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# 1 Incorporating microclimate into species 2 distribution models

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## 10 **Abstract**

11 Species distribution models (SDMs) are widely used to make predictions and assess questions  
12 regarding the spatial distribution and redistribution of species under environmental changes. Current  
13 SDMs are, however, often based on free-air or synoptic temperature conditions with a coarse  
14 resolution, and thus may fail to capture apparent temperature (cf. microclimate) experienced by living  
15 organisms within their habitats. Microclimate is nevertheless crucial in habitats characterized by a  
16 vertical component (e.g. forests, mountains, or cities) or by horizontal variation in surface cover. The  
17 mismatch between how we usually express climate (cf. coarse-grained free-air conditions) and the  
18 apparent microclimatic conditions that living organisms experience has only recently been  
19 acknowledged in SDMs, yet several studies have already made considerable progress in tackling this  
20 problem from different angles. In this review, we summarize the currently available methods to obtain  
21 meaningful microclimatic data for use in distribution modelling. We discuss the issue of extent and  
22 resolution, and propose an integrated framework using a selection of appropriately-placed sensors in  
23 combination with both detailed measurements of the habitat 3D structure, for example derived from  
24 digital elevation models or airborne laser scanning, and long-term records of free-air conditions from  
25 weather stations. As such, we can obtain microclimatic data with finer spatiotemporal resolution and  
26 of sufficient extent to model current and future species distributions.

27 **Keywords:** biodiversity, climate change, environmental niche modeling, humidity, microclimate,  
28 microrefugia, remote sensing, temperature

29

## 30 **Introduction**

31 Species distribution models (SDMs), also known as environmental niche models, are widely used to  
32 make predictions and assess questions regarding the spatial distribution and redistribution of species  
33 under environmental changes (Elith and Leathwick 2009). Applications of SDMs range from studies on  
34 the effects of anthropogenic climate change to predictions of biological invasions (Guisan and Thuiller  
35 2005). SDMs are usually created by relating known species occurrence (or presence-absence) data with  
36 information about the environmental conditions at these locations (Guisan and Thuiller 2005, Elith and  
37 Leathwick 2009, Jiménez-Valverde et al. 2011). The most common strategy is to work with a set of  
38 bioclimatic variables at 30 arc-second resolution (ca. 1 km at the equator) or coarser (Hijmans et al.  
39 2005, Warren et al. 2008, Sears et al. 2011, Slavich et al. 2014, Gonzalez-Moreno et al. 2015) which  
40 usually represent free-air conditions averaged over 30 years or more. While such macroclimatic data  
41 might be sufficient in flat terrains with little variation in land use, they may not adequately characterize  
42 the microclimatic conditions organisms experience. Differences between macro- and microclimate are  
43 expected to be particularly pronounced where habitat includes a vertical dimension with significant  
44 variation along it, originating from either biotic, abiotic or human-made features (e.g. in mountains,  
45 forests, or cities) (Bramer et al. 2018).

46 For example, in mountain regions with heterogeneous topography, microclimate can vary  
47 noticeably over short distances due to a steep elevational gradient and rugged terrain (Gottfried et al.  
48 1999, Holden et al. 2011, Sears et al. 2011, Opedal et al. 2015, Graae et al. 2018). Annual average  
49 temperatures have been found to vary up to 6°C within spatial units of 1 km<sup>2</sup> in Northern Europe  
50 (Lenoir et al. 2013). This large temperature variation also affects snow distribution (both snow depth  
51 and cover) in cold environments and consequently the local length of the growing season and many  
52 associated processes (Körner 2003, Aalto et al. 2018). The fine-grained thermal variability in mountains  
53 is usually attributed to physical processes such as air motion and solar radiation, interacting with  
54 topographic complexities such as aspect, slope angle and roughness; i.e. topoclimate (Geiger and Aron  
55 2003), with vegetation cover and anthropogenic disturbance additionally known to affect local  
56 temperatures (Lembrechts et al. 2017). Consequently, the necessity to incorporate topoclimatic  
57 processes into SDMs for organisms in mountainous regions is now well acknowledged (Randin et al.  
58 2009, Dobrowski 2011).

59 Similar microclimate heterogeneity has been reported for forest systems, where daily maximum  
60 temperatures in the understory, i.e. sub-canopy temperatures, have been found to be more than 5°C  
61 lower – and occur significantly later in the day – than in comparable clear-cuts (Chen et al. 1999). It  
62 has also been recently suggested that sub-canopy temperatures are not only instantly buffered, but  
63 also partially decoupled from free-air temperatures (Ewers and Banks-Leite 2013, Varner and Dearing

64 2014, Locosselli et al. 2016, Lenoir et al. 2017, Aalto et al. 2018), with important consequences for  
65 forest-dwelling species redistribution under anthropogenic climate change (Lenoir et al. 2017).  
66 Temperature buffering is defined here as a reduction in climatic extremes, which increases stability  
67 over time, while the term decoupling is used for a deviation from the 1:1 reference line of perfect  
68 coupling between sub-canopy and free-air temperatures. In cities, the urban heat island (UHI) effect  
69 results in higher air and surface temperatures than in rural surroundings, especially at night (Grimm et  
70 al. 2008). Differences between urban and adjacent rural temperatures are increasing (from around  
71 0.5°C differences in 1950 to 1.5°C in 2005 for Brussels) as urbanisation has increased in the last decade  
72 (Hamdi 2010), indicating a similar decoupling between urban microclimate and the background free-  
73 air conditions as observed in forests. The UHI effect results from the interaction between the vertical  
74 use of space (e.g. buildings) with the different land cover in urbanised areas, with a lower evaporative  
75 cooling and reductions in heat convection to the atmosphere thought to be the driving factors (Zhao  
76 et al. 2014). In general, temperature variation occurs at multiple scales, from the smallest boundary  
77 layer of air to the landscape level (Pincebourde et al. 2016, Bramer et al. 2018).

78 In order to accurately predict species distributions in natural or anthropogenic environments  
79 with such small-scale climatic variability (e.g. arctic-alpine, forest, urban), fine resolution climate data  
80 is needed (Illan et al. 2010, Scherrer and Körner 2011, Suggitt et al. 2011, Graae et al. 2012, Opedal et  
81 al. 2015). This is important for example in regard to holdouts, which are isolated populations that  
82 persist in a favourable microclimate for a limited period of time amidst deteriorating climatic  
83 conditions; and microrefugia, where these isolated populations can persist for a longer time until  
84 climatic conditions return to baseline or suitable (Ashcroft 2010, Dobrowski 2011, Hannah et al. 2014,  
85 Lenoir et al. 2017, Meineri and Hylander 2017). Indeed, the spatial heterogeneity in temperature  
86 computed from local measurements has been shown to be almost twice as large as the one computed  
87 from global interpolated temperatures (Lenoir et al. 2013), suggesting local persistence opportunities  
88 through short-distance escapes for populations experiencing anthropogenic climate change (Graae et  
89 al. 2018). Overlooking such microrefugia likely results in overestimations of future species' range shifts  
90 (Lenoir et al. 2013). Climatic variability within an area can also buffer climate warming effects  
91 considerably (Lenoir et al. 2013, Lenoir et al. 2017), yet this buffering likewise often remains  
92 undetected using macroclimatic data at coarse spatial resolution (e.g. CHELSA (Karger et al. 2017),  
93 WorldClim (Fick and Hijmans 2017), TerraClimate (Abatzoglou et al. 2018) or ENVIREM (Title and  
94 Bemmels 2017)). Overlooking this buffering can lead to overestimation of extinction rates (Willis and  
95 Bhagwat 2009). Another use of microclimatic data lies in the assessment of stepping stones, referring  
96 to areas with favourable microclimates that facilitate species' range shifts, e.g. upward or poleward  
97 movement during climate change (Hannah et al. 2014). Such stepping stones can exist in mountain

98 environments (Lembrechts et al. 2017), yet the urban matrix can also act as such for the poleward  
99 expansion of both heat-loving native and non-native species (Menke et al. 2011).

100 This mismatch between how we traditionally use climate (cf. free-air conditions) and the  
101 apparent microclimatic conditions that living organisms experience has only recently been  
102 acknowledged in SDMs (Dobrowski 2011, Pradervand et al. 2014, Slavich et al. 2014), yet considerable  
103 progress in tackling this problem has been made and has produced improvements in SDM predictions  
104 (e.g. Ashcroft et al. 2008, Dobrowski 2011, Pradervand et al. 2014, Slavich et al. 2014, Meineri and  
105 Hylander 2017, Bramer et al. 2018). In the following sections, we shortly summarize the current  
106 available methods to obtain meaningful microclimatic data for ecology, after which we show their  
107 current application in SDMs.

## 108 **Sources of microclimatic data**

### 109 **In-situ measurements**

110 Miniature data-loggers can provide high-resolution measurements of surface, soil and air  
111 temperatures, with the major advantage that conditions can be measured where they are expected to  
112 be ecologically most relevant to living organisms (Rae et al. 2006, Ashcroft et al. 2008, Bramer et al.  
113 2018). Small sensors can even be attached to the organisms themselves to obtain temperature  
114 information at the level of the study object (Potter et al. 2013). Such measurements also allow high  
115 temporal detail, and focusing on extreme weather conditions has as such been shown to be often more  
116 relevant for species distributions than the average climate over seasons with many different weather  
117 patterns (Ashcroft and Gollan 2012). However, a drawback of microclimate data from in-situ loggers  
118 lies in the short temporal extent (Table 1). These techniques are currently indeed limited to the  
119 measurement of “micro-weather” data instead of microclimate data. To improve the accuracy of  
120 SDMs, the high spatial and temporal accuracy of these in-situ measurements will need to be combined  
121 with long-term records, either by maintaining loggers in the field over periods of several years or by  
122 coupling these loggers with historical data from the long-established networks of national weather  
123 stations. The use of such loggers over large geographic extents is also still limited by the cost (Lenoir  
124 et al. 2013), despite the increasing availability of small, relatively cheap and robust temperature  
125 sensors (Bramer et al. 2018). In-situ measurements with miniature data-loggers additionally provide  
126 opportunities to measure air humidity (Ashcroft and Gollan 2012), yet techniques to accurately  
127 measure long-term soil moisture and precipitation at numerous locations are currently not readily  
128 available (Lenoir et al. 2017), even though global databases of soil moisture have been under  
129 development for decades (Robock et al. 2000, Dorigo et al. 2011).

### 130 **Modelling microclimate**

131 For spatial predictions in SDMs, the above-mentioned in-situ measurements first have to be converted  
132 into gridded data across the spatial extent covered by the network of sensors, using interpolation  
133 techniques similar to those used to create global climate models based on a global network of weather  
134 station data (e.g. WorldClim) (Ashcroft et al. 2008, Meineri and Hylander 2017). As for interpolation  
135 techniques, one can use mixed-effects models or geostatistical approaches such as spatial kriging or  
136 geographically weighted regressions (Fotheringham et al. 2003, Ashcroft et al. 2008, Fridley 2009,  
137 Ashcroft and Gollan 2012, Meineri and Hylander 2017). Although geostatistical approaches may  
138 outperform mixed-effects models to spatially interpolate microclimate, the former cannot be used to  
139 extrapolate microclimate outside the spatiotemporal extent covered by the data. Mixed-effect models  
140 can be used to extrapolate microclimate, yet spatiotemporal extrapolations should always be used  
141 with extreme care, and must remain inside the range of conditions covered by the predictor variables  
142 used to calibrate the model. This is an important limitation with repercussions for SDMs. These  
143 interpolation techniques allow the integration of detailed regional variables (e.g. derived from digital  
144 elevation models (DEMs) or similar datasets) in accurate interpolations of microclimate (Bramer et al.  
145 2018). Such methods accounting for well-known topographic climate-forcing have been shown to  
146 significantly improve SDMs in regional trials (Ashcroft et al. 2008, Ashcroft and Gollan 2012).  
147 Microclimatic interpolation can capture variation at high temporal resolution, yet is limited in its  
148 temporal extent by the baseline in-situ temperature data (e.g. Ashcroft et al. 2008) (Table 1). The  
149 combination of a high (hourly) temporal resolution and a long temporal extent has however been  
150 realized thanks to the application of similar techniques (e.g. mixed-effect models) to interpolate long-  
151 term hourly weather station data at 25-m<sup>2</sup> resolution (with the help of fine-scaled DEMs , e.g. Bennie  
152 et al. 2013, Meineri and Hylander 2017) or lower (< 10 m, thanks to airborne light detection-and-  
153 ranging (LiDAR) images, George et al. 2015; see the last paragraph of this section and the next section  
154 for the use of remote sensing technologies). However, such interpolations are currently limited to free-  
155 air temperature (Table 1).

156 Similar statistical approaches can be used to downscale macroclimate, i.e. translating  
157 macroclimatic variables to a finer spatial resolution by linking global climate models to regional or local  
158 variables at that finer resolution. Such downscaling approaches use statistical relationships between  
159 local and global climate patterns to estimate local climate (Dobrowski et al. 2009, Ashcroft and Gollan  
160 2013a). They can provide long-term averages of local climate with a long temporal extent, yet have a  
161 coarse temporal resolution and are again limited to free-air temperatures (Table 1, Woods et al. 2015,  
162 Carroll et al. 2016). Additionally, while regional datasets often include estimates of climate extremes  
163 (e.g. the warmest temperature of the warmest month, Hijmans et al. 2005), they do not allow the

164 assessment of variation in frequency and/or intensity of climate extremes over time, as is possible with  
165 in-situ measurements.

166 As opposed to the above-mentioned statistical models, process-based or mechanistic methods  
167 seek to model microclimate using mathematical relationships between the processes driving it (e.g.  
168 coastal influences, altitudinal effects or cold-air drainage). They originate in meteorology and  
169 incorporate the physical processes like energy and mass fluxes or wind speed to predict climate at the  
170 local scale, which makes them more likely to provide reliable predictions under future conditions  
171 (Bennie et al. 2008, Evans and Westra 2012, Felicísimo Pérez and Martín-Tardío 2017, Kearney and  
172 Porter 2017). Mechanistic models still require inputs from weather stations or climate models, but  
173 crucially the downscaling process is based on known mechanisms rather than using interpolation or  
174 statistical algorithms (Bramer et al. 2018). Finally, one can also use empirically calibrated mechanistic  
175 models, which combine a mechanistic understanding of microclimatic processes (e.g. cold-air  
176 drainage) with empirical testing using in-situ measurements (Maclean et al. 2017). Such a hybrid model  
177 combines the accuracy of empirical models with the transferability of mechanistic models.

178 The spatial resolution of interpolation and downscaling approaches is unavoidably linked to the  
179 resolution of the underlying environmental data: it can only 'fill in the gaps' in a coarser dataset if other  
180 fine-grained environmental information is available. Most downscaling approaches make use of DEMs  
181 to capture topoclimate. High-resolution DEMs are currently available at horizontal resolutions of 25 m  
182 or finer at the global extent (Randin et al. 2009, Hannah et al. 2014, Davis et al. 2016), allowing a  
183 significant improvement over the 1-km resolution of global climate data (e.g. WorldClim, CHELSA,  
184 ENVIREM). With not only elevation defining microclimate, other topoclimatic variables (e.g. aspect,  
185 cold-air drainage, solar insolation) are being derived from high-resolution DEMs to further improve  
186 models (Dobrowski 2011, Ashcroft and Gollan 2013b, Lenoir et al. 2017). Recent years have also seen  
187 a rapid increase in remote sensing techniques using satellite-based, airborne or terrestrial sensors, and  
188 consequently a strong increase in the accuracy and resolution of remotely-sensed gridded data (Table  
189 1, Parmentier et al. 2014, Pradervand et al. 2014, Bramer et al. 2018). At resolutions finer than the 25  
190 x 25 m available in DEMs, both physiographic and biophysical processes affect microclimate (Suggitt  
191 et al. 2011, Lenoir et al. 2017, Greiser et al. 2018). Remote sensing techniques such as airborne LiDAR  
192 sensors as well as hyperspectral images can provide a 3D analysis of canopy structure and height of  
193 the vegetation and ground surface at an unprecedented resolution (Lefsky et al. 2002, Bramer et al.  
194 2018), thus providing structural properties of the landscape. To transform this information into  
195 microclimatic values, one can use either empirical regressions, or a process-based modelling approach,  
196 in which the effects of microtopography and vegetation on temperature are incorporated (Lenoir et  
197 al. 2017). Using remote sensing data thus provides climate data with a high spatial resolution and broad

198 extent, and either a high temporal resolution (from interpolation of in-situ data), a broad temporal  
199 extent (from downscaling of coarse-grained climatic grids) or both (from interpolation of weather  
200 station data). Although the potential of LiDAR tools to assess detailed physiographic and biophysical  
201 processes has recently been highlighted (Keppel et al. 2012), their use in SDMs is relatively  
202 underexplored (Lenoir et al. 2017). Finally, note that downscaling and interpolation approaches  
203 become exponentially more computationally intense with each linear increase in scale-precision (cf.  
204 finer resolutions for a given extent), both temporarily and spatially (Potter et al. 2013, Hannah et al.  
205 2014).

206

### 207 **Remotely-sensed land surface temperature**

208 The most straightforward option to infer microclimate from remote sensing is by directly measuring  
209 it through thermal remote sensing – via satellites (e.g. MODIS, Wan et al. 2015) or portable infra-red  
210 (IR) cameras (Scherrer and Körner 2010). These techniques can play a crucial role when spatial  
211 variation in temperature needs to be measured with extreme accuracy, or in out-of-reach areas such  
212 as forest canopies (Faye et al. 2016). However, the outcomes have so far only been occasionally used  
213 as microclimatic data input in SDMs (e.g. Bisrat et al. 2012, Neteler et al. 2013), as IR images are  
214 limited to surface temperatures, and suffer from either temporal extent or spatial resolution  
215 limitations when using airborne or satellite-borne sensors, respectively (Potter et al. 2013).  
216 Moreover, the use of both airborne and satellite-borne sensors is usually biased towards cloudless  
217 days, which mathematically leads to biased spatial representations of climatic conditions. The  
218 currently available spatial resolution of land surface temperatures (LSTs) (ca. 1 km at the equator)  
219 (Wan et al. 2015) does however not provide an absolute increase in spatial resolution compared to  
220 the traditionally used free-air temperature gridded datasets like WorldClim or CHELSA (yet see  
221 EuroLST at 250-m resolution across Europe: Neteler et al. 2014). LSTs nevertheless give the  
222 advantage of a direct measurement for each pixel, instead of an interpolation of weather station  
223 data. In addition to the direct measurement of surface temperature, remote sensing can also play an  
224 important role in obtaining information on other variables that matter for microclimate, like cloud  
225 cover (Wilson and Jetz 2016) and much-needed information on soil moisture (Njoku et al. 2003,  
226 Entekhabi et al. 2010).

227



## 228 **Inclusion of microclimatic data in SDMs**

### 229 **Current status of microclimate in SDMs**

230 With the recent rapid advances in microclimatic data sources described above, there has been a  
231 corresponding steady increase in the application of this data in SDMs (Fig. 1, Table 2), with existing  
232 examples often showing significant improvement of model accuracy compared to models using coarse-  
233 grained climate data. For example, Ashcroft et al. (2008) showed that local temperature better  
234 predicted the distribution of 68% of their 37 studied plant species, and model performance also  
235 improved significantly using topoclimate for most species living in cold extremes in a study on  
236 mountain grasses and ferns (Slavich et al. 2014).

237 Current applications of microclimate modelling techniques into SDMs include both interpolation  
238 of in-situ measurements (e.g. Ashcroft et al. 2008, Ashcroft et al. 2009, Slavich et al. 2014) and  
239 statistical downscaling to regional topoclimate (e.g. Randin et al. 2009), with studies across a range of  
240 spatiotemporal scales (Fig. 1). However, as microclimate data with a spatial resolution of less than 10  
241 m<sup>2</sup> have only recently become available through the use of high-resolution LiDAR-techniques (George  
242 et al. 2015, Lenoir et al. 2017), fine-scale data has currently not been integrated into SDMs at broad  
243 spatial extents (dashed line in Fig. 1a). Up till the recent introduction of LiDAR into SDMs (Lenoir et al.  
244 2017), microclimatic data with the highest spatial resolution for use in SDMs was usually obtained  
245 through mechanistic modelling using fine-scaled DEMs at 25 m<sup>2</sup> (as in Gillingham et al. 2012). Using  
246 such techniques in combination with long-term hourly weather station data also allows for the desired  
247 combination of a broad temporal scale with a high temporal resolution (Fig. 1b, top left). Such a  
248 combination of high temporal accuracy and large temporal extent obtained with downscaling  
249 approaches has however not yet been applied in SDMs.

250 In-situ measurements of temperature and other microhabitat characteristics – without  
251 interpolation – have additionally been shown to be valuable for descriptive distribution modelling at  
252 the local scale (Opedal et al. 2015, Frey et al. 2016). For example, strong correlations have been  
253 observed between changes in the frequency of plant species over time and the in-situ temperature of  
254 their preferred microhabitat on mountain summits in Switzerland (Kulonen et al. 2018). Sometimes,  
255 topoclimatic variables derived directly from DEMs (like elevation, solar radiation or cold-air pooling)  
256 are also used independently in SDMs, thus using an indirect topoclimatic derivative instead of actually  
257 downscaled climate to improve the spatial resolution of SDMs (see e.g. Roslin et al. 2009, Maclean et  
258 al. 2015, Shinneman et al. 2016, Patsiou et al. 2017).

259 The use of microclimatic data in SDMs in a changing future climate has been explored less  
260 frequently, yet some recent papers have shown that the inclusion of higher temporal and spatial

261 resolution data can improve such predictions, for example by identifying windows of opportunity with  
262 both a limited spatial and temporal extent for oak seedlings (Davis et al. 2016). Incorporating  
263 microclimatic processes into projections of SDMs under climate change also resulted in lower rates of  
264 predicted local extinctions of Swedish alpine species by 2085 (Meineri and Hylander 2017), while it  
265 also increased the probability of occurrence of a theoretical species at its warm range edge (Lenoir et  
266 al. 2017).

267 Even though several studies have thus successfully demonstrated the usefulness of accounting  
268 for microclimatic processes into SDMs, we identified the need for an integrative approach, maximizing  
269 both the spatiotemporal scale and resolution, whilst allowing both descriptive and predictive models  
270 at scales relevant to the study species. We propose our framework in the next sections.

### 271 **Scale: a matter of choosing the right extent and resolution at which key processes operate** 272

273 First of all, we want to highlight the importance of the scale – both the extent and the resolution –  
274 issue when relating climatic data to species distributions. In order to maximally improve the descriptive  
275 and predictive power of SDMs, researchers should be aware of the scale at which species experience  
276 the microclimate (Potter et al. 2013, Hannah et al. 2014, Carroll et al. 2016). Importantly, the scale of  
277 microclimate does not necessary imply fine spatiotemporal resolutions; the temporal extents of the  
278 data matters as well, as does the spatiotemporal resolution at which the underlying processes operate:  
279 the “process resolution”. For example, the geographic distribution of tree species will be strongly  
280 dependent on long-term patterns of average air temperature, yet also on extremes like minimum  
281 winter air temperatures, as the latter affects the vulnerable aboveground tissues (Körner 2003,  
282 Williams et al. 2015). Moreover, a tree species could be persisting outside its climatic niche for  
283 substantial parts of its life span, e.g. when climate changes throughout its life span (cf. tolerance niche)  
284 (Sax et al. 2013) or just due to changing requirements for the growing individual (cf. ontogenetic niche  
285 shift) (Werner and Gilliam 1984, Bond and Midgley 2001). Seedlings will react more strongly to  
286 seasonal fluctuations in temperatures at the soil surface than later growth stages. Indeed, the  
287 environment experienced by germinating seeds, as compared to the one experienced by adult trees,  
288 is likely more decoupled from free-air temperatures and more constrained by temperatures near the  
289 ground. Yet, the meaningful spatial resolution at which microclimatic processes are operating for a  
290 sessile tree seedling is still likely greater than the centimetre scale, as it also depends on the vertical  
291 complexity of the vegetation layers from the surrounding individuals that could be located several  
292 metres away.

293 While the necessary spatiotemporal resolution at which microclimatic processes operate is usually  
294 finer than the available coarse-grained global and long-term climatic data, this spatiotemporal  
295 resolution will thus likely be different for different species, species groups or even different life stages  
296 or ontogenetic stages of the same species (e.g. life cycle of a tree or a dragonfly). In general, refining  
297 the spatial resolution has been shown to be less important for organisms in spatially homogeneous  
298 environments, while fine temporal resolution might matter less in environments where diurnal or  
299 seasonal variability is smaller than the environmental tolerance of the studied species (like for plants)  
300 (Hannah et al. 2014). For small animals, however, which can buffer their environment by moving, both  
301 a fine spatial and temporal resolution could be key. For a temperature-sensitive mammal like the  
302 American pika (*Ochotona princeps*), for example, their preferred micro-environment under rocks has  
303 been shown to be up to 30°C cooler than ambient temperature maxima (Varner and Dearing 2014),  
304 implying that both the availability of habitat at low elevations and the possibility of survival under  
305 warming climate conditions is being underestimated in SDMs that do not incorporate these  
306 microclimatic effects..

307 Process resolution also relates to the data quality of the explanatory variables. For example, one  
308 could use a limited, or spatially unbalanced, climatic dataset, use too simple extrapolation techniques  
309 or ignore important microclimatic process (e.g. cold-air drainage) when applying downscaling  
310 procedures (Daly 2006). Even though the resulting spatiotemporal resolution might still be high, the  
311 process resolution – and thus true accuracy – of the data would then be lower. It is thus critical to focus  
312 not only on the use of high-resolution datasets, yet to also include the relevant spatiotemporal  
313 resolution of the underlying climate-forcing factors and ground-truth models with in-situ  
314 measurements. In Table 2, we give additional insight in the realized process resolution of the studies  
315 depicted in Fig. 1 by listing the used techniques, included drivers, the use of in-situ measurements, and  
316 whether climate was extrapolated in space or time.

317 Finally, the search for better microclimatic data thus does not necessarily imply a blind run for  
318 an increasing refinement in the spatiotemporal resolution of climatic data at the global extent. While  
319 thermal physiology is interesting in its own regard, coarse-grained SDMs should maintain their focus  
320 on the actual distribution of the species, on a regional, continental or even global scale. Microclimatic  
321 precision or resolution is thus only valuable down to the level at which an increased resolution does  
322 not affect the actual distribution of a species anymore (Bennie et al. 2014). For example, microclimatic  
323 data improved models of moth distribution at the site level, yet not at the regional scale of the full  
324 species range in the tropical Andes (Rebaudo et al. 2016). The question of scale thus also relates to the  
325 accuracy at which predictions are needed and to situations where mean field approximations are not  
326 accurate (Bennie et al. 2014), as is for example the case for microrefugia, holdouts and stepping stones.

327 However, when fine resolution data are available, one can also add the assessment of (both spatial  
328 and temporal) heterogeneity within a certain pixel to the commonly used averages and extremes. By  
329 doing so, it is possible to capture and assess the impact of local environmental heterogeneity on  
330 metapopulation and metacommunity dynamics (Graae et al. 2018). Such a hierarchical approach,  
331 including environmental variation obtained at finer resolution into models of a species distribution at  
332 a coarser scale promises to bridge the gap between local and global species distribution questions.

### 333 **A framework to obtain adequate microclimatic data for use in SDMs**

334 How do we best answer to both the need for an increased level of detail and a high flexibility and  
335 adaptability to specific case studies? Certainly our goal should not be to fill the entire climatic grid with  
336 in-situ temperature sensors, as this is neither desirable nor possible (Potter et al. 2013). On the other  
337 hand, however, mechanistically or statistically downscaling macroclimate without relying on  
338 microclimate measurements is also limited, as we need a better understanding and validation of the  
339 processes underlying microclimate at very fine spatial and temporal resolutions in order to improve  
340 the accuracy or process resolution of our models. Combining in-situ microclimate measurements with  
341 fine-grained environmental variables derived from remotely sensed images to spatially interpolate  
342 microclimate helps solve the spatial issue (Greiser et al. 2018). However, these microclimatic grids are  
343 unlikely to reflect the long-term dynamics of climate over time (Lenoir et al. 2017) and instead capture  
344 the weather conditions that prevailed during the year the microclimatic data were recorded. To solve  
345 this issue, we argue in favour of an improved and unified statistical framework of spatiotemporal  
346 interpolations that would combine the use of in-situ microclimate measurements, long-term synoptic  
347 measurements from meteorological stations and high-resolution remote sensing images (e.g. airborne  
348 LiDAR and hyperspectral images) (Fig. 2). Linking in-situ microclimate measurements at fine temporal  
349 resolution with variables derived from remote sensing images at high spatial resolution and with a  
350 broad spatial extent will help facilitate spatial interpolation of microclimate (Lenoir et al. 2017, see the  
351 left side in Fig. 2). At the same time, linking the high temporal resolution of in-situ microclimate  
352 measurements with long-term synoptic measurements from the closest meteorological stations with  
353 a broad temporal extent will allow the reconstruction of long-term temporal dynamics of climate  
354 change (Wason et al. 2017, see the right side in Fig. 2). The generated grids of microclimate time series  
355 at fine spatiotemporal resolution and with a rather broad spatiotemporal extent (e.g. from landscape  
356 to regional level) can then be used to generate meaningful predictor variables in SDMs.

357 The framework described above highlights the need for accurate in-situ climate measurements,  
358 as they provide our best option for assessing microclimate at the level of the studied organism.  
359 However, by linking microclimate measurements with remote sensing data at fine spatial resolution,

360 and long-term data from meteorological stations, both the amount of sensors as well as the extent of  
361 the measurement period can be limited. This does require a careful sampling design, however, as one  
362 should attempt to cover the full range of microclimatic variation available within the study region to  
363 avoid the need for extrapolation outside the measured range, and measurements at locations and time  
364 intervals relevant to the study organism (Ashcroft and Gollan 2013a). As stated earlier, the selection  
365 of candidate predictor variables and the choice of the meaningful spatial resolution for averages,  
366 extremes and heterogeneity should also be done carefully and in light of the biology of the studied  
367 species. For example, it has been shown that the degree of deviation from perfect coupling between  
368 microclimate and the ambient climate depends on the assessed bioclimatic variable, implying that the  
369 beneficial effects of microrefugia are limited to species that are restricted by these climatic conditions  
370 that are partially decoupled from the regional climate (Hylander et al. 2015, Wason et al. 2017).

371 To spatially interpolate the microclimate measurements from physiographic, biophysical and  
372 anthropogenic variables derived from the above-mentioned remotely-sensed images (e.g. aspect,  
373 slope, solar insolation, land cover, disturbance intensity), geostatistical tools (e.g. geographically  
374 weighted regressions; Fotheringham et al. 2003) can be used. These tools extend traditional regression  
375 techniques by adding variation across space to the estimated regression parameters within the  
376 spatiotemporal limits of the available data. The ability to accommodate spatial variation makes  
377 geostatistical tools highly relevant for exploring the scale-dependent and spatially variable  
378 relationships between measured temperatures and physiographic, biophysical or anthropogenic  
379 drivers of temperature (Su et al. 2012). Depending on the scale of the study and the focal organism  
380 under study, remote sensing data can be satellite-borne, airborne or even ground-based (e.g. Lenoir  
381 et al. 2017). As more and more – mostly satellite-borne – remote sensing data is becoming freely  
382 available, the actual costs of our proposed approach can even be limited to those that are related to  
383 the maintenance of a carefully designed in-situ sensor network.

384 To perform temporal extrapolation, an approach as used in George et al. (2015) could be  
385 applied. They used temperature logger measurements spread across a forest in Missouri (USA) as the  
386 response variable and different combinations of both spatial variables, derived from LiDAR images,  
387 and temporal covariates, derived from the closest weather station, as predictors in a mixed-effect  
388 model to estimate air temperatures at any time (hourly) of any day between 2012 and 2013,  
389 corresponding to the calibration period. Extrapolation before this period is then possible thanks to the  
390 long-term records from the weather station. However, extrapolation should be handled with care as  
391 one would also need historical information on the likely spatial distribution of the LiDAR-derived  
392 variables. In the case of the forest in Missouri, this extrapolation would be possible only if older LiDAR  
393 images are available across the study area or by hindcasting tree growth based on a combined use of

394 allometric equations (i.e. a mechanistic approach) and information on past forest management  
395 practices. In general, however, hybrid models that combine a mechanistic understanding of the  
396 processes underlying microclimate (e.g. dynamic changes in vegetation cover) with a statistical  
397 validation based on in-situ measured data provide a promising research avenue to accurately predict  
398 microclimatic conditions in space and time (Maclean et al. 2017), especially if applied in multi-regional  
399 studies.

400         Once calculated, the microclimate data can be used to calibrate SDMs and predict the  
401 distribution of the studied species at the desired scale (spatiotemporal extent and resolution) (Fig. 2).  
402 Ideally, one integrates metapopulation and metacommunity dynamics in dynamic SDMs of the focal  
403 species to include their potential to actually explore the thermal heterogeneity within the environment  
404 (Graae et al. 2018). The broad temporal extent (e.g. several decades) and high temporal resolution  
405 (e.g. daily maxima or minima) of the microclimatic data creates unprecedented opportunities here to  
406 link available long-term species distribution data to the actual environmental conditions at the  
407 moment of the measurement, or to the past environmental conditions occurring several days, weeks,  
408 months or years before (cf. legacy or lagging effects). This does, however, require (process-based or  
409 empirical) assessments of the relevant temporal window to consider for a certain (group of) focal  
410 species. It will also prove valuable to compare the obtained models with “control” or “baseline” models  
411 using the traditional coarse-grained climate data to quantify the actual improvement of the SDMs by  
412 including microclimate. This can help in the interpretation of the role of microclimate in describing and  
413 predicting actual species distributions.

#### 414 **Extrapolating microclimate to the future**

415 The same framework as described in the previous chapter can now be applied to improve our  
416 extrapolations of microclimate into the future (Fig. 2, Box). Current practice involves downscaling  
417 approaches to obtain future microclimate (Davis et al. 2016). Again, statistical methods can be used,  
418 linking current downscaled climate to scenarios of climate change (Lenoir et al. 2017). Yet these  
419 approaches starting from a static climate scenario miss many of the dynamics that can be expected  
420 from climate change at the smallest scale, like local climatic stability, the process by which local  
421 microclimatic conditions are partially decoupled from macroclimatic fluctuations over time (Keppel et  
422 al. 2015, Lenoir et al. 2017).

423         The above-mentioned integration of the high temporal resolution of in-situ microclimate  
424 measurements with the long-term measurements from the closest meteorological stations can  
425 however be used to reconstruct long-term temporal dynamics by calculating the offset and the thermal  
426 coupling between the measurement location (e.g. near-surface soil temperatures) and the atmosphere

427 for use in predictions of the future microclimate (Pepin et al. 2011, Joly and Gillet 2017, Lenoir et al.  
428 2017). Aalto et al. (2018) have recently shown that estimation of the offset and thermal coupling has  
429 potential, even for one year of in-situ temperature data, yet they also stress the need for continuous  
430 multi-year measurements to improve validity. Nevertheless, with the recent explosive interest in  
431 microclimate, dataset quality and spatial and temporal extent of in-situ measurements is growing  
432 steadily, indicating that spatiotemporal extrapolation of microclimate will soon become feasible.  
433 Integrating these dynamic processes in our predictions of future (micro)climate will greatly increase  
434 the accuracy of our predictions of future species distributions under climate change (Wason et al.  
435 2017).

### 436 **Conclusions**

437 Recent advances in both measuring and modelling techniques have greatly enhanced the resolution of  
438 the climatic data available for SDMs. In this review, we suggested that all the necessary techniques and  
439 resources are now available to obtain a wide range of spatiotemporal microclimatic resolutions, if  
440 needed over regional and decadal extents. With the help of statistical models to link in-situ  
441 microclimate measurements with remote sensing data at fine spatial resolutions and synoptic  
442 measurements from meteorological stations covering several decades, accurate microclimatic data for  
443 the past, present and the future can now be obtained to dynamically model species distributions and  
444 redistributions at exactly the scale that matters. Developing microclimatic datasets at very fine  
445 spatiotemporal resolutions should however not be a goal on its own, yet be embedded in a framework  
446 to obtain environmental predictor variables at relevant spatiotemporal resolutions to improve the  
447 ecological validity of SDMs, and that similar frameworks can be developed for other relevant  
448 predictors, like land use change and habitat availability.

449

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451

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## Tables and figures

*Table 1: Measurement locations and main advantages (+) and disadvantages (-) of the different sources of microclimatic data for use in SDMs. Spatial and temporal resolution: a more detailed spatiotemporal accuracy provides an advantage. Spatial and temporal extent: data across a larger area and over a longer period provides an advantage.*

	<i>Measurement location</i>	<i>Spatial resolution</i>	<i>Temporal resolution</i>	<i>Spatial extent</i>	<i>Temporal extent</i>
<i>In-situ measurements</i>	<i>In-situ</i>	-	+	-	-
<i>Interpolation of in-situ measurements</i>	<i>In-situ</i>	+	+	+	-
<i>Interpolation of weather station data</i>	<i>Free-air</i>	+	+	+	+
<i>Downscaling of macroclimate</i>	<i>Free-air</i>	+	-	+	+
<i>Remote sensed land surface temperature</i>	<i>Surface</i>	+	-	+	-

Table 2: Specifics of the studies described in Fig. 1, including drivers and techniques, whether microclimate was validated with in-situ data, whether microclimate was extrapolated across space or time, and for which and how many species the data was used in SDMs.

Paper	Used technique (included drivers)	In-situ measurements	Extrapolated relationship in space or time	Modelled species
1 Ashcroft et al. (2008)	Linear regression (elevation, exposure, moisture, radiation)	Yes	Space	37 plant sp.
2 Trivedi et al. (2008)	Linear regression (elevation)	No	Time	20 plant sp.
3 Randin et al. (2009)	Inverse distance weighted interpolations (elevation)	No	Time	78 plant sp.
4 Ashcroft et al. (2009)	Linear regression linking air and soil temperatures	Yes	Time	37 plant sp.
5 Gillingham et al. (2012)	Mechanistic model (wind speed, air temperature, radiation, slope, aspect, topographic shading)	Yes	Space and time	2 insect sp.
6 Haby et al. (2012)	Thin-plate spline models (elevation)	No	Space	4 mammal sp.
7 Franklin et al. (2013)	Gradient-Inverse-Distance-Squared downscaling (elevation)	No	Time	52 plant sp.
8 Peterman and Semlitsch (2013)	Hierarchical mixed-effects model (elevation, exposure, vegetation cover)	Yes	Space	<i>Plethodon albagula</i> (amphibia)
9 Bennie et al. (2013)	Mechanistic model (wind speed, air temperature, radiation, slope, aspect, topographic shading)	Yes	Space	<i>Hesperia comma</i> (insect)
10 Slavich et al. (2014)	Linear regression (elevation, exposure, relative elevation, canopy cover, distance to coast)	Yes	Space and time	295 plant sp.
11 Ashcroft et al. (2014)	Thin-plate spline smoothing (elevation, latitude, longitude)			
	Topoclimate: linear regression (elevation, exposure, relative elevation, canopy cover, distance to coast)	Yes	Space	<i>Petrogale penicillata</i> (mammal)
	Macroclimate: thin-plate spline smoothing (elevation, latitude, longitude)			
12 Hodgson et al. (2015)	Mechanistic model (wind speed, air temperature, radiation, slope, aspect)	Yes	Space and time	<i>Plebejus argus</i> (insect)
13 West et al. (2015)	Partial derivative functions of temperature change	Yes	Time	<i>Bromus tectorum</i> (plant)
	Elevation			
14 Davis et al. (2016)	Gradient-Inverse-Distance-Squared downscaling (elevation)	No	Time	2 plant sp.
15 Rebaudo et al. (2016)	Linear regression linking air and sub-canopy temperatures	Yes	Time	<i>Phthorimaea operculella</i> (insect)
16 Meineri and Hylander (2017)	Linear regression + thin-plate spline geographic interpolation	Yes	No	78 plant sp.
	Latitude, elevation, solar radiation, aspect, relative elevation, topographic wetness index, distance to sea/water bodies			
17 Keppel et al. (2017)	Cubic convolution resampling	No	Space	2 plant sp.
18 Lenoir et al. (2017)	Geographically weighted regression + mechanistic transformation	No	Time	1 virtual plant sp.
	Physiographic: elevation, slope, eastness, northness, distance to the coast, clear-sky insolation time, land cover, relative concavity			
	Biophysical: canopy density			
19 Isaak et al. (2017)	Moving averages	Yes	Space and time	14 fish and amphibian sp.

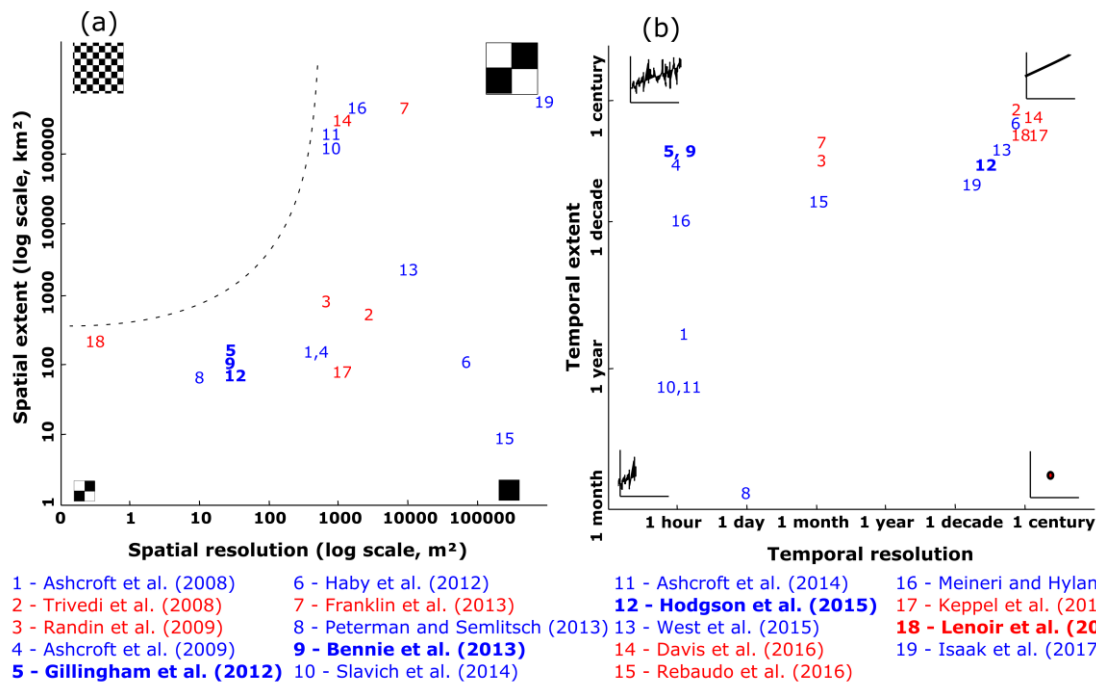


Figure 1: Overview of the use of microclimate data in SDMs as a function of their spatial resolution and extent (a, log-scale) and temporal resolution and extent (b, pseudo log-scale). Studies marked in blue used interpolation techniques (with mechanistic modelling approaches in bold), while studies marked in red used topographic downscaling. Infographics in each corner of each graph visualise the theoretical look of the data in question. The dashed line in (a) marks a trade-off, i.e. the lack of studies incorporating microclimate into SDMs with both a high spatial resolution and a broad spatial extent. Literature list obtained through a search of Google Scholar and Web of Science using the search term ‘species distribution modelling microclimate’, and following appropriate citation trails. Studies using in-situ climate measurements without interpolation (i.e. no clear spatial resolution nor extent), as well as studies using topoclimatic proxies (e.g. solar radiation intensity) are excluded.

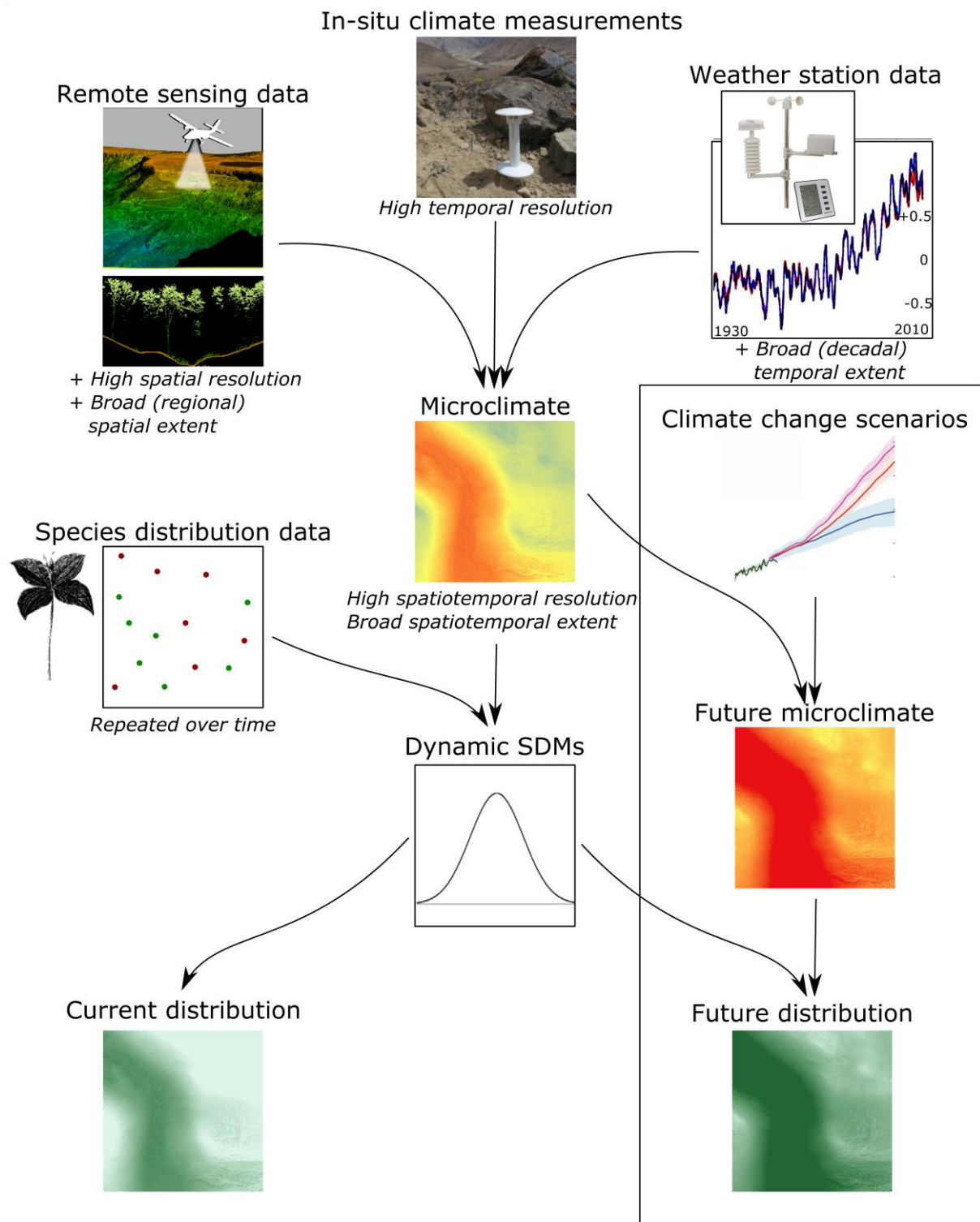


Figure 2: Schematic overview of the proposed strategy for integrated interpolation, in space and time, of microclimate and its implementation in species distribution modelling. The strength of this unified framework is to combine environmental data at fine spatial resolution thanks to remote sensing approaches with long-term time series from weather stations, and link these data to in-situ microclimatic measurements. For more details, see main text.