

1 **Stay or go – how topographic complexity influences alpine plant population and**
2 **community responses to climate change**

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46

47 **Abstract**

48 In the face of climate change, populations have two survival options – they can remain *in*
49 *situ* and tolerate the new climatic conditions (“stay”), or they can move to track their
50 climatic niches (“go”). For sessile and small-stature organisms like alpine plants, staying
51 requires broad climatic tolerances, realized niche shifts due to changing biotic
52 interactions, acclimation through plasticity, or rapid genetic adaptation. Going, in
53 contrast, requires good dispersal and colonization capacities. Neither the magnitude of
54 climate change experienced locally nor the capacities required for staying/going in
55 response to climate change are constant across landscapes, and both aspects may be
56 strongly affected by local microclimatic variation associated with topographic
57 complexity. We combine ideas from population and community ecology to discuss the
58 effects of topographic complexity in the landscape on the immediate “stay” or “go”
59 opportunities of local populations and communities, and on the selective pressures that
60 may have shaped the stay or go capacities of the species occupying contrasting
61 landscapes. We demonstrate, using example landscapes of different topographical
62 complexity, how species’ thermal niches could be distributed across these landscapes,
63 and how these, in turn, may affect many population and community ecological processes
64 that are related to adaptation or dispersal. Focusing on treeless alpine or Arctic
65 landscapes, where temperature is expected to be a strong determinant, our theoretical
66 framework leads to the hypothesis that populations and communities of topographically

67 complex (rough and patchy) landscapes should be both more resistant and more resilient
68 to climate change than those of topographically simple (flat and homogeneous)
69 landscapes. Our theoretical framework further points to how meta-community dynamics
70 such as mass effects in topographical complex landscapes and extinction lags in simple
71 landscapes, may mask and delay the long-term outcomes of these landscape differences
72 under rapidly changing climates.

73

74 **Keywords:** adaptation, dispersal, microclimate, niche, refugia, resilience.

75

76 ***Introduction***

77 Our understanding of the magnitude and ecological implications of climatic variation in
78 space and time has greatly developed over the past decades. Studies focusing on the
79 capacity for species to track their climatic niches over large spatial extents, including
80 palaeoecological reconstructions (reviewed in Feurdean *et al.*, 2013) and climate
81 envelope models (Pearson and Dawson, 2003; Sykes *et al.*, 1996), typically suggest high
82 migration rates in response to rapid redistribution of climates at the global scale (Clark *et*
83 *al.*, 1998; Loarie *et al.*, 2009). For plants, these findings have been challenged by more
84 recent molecular (Westergaard *et al.*, 2010, 2011), palaeoecological (Birks and Willis,
85 2008; Cheddadi *et al.*, 2014) and meso- to micro-scale climate envelope modelling
86 (Franklin *et al.*, 2013; Lenoir *et al.*, 2017; Randin *et al.*, 2009; Trivedi *et al.*, 2008;), all
87 suggesting occasional species persistence within refugia or through short-distance
88 escapes (Hampe and Jump 2011). Here, we discuss how the propensity for species to
89 “stay”, through adaptation processes, or “go”, through dispersal processes, so as to
90 survive in the face of climate change, depends not only on the magnitude of climate-
91 change exposure and the climate-change sensitivity of the constituent species and
92 communities (Dickinson *et al.*, 2014; Bertrand *et al.*, 2016), but also on the spatial
93 structure of the landscapes in which the species occur (Körner, 2004; Slavich *et al.*,
94 2014).

95 Topography is a key determinant of climatic variation across spatial scales
96 ranging from regions, covering hundreds of square kilometres, to microsites of less than a

97 square metre, especially in treeless areas like the high Arctic and alpine regions (see Box
98 1). Across these spatial scales, we can find regions, landscapes, patches, and microsites
99 that are relatively topographically uniform, as well as others that are topographically
100 complex, with associated differences in climatic heterogeneity. For example, there are
101 clear differences in topographic complexity between mountainous *vs.* flat landscapes in
102 high-latitude regions (Lenoir *et al.*, 2013), flat areas *vs.* ridge-snowbed gradients in alpine
103 landscapes (Graae *et al.*, 2011; Körner, 2003), and flat *vs.* microtopographically complex
104 patches within grassland and tundra vegetation (Armbruster *et al.*, 2007; Moeslund *et al.*,
105 2013; Opedal *et al.*, 2015). The topographic complexity at scales of a few tens of metres
106 can give rise to microclimatic variation in e.g., mean temperatures that often matches
107 what is expected under future climate change scenarios (2-6°C; Armbruster *et al.*, 2007;
108 Dobrowski *et al.*, 2013; Graae *et al.*, 2012; Lenoir *et al.*, 2013; Opedal *et al.*, 2015;
109 Scherrer and Körner, 2010; Scherrer and Körner, 2011).

110 It is important to focus on high-latitude and high-elevation landscapes beyond
111 treeline, not only because the complex topography there provides more spatial
112 heterogeneity in temperature, but especially because temperature itself is expected to be
113 the main determinant of plant distribution in these landscapes (Körner, 2003; Raunkiær
114 1934). Indeed, temperature has both direct effects on alpine plant life through setting
115 limits to species' fundamental niches, as well as indirect effects through determining, for
116 instance, decomposition and nutrient cycling, access to water, as well as the abundance of
117 herbivores, pathogens, pollinators, and seed dispersers. Some of these variables are also

118 influenced by other factors – for instance anthropogenic disturbances and herbivore
119 density that are often also regulated by humans. As Box 1 illustrates, we need to
120 incorporate all these various components of temperature into the thermal niche concept of
121 alpine plants. Hence, the thermal niche of an alpine plant species becomes a somewhat
122 theoretical object for which one has to make the often unrealistic assumption of *ceteris*
123 *paribus* (“other things being equal”). Though the realized niche for a species is difficult
124 to describe because of the complexity of interacting limiting factors, there are good
125 evidence for the existence of microclimatic niches (Lenoir et al 2013, Scherrer and
126 Körner 2011). In this paper we will make use of this theoretical niche concept, arguing
127 that realised microclimatic niches are important for plants and improving our
128 understanding of the distribution of these thermal niches across the landscape is
129 important for predicting species’ capacities to adapt or disperse in response to changing
130 climate.

131 Here, we synthesise theories relevant for how the topographic complexity of
132 landscapes at high elevations or latitudes influences the resistance (the lack of sensitivity
133 and response to perturbation or disturbance) and resilience (the capacity to recover after
134 perturbation or disturbance) of alpine plant populations and communities in response to
135 climate change. Specifically, we explore (1) how populations in landscapes of different
136 topographical complexity are affected by microclimatic heterogeneity under the current
137 climate, and (2) how this may affect their responses to climate change. We then turn to
138 communities, and (3) develop a framework for community response to landscape

139 microclimatic heterogeneity, before we (4) ask how this may affect community-level
140 responses to climate change in landscapes of different topographic complexity. Although
141 we focus on small-stature plants in cold ecosystems, many of the processes we describe
142 here would hold for other groups of organisms, with modifications to account for
143 differences in organism mobility and scale (Roth et al. 2014), as well as other important
144 factors of specific relevance. For example, for small-stature plants in the lowlands, one
145 would also have to consider, in addition to topography, the effect that tree or shrub
146 canopy cover exerts on microclimate (De Frenne et al., 2013; Grimmond et al. 2000) and
147 its consequences for forest plant species distribution (e.g. Wesser and Armbruster 1991;
148 Lenoir et al. 2017).

149

150 ***The spatial components of microclimatic niche heterogeneity***

151 Microclimatic heterogeneity affects populations and communities in two general ways.
152 First, by increasing the range of climatic conditions, it increases the climatic niche space
153 that is available within a given surface area and creates potential niche space for more
154 species. At the same time, this inevitably comes at the expense of reduced available
155 habitat area (Kerr and Packer, 1997; Scherrer and Körner, 2011) and thus increases
156 habitat fragmentation (Reino et al., 2013) for species with specialised thermal niches. In
157 alpine and Arctic ecosystems, topography is the main physiographic feature that can
158 enhance microclimatic heterogeneity in space. As a general and simplified example,
159 consider seven hypothetical landscapes of equal size (e.g., 1 km²), sharing a regional

160 plant species pool (Zobel, 1997), but varying in topographic complexity (Fig. 1).
161 Microclimatic heterogeneity due to topographic complexity has two dimensions: the
162 range of climatic conditions available (increasing from left to right in Fig. 1), and the
163 climatic patchiness or fragmentation (increasing from top to bottom in Fig. 1). The
164 species in the regional pool will be distributed differently among and within the
165 landscapes, depending on niche availability and landscape heterogeneity (in Figure 1,
166 species are represented by rings and curves of different colours). In addition to
167 experiencing long-term changes in climatic conditions, our hypothetical landscapes can
168 experience different levels of disturbance and seasonal fluctuation, which will naturally
169 influence the population and community dynamics of the plants inhabiting these
170 landscapes. Additionally, alpine plant species have different life histories, sizes and
171 dispersal capacities, involving different spatial scales (cf. the spatial extent and resolution
172 of our hypothetical landscapes). Here, we only focus on the spatial arrangement of
173 microclimatic conditions across a 1-km² landscape and the impact of climate change on
174 the “stay” or “go” processes.

175 Our first example landscape, L0, is climatically homogeneous, with a narrow
176 range of climatic conditions (or niche space), such as can be found for temperature across
177 a flat and smooth landscape. For species whose realised niche requirements are fulfilled
178 in this landscape (species represented by the brown and green curves and rings in Fig. 1),
179 a large and continuous habitat area is available, and the probability of local extinction
180 under stable conditions is hence low (Hanski, 1998; Lande, 1993; MacArthur and

181 Wilson; 1963). L1 and L2 encompass increasingly wider ranges of thermal conditions
182 that are distributed in a non-patchy way (positive spatial autocorrelation) such as on a
183 gentle (L1) or a steep (L2) hillside. The available niche space, and hence the potential
184 number of species in the landscape increases from L0 via L1 to L2 (Fig. 1). Depending
185 on the species' niche width and the climatic niche availability, species may occur in the
186 whole or in parts of the landscape, and there is, for most species, less habitable area
187 available in L2 than in L1 and L0.

188 L3 has the same available niche space for any given species as L1, but suitable
189 areas for each species are more patchily distributed in space, and the populations will
190 therefore tend to be more spatially scattered, as in a hilly landscape with fine-scale
191 topographic complexity. Landscapes L2 and L4 have the same difference in patchiness as
192 between L1 and L3 but with a larger climatic range. Thus, L3 and L4 have, on average,
193 smaller patches, but also shorter distances between patches of suitable habitat, compared
194 to landscapes L1 and L2, respectively. Landscapes L5 and L6 are even more fragmented,
195 to the extent that they may appear quasi-homogeneous.

196 Below, we evaluate how the increasing landscape heterogeneity affects the
197 populations and communities inhabiting these different landscapes. We outline the
198 consequences of this landscape heterogeneity for the selective pressures within the
199 different landscapes, and for how the populations and communities are equipped to
200 respond to climate change.

201

202 ***Populations in landscapes of varying climatic heterogeneity***

203 For species with narrow niches and/or only occurring in part of the climatic range of the
204 landscape (i.e. purple species in L1, L3 and L5 and blue species in L2, L4 and L6),
205 populations will be smaller in size and/or more fragmented in space going from L0
206 towards L6. This may lead to higher local extinction rates due to stochastic processes in
207 the smaller populations of fragmented landscapes (Fig. 1). However, when moving from
208 L3 to L5 or from L4 to L6 the existence of many small patches will reduce the average
209 distance between patches of suitable habitat in these landscapes, potentially improving
210 connectivity between the fragmented populations and reducing extinction risks via rescue
211 effects (Brown and Kodric-Brown, 1977; Hanski, 1998). Note that this potential increase
212 in connectivity can only happen if the average dispersal distance of the focal plant species
213 within the landscape exceeds the average distance between patches of suitable habitat
214 (i.e., the patches are part of a population or meta-population, *sensu* Hanski, 1998). In our
215 example with a fixed sized landscape window, the balance between extinctions, caused
216 by reduced patch sizes, and colonisations, caused by reduced distances between the
217 patches and by the area-related colonization capacity, will depend on the organisms' life
218 history. Small sized and well-dispersed plant species will most likely be less affected by
219 decreasing habitat sizes and increasing isolation than plant species with high area
220 requirement or more limited colonisation capacities.

221 Interestingly, the population processes in climatically variable and patchy
222 landscapes, like L6, may converge towards the situation in homogeneous landscapes such

223 as L0 if distances are so small that individuals can easily move between patches so that
224 populations are no longer fragmented. However, in contrast to L0, highly heterogeneous
225 landscapes as in L6 may allow populations with different niche requirements to coexist,
226 as long as the patch area across the landscape is still large enough for populations to
227 survive locally. Therefore, the constraint due to dispersal limitation towards a climatically
228 suitable location may become less important towards both L6 (i.e. similar microclimates
229 can be very close) and L0 (i.e. homogeneous microclimatic conditions), and may be most
230 important under intermediate microclimatic heterogeneity (relative to the organism under
231 study).

232 The microclimatic heterogeneity in the landscape will also alter the selective
233 forces acting on populations in the different landscape types. Populations inhabiting
234 climatically heterogeneous landscapes may be under selection for broader niches in order
235 to maintain sustainable population sizes in a heterogeneous environment. When
236 microclimatic heterogeneity increases, either moving from left to right or top to bottom in
237 Fig. 1, species with broad climatic niches, represented by the green curve, will have an
238 advantage compared to the species with narrower niches. Selection for broader niches
239 may result in greater phenotypic plasticity within local populations, with important
240 consequences for the capacity of these populations to respond to environmental changes
241 (Chevin *et al.*, 2010; Jump and Peñuelas, 2005; Nicotra *et al.*, 2010). Whether selection
242 in response to environmental heterogeneity favours phenotypic plasticity, genetic
243 differentiation, or a combination of the two, depends on several factors, including the

244 temporal and spatial scale of climatic variation (Alpert and Simms, 2002; Botero *et al.*,
245 2015). More effective dispersal in space or time may also counteract the negative effects
246 of fragmentation. Populations in fragmented landscapes may therefore also be under
247 selection towards better dispersal abilities, or they may be under selection towards better
248 survival in dormant or other long-lived stages, thus contributing to extinction time-lags,
249 until opportunities for continued growth and reproduction (re)appear locally (dispersal in
250 time or remnant population strategy *sensu* Eriksson, 1996).

251

252 ***Consequences of microclimatic heterogeneity for populations under changing climate***

253 Populations in different landscape types, such as topographically simple vs. complex
254 terrains, may be very differently positioned, and also equipped, to meet ecological
255 challenges of climate change. In a climatically homogeneous landscape, like L0,
256 populations can remain within the landscape if they tolerate the new climatic conditions,
257 either through intrinsic ability of individuals to tolerate changing climatic conditions
258 (Bertrand *et al.*, 2016), or through intraspecific variation in the position of the climatic
259 niche optima (Valladares *et al.* 2014). Alpine plant species within the homogeneous
260 landscapes are expected to have rather narrow niches, but those with the widest climatic
261 niches, represented by the green curve in Fig. 1, will have the highest chance of surviving
262 in this type of landscape and adapting to the new climatic conditions through realised
263 niche shifts (Wasof *et al.*, 2013, 2015). Indeed, in L0, distances to new suitable habitats
264 might be relatively large (i.e., somewhere outside the landscape), thus favouring

265 adaptation (“stay”) processes over dispersal and colonisation (“go”) processes. In
266 addition, low immigration rates into patches in these landscapes (i.e., long distance to
267 source populations of species with different climatic optima) means that the resident
268 species will have a relatively low risk of being exposed to competition from immigrant
269 species better adapted to the new climate (Ackerly, 2003; Bertrand *et al.*, 2011). This
270 may allow persistence under a new suboptimal climate and hence a longer time during
271 which adaptation to the new climate can occur (Ackerly, 2003; Svenning and Sandel,
272 2013). Species with high persistence capacity, for instance with very long-lived
273 individuals or dormant stages, may remain for extended periods in this type of landscape
274 (L0) compared to those predicted from their climatic niche (Eriksson, 1996, 2000; May *et*
275 *al.*, 2009; Migliore *et al.*, 2013), contributing to the extinction debt (Tilman *et al.*, 1994).
276 Related to this, “staying” may also be possible through expansion of the realised niche to
277 encompass the new climate, for example due to changes in biotic interactions (e.g.
278 competitive release (Lenoir *et al.*, 2010)).

279 In contrast, populations experiencing changing climate in more heterogeneous
280 landscapes (to the right or down in Fig. 1) are more likely to have a suitable microclimate
281 patch nearby. At the same time, these populations are likely to have been under selection
282 for better dispersal capacity and wider niches because they have been exposed to such.
283 The populations remaining in these landscapes should thus be better equipped to stay
284 within the landscape. In L1-L6, in contrast to L0, for which species have to migrate
285 outside the landscape if they cannot adapt locally, species can move across the landscape

286 to track the climatic change. Species may go extinct within the landscape if (i) dispersal
287 distances to track the species' niche exceed the species' dispersal capacity and life-
288 history traits, (ii) the available habitat area within the landscape becomes too small to
289 support a viable (meta-)population or (iii) the species' climatic niche is no longer
290 available within the landscape (e.g., very cold-adapted species represented by the blue
291 curve). In L1 the risk of colonisation time-lags and extinctions is expected to be higher
292 than in L2 but this will depend heavily on species climatic tolerance, dispersal capacity
293 and life-history traits (Alsos *et al.*, 2012, 2015; Bertrand *et al.*, 2011; Lenoir *et al.*, 2008).

294 The average dispersal distance required to track a given climate change within the
295 landscape window decreases from L1 via L3 to L5, requiring successively smaller
296 dispersal capacity for survival. L4 and L6 will offer even better opportunities to disperse
297 between patches under dramatic climate changes, even for dispersal-limited species.
298 There is a high probability of encountering a patch nearby with suitable microclimate
299 unless the microclimatic niche has vanished for that species (i.e. the species represented
300 by blue and purple curves in Fig. 1 may lose their niches after warming), resulting in
301 low dispersal limitation-related extinction rates and short time-lags. New neighbours will
302 colonise at a faster rate. We expect that such rapid changes will pose challenges for
303 species with slow life histories (cf. long-lived species with limited colonisation capacity)
304 (Lenoir and Svenning, 2013; Tscharrntke *et al.*, 2012; Vranckx *et al.*, 2012), and they will
305 rely more on their ability to tolerate climate changes (De Witte and Stocklin, 2010). The
306 more fragmented landscapes, however, will also encompass smaller and more fragmented

307 populations that may be more vulnerable to climatic fluctuations.

308 Our example landscapes illustrate how the adaptations resulting from the selective
309 pressures that have been shaping the populations inhabiting homogeneous versus
310 heterogeneous landscapes may be the opposite of the adaptations populations will need to
311 survive in those landscapes under a rapid climate change. Populations in homogeneous
312 landscapes have been under selection for traits allowing them to persist under rather
313 homogeneous conditions, but may, in the face of climate change, be required to migrate
314 over large distances (outside the landscape) if they cannot tolerate or adapt to the new
315 conditions. In contrast, populations inhabiting heterogeneous landscapes have better
316 opportunities to “stay” within their landscape throughout short-distance displacements
317 and yet are also better adapted to disperse over longer distances and establish in a wider
318 range of conditions due to historical selection pressures towards better dispersal and
319 wider niches.

320

321 ***Communities in landscapes of varying climatic heterogeneity***

322 Landscape structure and the associated differences in climatic range and patchiness will
323 have consequences for community-level processes in the landscape (Tscharntke *et al.*,
324 2012). The meta-community paradigm (Box 2), as described by Chesson (2000) and
325 Leibold *et al.* (2004), is a useful starting point for exploring these implications. Here we
326 assume that meta-community dynamics are driven to various degrees by neutral
327 processes, patch dynamics, species sorting, and mass effects (Leibold *et al.* 2004).

328 Climatically homogeneous landscapes, as exemplified by L0, are not likely to support
329 communities in which climate niche-based processes, such as species sorting or mass
330 effects, play important roles in maintaining species diversity (Fig. 2). There is no climate-
331 driven habitat variation, and the populations that inhabit these landscapes share the same
332 climate niche (see above). The total suitable habitat area is large and climatically
333 homogeneous, which will increase the probability of community assembly based on
334 either neutral processes, where the co-existence results from the very slow stochastic
335 extinction rates of demographically equivalent species within a relatively large
336 population area, or patch dynamics, with species co-existence permitted by a trade-off
337 between dispersal and competitive abilities (Fig. 2).

338 In contrast, landscapes encompassing a wider range of climatic conditions (L1-
339 L6) have more climate niche space available and there is scope for coexistence based on
340 climate niche partitioning and hence for species sorting and/or mass effects to operate
341 (Fig. 2). The climatic range is equal for all landscapes at the same position along the
342 climate range gradient (for L1, L3, and L5 or for L2, L4, and L6), and the total area of
343 suitable microclimate for any particular species is therefore also equal for the landscapes
344 within each of these columns. It follows that climatic niche-partitioning processes (i.e.,
345 species sorting and/or mass effects) is likely to be intermediately important across L1, L3,
346 and L5, and of overriding importance across L2, L4 and L6. As we move from L0 via L1
347 to L2, the average habitat area available for each species decreases, but for each species
348 the available area is not fragmented (high auto-correlation), leading to an overall decrease

349 in the relative contribution of dispersal to community dynamics.

350 Towards the lower parts of Fig. 2, both the average patch size of suitable habitats
351 and the dispersal distance between patches decreases, leading to increased probabilities of
352 both local extinction and re-colonisation of locally-extinct populations. The climate
353 gradient length is equal within each column (e.g., L2, L4 and L6) and the importance of
354 climatic niche-partitioning processes (the combined effect of species sorting and mass
355 effects) is hence constant. However, with increased fragmentation, the probability that a
356 dispersed propagule ends up in a 'sink' population increases, and the relative importance
357 of mass effects is therefore expected to increase at the cost of efficient species sorting
358 (Fig. 2). In L6, however, the decrease in dispersal distances between patches might be so
359 important that, for some species, the landscape is perceived as more homogeneous than
360 L3 and L4. Hence, neutral dynamics could be expected to operate, but within several
361 "parallel communities" each consisting of few species with very specific climatic
362 tolerances. Mass effects are then occurring between these parallel communities, causing
363 all the species to seemingly coexist in the same landscape.

364

365 *Consequences of microclimatic heterogeneity for communities under climate change*

366 In large homogeneous landscapes where diversity is maintained by neutral and patch-
367 dynamics processes, such as L0, there is little climate niche variation among species.

368 Under climate change, persistence due to shifts in species' realised niche is possible as
369 long as the climate change is within the fundamental niche limits of the species (Lenoir

370 and Svenning, 2015). As the current climate no longer overlaps with the fundamental
371 climatic niches of many of the species in the community, extinction rates are likely to
372 increase sharply, and the ensuing gaps will mostly receive non-suitable recruits. This will
373 result in unsaturated communities, probably with decreased levels of interspecific
374 competitive interactions, which could lead to shifts or expansion of realised niches (cf.
375 Lenoir et al., 2010) and increased probability of persistence for the remaining species.
376 Long-term maintenance of biodiversity and ecological functions in such landscapes will
377 require local extinctions and immigration, and hence remnant population dynamics
378 (Eriksson, 1996, 2000), storage effects (Chesson and Warner, 1981) and dispersal
379 limitation on long-distance dispersal from outside the landscape will result in severe
380 time-lags. Such communities may exhibit considerable unpaid extinction debts (Jackson
381 and Sax, 2010; Kuussaari *et al.*, 2009), as species sorting processes will be inefficient in
382 increasingly unsaturated communities consisting of species poorly adapted to the new
383 climatic conditions. On the other hand, when individuals dispersing in from outside the
384 landscape do eventually arrive, these unsaturated communities are likely to be readily
385 invisable (colonisable) and new species with good dispersal and establishment capacities
386 are likely to be favoured. We therefore expect communities in homogeneous landscapes
387 to experience relatively slow species loss, and low levels of landscape-scale reshuffling
388 over time (cf. time lag and climatic debt, *sensu* Bertrand et al., 2016). In the long term
389 and with dramatic climate change exceeding the tipping point, we expect greater
390 proportional species loss (climatic debt being paid off) here than in heterogeneous

391 landscapes.

392 In heterogeneous landscapes (L1-L6), climate change is likely to result in species
393 displacement along the climatic gradient, with direction and rate of the realized
394 community change shaped by the interplay between local dispersal and species-sorting
395 processes operating within the landscape (i.e., paralleling the processes operating in the
396 landscape under a stable climate; Fig. 2). In general terms, landscapes with broader
397 climatic ranges will have smaller available habitat area for any given climatic regime and
398 hence higher extinction probability under climate change compared to more
399 homogeneous landscapes. However, the finer-grained spatial heterogeneity of patchy
400 landscapes implies, on average, that a broader range of climatic conditions are available
401 within a given distance from any particular point in the landscape, and hence an influx to
402 patches of species with a broad range of climatic-niche requirements. As discussed
403 above, a species pool adapted to survival in a fragmented landscape may also be better
404 equipped for dispersal within the landscape. The net effect is less dispersal limitation,
405 shorter establishment time-lags, and faster equilibration of the communities to new
406 climatic conditions in patchy compared to homogeneous landscapes. Only the warmest
407 patches may experience problems getting new species from within the landscape.
408 However, at the same time, good dispersal abilities coupled with greater proximity
409 between different habitat types will also result in greater impacts of mass effects on
410 communities within these heterogeneous landscapes (Fig. 2). These mass effects will tend
411 to delay the realized community change in response to climate change in patchy

412 landscapes. Indeed, as long as a sufficient number of source populations are still
413 available within the landscape, communities may appear resistant to climate change (Fig.
414 2). These contrasting effects of niche availability and patchiness on metacommunity
415 processes within the landscapes thus predicts better climatic-niche tracking across
416 intermediate landscapes (L1 to L5), with shorter time-lags here than in less (L0) or more
417 (L6) fragmented landscapes where greater tolerances to climate change and greater mass
418 effects, respectively, delay community turnover in species composition.

419 The shift in relative importance of underlying meta-community processes (from
420 neutral processes and patch dynamics via species sorting to mass effects; Fig. 2) as well
421 as the differences in selective pressures (increasing dispersal ability, Fig. 1) may be
422 instrumental in driving differences in community-level response along the gradient from
423 homogeneous to heterogeneous landscapes. At the same time, these same processes
424 (notably, the mass effects) will tend to delay the change in underlying community
425 dynamics in heterogeneous landscapes, resulting in an apparent resistance to climate
426 change.

427

428 **The impact of temporal variation, and non-climatic confounding factors**

429 In addition to the general framework discussed above, other aspects of scale, temporal
430 climatic variation, other niche requirements, biotic interactions, and disturbance will
431 affect populations and communities under climate change. First, climatic heterogeneity
432 varies in time as well as in space, and this also shapes the characteristics of populations

433 and communities, and we may, for example, expect populations and communities with a
434 history of exposure to strong temporal climatic variation due to seasonality or recurring
435 extreme events to cope better with climate changes compared to landscapes in regions
436 with less variable weather and climate. Second, biotic interactions can modify both
437 microclimate and the ability of species to track their climate (Leathwick and Austin,
438 2001; Wisz et al., 2013). For instance, species colonisation rates may be enhanced by
439 facilitation (Anthelme et al., 2014) or by zoochory (Cunze et al., 2013), and they may be
440 delayed by interference (Pellissier et al., 2010). The strength of biotic interactions are
441 however themselves often dependent on climate (Pellissier et al., 2013; Anthelme et al.,
442 2014; Alexander et al., 2015; Olsen et al., 2016), and may therefore also enforce
443 processes determined by landscape heterogeneity.

444 The rate and magnitude of climate change will partly determine the need for
445 adaptation or required dispersal capacity for climate tracking (Sandel *et al.*, 2011), and
446 the disturbance frequency in a landscape, whether topographically homogeneous or
447 heterogeneous, also imposes selective pressures on the species. Disturbance creates
448 additional temporal and spatial heterogeneity in plant populations and communities,
449 imposes distinct selective pressures (Tschardtke *et al.*, 2012), and interacts with
450 community dynamics (Levins and Culver, 1971; Tilman, 1994). Communities dominated
451 by disturbance-adapted species will hence change faster than communities dominated by
452 more stress-tolerant or competitive species (*sensu* Grime, 2001). This is not only because
453 the species in the landscape are adapted to rapid changes, but also because the landscape

454 itself will likely be subjected to disturbance in the future providing gaps in the vegetation
455 for new colonisations (Vandvik and Goldberg, 2005; 2006). Many areas with high
456 disturbance are associated with intense use by human or other animals and are often
457 found in flat areas. Therefore, disturbance may cause topographically homogeneous
458 landscapes to change faster than expected from the microclimatic variation patterns
459 outlined above.

460

461 **Conclusion**

462 A growing number of studies points to the importance of landscape topography in
463 modifying the rate of change in populations and communities (Tscharrntke *et al.*, 2012).
464 For instance, findings from Bertrand *et al.* (2011) suggest that the extinction debt in
465 forest plant communities is much more important in the lowlands than in the highlands in
466 France. Spasojevic *et al.* (2013) and De Frenne *et al.* (2013) however, showed that alpine
467 and forest plant communities are dynamic through time when studied at a fine spatial
468 scale, even for the species distributions that on a broad scale seem to show extinction
469 debts (Bertrand *et al.*, 2011). We argue that landscapes with high microclimatic
470 heterogeneity will contain populations and communities that have better opportunities for
471 coping with climate change than those of climatically more homogeneous landscapes.
472 However, at the same time, the characteristics of populations in heterogeneous landscapes
473 may also compromise the monitoring of species-environment relationships, due to mass
474 effects. In contrast, populations and communities of climatically more homogeneous

475 landscapes may be relatively more vulnerable to climate change as they can only persist
476 in the long run if they adapt to the new environment, if their realised niches are relaxed,
477 or if they persist through extreme longevity and remnant populations. Nevertheless, lower
478 immigration rates and less-saturated communities may provide opportunities for niche
479 expansion and rapid evolution in homogeneous landscapes under a changing climate.
480 Species and communities in homogeneous landscapes may therefore be more resistant to
481 climate change than predicted solely from the current realised niches of the species and
482 the current community dynamics.

483 To improve our understanding of population and community responses to climatic
484 change, future studies need to consider the microclimatic heterogeneity of the landscapes
485 in which the species are found and the selective pressures that may have shaped the
486 populations and communities in these landscapes. We here introduced a very simplified
487 theoretical framework to illustrate how the spatial patterns in microclimatic range and
488 patchiness, closely associated to the various effects of topography and variables outlined
489 in Box 1, may affect alpine community dynamics in response to climate change.

490 Synthesis and tests of the importance of temporal climatic variation for the capacity for
491 persistence or migration of populations and communities are also needed. Considering
492 the microclimatic heterogeneity driven by topographic complexity in Arctic and alpine
493 ecosystems may help us better understand the resistance and resilience of populations and
494 communities to changing climate.

495

496 **Acknowledgments**

497 This paper is the outcome of discussions during network meetings of the Stay or Go
 498 network funded by Nordforsk from 2011-2013 (Project number 29662 to BJB). JCS was
 499 supported by the European Research Council (ERC-2012-StG-310886-HISTFUNC).

500

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795 **Legends to figs**

796 Figure 1.

797 Species response curves along a temperature gradient (upper panel) and the species'
798 spatial distributions (lower panels) across seven landscapes differing in two important
799 determinants of climatic heterogeneity; the range of climatic conditions available (cf.
800 increasing climatic range from left to right) and the degree of fragmentation in climatic
801 conditions (cf. increasing climatic patchiness from top to bottom). The available climate
802 within the landscapes in each column is represented by a vertical dotted line [mean] and
803 a grey box [range] in the upper panel. For illustrative purpose, a theoretical species pool
804 is provided, containing five different species (represented by colours) with different
805 climatic niches (upper panel). Each of the seven (L0-L6) landscape panels gives
806 exemplified spatial distribution of the climatic niche space (colour scale from cold to
807 warm) and of local populations of the species in the species pool (coloured rings). Note
808 that the mean temperature is similar across all seven landscapes – illustrated by the black
809 triangle on the key to the right.

810

811 Figure 2.

812 Prediction of the relative importance of different meta-community dynamics (Neutral
813 processes NP, Patch dynamics PD, Species sorting SS and Mass effects ME (see Box 2
814 for explanation)) (upper panel) in response to the climatic heterogeneity in the landscape
815 (lower panels). The seven landscapes are the same as in Figure 1.

816

817

818 **Box 1: The thermal niche of alpine plants**

819 The thermal niche of plants is often described in a highly simplified manner with a strong
820 focus on synoptic or ambient air temperature characterizing macroclimate. For small-
821 stature and slow-growing alpine and Arctic plants there is a major difference and
822 decoupling between the temperature that the plants experience near the ground and the
823 temperature conditions obtained from weather stations measuring synoptic temperature at
824 2 m height (Graae et al. 2012, Lenoir et al 2013, Körner 2003, Scherrer and Körner 2010,
825 2011). During summer, the difference and decoupling between temperature conditions
826 near the ground and synoptic temperature is to a high degree controlled by topography,
827 vegetation structure, proximity to ground and, in the soil, also the moisture level.
828 During winter, difference and decoupling is also caused by topography, vegetation
829 structure and proximity to ground, but this is mostly due to its effect on snow cover
830 and depth that determines the microclimate (temperature and moisture) and light
831 conditions to the plants. Körner (2003) as well as Wipf and Rixen (2010) describes in
832 detail how snow cover and duration matters for alpine and Arctic vegetation.

833 In addition to these scale effects, it is well established that the multifaceted nature
834 of temperature (maximum, minimum, mean, growing season length, etc.) affects different
835 life cycle and phenological stages to various extent. For instance, extreme temperatures
836 are mostly associated with mortality events and the timing of these extreme events is
837 crucial, whereas mean temperatures are chiefly associated with growth processes. Körner
838 et al. (2016) describe how the many different components of climate affect tree
839 distribution, and this complexity of niche limiting factors and interactions is expected to
840 be even greater for small-stature plants occurring near the ground. Understanding the

841 ecophysiological and ecological mechanisms underlying plant species distribution needs
842 to take such microclimatic considerations into account. Accounting for all these limiting
843 factors to model alpine plant species distribution is rarely done in the scientific literature.
844 The more simplified concept of thermal niche has, however, shown useful because plant
845 species distribution, especially trees for which most studies are done, correlate well with
846 macroclimatic variables such as mean summer and winter temperatures. However, for
847 mechanistic understanding of what is driving these correlations we need to go beyond
848 mean temperatures (Körner et al. 2016) and assess the importance of this topographically-
849 driven heterogeneity in temperature conditions near the ground and its consequences for
850 alpine plant distribution and redistribution under climate change.

851

852 Legend to Figure Box 1:

853 Diagram showing the many factors shaping the microclimatic niche in alpine plant
854 communities. The growing season macroclimate is filtered into microclimate by factors
855 listed in the red arrow and winter macroclimate is filtered into microclimate by factors
856 listed in the blue arrow. The resulting summer microclimatic niche in green for survival
857 growth and reproduction of plants are determined by temperature extremes (max and min
858 temperatures mostly for survival), season length and growing degree hours (GDH) that
859 gives the accumulated temperature for growth and reproduction. Also the winter
860 microclimatic niche in blue is determined by the temperature extremes for survival while
861 season length, that also to a high extent is driven by snow cover, determines important
862 winter processes, for instance respiration and dormancy break.

863

864 **Box 2: The meta-community paradigm**

865 The meta-community paradigm defines a meta-community as a set of local communities,
 866 linked by dispersal, and describes how the dynamics of the meta-community at large is
 867 driven by the interactive effects of local niche processes operating within each patch, and
 868 by dispersal between patches (Leibold *et al.*, 2004). **Four general and non-mutually**
 869 **exclusive perspectives** on meta-community dynamics are typically recognized:

- 870 • **Neutral** processes assume that all species within a trophic level and all patches
 871 are functionally equivalent and coexistence is permitted by stochastic processes
 872 and slow competitive exclusion relative to immigration and evolutionary rates
 873 (Hubbell, 2001).
- 874 • **Patch dynamics** models describe a system where coexistence is permitted by a
 875 trade-off between dispersal and competitive ability, so that the most successful
 876 colonizers of available patches are relatively poor competitors, and vice versa
 877 (Levins and Culver, 1971; Tilman, 1994).
- 878 • **Species sorting** models assume an environmentally heterogeneous environment
 879 and consider how species' niche requirements 'sort' them into local communities
 880 (Chase and Leibold, 2003; Whittaker, 1962).
- 881 • **Mass effects** models build on species sorting, but with the added feature that
 882 dispersal between communities may allow maintenance of local 'sink'
 883 populations also in sites where the niche requirements of that species are not met
 884 (Holt, 1993; Mouquet and Loreau, 2003).

885 In the past decade, the meta-community paradigm has been highly influential in setting
 886 the research agenda in community ecology, and it has inspired a substantial literature on
 887 the interplay between dispersal and niche processes, covering a wide range of spatial and
 888 temporal scales, biomes, and organism groups, and giving rise to both theoretical,
 889 observational and experimental advances (Leibold *et al.*, 2010; Murphy and Foster, 2014;
 890 Myers and Harms, 2009; Pillar and Duarte, 2010; Telford *et al.*, 2006; Tschamntke *et al.*,
 891 2012; Urban *et al.*, 2008). However, questions of the relative importance of the different
 892 meta-community processes in determining the patterns in community composition we
 893 observe in nature, and indeed how and if the relative importance of these processes can
 894 even be quantitatively assessed, have been highly debated and are far from being resolved

895 (e.g., Logue *et al.*, 2011).