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

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48

49 **Abstract**

50 In the face of climate change, populations have two survival options – they can tolerate
51 the new climatic conditions, though broad tolerance, plasticity, or adaptation ('stay'), or
52 they can disperse to new locations, tracking their climatic niches ('go'). For sessile and
53 small-stature organisms like alpine plants, "going" requires good dispersal and
54 establishment capacities. Staying, in contrast, requires broad climatic tolerances, niche
55 shifts due to changing biotic interactions, acclimation through plasticity, or rapid genetic
56 adaptation. Neither the magnitude of climate change experienced locally nor the
57 capacities required for staying/going in response to climate change are constant across
58 landscapes, and these may be strongly affected by local microclimatic variation
59 associated with topographic complexity. We combine ideas from population and
60 community ecology to discuss the effects of topographic complexity in the landscape on
61 the immediate "stay" or "go" opportunities of local populations and communities, and on
62 the selective pressures that may have shaped the "stay" or "go" capacities of the species
63 occupying contrasting landscapes. We here demonstrate, using example landscapes of
64 different topographical complexity, how species' thermal niches could be distributed
65 across these landscapes, and how these, in turn, may affect many population and
66 community ecological processes that are related to adaptation or dispersal. With a focus

67 on treeless, high-elevation or Arctic landscapes, where the vegetation consist of slow-
68 growing species and temperature is expected to be a strong determinant, we suggest that
69 populations and communities of topographically complex (rough and patchy) landscapes
70 should be both more resistant and more resilient to climate change than those of
71 topographically simple (flat and homogeneous) landscapes. However, meta-community
72 mass effects in rough and patchy landscapes, as well as extinction lags in flat and
73 homogeneous landscapes, may sometimes mask and delay the effects of these landscape
74 differences under rapidly changing climates.

75

76 **Keywords:** adaptation, dispersal, microclimate, niche, refugia, resilience, resistance,
77 topoclimate.

78

79 ***Introduction***

80 Our understanding of the magnitude and ecological implications of climatic variation in
81 space and time has greatly developed over the past decades. Most studies focused on the
82 global distribution of climate and the capacity for species to track their climatic niches;
83 palaeoecological reconstructions (reviewed in Feuderan *et al.*, 2013) and climate
84 envelope models (Pearson and Dawson, 2003; Sykes *et al.*, 1996) suggest high migration
85 rates in response to the rapid redistribution of climate at the global scale (Clark *et al.*,
86 1998; Loarie *et al.*, 2009). For plants, these findings have been challenged by molecular
87 (Westergaard *et al.*, 2010, 2011), palaeoecological (Birks and Willis, 2008; Cheddadi *et al.*,
88 2014) and mesoscale to microscale climate envelope-modelling studies (Randin *et al.*,
89 2009), all suggesting occasional survival in refugia in, for example, the periglacial
90 landscapes of Europe and North America (Birks and Willis, 2008; Davis and Shaw, 2001;
91 Stewart *et al.*, 2010). These discrepancies illustrates how an appreciation of the spatial
92 variation in climate is key to understanding spatial and temporal dynamics of species and
93 communities (Ackerly *et al.*, 2010; Dobrowski, 2011; Dobrowski *et al.*, 2011, Lenoir and
94 Svenning, 2013; Svenning and Sandel, 2013). Indeed, the propensity for species to
95 “stay”, through adaptation processes, or “go”, through dispersal processes, so as to
96 survive in the face of climate change, not only depends on the magnitude of climate-
97 change exposure and the climate-change sensitivity of the constituent species and
98 communities (Dickinson *et al.*, 2014; Bertrand *et al.*, 2016), but also on the spatial
99 structure of the landscapes in which the species occur (Körner 2004, Slavich *et al.*, 2014).

100 Topography is a key determinant of climatic variation across spatial scales
101 ranging from regions, covering hundreds of square kilometres, to microsites of less than a
102 square metre, especially in treeless areas like the high Arctic and alpine regions (see Box
103 1). Across these ecosystems, we can find regions, landscapes, patches, and microsites that
104 are relatively topographically uniform or topographically complex, with associated
105 differences in climatic heterogeneity. For example, there are clear differences in
106 topographic complexity between mountainous *vs.* flat landscapes in high-latitude regions
107 (Lenoir *et al.*, 2013), flat areas *vs.* ridge-snowbed gradients in alpine landscapes (Graae *et*
108 *al.*, 2011; Körner, 2003), and flat *vs.* microtopographically complex patches within
109 grassland and tundra vegetation (Armbruster *et al.*, 2007; Moeslund *et al.*, 2013; Opedal
110 *et al.*, 2015). It is widely acknowledged that topographic complexity in these treeless
111 areas exerts a strong control on vegetation structure and soil moisture during summer as
112 well as on snow cover distribution during winter, which subsequently affects the spatial
113 distribution of temperature near the ground and its decoupling from synoptic and free-air
114 temperature (Box 1). The impact of this topographically-driven heterogeneity in
115 temperature conditions near the ground on alpine plant communities is therefore of
116 particular interest under the current circumstances of anthropogenic climate change. For
117 instance, topographic complexity at scales of a few tens of metres can give rise to
118 microclimatic variation in e.g., mean temperatures that often matches what is expected
119 under future climate change scenarios (2-6°C; Armbruster *et al.*, 2007; Dobrowski *et al.*,
120 2013; Graae *et al.*, 2012; Lenoir *et al.*, 2013; Opedal *et al.*, 2015; Scherrer and Körner,

121 2010; Scherrer and Körner, 2011).

122 It important to focus on high-latitude and high-elevation landscapes beyond
123 treeline, not only because the complex topography there provides more spatial
124 heterogeneity in temperature, but especially because temperature itself is expected to be
125 the main determinant of plant distribution (Körner 2003, Raunkjær 1934). Indeed,
126 temperature has direct effects on alpine plant life, setting limits to their fundamental
127 niches. Temperature also has a number of indirect effects on alpine plants determining,
128 for instance, plant water balance, decomposition rates of organic matter, rates of nutrient
129 cycling, access to water, and the abundance of herbivores, pathogens, pollinators, and
130 seed dispersers. Some of these variables are also influenced by other factors – for
131 instance anthropogenic disturbances. As Box 1 demonstrates, we need to incorporate all
132 these various components of temperature into the thermal niche concept of alpine plants.
133 Describing the thermal niche for a species is difficult because of the complexity of other
134 interacting and limiting factors. Here, the thermal niche of an alpine plant species
135 becomes a somewhat theoretical object for which one has to make the often unrealistic
136 assumption of *ceteris paribus* (“other things being equal”). Improving our understanding
137 of the distribution of these thermal niches across the landscape is important for predicting
138 species' capacities to adapt and disperse in response to changing climate.

139 Here, we synthesise theories relevant for how the topographic complexity of a
140 landscape at high latitudes or altitudes influences the resistance (the lack of sensitivity
141 and response to perturbation or disturbance) and resilience (the capacity to recover after

142 perturbation or disturbance) of alpine plant populations and communities in response to
143 climate change. Specifically, we explore (1) how populations in landscapes of different
144 topographical complexity are affected by microclimatic heterogeneity under the current
145 climate, and (2) how this may affect their responses to climate change. We then turn to
146 communities, and (3) develop a framework for community response to landscape
147 microclimatic heterogeneity, before we (4) ask how this may affect community-level
148 responses to climate change in landscapes of different topographic complexity. Although
149 we focus on small-stature plants in cold ecosystems, many of the processes we describe
150 here would hold for other groups of organisms, with modifications to account for
151 differences in organism mobility and scale (Roth et al. 2014). For small-stature plants in
152 the lowlands, one would also have to consider, in addition to topography, the effect that
153 tree or shrub canopy cover exerts on microclimate (Grimmond et al. 2000) and its
154 consequences for forest plant species distribution (e.g. Wesser and Armbruster 1991;
155 Lenoir et al. 2017).

156

157 *The spatial components of microclimatic heterogeneity*

158 Microclimatic heterogeneity affects populations and communities in two general ways.
159 First, by increasing the range of climatic conditions, it increases the climatic niche space
160 that is available within a given surface area and creates potential niche space for more
161 species. At the same time, this inevitably comes at the expense of reduced available
162 habitat area (Kerr & Packer 1997, Scherrer and Körner 2011) and thus increases habitat

163 fragmentation (Reino et al. 2013) for species with specialised thermal niches.

164 Topography in alpine and Arctic ecosystems is the main physiographic feature that can
165 enhance microclimatic heterogeneity in space. As a general and simplified example,
166 consider seven hypothetical landscapes of equal size (e.g., 1 km²), sharing a regional
167 plant species pool (Zobel, 1997), but varying in topographic complexity (Fig. 1).

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

183 Our first example landscape, L0, is climatically homogeneous, with a narrow

184 range of climatic conditions (or niche space), such as can be found for temperature across
185 a flat and smooth landscape. For species whose realised niche requirements are fulfilled
186 in this landscape (species represented by the brown and green curves and rings in Fig. 1),
187 a large and continuous habitat area is available, and the probability of local extinction
188 under stable conditions is hence low (Hanski, 1998; Lande, 1993; MacArthur and
189 Wilson; 1963). L1 and L2 encompass increasingly wider ranges of thermal conditions
190 that are distributed in a non-patchy way (positive spatial autocorrelation) such as on a
191 gentle (L1) or a steep (L2) hillside. The available niche space, and hence the potential
192 number of species in the landscape increases from L0 via L1 to L2 (Fig. 1). Depending
193 on the species' niche width and the climatic niche availability, species may occur in the
194 whole or in parts of the landscape, and there is, for most species, less habitable area
195 available in L2 than in L1 and L0.

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

204 Below, we evaluate how the increasing landscape heterogeneity affects the

205 populations and communities inhabiting these different landscapes. We outline the
206 consequences of this landscape heterogeneity for the selective pressures within the
207 different landscapes, and for how the populations and communities are equipped to
208 respond to climate change.

209

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

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

226 history. Small sized and well-dispersed plant species will most likely be less affected by
227 decreasing habitat sizes and increasing isolation than plant species with high area
228 requirement or more limited colonisation capacities.

229 Interestingly, the population processes in climatically variable and patchy
230 landscapes, like L6, may converge towards the situation in homogeneous landscapes such
231 as L0 if distances are so small that individuals can easily move between patches so that
232 populations are no longer fragmented. However, in contrast to L0, highly heterogeneous
233 landscapes as in L6 may allow populations with different niche requirements to coexist,
234 as long as the patch area across the landscape is still large enough for populations to
235 survive locally. Therefore, the constraint due to dispersal limitation towards a climatically
236 suitable location may become less important towards both L6 (i.e. similar microclimates
237 can be very close) and L0 (i.e. homogeneous microclimatic conditions), and may be most
238 important under intermediate microclimatic heterogeneity (relative to the organism under
239 study).

240 The microclimatic heterogeneity in the landscape will also alter the selective
241 forces acting on populations in the different landscape types. Populations inhabiting
242 climatically heterogeneous landscapes may be under selection for broader niches in order
243 to maintain sustainable population sizes in a heterogeneous environment. When
244 microclimatic heterogeneity increases, either moving from left to right or top to bottom in
245 Fig. 1, species with broad climatic niches, represented by the green curve, will have an
246 advantage compared to the species with narrower niches. Selection for broader niches

247 may result in greater phenotypic plasticity and/or genetic differentiation within local
248 populations, with important consequences for the capacity of these populations to
249 respond to environmental changes (Chevin *et al.*, 2010; Jump and Peñuelas, 2005;
250 Nicotra *et al.*, 2010). Whether selection in response to environmental heterogeneity
251 favours phenotypic plasticity, genetic differentiation, or a combination of the two,
252 depends on several factors, including the temporal and spatial scale of climatic variation
253 (Alpert and Simms, 2002; Botero *et al.*, 2015). More effective dispersal in space or time
254 may also counteract the negative effects of fragmentation. Populations in fragmented
255 landscapes may therefore also be under selection towards better dispersal abilities, or they
256 may be under selection towards better survival in dormant or other long-lived stages, thus
257 contributing to extinction time-lags, until opportunities for continued growth and
258 reproduction (re)appear locally (dispersal in time or remnant population strategy *sensu*
259 Eriksson, 1996).

260

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

262 Populations in different landscape types, such as topographically simple vs. complex
263 terrains, may be very differently positioned, and also equipped, to meet ecological
264 challenges of climate change. In a climatically homogeneous landscape, like L0,
265 populations can remain within the landscape if they tolerate the new climatic conditions,
266 either through intrinsic ability of individuals to tolerate changing climatic conditions
267 (Bertrand *et al.*, 2016), or through intraspecific variation in the position of the climatic

268 niche optima (Valladares et al. 2014). Alpine plant species within the homogeneous
269 landscapes are expected to have rather narrow niches, but those with the widest climatic
270 niches, represented by the green curve in Fig. 1, will have the highest chance of surviving
271 in this type of landscape and adapting to the new climatic conditions through realised
272 niche shifts (Wasof *et al.*, 2013, 2015). Indeed, in L0, distances to new suitable habitats
273 might be relatively large (i.e., somewhere outside the landscape), thus favouring
274 adaptation ("stay") processes over dispersal and colonisation ("go") processes. In
275 addition, low immigration rates into patches in these landscapes (i.e., long distance to
276 source populations of species with different climatic optima) means that the resident
277 species will have a relatively low risk of being exposed to competition from immigrant
278 species better adapted to the new climate (Ackerly, 2003; Bertrand *et al.*, 2011). This
279 may allow persistence under a new suboptimal climate and hence a longer time during
280 which adaptation to the new climate can occur (Ackerly, 2003; Svenning and Sandel,
281 2013). Species with high persistence capacity, for instance with very long-lived
282 individuals or dormant stages, may remain for extended periods in this type of landscape
283 (L0) compared to those predicted from their climatic niche (Eriksson, 1996, 2000; May *et*
284 *al.*, 2009; Migliore *et al.*, 2013), contributing to the extinction debt (Tilman et al., 1994).
285 Related to this, "staying" may also be possible through expansion of the realised niche to
286 encompass the new climate, for example due to changes in biotic interactions (e.g.
287 competitive release (Lenoir *et al.*, 2010)).

288 In contrast, populations experiencing changing climate in more heterogeneous

289 landscapes (to the right or down in Fig. 1) are more likely to have a suitable microclimate
290 patch nearby. At the same time, these populations are likely to have been under selection
291 for better dispersal capacity and wider niches because they have been exposed to such.
292 The populations remaining in these landscapes should thus be better equipped to stay
293 within the landscape. In L1-L6, in contrast to L0, for which species have to migrate
294 outside the landscape if they cannot adapt locally, species can move across the landscape
295 to track the climatic change. Species may go extinct within the landscape if (i) dispersal
296 distances to track the species' niche exceed the species' dispersal capacity and life-
297 history traits, (ii) the available habitat area within the landscape becomes too small to
298 support a viable (meta-)population or (iii) the species' climatic niche is no longer
299 available within the landscape (e.g., very cold-adapted species represented by the blue
300 curve). In L1 the risk of colonisation time-lags and extinctions is expected to be higher
301 than in L2 but this will depend heavily on species climatic tolerance, dispersal capacity
302 and life-history traits (Alsos *et al.*, 2012, 2015; Bertrand *et al.*, 2011; Lenoir *et al.*, 2008).

303 The average dispersal distance required to track a given climate change within the
304 landscape window decreases from L1 via L3 to L5, requiring successively smaller
305 dispersal capacity for survival. L4 and L6 will offer even better opportunities to disperse
306 between patches under dramatic climate changes, even for dispersal-limited species.
307 There is a high probability of encountering a patch nearby with suitable microclimate
308 unless the microclimatic niche has vanished for that species (i.e. the species represented
309 by blue and purple curves in Fig. 1 may lose their niches after warming), resulting in

310 low dispersal limitation-related extinction rates and short time-lags. New neighbours will
311 colonise at a faster rate. We expect that such rapid changes will pose challenges for
312 species with slow life histories (cf. long-lived species with limited colonisation capacity)
313 (Lenoir and Svenning, 2013; Tschardtke *et al.*, 2012; Vranckx *et al.*, 2012), and they will
314 rely more on their ability to tolerate climate changes (De Witte and Stocklin, 2010). The
315 more fragmented landscapes, however, will also encompass smaller and more fragmented
316 populations that may be more vulnerable to climatic fluctuations.

317 Our example landscapes illustrate how the selective pressures that have been
318 shaping the populations inhabiting homogeneous versus heterogeneous landscapes may
319 be the opposite of what the populations need to survive a rapid climate change.
320 Populations in homogeneous landscapes have been under selection for traits allowing
321 them to persist under rather homogeneous conditions, but may, in the face of climate
322 change, be required to migrate over large distances (outside the landscape) if they cannot
323 adapt to the new conditions. In contrast, populations inhabiting heterogeneous landscapes
324 have better opportunities to “stay” within their landscape throughout short-distance
325 displacements and yet are also better adapted to disperse and establish outside the
326 landscape due to historical selection pressures towards better dispersal and wider niches.

327

328 *Communities in landscapes of varying climatic heterogeneity*

329 Landscape structure and the associated differences in climatic range and patchiness will
330 have consequences for community-level processes in the landscape (Tschardtke *et al.*,

331 2012). The meta-community paradigm (Box 2), as described by Chesson (2000) and
332 Leibold et al. (2004), is a useful starting point for exploring these implications. Here we
333 assume that meta-community dynamics are driven to various degrees by neutral
334 processes, patch dynamics, species sorting, and mass effects (Leibold et al. 2004).
335 Climatically homogeneous landscapes, as exemplified by L0, are not likely to support
336 communities in which climate niche-based processes, such as species sorting or mass
337 effects, play important roles in maintaining species diversity (Fig. 2). There is no climate-
338 driven habitat variation, and the populations that inhabit these landscapes share the same
339 climate niche (see above). The total suitable habitat area is large and completely
340 homogeneous, which will increase the probability of community assembly based on
341 either neutral processes, where the co-existence results from the very slow stochastic
342 extinction rates of demographically equivalent species within a relatively large
343 population area, or patch dynamics, with species co-existence permitted by a trade-off
344 between dispersal and competitive abilities (Fig. 2).

345 In contrast, landscapes encompassing a wider range of climatic conditions (L1-
346 L6) have more climate niche space available and there is scope for coexistence based on
347 climate niche partitioning and hence for species sorting and/or mass effects to operate
348 (Fig. 2). The climatic range is equal for all landscapes at the same position along the
349 climate range gradient (for L1, L3, and L5 or for L2, L4, and L6), and the total area of
350 suitable microclimate for any particular species is therefore also equal for the landscapes
351 within each of these columns. It follows that climatic niche-partitioning processes (i.e.,

352 species sorting and/or mass effects) is likely to be intermediately important across L1, L3,
353 and L5, and of overriding importance across L2, L4 and L6. As we move from L0 via L1
354 to L2, the average habitat area available for each species decreases, but for each species
355 the available area is not fragmented (high auto-correlation), leading to an overall decrease
356 in the relative contribution of dispersal to community dynamics.

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

371

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

373 In large homogeneous landscapes where diversity is maintained by neutral and patch-
374 dynamics processes, such as L0, there is little climate niche variation among species.
375 Under climate change, persistence is possible as long as the new climate is within the
376 fundamental niche limits of the species. Otherwise, persistence will involve shifts in
377 species' realised niche (Lenoir and Svenning, 2015) or remnant population dynamics
378 (Eriksson, 1996, 2000) and storage effect (Chesson and Warner, 1981). As these systems
379 reach a situation, in which the current climate no longer overlaps with the fundamental
380 climatic niches of many of the species in the community, extinction rates are likely to
381 increase sharply, and the ensuing gaps will mostly receive non-suitable recruits. This will
382 result in unsaturated communities, probably with decreased levels of interspecific
383 competitive interactions, which could lead to shifts or expansion of realised niches (cf.
384 Lenoir et al., 2010) and increased probability of persistence for the remaining species.
385 Maintenance of biodiversity and ecological functions in such landscapes may depend on
386 immigration and hence on long-distance dispersal from outside the landscape, and severe
387 immigration time-lags can be expected. On the other hand, when individuals dispersing in
388 from outside the landscape do eventually arrive, these unsaturated communities are likely
389 to be readily invasible (colonisable) and new species with good dispersal and
390 establishment capacities are likely to be favoured. Such communities may exhibit
391 considerable unpaid extinction debts (Jackson and Sax, 2010; Kuussaari *et al.*, 2009), as
392 species sorting processes will be inefficient in increasingly unsaturated communities
393 consisting of species poorly adapted to the new climatic conditions. We therefore expect

394 communities in homogeneous landscapes to experience relatively slow species loss, and
395 low levels of landscape-scale reshuffling over time (cf. time lag and climatic debt, *sensu*
396 Bertrand et al., 2016). In the long term and with dramatic climate change exceeding the
397 tipping point, we expect greater proportional species loss (climatic debt being paid off)
398 here than in heterogeneous landscapes.

399 In heterogeneous landscapes (L1-L6), climate change is likely to result in species
400 displacement along the climatic gradient based on local dispersal and species-sorting
401 processes (i.e., paralleling the processes operating in the landscape under a stable climate;
402 Fig. 2). Towards L6, the successively smaller available habitat area for any given climatic
403 regime may increase the extinction probability, but the relatively shorter dispersal
404 distances needed to track climate change will increase the probability for niche filling and
405 community saturation compared to L0. With climate warming, extinctions will primarily
406 occur among the relatively cold-adapted species, which will lose habitat area as their
407 fundamental-niche requirements are no longer met, and/or as the new community get
408 filled and they are outcompeted by more competitive species from relatively warmer
409 conditions (Alexander et al. 2015).

410 L3-L5 and L2-L4 have the same range of climatic conditions as L1 and L2,
411 respectively, and are therefore equally prone to extinctions of the most cold-adapted
412 species due to habitat-area loss and/or new competitors following climate change (Fig. 2).
413 However, the finer-grained spatial heterogeneity of these landscapes results, on average,
414 in a broader range of climatic conditions within a given distance from any particular point

415 in the landscape, and hence an influx of species with a broad range of climatic-niche
416 requirements. A species pool adapted to survival in a fragmented landscape (L3-L6 in
417 Fig. 2) may also be better equipped to disperse to new habitats in face of climate change.
418 This results in increased variation on which species sorting processes can act, resulting in
419 shorter dispersal and establishment time-lags and faster filling up of the communities
420 compared to L1. L4 and L6 are also even more fragmented than L3 and L5, respectively
421 (Fig. 2), and will therefore have the highest influx of colonisers from different climatic
422 conditions into any particular habitat patch, and hence a faster colonisation and a larger
423 degree of filling up, species sorting and reshuffling under a changing climate. At the
424 same time, good dispersal abilities coupled with greater proximity between different
425 habitat types are also responsible for the greater impacts of mass effects on communities
426 within these heterogeneous landscapes (Fig. 2). These mass effects will tend to delay the
427 overall impacts of climate change on the community dynamics of these landscapes, as
428 community composition will change less than predicted from species niches. Indeed, as
429 long as one or several populations are still acting as sources within the landscape, these
430 will supply sink populations with individuals resulting in apparent resilience despite
431 climate change and inertia before all source populations turn to sink populations across
432 the landscape (Fig. 2). The extinction debt in L6 will only be paid off when all
433 populations will turn into sink populations across the landscape, which may take some
434 time (cf. strong inertia). We thus expect better climatic-niche tracking across intermediate
435 landscapes (L1 to L5), with shorter time-lags than in less (L0) or more (L6) fragmented

436 landscapes where greater tolerances to climate change and mass effects, respectively,
437 delay turnover in species composition.

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

446

447 **The impact of scale, temporal variation, and non climatic confounding factors**

448 In addition to the general framework discussed above, other aspects of scale, temporal
449 climatic variation, other niche requirements, biotic interactions, and disturbance will
450 affect populations and communities under climate change. First, climatic heterogeneity
451 varies in time as well as in space, and this also shapes the characteristics of populations
452 and communities, and we may, for example, expect populations and communities with a
453 history of exposure to strong temporal climatic variation due to seasonality or recurring
454 extreme events to cope better with climate changes compared to landscapes in regions
455 with less variable weather and climate. Second, species will respond differently to the
456 same landscape characteristics, depending on their life history traits, e.g. size of the

457 individuals, dispersal capacity, and area requirements (Potter *et al.*, 2013; Tschardtke *et*
458 *al.*, 2012). Finally, as mentioned in the beginning of the paper, species distributions on all
459 scales are affected by other niche dimensions in addition to climate *per se*, including
460 substrate, hydrology, and interactions with mutualists, predators and competitors, etc..

461 Biotic interactions can modify both microclimate and the ability of species to
462 track their climate (Leathwick and Austin, 2001; Wisz *et al.*, 2013). For instance, species
463 colonisation rates may be enhanced by facilitation (Anthelme *et al.*, 2014) or by zoochory
464 (Cunze *et al.*, 2013), and they may be delayed by interference (Pellissier *et al.*, 2010). The
465 strength of biotic interactions are however themselves often dependent on climate
466 (Pellissier *et al.*, 2013; Anthelme *et al.*, 2014; Alexander *et al.*, 2015; Olsen *et al.*, 2016),
467 and may therefore also enforce processes determined by landscape heterogeneity.

468 The rate and magnitude of climate change will partly determine the need for
469 adaptation or required dispersal capacity for climate tracking (Sandel *et al.*, 2011), and
470 the disturbance frequency in a landscape, whether topographically homogeneous or
471 heterogeneous, also imposes selective pressures on the species. Disturbance creates
472 additional temporal and spatial heterogeneity in plant populations and communities,
473 imposes distinct selective pressures, and may interact with community dynamics and
474 heterogeneity-driven selective pressures. Disturbance is integral to coexistence based on
475 patch dynamics processes (Levins and Culver, 1971; Tilman, 1994). High disturbance
476 rates select for good dispersal capacity and dynamic populations and communities
477 (Tschardtke *et al.*, 2012). Landscapes dominated by disturbance-adapted species will

478 hence change faster than topographically similar landscapes dominated by more stress-
479 tolerant or competitive species (*sensu* Grime, 2001). This is not only because the species
480 in the landscape are adapted to rapid changes, but also because the landscape itself will
481 likely be subjected to disturbance in the future providing gaps in the vegetation for new
482 colonisations (Vandvik and Goldberg, 2005, 2006). Many areas with high disturbance are
483 associated with intense use by human or other animals and are often found in flat areas.
484 Therefore, disturbance may cause topographically homogeneous landscapes to change
485 faster than expected from the microclimatic variation patterns outlined above.

486

487 **Conclusion**

488 A growing number of studies points to the importance of landscape topography in
489 modifying the rate of change in populations and communities (Tschardt *et al.*, 2012).
490 For instance, it has been recently demonstrated that the extinction debt in forest plant
491 communities is much more important in the lowlands than in the topographically more
492 complex highlands (Bertrand *et al.* 2011). However, the characteristics of populations in
493 heterogeneous landscapes may also compromise the monitoring of species-environment
494 relationships due to mass effects. In contrast, the populations and communities of
495 climatically more homogeneous landscapes can only persist in the long run if they adapt
496 to the new environment, if their realised niches are relaxed, or if they persist through
497 extreme longevity and remnant populations. Nevertheless, lower immigration rates and
498 less-saturated communities may provide opportunities for niche expansion and rapid

499 evolution in homogeneous landscapes under a changing climate. Species and
500 communities in homogeneous landscapes may therefore be more resistant to climate
501 change than predicted solely from the current realised niches of the species and the
502 current community dynamics.

503 To improve our understanding of population and community responses to climatic
504 change, future studies need to consider the microclimatic heterogeneity of the landscapes
505 in which the species are found and the selective pressures that may have shaped the
506 populations and communities in these landscapes. Considering the microclimatic
507 heterogeneity driven by topographic complexity in high Arctic and alpine ecosystems
508 may help us better understand the resistance and resilience of populations and
509 communities to changing climate.

510

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515

516 **References:**

- 517 Ackerly D.D., 2003. Community assembly, niche conservatism, and adaptive evolution in
518 changing environments. *Int. J. Plant Sci.* 164, S165-S184.
519 Ackerly D.D., Loarie S.R., Cornwell W.K., Weiss S.B., Hamilton H., Branciforte R.,
520 Kraft N.J.B., 2010. The geography of climate change: implications for
521 conservation biogeography. *Divers. Distrib.* 16, 476-487.

- 522 Alexander J.M., Diez. J.M., Levine, J.M., 2015. Novel competitors shape species'
523 responses to climate change, *Nature* 525, 515-518.
- 524 Alpert P., Simms E.L., 2002. The relative advantages of plasticity and fixity in different
525 environments: when is it good for a plant to adjust? *Evol. Ecol.* 16, 285-297.
- 526 Alsos I.G., Ehrich D., Eidesen P.B. Solstad H., Westergaard K.B., Schonswetter P.,
527 Tribsch A., Birkeland S., Elven R., Brochmann C., 2015. Long-distance plant
528 dispersal to North Atlantic islands: colonization routes and founder effect. *Aob*
529 *Plants* 7.
- 530 Alsos I.G., Ehrich D., Thuiller W. Eidesen P.B., Tribsch A., Schonswetter P., Lagaye C.,
531 Taberlet P., Brochmann C., 2012. Genetic consequences of climate change for
532 northern plants. *P. Roy. Soc. B-Biol. Sci.* 279, 2042-2051.
- 533 Anthelme F., Cavieres L.A., Dangles O., 2014. Facilitation among plants in alpine
534 environments in the face of climate change. *Frontiers Plant Sci.* 5,
535 doi:10.3389/fpls.2014.00387.
- 536 Armbruster W.S., Rae D., Edwards M.E., 2007. Topographic complexity and biotic
537 response to high-latitude climate change: variance is as important as the mean. In:
538 Arctic-Alpine Ecosystems and People in a Changing Environment. (eds Ørbæk
539 JB, Kallenborn R, Tombre I, Hegseth EN, Falk-Petersen S, Hoel AH) Springer
540 Verlag pp 105-122,
- 541 Bertrand R., Lenoir J., Piedallu C., Riofrío-Dillon G., de Ruffray P., Vidal C., Pierrat
542 J.C., Gégout J.C., 2011. Changes in plant community composition lag behind
543 climate warming in lowland forests. *Nature* 479, 517-520.
- 544 Bertrand, R., Riofrío-Dillon G., Lenoir J., Drapier J., de Ruffray P., Gégout J.C., Loreau
545 M., 2016. Ecological constraints increase the climatic debt in forests. *Nature*
546 *Comm.*, 10.1038/ncomms12643
- 547 Birks H.J.B., Willis K.J., 2008. Alpines, trees, and refugia in Europe. *Plant Ecol. Divers.*
548 1, 147-160.
- 549 Botero C.A., Weissing F.J., Wright J., Rubenstein D.R., 2015. Evolutionary tipping
550 points in the capacity to adapt to environmental change. *P. Natl. Acad. Sci. USA*
551 112, 184-189.
- 552 Brown J.H., Kodric-Brown A., 1977. Turnover Rates in Insular Biogeography - Effect of
553 Immigration on Extinction. *Ecology* 58, 445-449.
- 554 Chase J.M., Leibold M.A., 2003. *Ecological Niches*, Chicago, IL, University of Chicago
555 Press.
- 556 Cheddadi R., Birks H.J.B., Tarroso P. Liepelt S., Gomory D., Dullinger S., Meier E.S.,
557 Hulber K., Maiorano L., Laborde H., 2014. Revisiting tree-migration rates: *Abies*
558 *alba* (Mill.), a case study. *Veg. Hist. Archaeobot.* 23, 113-122.
- 559 Chesson P., 2000. Mechanisms of maintenance of species diversity. *Annu. Rev. Ecol.*
560 *Syst.* 31, 343-366.
- 561 Chesson P.L., Warner R.R., 1981. Environmental Variability Promotes Coexistence in
562 Lottery Competitive-Systems. *Am. Nat.* 117, 923-943.
- 563 Chevin L.M., Lande R., Mace G.M., 2010. Adaptation, Plasticity, and Extinction in a
564 Changing Environment: Towards a Predictive Theory. *Plos Biol.* 8.
- 565 Clark J.S., Fastie C., Hurr G. Jackson S.T., Johnson C., King G.A., Lewis M., Lynch J.,
566 Pacala S., Prentice C., Schupp E.W., Webb T., Wyckoff P., 1998. Reid's paradox

- 567 of rapid plant migration - Dispersal theory and interpretation of paleoecological
 568 records. *Bioscience* 48, 13-24.
- 569 Cunze A., Heidel F., Tackenberg O., 2013. Are plant species able to keep pace with the
 570 rapidly changing climate? *PLoS ONE* 8, doi:10.1371/journal.pone.0067909.
- 571 Davis M.B., Shaw R.G., 2001. Range shifts and adaptive responses to Quaternary climate
 572 change. *Science* 292, 673-679.
- 573 De Frenne P., Rodriguez-Sanchez F., Coomes D.A., Baeten L., Verstraeten G., Vellend
 574 M., Bernhardt-Romermann M., Brown C.D., Brunet J., Cornelis J., Decocq G.M.,
 575 Dierschke H., Eriksson O., Gilliam F.S., Hedl R., Heinken T., Hermy M.,
 576 Hommel P., Jenkins M.A., Kelly D.L., Kirby K.J., Mitchell F.J.G., Naaf T.,
 577 Newman M., Peterken G., Petrik P., Schultz J., Sonnier G., Van Calster H.,
 578 Waller D.M., Walther G.R., White P.S., Woods K.D., Wulf M., Graae B.J.,
 579 Verheyen K., 2013. Microclimate moderates plant responses to macroclimate
 580 warming. *P. Natl. Acad. Sci. USA* 110, 18561-18565.
- 581 De Witte L.C., Stöcklin J., 2010. Longevity of clonal plants: why it matters and how to
 582 measure it. *Ann. Bot.-London*, 106, 859-870.
- 583 Dickinson M.G., Orme C.D.L., Suttle K.B., Mace G.M., 2014. Separating sensitivity
 584 from exposure in assessing extinction risk from climate change. *Sci. Rep.* 4.
- 585 Dobrowski S.Z., 2011. A climatic basis for microrefugia: the influence of terrain on
 586 climate. *Global Change Biol.* 17, 1022-1035.
- 587 Dobrowski S.Z., Abatzoglou J., Swanson A.K., Greenberg J.A., Mynsberge A.R., Holden
 588 Z.A., Schwartz M.K., 2013. The climate velocity of the contiguous United States
 589 during the 20th century. *Global Change Biol.* 19, 241-251.
- 590 Dobrowski S.Z., Thorne J.H., Greenberg J.A., Safford H.D., Mynsberge A.R., Crimmins
 591 S.M., Swanson A.K., 2011. Modeling plant ranges over 75 years of climate
 592 change in California, USA: temporal transferability and species traits. *Ecol.*
 593 *Monogr.* 81, 241-257.
- 594 Eriksson O., 1996. Regional dynamics of plants: A review of evidence for remnant,
 595 source-sink and metapopulations. *Oikos* 77, 248-258.
- 596 Eriksson O., 2000. Functional roles of remnant plant populations in communities and
 597 ecosystems. *Global Ecol. Biogeogr.* 9, 443-449.
- 598 Feurdean A., Bhagwat S.A., Willis K.J., Birks H.J.B., Lischke H., Hickler T., 2013. Tree
 599 Migration-Rates: Narrowing the Gap between Inferred Post-Glacial Rates and
 600 Projected Rates. *Plos One* 8.
- 601 Graae B.J., De Frenne P., Kolb A., Brunet J., Chabrerie O., Verheyen K., Pepin N.,
 602 Heinken T., Zobel M., Shevtsova A., Nijs I., Milbau A 2012. On the use of
 603 weather data in ecological studies along altitudinal and latitudinal gradients.
 604 *Oikos* 121, 3-19.
- 605 Graae B.J., Ejrnaes R., Lang S.I., Meineri E., Ibarra P.T., Bruun H.H., 2011. Strong
 606 microsite control of seedling recruitment in tundra. *Oecologia* 166, 565-576.
- 607 Hanski I., 1998. Metapopulation dynamics. *Nature* 396, 41-49.
- 608 Grime J.P. 2001. *Plant Strategies, Vegetation Processes, and Ecosystem Properties.*
 609 Chichester, John Wiley & Sons.
- 610 Holt R.D., 1993. Ecology at the mesoscale: The influence of regional processes on local
 611 communities. In: *Species diversity in ecological communities.* Ricklefs R.E.,
 612 Schluter D. (eds). University of Chicago Press, Chicago, Illinois. pp 77-88.

- 613 Hubbell S.P., 2001. The Unified Neutral Theory of Biodiversity and Biogeography
 614 Princeton, Princeton University Press.
- 615 Jackson S.T., Sax D.F., 2010. Balancing biodiversity in a changing environment:
 616 extinction debt, immigration credit and species turnover. *Trends Ecol. Evol.* 25,
 617 153-160.
- 618 Jump A.S., Peñuelas J., 2005. Running to stand still: adaptation and the response of
 619 plants to rapid climate change. *Ecol. Lett.* 8, 1010-1020.
- 620 Kerr J.T., Packer L., 1997. Habitat heterogeneity as a determinant of mammal species
 621 richness in high-energy regions. *Nature* 385, 252-254.
- 622 Körner C., 2003. *Alpine Plant Life. Functional Plant Ecology of High Mountain*
 623 *Ecosystems*, Heidelberg, Springer-Verlag.
- 624 Kuussaari M., Bommarco R., Heikkinen R.K. Helm A., Krauss J., Lindborg R., Öckinger
 625 E., Pärtel M., Pino J., Rodà F., Stefanescu C., Teder T., Zobel M., Steffan-
 626 Dewenter I., 2009. Extinction debt: a challenge for biodiversity conservation.
 627 *Trends Ecol. Evol.* 24, 564-571.
- 628 Lande R., 1993. Risks of Population Extinction from Demographic and Environmental
 629 Stochasticity and Random Catastrophes. *Am. Nat.* 142, 911-927.
- 630 Leathwick J. R., and Austin, M.P., 2001. Competitive interactions between tree species in
 631 New Zealand's old-growth indigenous forests. *Ecology* 82, 2560–2573.
- 632 Leibold M.A., Economo E.P., Peres-Neto P., 2010. Metacommunity phylogenetics:
 633 separating the roles of environmental filters and historical biogeography. *Ecol.*
 634 *Lett.* 13, 1290-1299.
- 635 Leibold M.A., Holyoak M., Mouquet N. Amarasekare P., Chase J.M., Hoopes M.F., Holt
 636 R.D., Shurin J.B., Law R., Tilman D., Loreau M., Gonzalez A., 2004. The
 637 metacommunity concept: a framework for multi-scale community ecology. *Ecol.*
 638 *Lett.* 7, 601-613.
- 639 Lenoir J., Gégout J.C., Guisan A., Vittoz P., Wohlgemuth T., Zimmermann N.E.,
 640 Dullinger S., Pauli H., Willner W., Svenning J.C., 2010. Going against the flow:
 641 potential mechanisms for unexpected downslope range shifts in a warming
 642 climate. *Ecography* 33, 295-303.
- 643 Lenoir J., Gégout J.C., Marquet P.A., De Ruffray P., Brisse H., 2008. A significant
 644 upward shift in plant species optimum elevation during the 20th century. *Science*
 645 320, 1768-1771.
- 646 Lenoir J., Graae B.J., Aarrestad P.A., Alsos I.G., Armbruster W.S., Austrheim G.,
 647 Bergendorff C., Birks H.J.B., Brathen K.A., Brunet J., Bruun H.H., Dahlberg C.J.,
 648 Decocq G., Diekmann M., Dynesius M., Ejrnaes R., Grytnes J.A., Hylander K.,
 649 Klanderud K., Luoto M., Milbau A., Moora M., Nygaard B., Odland A.,
 650 Ravolainen V.T., Reinhardt S., Sandvik S.M., Schei F.H., Speed J.D.M.,
 651 Tveraabak L.U., Vandvik V., Velle L.G., Virtanen R., Zobel M., Svenning J.C.
 652 2013. Local temperatures inferred from plant communities suggest strong spatial
 653 buffering of climate warming across Northern Europe. *Global Change Biol.* 19,
 654 1470-1481.
- 655 Lenoir J., Svenning J.C., 2013. Latitudinal and elevational range shifts under
 656 contemporary climate change. In: *Encyclopedia of biodiversity.* (ed. Levin S.A.),
 657 Academic Pres, 599-611.

- 658 Lenoir J., Svenning J.C., 2015. Climate-related range shifts – a global multidimensional
659 synthesis and new research directions. *Ecography* 38, 15-28.
- 660 Levins R., Culver D., 1971. Regional coexistence of species and competition between
661 rare species. *P Natl Acad Sci USA* 68, 1246-1248.
- 662 Loarie S.R., Duffy P.B., Hamilton H., Asner G.P., Field C.B., Ackerly D.D., 2009. The
663 velocity of climate change. *Nature* 462, 1052-U1111.
- 664 Logue J.B., Mouquet N., Peter H., Hillebrand H., Metacommunity Working G., 2011.
665 Empirical approaches to metacommunities: a review and comparison with theory.
666 *Trends Ecol. Evol.* 26, 482-491.
- 667 Luoto M., Heikkinen R.K., 2008. Disregarding topographical heterogeneity biases
668 species turnover assessments based on bioclimatic models. *Global Change Biol.*
669 14, 483-494.
- 670 MacArthur R.H., Wilson E.O., 1963. An equilibrium theory of insular zoogeography.
671 *Evolution* 17, 373-387.
- 672 May MR, Provance MC, Sanders AC, Ellstrand NC, Ross-Ibarra J., 2009. A Pleistocene
673 Clone of Palmer's Oak Persisting in Southern California. *Plos One*, 4.
- 674 Migliore J., Baumel A., Juin M., Fady B., Roig A., Duong N., Medail F., 2013. Surviving
675 in Mountain Climate Refugia: New Insights from the Genetic Diversity and
676 Structure of the Relict Shrub *Myrtus nivellei* (Myrtaceae) in the Sahara Desert.
677 *Plos One*, 8.
- 678 Moeslund J.E., Arge L., Bøcher P.K., Dalgaard T., Ejrnæs R., Odgaard M.V., Svenning
679 J.C., 2013. Topographically controlled soil moisture drives plant diversity patterns
680 within grasslands. *Biodivers. Conserv.* 22, 2151-2166.
- 681 Mouquet N., Loreau M., 2003. Community patterns in source-sink metacommunities. *Am.*
682 *Nat.* 162, 544-557.
- 683 Murphy C.A., Foster B.L., 2014. Soil Properties and Spatial Processes Influence
684 Bacterial Metacommunities within a Grassland Restoration Experiment. *Restor.*
685 *Ecol.* 22, 685-691.
- 686 Myers J.A., Harms K.E., 2009. Seed arrival, ecological filters, and plant species richness:
687 a meta-analysis. *Ecol. Lett.* 12, 1250-1260.
- 688 Nicotra A.B., Atkin O.K., Bonser S.P. Davidson A.M., Finnegan E.J., Mathesius U., Poot
689 P., Purugganan M.D., Richards C.L., Valladares F., van Kleunen M., 2010. Plant
690 phenotypic plasticity in a changing climate. *Trends Plant Sci.* 15, 684-692.
- 691 Opedal O.H., Armbruster W.S., Graae B.J., 2015. Linking small-scale topography with
692 microclimate, plant species diversity and intra-specific trait variation in an alpine
693 landscape. *Plant Ecol. Divers.* 8, 305-315.
- 694 Olsen S.L., Töpper J.P., Skarpaas O., Vandvik V., Klanderud K., 2016. From facilitation
695 to competition: temperature-driven shift in dominant plant interactions affects
696 population dynamics in semi-natural grasslands. *Glob. Change Biol.* 22, 1915-
697 1926.
- 698 Pearson R.G., Dawson T.P., 2003. Predicting the impacts of climate change on the
699 distribution of species: are bioclimate envelope models useful? *Global Ecol.*
700 *Biogeogr.* 12, 361-371.
- 701 Pellissier L., Bråthen K.A., Pottier J., Randin C.F., Vittoz P., Dubuis A., Yoccoz N.G.,
702 Alm T., Zimmermann N.E., Guisan A., 2010. Species distribution models reveal

- 703 apparent competitive and facilitative effects of a dominant species on the
704 distribution of tundra plants. *Ecography* 33, 1004-1014.
- 705 Pellissier L., Bråthen, K.A., Vittoz P., Yoccoz N.G., Dubuis A., Meier E.S.,
706 Zimmermann N.E., Randin C.F., Thuiller W., Garraud L., Van Es J., Guisan, A.,
707 2013 Thermal niches are more conserved at cold than warm limits in arctic-alpine
708 plant species. *Global Ecol. Biogeogr.* 22, 933-941.
- 709 Pillar V.D., Duarte L.D.S., 2010. A framework for metacommunity analysis of
710 phylogenetic structure. *Ecol. Lett.*, 13, 587–596.
- 711 Potter K.A., Woods H.A., Pincebourde S., 2013. Microclimatic challenges in global
712 change biology. *Global Change Biol.* 19, 2932-2939.
- 713 Randin C.F., Engler R., Normand S. Zappa M., Zimmermann N.E., Pearman P.B., Vittoz
714 P., Thuiller W., Guisan A., 2009. Climate change and plant distribution: local
715 models predict high-elevation persistence. *Global Change Biol.* 15, 1557-1569.
- 716 Reino L., Beja P., Araujo M.B., Dray S., Segurado P., 2013. Does local habitat
717 fragmentation affect large-scale distributions? The case of a specialist grassland
718 bird. *Divers. Distrib.* 19, 423-432.
- 719 Sandel B., Arge L., Dalsgaard B., Davies R.G., Gaston K.J., Sutherland W.J., Svenning
720 J.C., 2011. The Influence of Late Quaternary Climate-Change Velocity on
721 Species Endemism. *Science* 334, 660-664.
- 722 Scherrer D., Körner C., 2010. Infra-red thermometry of alpine landscapes challenges
723 climatic warming projections. *Global Change Biol.* 16, 2602-2613.
- 724 Scherrer D., Körner C., 2011. Topographically controlled thermal-habitat differentiation
725 buffers alpine plant diversity against climate warming. *J. Biogeogr.* 38, 406-416.
- 726 Slavich E., Warton D.I., Ashcroft M.B., Gollan J.R., Ramp D., 2014. Topoclimate versus
727 macroclimate: how does climate mapping methodology affect species distribution
728 models and climate change projections? *Divers. Distrib.* 20, 952-963.
- 729 Spasojevic M.J., Bowman W.D., Humphries H.C., Seastedt T.R., Suding K.N., 2013.
730 Changes in alpine vegetation over 21 years: Are patterns across a heterogeneous
731 landscape consistent with predictions? *Ecosphere* 4, 117.
- 732 Stewart J.R., Lister A.M., Barnes I., Dalen L., 2010. Refugia revisited: individualistic
733 responses of species in space and time. *P. Roy. Soc. B-Biol. Sci.* 277, 661-671.
- 734 Svenning J.C., Sandel B., 2013. Disequilibrium Vegetation Dynamics under Future
735 Climate Change. *Am. J. Bot.* 100, 1266-1286.
- 736 Sykes M.T., Prentice I.C., Cramer W., 1996. A bioclimatic model for the potential
737 distributions of north European tree species under present and future climates. *J.*
738 *Biogeogr.* 23, 203-233.
- 739 Telford R.J., Vandvik V., Birks H.J.B., 2006. Dispersal limitations matter for microbial
740 morphospecies. *Science* 312, 1015-1015.
- 741 Tilman D., 1994. Competition and biodiversity in spatially structured habitats. *Ecology*
742 75, 2-16.
- 743 Tschardtke T., Tylianakis J.M., Rand T.A. Didham R.K., Fahrig L., Peter B., Bengtsson
744 J., Clough Y., Crist T.O., Dormann C.F., Ewers R.M., Freund J., Holt R.D.,
745 Holzschuh A., Klein A.M., Kleijn D., Kremen C., Landis D.A., Laurance W.,
746 Lindenmayer D., Scherber C., Sodhi N., Steffan-Dewenter I., Thies C., van der
747 Putten W.H., Westphal C., 2012. Landscape moderation of biodiversity patterns
748 and processes - eight hypotheses. *Biol. Rev.* 87, 661-685.

- 749 Urban M.C., Leibold M.A., Amarasekare P., De Meester L., Gomulkiewicz R., Hochberg
750 M.E., Klausmeier C.A., Loeuille N., de Mazancourt C., Norberg J., Pantel J.H.,
751 Strauss S.Y., Vellend M., Wade M.J., 2008. The evolutionary ecology of
752 metacommunities. *Trends Ecol. Evol.* 23, 311-317.
- 753 Vandvik V., Goldberg D.E., 2006. Sources of diversity in a grassland metacommunity:
754 quantifying the contribution of dispersal to species richness. *Am. Nat.* 168, 157-
755 167.
- 756 Vandvik V., Goldberg D.E., 2005. Distinguishing the roles of dispersal in diversity
757 maintenance and in diversity limitation. *Folia Geobot.* 40, 45-52.
- 758 Vranckx G., Jacquemyn H., Muys B., Honnay O., 2012. Meta-Analysis of Susceptibility
759 of Woody Plants to Loss of Genetic Diversity through Habitat Fragmentation.
760 *Conserv. Biol.* 26, 228-237.
- 761 Wasof S., Lenoir J., Aarrestad P.A., Alsos I.G., Armbruster W.S., Austrheim G.,
762 Bakkestuen V., Birks H.J.B., Bråthen K.A., Broennimann O., Brunet J., Bruun
763 H.H., Dahlberg C.J., Diekmann M., Dullinger S., Dynesius M., Ejrnæs R., Gégout
764 J.-C., Graae B.J., Grytnes J.-A., Guisan A., Hylander K., Jónsdóttir I.S., Kapfer J.,
765 Klanderud K., Luoto M., Milbau A., Moora M., Nygaard B., Odland A., Pauli H.,
766 Ravolainen V., Reinhardt S., Sandvik S.M., Schei F.H., Speed J.D.M., Svenning
767 J.-C., Thuiller W., Tveraabak L.U., Vandvik V., Velle L.G., Virtanen R., Vittoz
768 P., Willner W., Wohlgemuth T., Zimmermann N.E., Zobel M., Decocq G., 2015.
769 Disjunct populations of European vascular plant species keep the same climatic
770 niches. *Global Ecol. Biogeogr.* 24, 1401-1412.
- 771 Wasof S., Lenoir J., Gallet-Moron E., Jamoneau A., Brunet J., Cousins S.A.O., De
772 Frenne P., Diekmann M., Hermy M., Kolb A., Liira J., Verheyen K., Wulf M.,
773 Decocq G., 2013. Ecological niche shifts of understorey plants along a latitudinal
774 gradient of temperate forests in north-western Europe. *Global Ecol. Biogeogr.* 22,
775 1130-1140.
- 776 Wesser S.D., Armbruster W.S., 1991. Species distribution controls across a forest-steppe
777 transition: a causal model and experimental test. *Ecol. Monogr.* 61, 323-342.
- 778 Westergaard K.B., Alsos I.G., Engelskjøn T., Flatberg K.I., Brochmann C., 2011. Trans-
779 Atlantic genetic uniformity in the rare snowbed sedge *Carex rufina*. *Conserv.*
780 *Genet.* 12, 1367-1371.
- 781 Westergaard K.B., Jørgensen M.H., Gabrielsen T.M., Alsos I.G., Brochmann C., 2010.
782 The extreme Beringian/Atlantic disjunction in *Saxifraga rivularis* (Saxifragaceae)
783 has formed at least twice. *J. Biogeogr.* 37, 1262-1276.
- 784 Whittaker R.H., 1962. Classification of natural communities. *Bot. Rev.* 28, 1-239.
- 785 Wisz M.S., Pottier J., Kissling W.D., Pellissier L., Lenoir J., Damgaard C.F., Dormann
786 C.F., Forchhammer M.C., Grytnes J.-A., Guisan A., Heikkinen R.K., Høye T.T.,
787 Kühn I., Luoto M., Maiorano L., Nilsson M.-C., Normand S., Öckinger E.,
788 Schmidt N.M., Termansen M., Timmermann A., Wardle D.A., Aastrup P.,
789 Svenning J.-C., 2013. The role of biotic interactions in shaping distributions and
790 realised assemblages of species: implications for species distribution modelling.
791 *Biol. Rev.* 88, 15-30.
- 792 Zobel M., 1997. The relative role of species pools in determining plant species richness.
793 An alternative explanation of species coexistence? *Trends Ecol. Evol.* 12, 266-
794 269.

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798 **Figure Legends**

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800 Figure 1.

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

814 Figure 2.

815 Prediction of the relative importance of different meta-community dynamics (Neutral
816 processes, Patch dynamics, Species sorting and Mass effects (see Box 1 for explanation))
817 (upper panel) in response to the climatic heterogeneity in the landscape (lower panels).

818 The seven landscapes are the same as in Figure 1.

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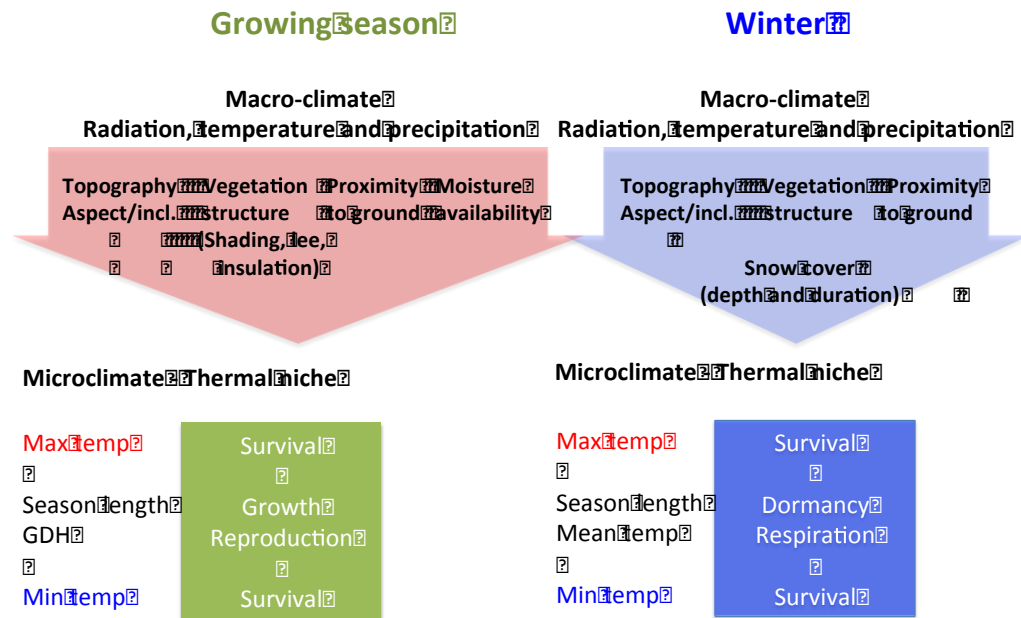
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821 **Box 1: The thermal niche of alpine plants**

822 The thermal niche of plants is often described in a highly simplified manner with a strong
823 focus on synoptic or ambient air temperature characterizing macroclimate. For small-
824 stature and slow-growing alpine and Arctic plants there is a major difference and
825 decoupling between the temperature that the plants experience near the ground and the
826 temperature conditions obtained from weather stations measuring synoptic temperature at
827 2 m height (Graae et al. 2012, Lenoir et al 2013, Körner 2003, Scherrer and Körner 2010,
828 2011). During summer, the difference and decoupling between temperature conditions
829 near the ground and synoptic temperature is to a high degree directly controlled by
830 topography but also indirectly via the effect of topography on vegetation structure and
831 soil moisture. During winter, the indirect effect of topography on temperature conditions
832 near the ground is strongly mediated by the distribution of snow and by snow depth (cf.
833 snowdrifts due to the interaction between wind and topography) rather than by vegetation
834 structure and soil moisture, Therefore, snow cover and duration exerts a strong control on
835 temperature conditions near the ground, partially determining the onset of the growing
836 season in alpine and Arctic ecosystems. Körner (2003) as well as Wipf and Rixen (2010)
837 demonstrate how snow cover and duration matters for alpine and Arctic vegetation.

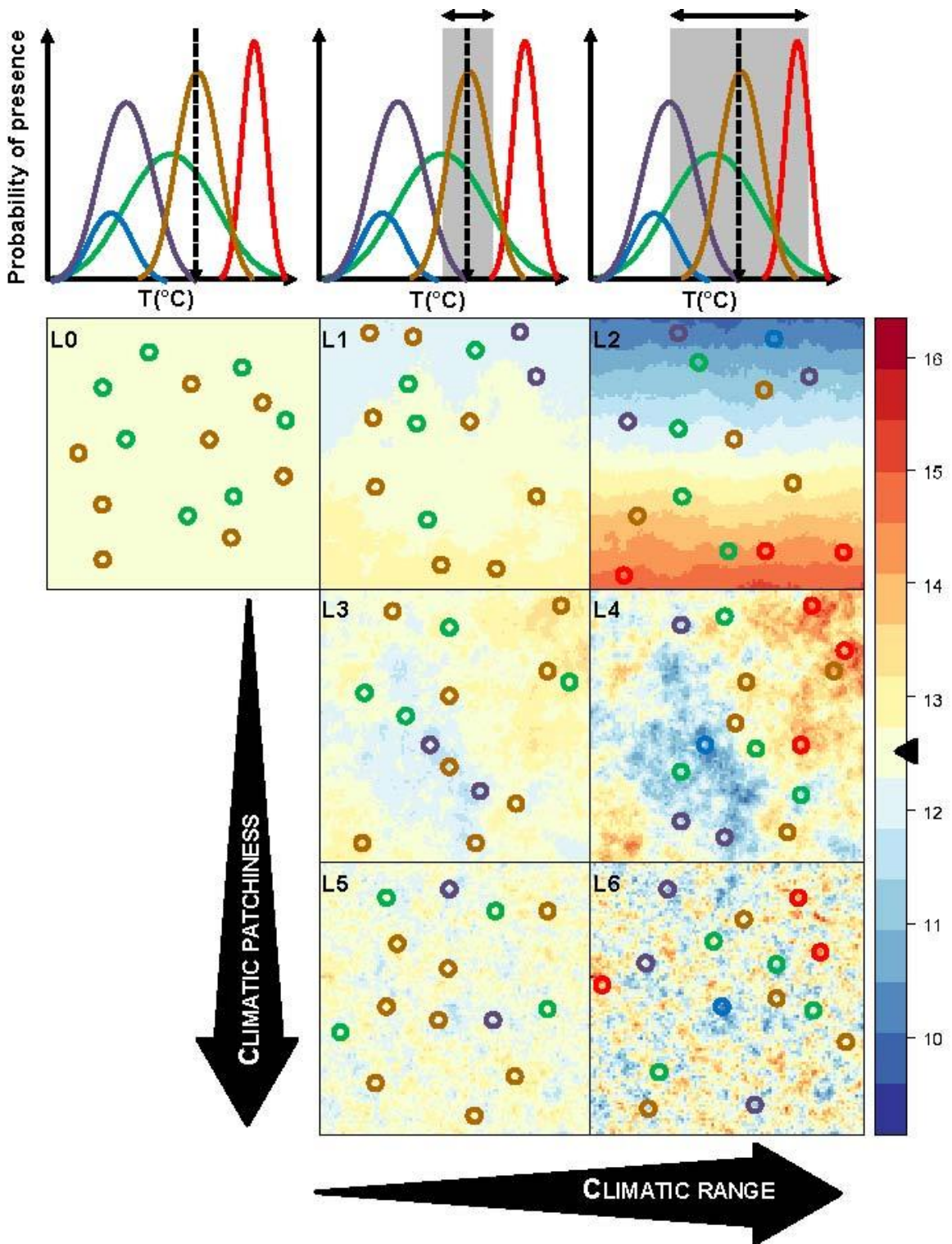
838 In addition to these scale effects, it is well established that the multifaceted nature
839 of temperature (maximum, minimum, mean, growing season length, etc.) affects different
840 life cycle and phenological stages to various extent. For instance, extreme temperatures
841 are mostly associated with mortality events and the timing of these extreme events is
842 crucial, whereas mean temperatures are chiefly associated with growth processes. Körner
843 et al. (2016) describe how the many different components of climate affect tree

844 distribution, and this complexity of niche limiting factors and interactions is expected to
845 be even greater for small-stature plants occurring near the ground. Understanding the
846 ecophysiological and ecological mechanisms underlying plant species distribution needs
847 to take such microclimatic considerations into account. Accounting for all these limiting
848 factors to model alpine plant species distribution is rarely done in the scientific literature.,
849 The more simplified concept of thermal niche has, however, shown useful because plant
850 species distribution, especially trees for which most studies are done, correlate well with
851 macroclimatic variables such as mean annual temperature. However, for mechanistic
852 understanding of what is driving these correlations we need to go beyond mean
853 temperatures (Körner et al. 2016) and assess the importance of this topographically-
854 driven, either directly or indirectly (via vegetation structure, soil moisture or snow cover),
855 heterogeneity in temperature conditions near the ground and its consequences for alpine
856 plant distribution and redistribution under climate change..
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861 **Figure 1.**



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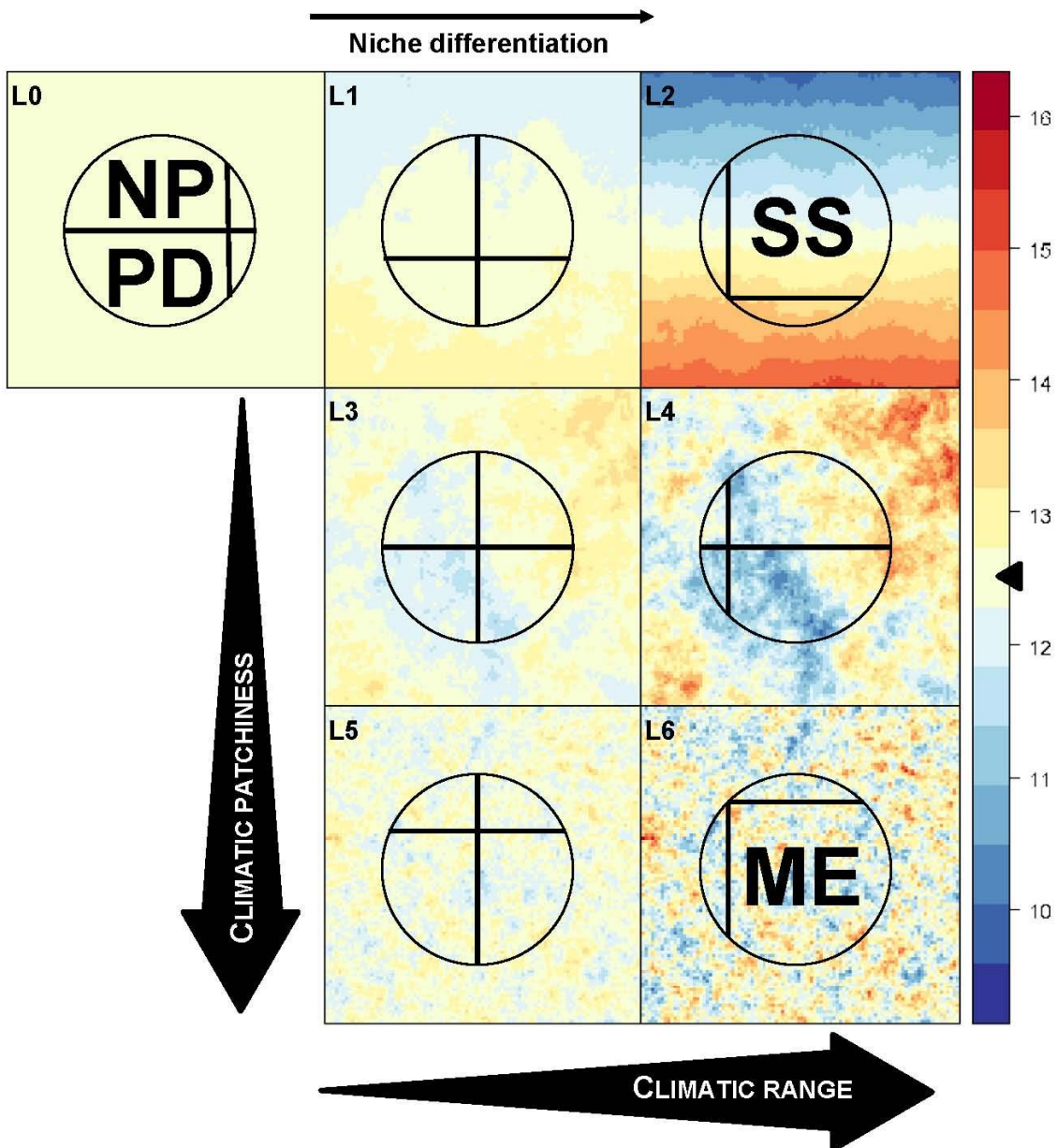
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868 Figure 2.



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

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

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

890 In the past decade, the meta-community paradigm has been highly influential in setting
 891 the research agenda in community ecology, and it has inspired a substantial literature on
 892 the interplay between dispersal and niche processes, covering a wide range of spatial and
 893 temporal scales, biomes, and organism groups, and giving rise to both theoretical,
 894 observational and experimental advances (Leibold *et al.*, 2010; Murphy and Foster, 2014;
 895 Myers and Harms, 2009; Pillar and Duarte, 2010; Telford *et al.*, 2006; Tschamtkke *et al.*,
 896 2012; Urban *et al.*, 2008). However, questions of the relative importance of the different
 897 meta-community processes in determining the patterns in community composition we
 898 observe in nature, and indeed how and if the relative importance of these processes can
 899 even be quantitatively assessed, have been highly debated and are far from being resolved

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