

1 **Refining predictions of population decline at species' rear edges**

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26 **Abstract**

27 According to broad-scale application of biogeographical theory, widespread retractions of  
28 species' rear edges should be seen in response to ongoing climate change. This prediction  
29 rests on the assumption that rear edge populations are 'marginal' since they occur at the limit  
30 of the species' ecological tolerance and are expected to decline in performance as climate  
31 warming pushes them to extirpation. However, conflicts between observations and  
32 predictions are increasingly accumulating and little progress has been made in explaining this  
33 disparity. We argue that a revision of the concept of marginality is necessary, together with  
34 explicit testing of population decline, which is increasingly possible as data availability  
35 improves. Such action should be based on taking the population perspective across a species'  
36 rear edge, encompassing the ecological, geographical and genetic dimensions of marginality.  
37 Refining our understanding of rear edge populations is essential to advance our ability to  
38 monitor, predict and plan for the impacts of environmental change on species range  
39 dynamics.

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## 51 **Introduction**

52 Climate change impacts species performance and distribution across the globe (Parmesan &  
53 Yohe, 2003). Biogeographical theory suggests that rising global temperatures should drive  
54 species to move poleward and upward in elevation as they track the climates to which they  
55 are adapted. Therefore, it is reasonable to expect that population loss and range retractions  
56 should be seen in the most low-latitude, drought-prone areas of a species' distribution (the  
57 rear edge, Hampe & Petit, 2005), given that widespread climate-driven extinction has been  
58 predicted (Thomas et al., 2004; Urban, 2015). However, assumptions of declining rear edge  
59 population performance are a long-lasting legacy of uncritical application of the centre-  
60 periphery hypothesis (Brown, 1984; Safriel, Volis, & Kark, 1994). This prediction assumes  
61 that rear edge populations are fundamentally at higher risk of extinction than those  
62 populations at the core of the species' range. This elevated extinction risk is attributed to the  
63 expectation that they occur in less favourable climates (or habitats) and are more at risk from  
64 demographic stochasticity because of lower and highly variable population sizes.  
65 Consequently, widespread 'marginality' is predicted at the species' rear edge, i.e. decreased  
66 population performance because populations occur at the limits of the species' physiological  
67 and ecological tolerance.

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69 The assumption of rear edge population decline in response to climate change appears well  
70 supported in the literature (e.g. Allen et al., 2010; Carnicer et al., 2011; Feeley et al., 2011;  
71 Lesica & Crone, 2016; Marqués, Camarero, Gazol, & Zavala, 2016; Reich et al., 2015).  
72 However, such support is often derived from an amalgamation of case-studies of decline,  
73 risking inaccurate predictions when attempting to extrapolate regionally across the rear edge  
74 of a species distribution. 'Marginality' at the population level is determined by the interaction  
75 of a variety of constraints, including climate and local-scale environmental conditions, habitat

76 fragmentation, species traits, physiology and biotic interactions, as well as population  
77 demography and genetics. At the same time, anthropogenic land-use changes shape how  
78 species are distributed, and their legacies strongly influence population dynamics. All  
79 together result in ecological and evolutionary mechanisms that are dependent upon far more  
80 than the biogeographical location of a population (Hampe & Petit, 2005; Pironon et al., 2016;  
81 Sexton, McIntyre, Angert, & Rice, 2009). Consequently, conflicts between predictions and  
82 observed population responses are increasingly accumulating (e.g. Bertrand et al., 2011;  
83 Cavin & Jump, 2017; Doak & Morris, 2010; Granda et al., 2018; Rabasa et al., 2013;  
84 Rapacciuolo et al., 2014). Here we examine the potential reasons for this disparity by  
85 decomposing the causes of marginality and discuss why simplifying assumptions on  
86 marginality have implications for predicting species' range shifts. We propose a generally  
87 applicable rationale for research design and analysis to better integrate population-level  
88 responses into a biogeographical context of species decline. Our focus is on plant – and  
89 especially tree – species because of the abundance of data available and the key roles forests  
90 play in global carbon and hydrological cycles and maintaining biodiversity. We argue that, as  
91 data availability increases, greater emphasis should be placed on recognising the scale-  
92 dependency of the factors determining population dynamics, which is fundamental in highly  
93 heterogeneous regions like the rear edges, where global change is strongly altering the  
94 structure and function of forest ecosystems.

95

#### 96 **Empirical evidence in agreement with biogeographical theory**

97 A broad range of studies in the literature provides empirical evidence of declining rear edge  
98 populations relative to those of the range-core or across low-altitude relative to high-altitude  
99 areas in concordance with biogeographical predictions. For example, sudden population  
100 mortality associated with elevated drought stress at species rear edges has been observed in

101 forest ecosystems across the globe (Allen et al., 2010). Equally, evidence of population  
102 decline that heralds range retractions is often provided by dendroecological approaches. For  
103 example, Scots pine (*Pinus sylvestris*) forests in the Gúdar range (southern Iberian Range,  
104 Iberian Peninsula) are representative populations of the species' rear edge. The species occurs  
105 in a mountainous orography, where low-altitude, dry-edge populations coexist with a more  
106 drought-tolerant pine species, the black pine (*Pinus nigra* subsp. *salzmannii*). In accordance  
107 with biogeographical predictions, Scots pine growth is enhanced by temperature at mid- and  
108 upper elevations, and constrained because of enhanced drought stress at low-elevations. In  
109 these low-altitude areas, where both species co-occur, black pine is more resilient than Scots  
110 pine to extreme drought events, suggesting that future changes in species composition are  
111 likely (Marqués et al., 2016). Experimental evidence of species' responses to climate  
112 manipulation also supports biogeographical predictions. For example, *in situ* experimental  
113 warming in northern Minnesota, North America, showed reductions in photosynthesis and  
114 growth near warm range limits and increases near cold range limits in juvenile trees of 11  
115 boreal and temperate forest species (Reich et al., 2015). Species' range shifts predicted by  
116 biogeographical theory have been observed in biodiversity hotspots like the Tropical Andes.  
117 Elevational shifts during a 4-year period were assessed for 38 tree genera across an  
118 elevational gradient from 950 to 3400 m in Manu National Park in south-eastern Peru. Mean  
119 migration rate was 2.5–3.5 vertical metres upslope per year and low-elevation genera also  
120 increased in abundance in most of the study plots. However, the rate of elevational migration  
121 was lower than predicted according to the temperature increase in the region, suggesting a  
122 lagged response to climate change of primary tropical montane forests (Feeley et al., 2011).  
123  
124 **Why disparities between biogeographical theory and population ecology matter**

125 Four complementary explanations drawn from empirical evidence clarify why rear edge  
126 population performance can deviate from biogeographical predictions:

127 *(i) Geographical and ecological edges do not always overlap at the population scale*

128 Assuming a complete overlap of geographical and ecological range limits at the rear edge of  
129 a species' distribution may explain counterintuitive population responses. For example,  
130 decline in the abundance of plant species with an arctic-alpine and boreal distribution across  
131 western North America has been observed across rear edge populations occurring in the  
132 northern Rocky Mountains. Although the overall trend of species' abundance decline is in  
133 agreement with biogeographical predictions, 50% of monitored populations remained stable  
134 or even increased in abundance (Lesica & Crone, 2016). Therefore, decreased population  
135 performance at rear edges cannot be assumed because ecological and geographical range  
136 margins do not always overlap.

137 *(ii) Interactions among ecological factors determine population dynamics*

138 Species distributions and population dynamics are determined by complex interactions of  
139 ecological factors (Harper, 1977). For example, soil phosphorus strongly limits tropical tree  
140 distributions along a gradient of dry-season moisture along the Panama Canal (Condit,  
141 Engelbrecht, Pino, Pérez, & Turner, 2013) and, in Mediterranean communities, several plant  
142 species only survive at the drier edge of their ranges in communities beneath the facilitative  
143 effects of the shrub "retama amarilla" (*Retama sphaerocarpa*) (Armas, Rodríguez-  
144 Echeverría, & Pugnaire, 2011). However, such complexity is typically simplified in large-  
145 scale studies because of methodological limitations when trying to represent population-level  
146 processes over broader spatial scales. Consequently, disparities between population responses  
147 and biogeographical predictions are likely to be common. For example, elevational range  
148 shifts inferred from adult and juvenile abundance in Mediterranean, temperate and boreal tree  
149 species in Europe are idiosyncratic rather than consistent with temperature-based predictions

150 (Rabasa et al., 2013). Similarly, downslope shifts in elevation are as common as upslope  
151 shifts across a broad range of taxa in California (Rapacciuolo et al., 2014). Common  
152 explanations for these unexpected responses are factors such as human land-use, water  
153 balance or soil quality, species physiological and dispersal traits, demographic dynamics and  
154 biotic interactions (Rabasa et al., 2013; Rapacciuolo et al., 2014).

155 *(iii) Decoupling between microclimates and macroclimates*

156 Large-scale predictions from bioclimatic models are generally derived from coarse gridded  
157 climatic data because fine-resolution or microclimatic data are rarely available over large  
158 spatial scales. Organisms, however, respond to their local environment. For instance,  
159 microclimatic variation due to topographic factors is generally not captured by the resolution  
160 of interpolated climatic data while differences between regional free-air and local  
161 temperatures may amount to several degrees (Dobrowski, 2011). At finer scales, biophysical  
162 processes have impressive effects. For example, structural characteristics of old-growth  
163 forests may provide microclimates cooler by as much as 2.5°C across forest stands (Frey et  
164 al., 2016). Therefore, it is not surprising that climate at resolution of 100 or more meters  
165 poorly explains variation of leaf and wood traits across populations of temperate and  
166 Mediterranean trees (Vilà-Cabrera, Martínez-Vilalta, & Retana, 2015). In the context of  
167 marginality, a highly illustrative example of mismatch between micro- and macroclimates is  
168 the persistence of rear edge populations such as the stands of pedunculated oak (*Quercus*  
169 *robur* L.) in Jerte valley, western Iberian Peninsula (Moracho, Moreno, Jordano, & Hampe,  
170 2016) which has a regional climate significantly hotter and dryer than that tolerated by this  
171 species. Consequently, a decoupling between micro- and macroclimates has strong  
172 implications for climate-based predictions on population decline (Hampe & Jump, 2011).

173 *(iv) Evolutionary processes*

174 Populations (or genotypes) are adapted to a specific range of ecological conditions and,  
175 consequently, each individual within a species may experience stress from climate change  
176 (Harte, Ostling, Green, & Kinzig, 2004). Therefore, the existence (or lack) of genetic  
177 adaptations to climatic stress may also explain some of the former unexpected responses. For  
178 example, greenhouse experiments show that dry-edge populations of the spurge olive  
179 (*Cneorum tricoccon*), a Mediterranean evergreen shrub with a narrow distribution, exhibit  
180 more drought-tolerant phenotypes, and growth of individuals inhabiting drier habitats is less  
181 affected by drought stress (Lázaro-Nogal et al., 2016). However, most empirical evidence on  
182 spatial variation of key species traits comes from observations across broad latitudinal  
183 gradients. For example, rear edge populations of the European beech tree show higher  
184 resistance to xylem embolism relative to mid-latitude, range-core populations (Stojnić et al.,  
185 2018). Yet, a proper understanding on whether variation in this and other traits relevant for  
186 species persistence occurs across rear edge populations is lacking.

187

188 The former explanations point to two subtly interrelated aspects that, if not acknowledged,  
189 strongly limit our understanding of marginality, and our ability to predict population loss.  
190 First, marginality is a multidimensional property of populations that encompasses ecological,  
191 geographical, and genetic components. Second, methodological limitations and lack of data  
192 restrict our capacity to link population ecology with biogeography (but see SDMs accounting  
193 for phenotypic plasticity and local adaptation in Benito Garzón, Robson, & Hampe, 2019).  
194 Consequently, local predictions of rear edge decline only based on distribution patterns at the  
195 regional scale become unrealistic (Thuiller et al., 2008). Overcoming such limitations is  
196 essential to reconcile population ecology with biogeographical theory at species' rear edges  
197 to enable a predictive understanding of their dynamics, function and management (Mouquet  
198 et al., 2015).



199

200 **Refining our predictive understanding of rear edge population decline**

201 We propose a rationale that integrates the ecological, geographical and genetic dimensions of  
202 marginality to determine the regional- and local-scale mechanisms shaping the probability of  
203 persistence (or extinction) of rear edge populations (Figure 1). Importantly, the scale-  
204 dependency of ecological mechanisms influencing the persistence probability of populations  
205 may result in contrasting predictions between the regional and local scales. Consequently, we  
206 argue that a hypothesis-driven approach is necessary, with population decline tested rather  
207 than assumed according to predicted marginality. At the core of the rationale lies a data-  
208 driven methodology that permits the incorporation of increasingly available data sources into  
209 experimental study design. Essentially, each marginality dimension can be inferred from  
210 multiple ecological components (e.g. climatic range, landscape connectivity, community  
211 composition, human-driven habitat degradation, etc.) across the species' rear edge. The  
212 distribution and edges of these components and their interactions can be identified and  
213 populations categorized across marginality types (Figure 2A) ensuring that, at the regional  
214 scale, the entire rear edge structure is represented (Figure 1). At the same time, population  
215 and individual parameters need to be measured with replication within- and compared across  
216 marginality types to ensure a balanced sampling and accurate parameter assessment (Figure  
217 2B). Observed population responses are then contrasted with regional-level predictions and,  
218 if disparities arise, local-scale mechanisms need to be considered (Figure 2B). We  
219 demonstrate how application of this rationale improves understanding of marginality and  
220 highlights the need to consider the scale-dependency of ecological suitability.

221

222 **(i) Conceptualising the dimensions of marginality**

223 Our understanding of marginality as a multidimensional concept, the rear edge structure, as  
224 well as the regional- and local-level hypotheses of population decline are illustrated in Figure  
225 1. In analogy with the limits of the realized niche (Hutchinson, 1957), abiotic and biotic  
226 factors define ecological marginality at the regional and local scales. The regional climate (or  
227 macroclimate) of the population location relative to the edge of the species' climatic  
228 distribution (or the threshold of species' climatic tolerance) is used to infer ecological  
229 marginality at the regional scale, while the range of population-scale habitat characteristics  
230 (e.g. microclimate, soil quality, land-use history) is used to derive local ecological  
231 marginality. Population decline is thus predicted to occur at the extremes of these factors, e.g.  
232 drier climates, poor soils or intense disturbance. Rear edge populations occur along  
233 bioclimatic transition zones (Jump, Mátyás, & Peñuelas, 2009), where species climatic  
234 suitability decreases and habitat heterogeneity is high over small spatial scales. Consequently,  
235 changes in the composition of communities can occur abruptly with shifts in habitat quality  
236 such that community composition can be used alongside abiotic conditions to infer ecological  
237 marginality. At the landscape scale, the composition of communities surrounding the focal  
238 rear edge population is used to infer regional-scale ecological marginality, which increases  
239 approaching the transition between bioclimatic zones. At the local scale, the community  
240 composition is used to infer interactions among organisms – within or across trophic levels –  
241 potentially determining ecological marginality. If co-occurring species, relative to the focal  
242 one, are competitors under an ecological advantage (e.g. drought-tolerant) or antagonists (e.g.  
243 biotic agents), such biotic interactions result in increased local ecological marginality.  
244 Contrary, biotic interactions result in decreased local ecological marginality if beneficial  
245 effects can emerge from species coexistence (e.g. facilitation, mutualism, or  
246 complementarity).

247

248 The rear edge is typically made up of populations of variable size and connectivity, defining a  
249 fragmented landscape (Hampe & Petit, 2005; Jump et al., 2009). Therefore, the spatial  
250 distribution, size and connectivity of populations (i.e. habitat configuration) are used to infer  
251 regional-scale geographical (and genetic) marginality. Increased fragmentation and isolation  
252 as a consequence of either natural processes or anthropogenic impacts, result in decreased  
253 population performance. This detrimental effect is associated with an altered habitat leading  
254 to edge effects (Murcia, 1995), increased metapopulation dynamics due to dispersal  
255 limitation (Hanski, 1991), disrupted biotic networks and novel interactions or invasion  
256 (Hagen et al., 2012), and the loss of genetic variation and individual fitness because of  
257 increased chance of genetic drift and inbreeding (Templeton, Shaw, Routman, & Davis,  
258 1990). However, in parallel with deviation of local ecological conditions from the regional  
259 scale, population responses that are the product of local-scale mechanisms (e.g. local  
260 adaptation) or biotic interactions (e.g. mutualistic symbioses) may contradict predicted  
261 marginality based on habitat configuration alone.

262

## 263 **(ii) Quantifying marginality and testing regional-scale hypotheses of population decline**

264 Marginality can be quantified along multiple axes at the regional scale using existing data  
265 sources, allowing hypothesis-testing on the regional mechanisms determining population  
266 decline (Figure 1). Climatic and geographic range-edges may not completely overlap (Cavin  
267 & Jump, 2017; Chardon, Cornwell, Flint, Flint, & Ackerly, 2015). Consequently, while  
268 geographical ranges frequently correlate with climate at the continental scale, it cannot be  
269 assumed that all rear edge populations are climatically limited. This idea can be understood,  
270 for example, from the variable relationship between the climatic characteristics and  
271 geographical location of populations of the European beech (*Fagus sylvatica* L.) tree from the  
272 Iberian Peninsula to Northern Scotland. Populations inhabiting dry and wet sites relative to

273 the species' climatic distribution can be found at the rear edge with contrasting implications  
274 for population performance (Cavin & Jump, 2017). Large-scale forest inventories or remotely  
275 sensed data layers such as land-cover maps can be used to determine geographical  
276 marginality, with gridded climate data used to infer ecological marginality relative to the  
277 climatic distribution of the species (Figure 2A). The interaction between both types of  
278 marginality results in variable predicted extinction risk across the rear edge (Figure 1).

279

280 At rear edges, abrupt bioclimatic transitions may not be explained by climate alone. For  
281 example, the pine–cloud forest ecotone on the windward slopes of the Cordillera Central,  
282 Dominican Republic, is primarily a result of high-elevation fire regimes. Declining  
283 temperature and precipitation with elevation together with trade wind inversion, and small-  
284 scale variation in topography and vegetation determine fire occurrence and ecotone formation  
285 (Martin, Sherman, & Fahey, 2007). Existing data sources that incorporate species  
286 composition data (e.g. inventories and land-cover maps) can be used to infer bioclimatic  
287 transitions at the landscape scale, and thus refine predictions on ecological marginality based  
288 on climate alone (Figure 2A; Figure 1). This idea can be exemplified by the exceptional range  
289 retraction of ponderosa pine (*Pinus ponderosa*) after a severe drought in mid-1950s at the  
290 ecotone between this species and piñon–juniper woodland (*Pinus edulis* and *Juniperus*  
291 *monosperma*) in northern New Mexico (Allen & Breshears, 1998). Forest dieback  
292 predominantly concentrated in low-altitude, drought-prone populations, but more climatically  
293 favourable areas along the entire altitudinal gradient were also affected likely because of a  
294 competitive disadvantage relative to more drought-tolerant species. The interaction between  
295 climate and community composition at the regional scale reflects a mosaic of ecological  
296 conditions at rear edges not only dependent on climate (Figure 1), and should, therefore, be  
297 incorporated into empirical study design (Figure 2A).

298

299 Populations at similar levels of ecological marginality are at higher risk of extinction with  
300 increasing geographical (and genetic) marginality at the regional-scale (Figure 1). Spatial-  
301 pattern and landscape-connectivity GIS analyses (e.g. Wegmann et al., 2018) on land-cover  
302 maps and other remote-sensing derived-sources can be used to accurately infer habitat  
303 configuration and test predictions of decreased population performance (Figure 2A).  
304 Population fragmentation is associated with ecological edge effects (Murcia, 1995). For  
305 example, in tropical montane forests in the Bolivian Andes, temperature gradients from the  
306 edge to the interior of forest patches are equivalent to a 100-m shift in elevation. Higher  
307 temperatures at forest edges cause warmer and drier habitats with corresponding elevation of  
308 drought stress, changes in species composition and increased fire risk (Lippok et al., 2014).  
309 Fragmentation may also strongly decrease individual fitness and alter population dynamics  
310 through rapid genetic changes. For example, loss of large-vertebrate dispersers because of  
311 human-driven habitat fragmentation across Brazilian Atlantic rainforests is associated with a  
312 rapid (< 100 years) evolutionary seed size reduction in a keystone palm species (*Euterpe*  
313 *edulis*). Seed size reduction results in increased seed vulnerability to desiccation and  
314 decreased seedling growth. At the same time, genetic diversity among seedlings in  
315 fragmented (defaunated) sites is lower than in non-fragmented sites. Altogether, these  
316 impacts have strong implications for population dynamics under predicted drier conditions in  
317 the studied forests (Carvalho, Galetti, Colevatti, & Jordano, 2016; Galetti et al., 2013).

318

### 319 **Shifting to the population perspective: refocusing on local-scale hypotheses**

320 Framing hypotheses of population decline based on marginality predicted at the regional-  
321 scale can result in disparities between regional predictions and observed population  
322 responses. Such disparities demonstrate the need to refocus studies exploring rear edge

323 performance on local-scale hypotheses (Figure 1; Figure 2B). Below we first address the  
324 strong influence that anthropogenic land-uses and their legacies have on our understanding of  
325 marginality and their likely prominent role to explain the mismatch between predictions and  
326 observations. Thereafter, we illustrate with selected examples from the literature how rapidly  
327 increasing data availability can be harnessed for the evaluation of local-scale mechanisms  
328 across marginality-types (Figure 2B), thereby refining our predictive understanding of rear  
329 edges.

### 330 **(i) Anthropogenic land-uses and their legacies**

331 Anthropogenic land-use during the last few hundred years has altered the realised niche of  
332 species and consequently their contemporary distribution is often not in equilibrium with the  
333 range of ecological conditions they are able to exploit. For example, using ‘pre-settlement’  
334 vegetation estimations inferred from survey records (1830–1910), and historical climate and  
335 contemporary data, Goring & Williams (2017) demonstrated that human land conversion  
336 shifted the past distribution of some tree genera in Midwestern United States, from drier and  
337 warmer climates in the past to wetter and cooler conditions today. Land-use changes and  
338 associated habitat modifications, therefore, complicate the identification of ‘ecological edges’  
339 of a species’ distribution (Figure 1). Anthropogenic land-use also interacts with climate  
340 change impacts on population dynamics. For example, human-driven forest loss prevails in  
341 warmer (low-latitude or altitude) regions and, rather than climate change, recent habitat loss –  
342 quantified from ~30-m resolution data generated from Landsat image analysis – explains the  
343 biotic attrition observed in these areas (Guo, Lenoir, & Bonebrake, 2018). On the other hand,  
344 tree species plantations for wood or food production and fire suppression can contribute to  
345 species expansion beyond their climatic limits, but increase the risk of dieback episodes and  
346 wildfires during extreme dry years (Maranz, 2009; Nowacki & Abrams, 2015; Sánchez-  
347 Salguero, Navarro-Cerrillo, Swetnam, & Zavala, 2012). At the same time, socioeconomic

348 changes can lead to widespread forest expansion over abandoned land (Meyfroidt & Lambin,  
349 2011). For example, the combination of forest inventory data with historical and modern  
350 land-cover maps generated from aerial images shows that the ~25% of current forests in the  
351 Iberian Peninsula, the rear edge of several temperate and boreal tree species, are growing on  
352 former agricultural and grazing land abandoned after the 1950s (Vilà-Cabrera, Espelta,  
353 Vayreda, & Pino, 2017). Consequently, anthropogenic habitat modification and its legacies  
354 represent a critical dimension of marginality as they may intensify, confound or delay  
355 climate-driven population decline at rear edges.

### 356 **(ii) Population demography and structure**

357 Forest inventory networks are very useful for assessing recent demographic dynamics over  
358 large geographical scales. However, the spatiotemporal resolution and the quantity of data are  
359 limited and need to be complemented with more detailed data and studies. Long-term  
360 population responses can be better understood taking advantage of the increasing availability  
361 of dendroecological data over large geographical areas (e.g. Sánchez-salguero et al., 2017),  
362 while field-based investigations can inform on particular persistence mechanisms such as  
363 compensatory changes in demographic rates (Doak & Morris, 2010) or stabilising processes  
364 (e.g. competition release) after extreme drought events (Lloret, Escudero, Iriondo, Martínez-  
365 Vilalta, & Valladares, 2012). However, detailed information on population structural  
366 characteristics including human uses needs to be assessed using inventory data and, together  
367 with observed population demography, explicitly placed in the context of past management  
368 and its legacy. Such characterisation of population structure is essential given that, for  
369 example, regular forest management (e.g. thinning) can assist a species to persist under  
370 chronic climatic stress (Linares, Camarero, & Carreira, 2009), delaying or even concealing  
371 the decline of the species if the less vigorous individuals are removed. However, when forest  
372 use is abandoned and the stand matures this beneficial effect can reverse due to greater

373 physiological constraints associated with larger trees (D'Amato, Bradford, Fraver, & Palik,  
374 2013). If coupled with long-term acclimation to favourable water availability, such structural  
375 shifts (i.e. bigger stems and higher leaf area) may lead to greater demand of water resources  
376 that are not available during extreme drought (Jump et al., 2017), resulting in increased  
377 population decline even across better-quality habitats (Figure 1).

### 378 **(iii) Local-scale environmental conditions**

379 Rear edges mostly occur within areas of high habitat heterogeneity at small spatial scales  
380 (Hampe & Petit, 2005). Micro-topography is an important driver of small-scale variation in  
381 habitat quality, and it can be modelled from existing data such as high-resolution digital  
382 elevation models (DEM) derived from remote sensing. For example, Adams et al. (2014)  
383 used 1-m resolution DEM to show how micro-topographic control on moisture conditions  
384 mediates tree growth and water-use responses to drought near the elevational range-limits of  
385 lodgepole pine (*Pinus contorta*) and ponderosa pine (*Pinus ponderosa*) in the Gordon Gulch  
386 catchment, Colorado. Such topographic variability together with a range of other physical  
387 (e.g. lithology, edaphic characteristics) and biophysical factors (e.g. vegetation structure and  
388 traits) facilitates the existence of microrefugia (Figure 1; McLaughlin et al., 2017). For  
389 instance, rock outcrops and associated habitat can create microclimates 4.9 °C cooler, 12%  
390 wetter, and less variable than the climate of the surrounding habitat. This microclimate is  
391 associated to the persistence of a rear edge population of *Podocarpus lambertii* at the species'  
392 drier range-edge located in a semiarid region in Brazil (Locosselli, Cardim, & Ceccantini,  
393 2016). Microclimate data can be derived from local networks of climate data loggers and  
394 combined with remotely sensed topographical and vegetation structural data. Improvements  
395 in data resolution are essential in highly variable regions in terms of habitat conditions, where  
396 the potential for microclimatic buffering strongly relies on microrefugia occurrence and  
397 human impacts on habitat structure. For example, along a land-use intensity gradient in



398 Borneo, from unlogged old-growth forests to mature oil-palm plantations, canopy structure  
399 and topography are strong drivers of small-scale variation in understory temperature and  
400 vapour pressure deficit. Assessing and modelling variation in microclimatic conditions is  
401 critical in regions like the lowland tropics, where many species reach their thermal tolerance  
402 limits (Jucker et al., 2018).

#### 403 **(iv) Biotic interactions**

404 Alterations to species coexistence can reflect an altered habitat, for example, such that more  
405 drought- and shade-tolerant species gain a competitive advantage. For example, the local  
406 coexistence between the boreal pine species Scots pine (*Pinus sylvestris*) and Mediterranean  
407 oak species (e.g. *Quercus ilex* and *Q. pubescens*) can be observed along altitudinal gradients  
408 in many European mountain systems, such as the Pyrenees. Oak seedling abundance and  
409 performance are higher under drought-induced Scots pine decline but this association is not  
410 only restricted to the most drought-prone stands at low-altitudes. Habitat deterioration and  
411 past species-selective management explain observed community dynamics at the local scale  
412 (Galiano, Martínez-Vilalta, Eugenio, Granzow-de la Cerda, & Lloret, 2013). The local  
413 community composition can be directly obtained from inventory data or field-based  
414 sampling, directly informing on ecological marginality, supporting a better understanding of  
415 marginality-type (Figure 1; Figure 2A).

416

417 Large-scale inventories are useful to assess how variation in biotic interactions scale-up over  
418 broad geographical areas, for example, those involving antagonistic interactions such as  
419 insect and fungal damage on trees (e.g. Carnicer et al., 2011). Although these large-scale  
420 analyses are often based on categorical data or species relative abundance, they provide a first  
421 identification of the spatial variation in species assemblages and should be used for setting  
422 more detailed experiments and studies on relevant biotic interactions. For example,

423 uncommon or novel interactions can be established if climate change or anthropogenic land-  
424 uses, like fire suppression, shift the identity of coexisting species. Experimental evidence  
425 demonstrates that the performance of populations failing to migrate as temperature increases  
426 will be strongly reduced by novel competitors migrating upwards in elevation (Alexander,  
427 Diez, & Levine, 2015). Other more complex situations, e.g. coevolution in mutualistic  
428 symbioses, need specific approaches but existing information can support hypothesis  
429 development and experimental design. For example, the structural characteristics of drought-  
430 tolerant, moth-susceptible pinyon pine (*Pinus edulis*) individuals differ from drought-  
431 intolerant, moth-resistant ones at the edge of the pine species' physiological tolerance in  
432 Northern Arizona. This information supported Gehring et al. (2017) to demonstrate that under  
433 drought stress, interactions between plant genotype, resistance to herbivory and mutualistic  
434 fungi operate differentially among individuals, providing an interpretation for landscape-scale  
435 patterns of population decline. Drought-tolerant, moth-susceptible trees have higher growth  
436 and survival than drought-intolerant, moth-resistant ones, and this differential performance  
437 correlates with distinct, genetically-based ectomycorrhizal communities.

438 **(v) Population genetics matters but within a context of ecological change**

439 The putative long-term stability of relict populations during Quaternary climatic oscillations  
440 – the result of microrefugia occurrence and evolutionary processes (Hampe & Jump, 2011;  
441 Hampe & Petit, 2005; Woolbright, Whitham, Gehring, Allan, & Bailey, 2014) – is an  
442 excellent example of the mismatch between predictions and observed responses at rear edges  
443 (Figure 1). Relict populations reinforce the idea that species' extinction risk depends on the  
444 interaction between population genetics and ecology. However, it has long been recognised  
445 that negative ecological impacts (e.g. demographic decline, restriction to dispersal, disruption  
446 of community dynamics) can often outweigh genetic factors in a context of rapid  
447 environmental change (Lande, 1988). Studies addressing questions of genetic marginality

448 primarily need to account for species-specific ecological requirements and demography. For  
449 example, along fragmented forests in southern Australia, decreased pollen diversity and  
450 increased selfing associate with fragmentation for two insect-pollinated eucalypt tree species,  
451 but not for a bird-pollinated one (Breed et al., 2015). Moreover, where fragmentation drives  
452 decreased genetic diversity and increased risk of inbreeding, population performance is not  
453 necessary reduced if, for instance, functional genetic variation is not altered (Reed &  
454 Frankham, 2001), genotypes are adapted to the local habitat (Kawecki, 2008) or the mating  
455 system evolves to ensure population viability (Ouayjan & Hampe, 2018). Furthermore, the  
456 amount of genetic variation (functional or neutral) and the degree of evolutionary adaptation  
457 to a marginal habitat may not matter when rapid environmental change drives abrupt shifts in  
458 population demography and increases species' regional extinction risk (Lande, 1988) (Figure  
459 1). Consequently, while population genetics can contribute toward refining predictions of rear  
460 edge population decline, it should be considered in the context of population ecology, with  
461 the focus on variation of functionally relevant phenotypic traits and demographic  
462 performance.

463

#### 464 **A population-focused study at the species' rear edge**

465 The European beech (*Fagus sylvatica* L.) tree is drought-sensitive and it is expected to be  
466 particularly vulnerable to deteriorating water balance across rear edge populations occurring  
467 in the north-eastern Iberian Peninsula. To highlight this approach to experimental design we  
468 used different existing data sources: (i) three regional forest inventories (the Ecological and  
469 Forest Inventory of Catalonia, the Spanish National Forest Inventory, and the Catalan  
470 Inventory of Singular Forests); (ii) an 8 m<sup>2</sup> resolution land-cover map (Land Cover Map of  
471 Catalonia); and (iii) 1 km<sup>2</sup> resolution gridded layer of the ratio of annual precipitation to  
472 potential evapotranspiration derived from the WorldClim database. Using these data, we

473 selected 40 beech populations classified into four main population types according to  
474 ecological marginality, based on climate and community composition, and geographical  
475 (genetic) marginality, based on plot spatial distribution (Figure 1 and 2). At each location we  
476 assessed population decline parameters, i.e. adult mortality and canopy defoliation based on  
477 measurements in one point in time (see Supporting information Appendix S1) and tested  
478 regional hypotheses on population decline (Figure 1). The direct comparison among  
479 marginality types provides evidence on two fundamental aspects. First, population decline  
480 seems to be occurring regionally but especially across ecologically marginal areas within the  
481 continuous range (Figure 3A), rather than at geographical edges where population extinction  
482 is first predicted to occur. Second, isolated populations inhabiting marginal habitats show  
483 lower levels of mortality and canopy decline than expected, which also are comparable to  
484 those observed in populations occurring across better-quality habitats. This mismatch  
485 between predictions and local observation is consistent with recent evidence showing high  
486 stability of rear edge beech populations (Cavin & Jump, 2017; Hackett-Pain & Friend, 2017;  
487 Stojnić et al., 2018).

488

489 We also show that differences across populations are mediated by the variability of decline  
490 along gradients resulting from interactions among marginality dimensions (Figure 3B). First,  
491 fragmentation and climate interact to explain patterns of population decline, evidencing  
492 regional population loss and local population retention. Second, climate and landscape-scale  
493 community composition interact to explain trends in population decline that might seem  
494 counterintuitive based on the effects of the dimensions separately. Broadly, mortality  
495 increases while approaching the transition area between bioclimates (i.e. from temperate to  
496 Mediterranean) across populations located in relatively wet habitats and, to the contrary, it  
497 decreases while approaching the transition area between bioclimates across populations

498 located in dry habitats, with a trend from continuous-range to isolated populations (Figure  
499 3B). All together, these results provide evidence on three main aspects. First, the mosaic of  
500 ecological conditions at the species' rear edge where climate alone cannot explain population  
501 responses. Second, the putative persistence of some relict populations across the species' rear  
502 edge. Third, the uneven but predictable pattern of population decline across populations, that  
503 can occur also in better-quality habitats.

504

505 This simple study-case application demonstrates that some disparities between predictions  
506 and observations can be reconciled accounting for simple interactions among marginality  
507 components, and that the potential scale-dependency of the mechanisms involved in  
508 population decline is a critical issue for modelling species distributions and regional  
509 biodiversity patterns at rear edges (Figure 1). By incorporating existing data sources to better  
510 infer the ecological structure of species rear edges through marginality-type classification and  
511 taking a hypothesis-driven approach, the rationale provided is flexible enough to be  
512 applicable to field-based approaches, *in situ* or controlled-condition experimentation,  
513 population genetic studies and approaches accounting for land-use changes, and allows better  
514 integration of population ecology and biogeography.

515

## 516 **Conclusions**

517 Taking the population perspective on marginality is challenging for empirical studies yet it is  
518 both possible and essential for our understanding of rear edge dynamics. It is of primary  
519 importance to determine interactions among ecological mechanisms driving population  
520 decline and the influence of anthropogenic land-use. Similarly, scaling-up the complexity of  
521 marginality to broader scales presents a critical challenge for biogeographical studies. The  
522 problem of data resolution driving a mismatch between regional predictions and local

523 observations can be improved as data availability increases, which is critical to plan for  
524 climate change impacts. For example, if management and conservation decisions are to be  
525 based on predictions and the actions implemented ‘locally’, we must know the spatial  
526 resolution of data that is needed to accurately predict rear edge dynamics. At the same time,  
527 data availability is distributed unevenly across spatial scales, systems and world regions, with  
528 regional scales, plant species and the Northern Hemisphere over-represented. Local  
529 environmental monitoring is essential to avoid scale-dependent hazards, and large-scale and  
530 systematic sampling protocols in the Southern Hemisphere and across taxa other than plants  
531 are needed. Increasingly, application of remote sensing methodologies and modelling can  
532 help fill data gaps, although ground truth data are still required. Importantly, the rationale  
533 presented allows the incorporation of other marginality dimensions not considered here. For  
534 example, it is critical to account for biological invasions, including novel competitors and  
535 pathogens, or nitrogen deposition and nutrient limitation. Such progress is essential to better  
536 understand and predict the impacts of a warming climate and how it interacts with other  
537 environmental changes to drive population retention or loss at species’ rear edges.

538

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548

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798 **Figure captions**

799 **Figure 1. Conceptual representation of the structure of species' rear edges and**  
800 **persistence probability of populations.** Marginality and the interactions among its  
801 dimensions, together with the regional- and local-level hypotheses on population decline are  
802 represented. Regional-level predictions: (i) the geographical edge (horizontal dashed line)  
803 represents the threshold between continuous range and isolated populations. Geographical  
804 (and genetic) marginality are higher with increasing fragmentation and population isolation;  
805 (ii) the climatic edge (vertical continuous line) represents the threshold of species' climatic  
806 tolerance. Ecological marginality is higher below this threshold. The direction of the line  
807 (bottom-right to top-left) represents higher abundance below the climatic edge in isolated  
808 populations relative to continuous range populations; (iii) the ecological edge (vertical dashed  
809 line) represents the threshold of species' ecological tolerance and a bioclimatic transition. It is  
810 defined by the interaction between the climatic edge and the community composition at the  
811 regional and/or local scale. Ecological marginality is higher below this threshold. The  
812 direction of the line (bottom-right to top-left) represents higher population abundance below  
813 the ecological edge in isolated populations relative to continuous range populations. Local-  
814 level predictions: the persistence probability may be higher or lower than expected at the  
815 regional scale because of population-level mechanisms. For a detailed description of  
816 mechanisms and examples, see section *Shifting to the population perspective: refocusing on*  
817 *local-scale hypotheses*.

818 **Figure 2. Guidelines for empirical study design.** (A) The distribution of marginality  
819 dimensions can be inferred from existing data sources (e.g. macroclimate, habitat  
820 configuration, community composition). The position of populations relative to the  
821 geographical, climatic and ecological edges is used to classify them into marginality-types  
822 according to the criteria of the flow diagram shown. The ecological edge results from the

823 interaction between the climatic edge and the community composition at the regional and/or  
824 local scale. The interaction between ecological marginality and geographical (and genetic)  
825 marginality results in four main marginality-types (see also Figure 1). (B) Population decline  
826 can be tested according to the predicted marginality-types, based on a balanced experimental  
827 design. Population/individual parameters need to be measured and regional-level hypotheses  
828 tested. Disparities between observed population responses and regional-scale predictions  
829 indicate that local-scale hypotheses need to be considered. For a practical application of this  
830 guidelines see section *A population-focused study at the species' rear edge*.

831 **Figure 3. Population decline of the European beech tree across marginality types and**  
832 **gradients.** (A) Tree mortality and canopy decline as a function of the four population  
833 marginality-types that result from the interaction between geographical (genetic) marginality  
834 (isolated/continuous range) and ecological marginality (ecologically-marginal/non-  
835 ecologically marginal); (B) population mortality across the gradients related to interactions  
836 between (i) climate (water balance expressed as the ratio of annual precipitation to potential  
837 evapotranspiration, P/PET) and geographical isolation (number of beech plots within a radius  
838 of 5 km around each sampled beech population), and (ii) climate (P/PET) and regional  
839 community composition surrounding sampled populations (% of Mediterranean communities  
840 relative to the total number of plots within a radius of 1.7 km around each beech population).  
841 Geographical, climatic and ecological edges (see Fig. 1 and 2) were derived from plot-level  
842 data of the Ecological and Forest Inventory of Catalonia and the Spanish National Forest  
843 Inventory, and 1-km<sup>2</sup> resolution interpolated climate derived from the WorldClim database  
844 (see supplementary material).

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848 **Supporting information**

849 **Appendix S1.** List and details of studies assessing rear edge population decline.

850 **Appendix S2.** Methodology used in the population-focused study presented.

851

852 **Graphical abstract**

853 Climate change is expected to drive population loss at the species' rear edge, however,  
854 disparities between predictions and observations are accumulating. We argue for a revision of  
855 the concept of marginality together with an explicit testing of population decline across the  
856 species' rear edge, given the scale-dependency of the ecological mechanisms determining  
857 population dynamics. Such progress is possible as data availability improves and essential to  
858 better predict the consequences of species range shifts.

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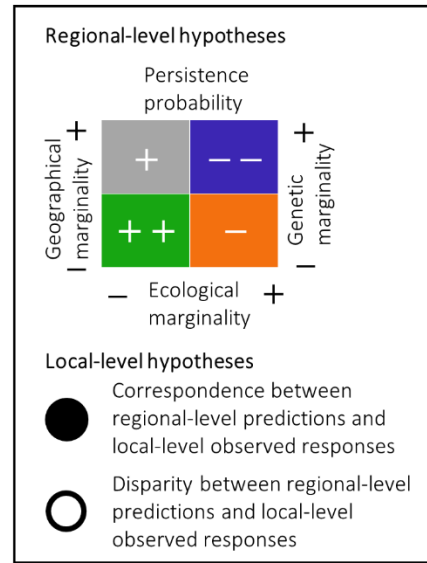
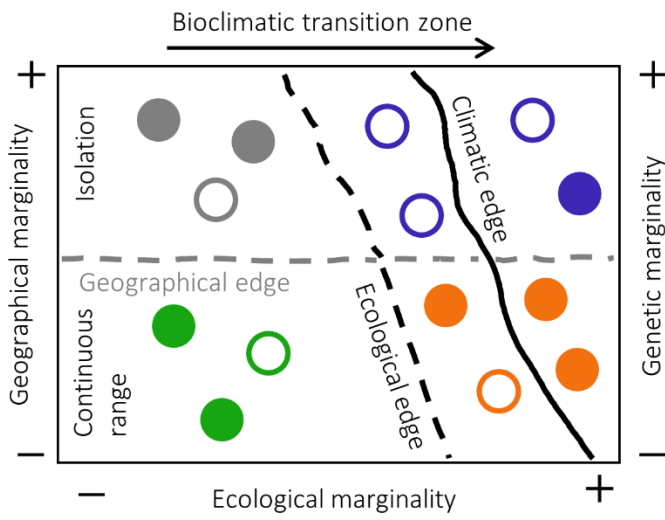
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873 **Figure 1**



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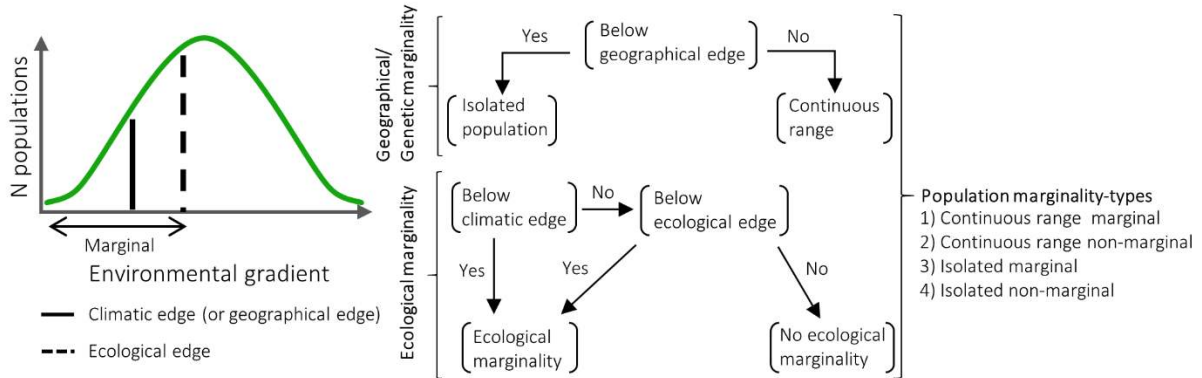
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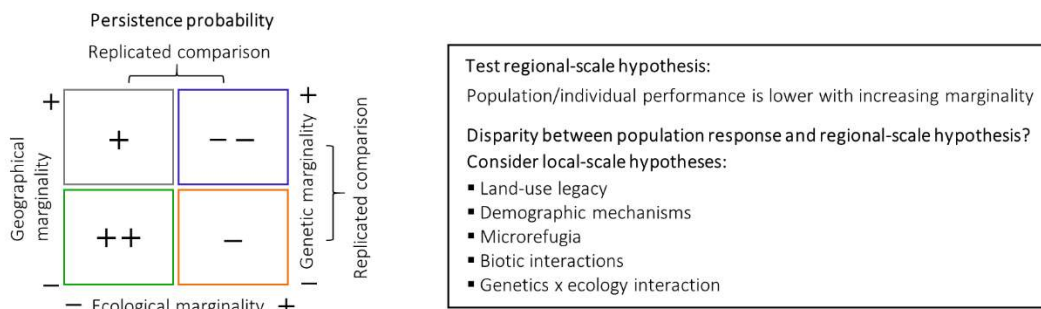
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894 **Figure 2**

(a) Example of classification of populations into population marginality-types



(b) Empirical study design for hypotheses testing on population decline at rear edges



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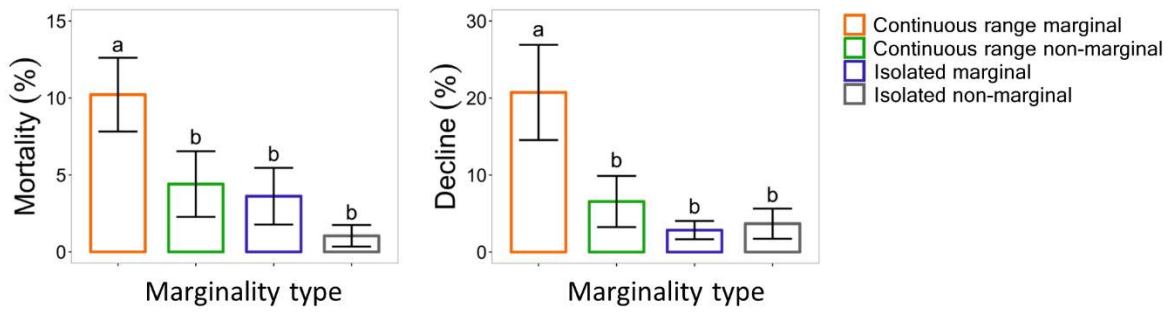
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(a) Mortality and canopy decline according to population marginality-type



(b) Mortality variation across population marginality-type

