

1 **Greater growth stability of trees in marginal habitats suggests a patchy pattern of**  
2 **population loss and retention in response to increased drought at the rear edge**

3 Albert Vilà-Cabrera<sup>1</sup> and Alistair S. Jump<sup>1,2</sup>

4 <sup>1</sup>Biological and Environmental Sciences. Faculty of Natural Sciences, University of Stirling,  
5 Stirling, FK9 4LA, Scotland, UK

6 <sup>2</sup>CREAF Cerdanyola del Vallès, Barcelona 08193, Catalonia, Spain

7 **E-mail addresses:** A Vilà-Cabrera: [albert.vilacabrera@stir.ac.uk](mailto:albert.vilacabrera@stir.ac.uk); AS Jump:

8 [a.s.jump@stir.ac.uk](mailto:a.s.jump@stir.ac.uk)

9 **Running title:** Tree growth responses at the rear edge

10 **Keywords:** biogeography, climate change, growth decline, periphery, range retraction,  
11 resilience, relict

12 **Type of article:** Letters

13 **N words abstract:** 148

14 **N words main text:** 4994

15 **N references:** 57

16 **N figures and tables:** 5

17 **Correspondence:** Albert Vilà-Cabrera. Email: [albert.vilacabrera@stir.ac.uk](mailto:albert.vilacabrera@stir.ac.uk), Tel: +44

18 1786467794

19 **Statement of authorship:** AVC and ASJ designed the study. AVC collected and analysed  
20 the data. AVC and ASJ interpreted the results. AVC drafted the manuscript and both authors  
21 contributed to editing.

22 **Data accessibility statement:** should the manuscript be accepted, the data supporting the  
23 results will be archived in the Dryad public repository and the data DOI will be included at  
24 the end of the article.

25

26 **ABSTRACT**

27 Species rear range-edges are predicted to retract as climate warms, yet evidence of population  
28 persistence is accumulating. Accounting for this disparity is essential to enable prediction and  
29 planning for species' range retractions. At the Mediterranean edge of European beech-  
30 dominated temperate forest, we tested the hypothesis that individual performance should  
31 decline at the limit of the species' ecological tolerance in response to increased drought. We  
32 sampled 40 populations in a crossed factor design of geographical and ecological marginality  
33 and assessed tree growth resilience and decline in response to recent drought. Drought  
34 impacts occurred across the rear edge, but tree growth stability was unexpectedly high in  
35 geographically isolated marginal habitat and lower than anticipated in the species' continuous  
36 range and better-quality habitat. Our findings demonstrate that, at the rear edge, range shifts  
37 will be highly uneven and characterised by reduction in population density with local  
38 population retention rather than abrupt range retractions.

39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50

## 51 INTRODUCTION

52 Climate change is driving global biodiversity redistribution with cascading effects on  
53 ecosystem functioning (Pecl *et al.* 2017). Understanding how the abundance and distribution  
54 of species are shifting is thus essential to plan for the conservation of biodiversity and  
55 management of natural resources. Forests cover ~30% of the land surface, represent 45% and  
56 50% of C stocks and net primary productivity, respectively (Bonan 2008), and provide  
57 habitat for much of terrestrial biodiversity (Petit & Hampe 2006). Consequently, the response  
58 of tree species will strongly influence the magnitude of climate change impacts. Since sessile  
59 and long-lived organisms such as trees are inevitably exposed to disturbance, population loss  
60 may occur if the impacts of increased disturbance exceed the species' tolerance limits  
61 (Scheffer *et al.* 2001). Therefore, it is reasonable to expect that, under increased drought,  
62 range retractions should occur at the rear edge of species' distributions (Morin *et al.* 2008).  
63 There is widespread evidence supporting this prediction across the globe (e.g. Reich &  
64 Oleksyn 2008; Allen *et al.* 2010; Galiano *et al.* 2010; Feeley *et al.* 2011; Matías & Jump  
65 2015; Barbeta & Peñuelas 2017; Rumpf *et al.* 2018). However, episodes of sudden species'  
66 range retractions are rarely documented (Jump *et al.* 2009).

67

68 A fundamental assumption underpinning expectations of range retraction is that rear edge  
69 populations are 'marginal' – i.e. they have lower individual performance and thus higher risk  
70 of extinction than those populations at the core of the species' range due to reduced habitat  
71 favourability and population size (Brown 1984). However, evidence for shifts at the rear edge  
72 of plant distributions is inconsistent (Lenoir & Svenning 2015) while population persistence  
73 is also well documented (e.g. Pulido *et al.* 2008; Bertrand *et al.* 2011; Hampe & Jump 2011;  
74 Lázaro-Nogal *et al.* 2015; Kolb *et al.* 2016; Granda *et al.* 2018). This lack of evidence on  
75 widespread rear edge population decline is evident at the regional scale, where variation in

76 performance rather than consistent decline among rear edge populations is often observed  
77 (e.g. Lesica & Crone 2016; Cavin & Jump 2017; Sánchez-Salguero *et al.* 2017).  
78  
79 This disparity between prediction and observation can be linked to oversimplification of the  
80 concept of marginality. Climate is a strong determinant of plant distribution (Harper 1977),  
81 so we can expect that individual performance decreases with increasing ecological  
82 marginality e.g. at the driest edge of a species' range. Predictions of ecological marginality  
83 based on climate alone can be improved with biotic patterns. Rear edge populations occur  
84 along bioclimatic transition areas (Jump *et al.* 2009), where changes in the composition of  
85 communities can occur over small spatial scales, with shifts in habitat quality (Forman 1995).  
86 For example, alterations to species coexistence can reflect deteriorating habitat quality even  
87 in climatically favourable areas (e.g. middle or high elevations), such that more stress-  
88 tolerant species gain a competitive advantage (Galiano *et al.* 2010). We might expect,  
89 therefore, that individual performance also depends on the community composition, with  
90 higher ecological marginality (and thus lower individual performance) where co-occurring  
91 species have a competitive advantage (but see Granda *et al.* 2018b).  
92  
93 Importantly, an incomplete overlap between geographical and ecological range limits can  
94 lead to unexpected population persistence at rear edges (e.g. Tegel *et al.* 2014) highlighting  
95 that we cannot assume that ecological marginality will drive decreased individual  
96 performance with increasing geographical marginality – e.g. where spatial isolation increases  
97 at the rear edge. At the same time, however, the fragmented habitat configuration at species'  
98 rear edges increases the chance of ecological edge effects and genetic erosion (Cheptou *et al.*  
99 2017). Consequently, we might expect lower individual performance in geographically  
100 isolated patches than in large and more continuous ones, under similar ecological conditions.

101 Although these general patterns of marginality can be quantified as data availability  
102 increases, we must remember that marginality is a property of populations not of distributions  
103 (Sexton *et al.* 2009). Consequently, each individual within a species may experience stress  
104 from climate change (Harte *et al.* 2004) while persistence may occur through local-scale  
105 ecological and evolutionary mechanisms such as micro-environmental buffering, biotic  
106 interactions or genetic adaptations (Kawecki 2008; Woolbright *et al.* 2014; McLaughlin *et al.*  
107 2017). We need, therefore, to test for reduced individual performance rather than assuming it  
108 according to position in a species' distribution.

109

110 The assessment of tree growth responses to drought provides an opportunity to test  
111 predictions of rear edge population decline. Tree radial growth (obtained from wood annual  
112 rings) is a parameter that allows individual performance to be assessed in response to  
113 environmental variability. For example, growth suppressions can indicate early signs of tree  
114 mortality in response to drought stress (Cailleret *et al.* 2017). Therefore, the potential for  
115 population loss can be inferred from tree growth responses to drought stress. Particularly,  
116 reduced tree growth stability (i.e. lower resilience to disturbance and greater growth decline  
117 over time) is expected to result from the impacts of recurrent droughts (Lloret *et al.* 2011).  
118 We know from a broad range of studies that decreased growth stability is associated with  
119 drought events (e.g. Peltier *et al.* 2016; Bottero *et al.* 2017; Gazol *et al.* 2018; Serra-  
120 Maluquer *et al.* 2018). However, the extent to which drought legacy over recurrent  
121 disturbances influences growth stability is rarely documented (Anderegg *et al.* 2015;  
122 Camarero *et al.* 2018). Considering the cumulative impact experienced by trees is thus  
123 essential to better understand and predict where population extinction may occur.

124

125 We sought to determine if reduced individual performance in response to increased drought is  
126 consistent with predicted population marginality at rear edges. To address this question, we  
127 examined tree growth resilience to successive drought events and trends over recent years  
128 across 40 rear edge populations of the European beech tree (*Fagus sylvatica* L.) distributed  
129 according to a crossed factor design of geographical and ecological marginality. Using these  
130 data, we test the hypotheses that increased geographical and ecological marginality is  
131 associated with: (1) decreased tree growth resilience to drought events, (2) stronger effects of  
132 past cumulative drought impacts on tree resilience to current disturbance, and (3) higher rates  
133 of growth decline over time consistent with increased cumulative drought impact.

134

## 135 **METHODS**

### 136 **Experimental design**

137 The research was conducted in Catalonia (north-eastern Iberian peninsula), along the rear  
138 edge of the European beech tree (*Fagus sylvatica* L.) (Fig. S1; Text S1). Following Vilà-  
139 Cabrera *et al.* (2019), we used existing forest inventory and climatic datasets to infer the  
140 distribution (and edges) of the species across the study area, in terms of the geography,  
141 climate and community composition of the populations (Text S1). Geographical marginality  
142 was assumed to increase with increasing habitat fragmentation and population isolation,  
143 while ecological marginality was assumed higher in drier climates and at the limit of the  
144 temperate-Mediterranean bioclimatic transition zone. We then classified the distribution of  
145 populations as follows: geographically isolated in non-marginal habitats (I–Non M),  
146 geographically isolated in marginal habitats (I–M), continuous range in non-marginal habitats  
147 (CR–Non M) and continuous range in marginal habitats (CR–M). We selected 40 beech  
148 populations (10 sites per population-type; Fig. S1b) for sampling to test our hypotheses  
149 relating to expected population marginality (Fig. 1).

150

## 151 **Field sampling and measurements**

152 Populations were sampled using a circular sampling plot (12.5 m radius). Within each plot,  
153 we identified species and measured diameter at breast height (dbh) for all adult trees (dbh  $\geq$   
154 7.5 cm). We also selected 10 trees (or  $< 10$  individuals if N beech trees within the plot was  
155 lower) and took two wood core samples per tree. We prepared cores and measured ring  
156 widths for the period 1985-2015 using standard dendroecological methods (Text S1). In total,  
157 we used 386 tree chronologies for analyses: 99 CR-M, 95 CR-Non M, 95 I-M and 97 I-Non  
158 M. Finally, we transformed ring width series to basal area increment (BAI) series using  
159 measured dbh and the equation:  $BAI_t = \pi \cdot (R_t^2 - R_{t-1}^2)$ , where  $R_t$  and  $R_{t-1}$  are the radius of  
160 the tree for year t and the preceding one, respectively.

161

## 162 **Selection of drought events**

163 We selected drought events using the standardized precipitation and evapotranspiration index  
164 (SPEI) (Vicente-Serrano *et al.* 2010) (Text S1). We selected four drought events: (i) 1989-  
165 1991-drought characterised by a highest intensity at the beginning and/or end of the period,  
166 (ii) 1994-drought characterised by extreme dry conditions during the growing season, (iii)  
167 1998-1999-drought characterised by moderate but continuous dry conditions, and (iv) 2005-  
168 2006-drought characterized by extreme dry conditions during two consecutive years.

169

## 170 **Resilience components: resistance and recovery**

171 Here we consider ‘resistance’ and ‘recovery’ as complementary components of resilience  
172 (Hodgson *et al.* 2015). Resistance is defined as the individual capacity for maintaining  
173 performance during disturbance, while recovery is defined as the individual ability for  
174 recovering the impact experienced. Both components are relative to the state of the individual

175 before disturbance. Following Lloret *et al.* (2011), we computed the two metrics at the  
176 individual level and for each drought:

177

$$178 \text{ Resistance} = \frac{BAI_{drought}}{BAI_{pre\ drought}},$$

$$179 \text{ Recovery} = \frac{(BAI_{post\ drought} - BAI_{drought})}{BAI_{pre\ drought}},$$

180

181 where  $BAI_{drought}$  is the growth during the corresponding drought (averaged across years for  
182 multi-year drought periods), while  $BAI_{pre\ drought}$  and  $BAI_{post\ drought}$  are the average growth for  
183 the 3 years preceding and following the drought, respectively (or 2 years in case of the 1989-  
184 1991 drought and the 1994 drought to avoid overlap between them, and with a drought  
185 occurring in 1986; Text S1). Note that there is an overlap between the period before the  
186 1989-91 drought and the period after a drought in 1986. The 1986 drought is not analysed  
187 here directly, however, we include its impact in the analyses (see below).

188

### 189 **Individual and plot-level characteristics**

190 To account for the cumulative effects of previous disturbance, we calculated for each tree and  
191 drought the cumulative impact of previous successive droughts (excluding the considered  
192 drought event) following the first drought considered (1989-1991) and including the impact  
193 of the 1986 drought. Cumulative impact was calculated as the sum of the impact experienced  
194 by the tree during previous droughts. The impact of a given drought was estimated as:

195

$$196 \text{ Impact} = \frac{(BAI_{pre\ drought} - BAI_{drought})}{BAI_{pre\ drought}},$$

197



198 where  $BAI_{\text{drought}}$  is the growth during the corresponding drought (averaged across years for  
199 multi-year drought periods), while  $BAI_{\text{pre drought}}$  is the average growth for the 3 years  
200 preceding the drought (or 2 years in case of the drought events 1989-1991 and 1994 to avoid  
201 overlap with the 1986–drought and 1989-1991–drought, respectively). In the case of the 1986  
202 drought, impact was calculated relative to the BAI of the previous year (1985) to minimise  
203 the inclusion of non-analysed background. Note that when  $BAI_{\text{drought}} > BAI_{\text{pre drought}}$  we set  
204 impact to zero.

205

206 We accounted for other tree- and plot-level characteristics: tree dbh, growth prior to the  
207 drought event (independent of tree size), plot basal area, and August SPEI at a time scale of 6  
208 months during and following each drought (Text S1).

209

## 210 **Data analysis**

211 To test the hypotheses that increased marginality results in (i) lower tree growth resilience to  
212 drought and (ii) stronger effects of cumulative drought impacts on resilience, we used mixed-  
213 effects models with plot identity as random factor on the intercept. We first modelled  
214 resistance and recovery as a function of the interaction term ‘drought x population-type’ to  
215 assess resilience patterns across the successive droughts and population-types. Drought was  
216 allowed to vary among populations in the random part of the model (lower AIC<sub>c</sub>, corrected  
217 Akaike information criterion). In a second step, and for each drought event, resistance and  
218 recovery were modelled as a function of the fixed effects population-type and its interaction  
219 with individual- and plot-level covariates, i.e. cumulative impact, dbh (log-transformed),  
220 previous growth, basal area and SPEI (during drought for resistance [ $SPEI_{\text{drought}}$ ] and  
221 following drought for recovery [ $SPEI_{\text{post drought}}$ ]). We included the interaction term ‘covariate  
222 x population-type’ to assess differences in covariate effects on resistance and recovery among

223 population-types. Starting from the full model that included all interaction terms, we created  
224 a set of models differing in the composition of interactions but always maintaining the single  
225 fixed terms and ranked them from lowest to highest AIC<sub>c</sub>. All the best models (lowest AIC<sub>c</sub>)  
226 within two AIC<sub>c</sub> units were considered equivalent in terms of fit. In case the model selection  
227 procedure yielded candidate models with similar Akaike weights, the simplest model was  
228 selected. Resistance was log-transformed and covariates were standardised.

229

230 To test the hypothesis that increased marginality results in higher rates of growth decline over  
231 time consistently with increased cumulative drought impact, we analysed growth trends also  
232 using a mixed-effects model. To assess growth trends across the rear edge, among  
233 population-types and according to the level of cumulative impact, tree BAI (log-transformed)  
234 was fitted successively as a function of the fixed effects ‘year’, ‘year x population-type’ and  
235 ‘year x population-type x cumulative impact’. Cumulative drought impact (i.e. the sum of  
236 suffered impacts over the study period) was included as 3-level factor variable based on the  
237 distribution of the variable: low <33rd percentile, middle 33rd-66th percentiles, and high >  
238 66th percentile. Additional models accounting for the effects of tree size were also fitted  
239 (Text S1). Plot and tree identity nested within plot were included as random factors on the  
240 intercept and year was included as random slope term at the plot and tree levels.

241

242 Parameter estimates were considered significant when the 95% confidence intervals (95% CI)  
243 did not include zero. Coefficients of determination were used to assess the percentage  
244 contribution of fixed effects ( $R^2_{marginal}$ ) and both fixed and random effects ( $R^2_{conditional}$ ) in  
245 explaining resistance, recovery and growth trend variability. Model diagnoses were overall  
246 satisfactory (Fig. S2). All analyses were carried out with R software version 3.4.4 (R

247 Development Core Team 2018), using the packages lme4 (Bates *et al.* 2015) and MuMIn  
248 (Barton 2011).

249

## 250 **RESULTS**

### 251 **Tree resistance**

252 Overall, tree resistance decreased over successive droughts, especially across continuous-  
253 range (CR-M and CR- Non M) and I-M populations though, in this last population-type, tree  
254 resistance did not decrease during the most recent drought (Table S1a; Fig. 2a). Differences  
255 in tree resistance among population-types were drought-specific. Consistently among  
256 population-types, tree resistance was variable among individuals, i.e. values varied around  
257 one, during the 1989-91 drought and it was low during the 2005-06 drought (Table S1a; Fig.  
258 2a). During the 1994 drought, tree resistance was variable across CR-Non M and I-M  
259 populations while growth reductions mostly occurred across I-Non M and CR-M populations  
260 (Table S1a; Fig. 2a). Contrastingly, trees occurring in I-Non M populations were overall  
261 resistant to the 1998-99 drought while growth reductions occurred across the rest of the  
262 species' rear edge (Table S1a; Fig. 2a). Explained variability by fixed effects was 19% and  
263 57% by fixed and random effects together.

264

265 Differences in tree resistance among population-types were dependent on the effects of some  
266 covariates (Table S2; Fig. 3). Cumulative impact had a negative effect on tree resistance to  
267 the 1994 drought across CR-M and I-Non M populations but this effect was not significant in  
268 the other population-types (Table S2; Fig. 3b). During the 1998-99 drought, cumulative  
269 impact positively associated with tree resistance in CR-M populations and, contrary,  
270 cumulative impact had a slight negative effect on resistance in CR-Non M and I-M  
271 populations (Figure 3e), though parameter estimates for this interaction were not significant

272 (Table S2). Tree growth prior to disturbance had a negative effect on tree resistance and this  
273 effect was consistent among droughts with the exception of the last one (Table S2).  
274 Furthermore, the interaction term ‘previous growth x population-type’ was included in the  
275 selected model for the 1989-91 and 1994 droughts (Table S2). In particular, tree resistance  
276 was higher for trees growing at slower rates before disturbance but lower for those growing  
277 faster, and this effect was more evident across I-M and CR-M populations (Table S2; Fig. 3a  
278 and 3c). We also found a positive effect of basal area on tree resistance in the 1994 drought  
279 across CR-M populations (Table S2; Fig 3d) while, in the 2005-06 drought, across all  
280 population-types (Table S2), and a positive effect of  $SPEI_{drought}$  on tree resistance that was  
281 consistent among population-types during the 1998-99 drought (Table S2). The effect of dbh  
282 on tree resistance was negative across all population-types in the 1989-91 and 1998-99  
283 droughts (Table S2). Finally, explained variability by fixed effects varied between 10% and  
284 47% among the best-selected models for each drought, while explained variability by fixed  
285 and random effects together varied between 44% and 72% (Table S2).

286

### 287 **Tree recovery**

288 Tree recovery increased over successive droughts especially in I-M populations and also in  
289 CR-M ones, while this trend was not as evident in CR-Non M and I-Non M populations  
290 (Table S1b; Fig. 2b). Note that tree resistance in general decreased over successive droughts  
291 across all population-types (Table S1a; Fig. 2a). Differences in recovery among population-  
292 types were drought-specific. Consistently among population-types but especially in I-M and  
293 CR-M populations, recovery values after the 1989-91 drought were low (i.e. around zero or  
294 negative) indicating decreased performance after drought despite resisting disturbance (Table  
295 S1b; Fig. 2b). Contrary, tree recovery after the 1994 drought was noticeable and similar  
296 among population-types, meaning that trees showing the lowest resistance (especially in I-

297 Non M and CR-M) were able to recover performance after drought (Table S1b; Fig. 2b).  
298 Similarly, tree recovery was overall similar among population-types after the 1998-99  
299 drought, meaning that trees experiencing the highest impact (especially in I-M populations)  
300 recovered performance better (Table S1b; Fig. 2b). Tree recovery after the 2005-06 drought  
301 was higher in I-M and CR-M populations (Table S1b; Fig. 2b). Note that the levels of (low)  
302 resistance were similar among population-types during this drought (Table S1a; Fig. 2a).  
303 Explained variability by fixed effects was 20% and 47% by fixed and random effects  
304 together.  
305  
306 Some covariate effects on tree recovery varied among population-types (Table S3; Fig. 4).  
307 Tree growth prior to disturbance had a significant positive effect on tree recovery in the  
308 1989-91 drought across I-M and CR-M populations, i.e. higher previous growth rates were  
309 related to higher recovery (Table S3; Fig. 4a). Note that trees showing higher previous  
310 growth rates displayed the lowest resistance during this drought, and this effect was stronger  
311 across I-M population (Table S2; Fig 3a). In contrast, previous growth had a significant  
312 negative effect on tree recovery across all population-types in the 1994 and 1998-99 droughts  
313 (Table S3). We also found a significant positive effect of  $SPEI_{\text{post drought}}$  in the 1989-91  
314 drought across CR-Non M populations and in the 1994 drought consistently among  
315 population-types, i.e. tree recovery was lower under a more negative water balance after the  
316 drought (Table S3; Fig. 4b). In contrast,  $SPEI_{\text{post drought}}$  had a significant negative effect on tree  
317 recovery across I-Non M populations in the 2005-06 drought (Table S3; Fig. 4c). Basal area  
318 was negatively associated with tree recovery only across CR-Non M populations in the 2005-  
319 06 drought (Table S3; Fig. 4d). Tree dbh had a significant negative effect in the 1989-91  
320 drought, while cumulative impact was always non-significant (Table S3). Finally, explained  
321 variability by fixed effects varied between 8% and 22% among the selected models for each

322 drought, while explained variability by fixed and random effects together varied between  
323 32% and 48% (Table S3).

324

### 325 **Tree growth trends**

326 Overall, tree growth slightly declined by a mean of 1.11% per year over the study period  
327 (95% CI  $-1.44\%$ ,  $-0.79\%$ ). Among populations, the growth trend was negative in 24 plots  
328 (i.e. the upper 95% CI was below 0), while stable in 15 (i.e. 95% CI included 0) and positive  
329 in 1 plot (i.e. the lower 95% CI was above 0) (Table S4). The percentage of plots showing  
330 significant growth decline was 80% in CR-M, 70% in CR-Non M, 60% I-Non M and 40% in  
331 I-M. There was variation in growth trends among population-types and according to the  
332 cumulative impact experienced by trees during the successive droughts (Table S5; Fig. 5).  
333 Tree growth was more stable in I-M populations than other population-types, while higher  
334 decline occurred in the continuous range:  $-0.89\%$  (95% CI  $-1.54\%$ ,  $-0.24\%$ ) for I-Non M,  $-$   
335  $0.76\%$  (95% CI  $-1.42\%$ ,  $-0.11\%$ ) for I-M,  $-1.58\%$  (95% CI  $-2.23\%$ ,  $-0.92\%$ ) for CR-Non  
336 M and  $-1.21\%$  (95% CI  $-1.85\%$ ,  $-0.56\%$ ) for CR-M. Furthermore, the effect of cumulative  
337 impact on tree growth decline was stronger across the continuous range (CR-M and CR-Non  
338 M) and better-quality habitat (CR-Non M and I-Non M). That is, growth decline change with  
339 increasing the level of cumulative impact was steeper in these population-types, reaching  
340 mean decline rates between  $-1.44\%$  and  $-3.36\%$  under high cumulative impact (Table S5;  
341 Fig. 5). In contrast, tree growth trends were more stable in I-M populations when high impact  
342 occurred (Table S5; Fig. 5). Explained variability by fixed effects was 6%, while explained  
343 variability by fixed and random effects together was 76%. Model diagnoses were satisfactory  
344 and predictions unbiased (Fig. S2.6), however, predictions are conservative with slight under-  
345 prediction of extreme growth reductions (Fig. S2.6, panel *b*). When accounting for the effects  
346 of tree size (final dbh), the best model included the term 'year x final dbh' and model fit

347 substantially increased (Table S6a). However, parameter estimates of the target term ‘year x  
348 population-type x cumulative impact’ were qualitatively equivalent (Table S6a). Finally,  
349 growth decline was steeper with increasing tree size (Table S6b) and consistently negative  
350 among dbh classes in the continuous range (Table S6c).

351

## 352 **DISCUSSION**

353 Widespread population decline is predicted to occur across the rear edge of species  
354 distributions in response to increased drought, prompting abrupt range retractions. Here we  
355 refine this prediction by decomposing causes of marginality and assessing individual  
356 performance under a population-focused framework that incorporates both ecological and  
357 geographical marginality. This approach identifies a patchy pattern of population decline and  
358 stability dependent on the type of marginality experienced by populations and demonstrates  
359 why population responses do not always support established assumptions of species’ range  
360 shifts. We emphasise three key findings. (1) Tree growth resilience is higher than expected in  
361 geographically isolated populations occurring across the most drought-prone climates at the  
362 temperate-Mediterranean bioclimatic transition. (2) Differences in tree growth resilience  
363 among population-types depend on individual- and stand-level components. Particularly, the  
364 cumulative impact experienced by trees during recurrent droughts may drive individuals to  
365 exceed their drought tolerance limits. (3) While growth stability is higher than expected  
366 across geographically isolated populations in marginal habitats there is a significant growth  
367 decline across rear edge populations, especially under increased ‘drought legacy’.

368

369 Other studies have attempted to document regional-scale evidence for species’ rear edge  
370 retractions. For example, Lesica & Crone (2016) found evidence for a declining trend for rear  
371 edge populations of arctic and boreal plant species in the Rocky Mountains. However, half of

372 the studied populations remained stable or increased in abundance over the study period.  
373 Many other study-cases report mixed evidence for rear edge population decline (e.g. Pulido *et*  
374 *al.* 2008; Galiano *et al.* 2010; Craven *et al.* 2013; Matías & Jump 2015; Kolb *et al.* 2016;  
375 Granda *et al.* 2018; Rumpf *et al.* 2018; Stojnić *et al.* 2018). This variation in population  
376 response agrees with the results reported here. However, our study suggests that variability in  
377 individual performance is predictable across the rear edge with a strong dependence on  
378 marginality type, itself a measurable characteristic that should not simply be assumed based  
379 on population location. To our knowledge, this work is the first study from field observations  
380 that explicitly accounts for the complexity of marginality and evidences why range shifts are  
381 heralded by declining regional population density, rather than occurring abruptly.

382

383 Our results indicate strong legacy effects of drought on tree performance, especially across  
384 continuous-range populations and/or better-quality habitats. First, tree resistance decreased  
385 over successive droughts especially across the continuous range, while recovery clearly  
386 increased across the most marginal habitats (Table S1; Fig. 2). Second, previous drought  
387 impact resulted in decreased resistance to the 1994 drought in CR-M and I-Non M  
388 populations and subtly to the 1998-99 drought in CR-Non M and I-M populations. In  
389 contrast, greater resistance under increased previous impact was observed in CR-M  
390 populations in the 1998-99 drought (Table S2; Fig. 3b and 3e). Third, greater decline in  
391 growth rates occurred across the continuous range and better-quality habitats and growth  
392 decline increased with increasing cumulative impact. Growth stability was, therefore, higher  
393 than expected in geographically isolated populations in marginal habitats (Fig. 5).

394

395 The geographical distribution of populations may contribute to the observed differences in  
396 individual performance among population-types, especially across I-Non M populations,



397 which show a differential pattern of resilience (e.g. Fig. 2) together with a marked  
398 distribution towards the NW of the study area (Fig. S1b). Other factors, such as regional  
399 variability in soil type, might also contribute but differences among population-types were  
400 not evident (Table S7; Fig. S3). Alternatively, a possible mechanism explaining variation in  
401 individual performance is an accumulated hydraulic deterioration and increased drought  
402 vulnerability after successive drought disturbances (Anderegg *et al.* 2013) but higher  
403 resistance to embolism and/or repair capacity of drought-induced damage than expected in  
404 the most marginal habitats. Ecological and evolutionary processes occurring at the local scale  
405 are plausible explanations for these differences in drought vulnerability.

406

407 Small-scale environmental variation due to topography, edaphic factors, vegetation structure  
408 and hydrologic processes may result in high-quality habitat within marginal regional  
409 environments, where populations have higher persistence probability despite chronic regional  
410 drought that exceeding their climatic tolerance limits (Lenoir *et al.* 2017; McLaughlin *et al.*  
411 2017). For example, the tree *Prunus lusitanica* occurs mainly in Macaronesian mountain  
412 cloud forests under subtropical conditions, but rear edge populations persist in riparian  
413 habitats under a Mediterranean climate in the Iberian peninsula (Pulido *et al.* 2008). Although  
414 differential patterns in topographic characteristics among population-types were not evident  
415 (Fig. S4), the occurrence of microrefugia is suggested by some subtle differences observed in  
416 some topographical factors (e.g. more northern and flatter, more sheltered terrain but lower  
417 elevations across I-M populations; Table S7). Within-species variation in hydraulic traits may  
418 also contribute to the observed patterns in growth responses. At the continental scale, rear  
419 edge populations of the European beech tree show higher resistance to xylem embolism than  
420 those occurring in the species range-core (Stojnić *et al.* 2018). Some evidence shows,  
421 however, that vulnerability to embolism does not vary with climate across beech populations

422 in the study area, but other hydraulic traits do (Rosas *et al.* 2019) and these might contribute  
423 to explain differential growth responses among population-types. Phenotypic variation over  
424 small (regional) spatial scales can occur partially as a result of selection of genotypes adapted  
425 to resource limitation, thereby contributing to greater than expected individual performance  
426 in marginal habitats. For example, experimental work with ponderosa pine (*Pinus ponderosa*)  
427 in northern Arizona shows higher biomass allocation to roots while greater survival capacity  
428 to extreme drought of seedlings coming from populations inhabiting low-elevation, drier  
429 habitats (Kolb *et al.* 2016). In contrast, decreased tree growth stability across better-quality  
430 habitats may result from lack of adaptation (or plasticity) and long-term exposure to climatic  
431 suitability and thus greater demand of water resources that are not available during drought  
432 (Jump *et al.* 2017).

433

434 Our results provide evidence of the potential long-term persistence of “relict” populations at  
435 the rear edge, resulting from the interaction between environmental microrefugia and  
436 adaptation to marginal habitats (Hampe & Petit 2005; Hampe & Jump 2011). Our findings  
437 also support a dependence of population decline on individual- and stand-level characteristics  
438 in interaction with population-type. For example, although growth rates were lower in  
439 marginal habitats we found that slow-growing trees in these habitats showed similar or higher  
440 resilience than comparable slow-growing trees in better-quality habitats or the continuous  
441 range. However, high-growth rates prior to drought were associated with lower resilience,  
442 especially across marginal habitats (Table S2 and S3; Fig. 3a and 3c; Fig. 4c). One possible  
443 explanation for this finding is a structural maladaptation to increased disturbance of fast-  
444 growing individuals. Higher drought susceptibility of fast-growing trees can be interpreted as  
445 structural and physiological disadvantages in water limited habitats (e.g. decreased root to

446 shoot ratio, higher leaf to sapwood area ratio or lower stomatal control) (Martínez-Vilalta *et*  
447 *al.* 2012).

448

449 We also found some contrasting effects of drought intensity and post-drought water  
450 availability. Growth reductions and legacy effects may occur independently of drought  
451 intensity when a certain intensity threshold is exceeded (Anderegg *et al.* 2015). This can  
452 contribute to explain why higher SPEI<sub>drought</sub> values were only related to higher resistance for  
453 the continuous but moderate 1998-1999 drought (Table S2), and why the effect of SPEI<sub>post</sub>  
454 <sub>drought</sub> on recovery was positive, neutral or even negative across droughts or population-types  
455 (Table S3; Fig. 4b and 4c). Finally, stand basal area also had an effect on growth responses,  
456 for example, it was positively related to resistance across CR-M populations in the 1994  
457 drought (Fig. 3d) and across all population-types in the 2005-06 drought (Table S2). Putative  
458 density-dependent tree mortality and consequent reduced intraspecific competition might  
459 explain this relationship (Jump *et al.* 2017). For example, across CR-M populations stand  
460 mortality (%) measured during the sampling was positively related with stand basal area of  
461 living trees in the 1994 drought ( $r = 0.27$ ,  $p < 0.05$ ) and in the 2005-06 drought ( $r = 0.19$ ,  $p <$   
462  $0.05$ ), and also with tree growth resistance during these drought events ( $r = 0.20$ ,  $p < 0.05$  and  
463  $r = 0.25$ ,  $p < 0.05$ , respectively). Consequently, greater intraspecific competition before or  
464 during disturbance followed by mortality-induced competition release might have provided  
465 survivors with higher capacity for resisting subsequent drought.

466

467 Reducing uncertainty of climate change impacts at the local scale to more accurately predict  
468 the pattern and consequence of species range shifts are key challenges for advancing our  
469 preparedness for global climate change. While we found regional-scale decline of *F.*  
470 *sylvatica*, we identified unexpectedly high growth stability across geographically isolated

471 populations in marginal habitats. Furthermore, across the continuous range and better-quality  
472 habitats growth stability was lower than anticipated. Our findings indicate a patchy, but  
473 predictable pattern of population loss and persistence in response to increased climate  
474 change-type drought. Understanding the impacts of changing frequency or magnitude of  
475 extreme events on tree growth remains a key challenge in part due to the difficulty of their  
476 prediction (Jentsch *et al.* 2007) (Fig S2.6). However, the approach demonstrated here can  
477 guide future research to better incorporate population-level ecology at broader spatial scales  
478 and demonstrates that we should be highly cautious about simply assuming marginality and  
479 thereby population decline as a constant property of a species' rear edge.

480

#### 481 **ACKNOWLEDGEMENTS**

482 We thank S. García, C. Mercer and S. Nieto for their support during fieldwork sampling, and  
483 P. Ruiz-Benito and A. Guardia for help in managing forest inventory and land-cover data. We  
484 also thank local stakeholders for their support and providing valuable information on the  
485 populations sampled. We thank the editor, anonymous reviewers and J. Lenoir for insightful  
486 comments on earlier drafts of the manuscript. AVC was funded by the European Union's  
487 Horizon 2020 research and innovation programme under Marie Skłodowska-Curie grant  
488 agreement No. 656300, and the 50<sup>th</sup> Anniversary Fellowship programme of the University of  
489 Stirling.

490

#### 491 **REFERENCES**

492 Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., *et*  
493 *al.* (2010). A global overview of drought and heat-induced tree mortality reveals  
494 emerging climate change risks for forests. *For. Ecol. Manage.*, 259, 660–684.

495 Anderegg, W.R.L., Plavcová, L., Anderegg, L.D.L., Hacke, U.G., Berry, J.A. & Field, C.B.

496 (2013). Drought's legacy: Multiyear hydraulic deterioration underlies widespread aspen  
497 forest die-off and portends increased future risk. *Glob. Chang. Biol.*, 19, 1188–1196.

498 Anderegg, W.R.L., Schwalm, C., Biondi, F., Camarero, J.J., Koch, G., Litvak, M., *et al.*  
499 (2015). Pervasive drought legacies in forest ecosystems and their implications for  
500 carbon cycle models. *Science (80-. )*, 349, 528–532.

501 Barbeta, A. & Peñuelas, J. (2017). Increasing carbon discrimination rates and depth of water  
502 uptake favor the growth of Mediterranean evergreen trees in the ecotone with temperate  
503 deciduous forests. *Glob. Chang. Biol.*, 23, 5054–5068.

504 Barton, K. (2011). *MuMIn: multi-model inference*. R package version 1.42.1. Available at:  
505 <https://cran.r-project.org/web/packages/MuMIn>. Last accessed .

506 Bates, D., Mächler, M., Bolker, B.M. & Walker, S.C. (2015). Fitting Linear Mixed-Effects  
507 Models Using lme4, 67, 48.

508 Bertrand, R., Lenoir, J., Piedallu, C., Dillon, G.R., De Ruffray, P., Vidal, C., *et al.* (2011).  
509 Changes in plant community composition lag behind climate warming in lowland  
510 forests. *Nature*, 479, 517–520.

511 Bonan, G.B. (2008). Forests and climate change: forcings, feedbacks, and the climate  
512 benefits of forests. *Science (80-. )*, 320, 1444–1449.

513 Bottero, A., D'Amato, A.W., Palik, B.J., Bradford, J.B., Fraver, S., Battaglia, M.A., *et al.*  
514 (2017). Density-dependent vulnerability of forest ecosystems to drought. *J. Appl. Ecol.*,  
515 54, 1605–1614.

516 Brown, J.H. (1984). On the Relationship between Abundance and Distribution of Species.  
517 *Am. Nat.*, 124, 255.

518 Cailleret, M., Jansen, S., Robert, E.M.R., Desoto, L., Aakala, T., Antos, J.A., *et al.* (2017). A  
519 synthesis of radial growth patterns preceding tree mortality. *Glob. Chang. Biol.*, 23,  
520 1675–1690.

521 Camarero, J.J., Gazol, A., Sangüesa-Barreda, G., Cantero, A., Sánchez-Salguero, R.,  
522 Sánchez-Miranda, A., *et al.* (2018). Forest Growth Responses to Drought at Short- and  
523 Long-Term Scales in Spain : Squeezing the Stress Memory from Tree Rings. *Front.*  
524 *Ecol. Evol.*, 6, 1–11.

525 Cavin, L. & Jump, A.S. (2017). Highest drought sensitivity and lowest resistance to growth  
526 suppression are found in the range core of the tree *Fagus sylvatica* L. not the equatorial  
527 range edge. *Glob. Chang. Biol.*, 23, 362–379.

528 Cheptou, P.-O., Hargreaves, A.L., Bonte, D. & Jacquemyn, H. (2017). Adaptation to  
529 fragmentation: evolutionary dynamics driven by human influences. *Philos. Trans. R.*  
530 *Soc. B Biol. Sci.*, 372, 20160037.

531 Craven, D., Hall, J.S., Ashton, M.S. & Berlyn, G.P. (2013). Water-use efficiency and whole-  
532 plant performance of nine tropical tree species at two sites with contrasting water  
533 availability in Panama. *Trees - Struct. Funct.*, 27, 639–653.

534 Feeley, K.J., Silman, M.R., Bush, M.B., Farfan, W., Cabrera, K.G., Malhi, Y., *et al.* (2011).  
535 Upslope migration of Andean trees. *J. Biogeogr.*, 38, 783–791.

536 Forman, R.T.. (1995). *Land mosaics: the ecology of landscapes and regions*. Cambridge  
537 University Press, Cambridge.

538 Galiano, L., Martínez-Vilalta, J. & Lloret, F. (2010). Drought-Induced Multifactor Decline of  
539 Scots Pine in the Pyrenees and Potential Vegetation Change by the Expansion of Co-  
540 occurring Oak Species. *Ecosystems*, 13, 978–991.

541 Gazol, A., Camarero, J.J., Vicente-Serrano, S.M., Sánchez-Salguero, R., Gutiérrez, E., de  
542 Luis, M., *et al.* (2018). Forest resilience to drought varies across biomes. *Glob. Chang.*  
543 *Biol.*, 24, 2143–2158.

544 Granda, E., Alla, A.Q., Laskurain, N.A., Loidi, J., Sánchez-Lorenzo, A. & Camarero, J.J.  
545 (2018a). Coexisting oak species, including rear-edge populations, buffer climate stress

546 through xylem adjustments. *Tree Physiol.*, 38, 159–172.

547 Granda, E., Gazol, A. & Camarero, J.J. (2018b). Functional diversity differently shapes  
548 growth resilience to drought for co-existing pine species. *J. Veg. Sci.*, 29, 265–275.

549 Hampe, A. & Jump, A.S. (2011). Climate Relicts: Past, Present, Future. *Annu. Rev. Ecol.*  
550 *Evol. Syst.*, 42, 313–333.

551 Hampe, A. & Petit, R.J. (2005). Conserving biodiversity under climate change: The rear edge  
552 matters. *Ecol. Lett.*, 8, 461–467.

553 Harper, J.L. (1977). *Population biology of plants*. London: Academic Press.

554 Harte, J., Ostling, A., Green, J.L. & Kinzig, A. (2004). Climate change and extinction risk.  
555 *Nature*, 430, 34–34.

556 Hodgson, D., McDonald, J.L. & Hosken, D.J. (2015). What do you mean, “resilient”? *Trends*  
557 *Ecol. Evol.*, 30, 503–506.

558 Jentsch, A., Kreyling, J. & Beierkuhnlein, C. (2007). A new generation of climate-change  
559 experiments : events , not trends. *Front. Ecol. Environ.*, 5, 365–374.

560 Jump, A.S., Mátyás, C. & Peñuelas, J. (2009). The altitude-for-latitude disparity in the range  
561 retractions of woody species. *Trends Ecol. Evol.*, 24, 694–701.

562 Jump, A.S., Ruiz-Benito, P., Greenwood, S., Allen, C.D., Kitzberger, T., Fensham, R., *et al.*  
563 (2017). Structural overshoot of tree growth with climate variability and the global  
564 spectrum of drought-induced forest dieback. *Glob. Chang. Biol.*, 23, 3742–3757.

565 Kawecki, T.J. (2008). Adaptation to marginal habitats. *Annu. Rev. Ecol. Evol. Syst.*, 39, 321–  
566 342.

567 Kolb, T.E., Grady, K.C., McEtrick, M.P. & Herrero, A. (2016). Local-Scale Drought  
568 Adaptation of Ponderosa Pine Seedlings at Habitat Ecotones. *For. Sci.*, 62, 641–651.

569 Lázaro-Nogal, A., Matesanz, S., Godoy, A., Pérez-Trautman, F., Gianoli, E. & Valladares, F.  
570 (2015). Environmental heterogeneity leads to higher plasticity in dry-edge populations

571 of a semi-arid Chilean shrub: Insights into climate change responses. *J. Ecol.*, 103, 338–  
572 350.

573 Lenoir, J., Hattab, T. & Pierre, G. (2017). Climatic microrefugia under anthropogenic climate  
574 change: implications for species redistribution. *Ecography (Cop.)*, 40, 253–266.

575 Lenoir, J. & Svenning, J. (2015). Climate-related range shifts – a global multidimensional  
576 synthesis and new research directions, 15–28.

577 Lesica, P. & Crone, E.E. (2016). Arctic and boreal plant species decline at their southern  
578 range limits in the Rocky Mountains. *Ecol. Lett.*, 166–174.

579 Lloret, F., Keeling, E.G. & Sala, A. (2011). Components of tree resilience: Effects of  
580 successive low-growth episodes in old ponderosa pine forests. *Oikos*, 120, 1909–1920.

581 Martínez-Vilalta, J., López, B.C., Loepfe, L. & Lloret, F. (2012). Stand- and tree-level  
582 determinants of the drought response of Scots pine radial growth. *Oecologia*, 168, 877–  
583 888.

584 Matías, L. & Jump, A.S. (2015). Asymmetric changes of growth and reproductive investment  
585 herald altitudinal and latitudinal range shifts of two woody species. *Glob. Chang. Biol.*,  
586 21, 882–896.

587 McLaughlin, B., Ackerly, D.D., Klos, P.Z., Natali, J., Dawson, T.E. & Thompson, S.E.  
588 (2017). Hydrologic refugia, plants and climate change. *Glob. Chang. Biol.*, 23, 000–000.

589 Morin, X., Viner, D. & Chuine, I. (2008). Tree species range shifts at a continental scale :  
590 new predictive insights from a process-based model. *J. Ecol.*, 96, 784–794.

591 Pecl, G.T., Araújo, M.B., Bell, J.D., Blanchard, J., Bonebrake, T.C., Chen, I., *et al.* (2017).  
592 Biodiversity redistribution under climate change: Impacts on ecosystems and human  
593 well-being, 9214.

594 Peltier, D.M.P., Fell, M. & Ogle, K. (2016). Legacy effects of drought in the southwestern  
595 United States: A multi-species synthesis. *Ecol. Monogr.*, 86, 312–326.



596 Petit, R.J. & Hampe, A. (2006). Some Evolutionary Consequences of Being a Tree. *Annu.*  
597 *Rev. Ecol. Evol. Syst.*, 37, 187–214.

598 Pulido, F., Valladares, F., Calleja, J.A., Moreno, G. & González-Bornay, G. (2008). Tertiary  
599 relict trees in a Mediterranean climate: Abiotic constraints on the persistence of *Prunus*  
600 *lusitanica* at the eroding edge of its range. *J. Biogeogr.*, 35, 1425–1435.

601 R Development Core Team. (2018). R: a language and environment for statistical computing.  
602 R Foundation for Statistical Computing, Vienna, Austria.

603 Reich, P.B. & Oleksyn, J. (2008). Climate warming will reduce growth and survival of Scots  
604 pine except in the far north. *Ecol. Lett.*, 11, 588–597.

605 Rosas, T., Mencuccini, M., Barba, J., Cochard, H., Saura-Mas, S. & Martínez-Vilalta, J.  
606 (2019). Adjustments and coordination of hydraulic, leaf and stem traits along a water  
607 availability gradient.

608 Rumpf, S.B., Hülber, K., Klöner, G., Moser, D., Schütz, M., Wessely, J., *et al.* (2018).  
609 Range dynamics of mountain plants decrease with elevation. *Proc. Natl. Acad. Sci.*, 115,  
610 1848–1853.

611 Sánchez-Salguero, R., Camarero, J.J., Carrer, M., Gutiérrez, E., Alla, A.Q. & Andreu-hayles,  
612 L. (2017). Climate extremes and predicted warming threaten Mediterranean Holocene  
613 firs forests refugia. *Proc. Natl. Acad. Sci.*

614 Scheffer, M., Carpenter, S., Foley, J.A., Folke, C. & Walker, B. (2001). Catastrophic shifts in  
615 ecosystems. *Nature*, 413, 591–596.

616 Serra-Maluquer, X., Mencuccini, M. & Martínez-Vilalta, J. (2018). Changes in tree  
617 resistance, recovery and resilience across three successive extreme droughts in the  
618 northeast Iberian Peninsula. *Oecologia*, 187, 343–354.

619 Sexton, J.P., McIntyre, P.J., Angert, A.L. & Rice, K.J. (2009). Evolution and ecology of  
620 species range limits. *Annu. Rev. Ecol. Syst.*, 40, 415–436.

621 Stojnić, S., Suchocka, M., Benito-Garzón, M., Torres-Ruiz, J.M., Cochard, H., Bolte, A., *et*  
622 *al.* (2018). Variation in xylem vulnerability to embolism in European beech from  
623 geographically marginal populations. *Tree Physiol.*, 38, 173–185.

624 Tegel, W., Seim, A., Hakelberg, D., Hoffmann, S., Panev, M., Westphal, T., *et al.* (2014). A  
625 recent growth increase of European beech (*Fagus sylvatica* L.) at its Mediterranean  
626 distribution limit contradicts drought stress. *Eur. J. For. Res.*, 133, 61–71.

627 Vicente-Serrano, S.M., Beguería, S. & López-Moreno, J.I. (2010). A multiscalar drought  
628 index sensitive to global warming: The standardized precipitation evapotranspiration  
629 index. *J. Clim.*, 23, 1696–1718.

630 Vilà-Cabrera, A., Premoli, A.C. & Jump, A.S. (2019). Refining predictions of population  
631 decline at species' rear edges. *Glob. Chang. Biol.*

632 Woolbright, S.A., Whitham, T.G., Gehring, C.A., Allan, G.J. & Bailey, J.K. (2014). Climate  
633 relicts and their associated communities as natural ecology and evolution laboratories.  
634 *Trends Ecol. Evol.*, 29, 406–416.

635

## Figure legends

**Figure 1.** Conceptual representation of hypothesised persistence probability according to population-type. Tree performance in response to increased drought is lower at the limit of the species' ecological tolerance, i.e. with decreasing habitat quality (sites in drier climates and at the limit of the temperate-Mediterranean transition zone) and increasing habitat fragmentation and population isolation. Consequently, persistence probability differs among population types according to the interaction between ecological and geographical marginality. Assuming ecological marginality > geographical marginality, from lower to higher persistence probability: I-M: geographically isolated in marginal habitats (– –); CR-M: continuous range in marginal habitats (–); I-Non M: geographically isolated in non-marginal habitats (+); CR-Non M: continuous range in non-marginal habitats (+ +).

**Figure 2.** Parameter estimates and 95% CI of (a) tree resistance and (b) tree recovery as a function of population type and drought event. Parameters were estimated in a mixed-effects model where resistance (log transformed) and recovery were modelled as a function of the interaction 'drought x population type'. Plot identity was included as random effect on the intercept and drought was allowed to vary among populations in the random part of the model. I-Non M: geographically isolated in non-marginal habitats; I-M: geographically isolated in marginal habitats; CR-Non M: continuous range in non-marginal habitats; CR-M: continuous range in marginal habitats. 1: 1989-91 drought; 2: 1994 drought; 3: 1998-99 drought; 4: 2005-06 drought.

**Figure 3.** Association for each population-type between tree resistance and (a) previous growth (independent of tree size) in 1989-91-drought, (b) cumulative impact in 1994-drought, (c) previous growth (independent of tree size) in 1994-drought, (d) basal area in 1994-drought, and (e) cumulative impact in 1998-1999-drought. Solid lines represent predicted effects; grey bands denote 95% confidence intervals. The other covariates were set

to their median. Tick lines on the x-axis represent individual cases. I–Non M: geographically isolated in non-marginal habitats; I–M: geographically isolated in marginal habitats; CR–Non M: continuous range in non-marginal habitats; CR–M: continuous range in marginal habitats.

**Figure 4.** Association for each population-type between tree recovery and (a) previous growth (independent of tree size) in 1989-1991–drought, (b)  $SPEI_{\text{post drought}}$  in 1989-1991–drought, (c)  $SPEI_{\text{post drought}}$  in 2005-2006–drought, and (d) basal area in 2005-2006–drought. Solid lines represent predicted effects; grey bands denote 95% confidence intervals. The other covariates were set to their median. Tick lines on the x-axis represent individual cases. I–Non M: geographically isolated in non-marginal habitats; I–M: geographically isolated in marginal habitats; CR–Non M: continuous range in non-marginal habitats; CR–M: continuous range in marginal habitats.

**Figure 5.** Parameter estimates and 95% CI of rates of tree growth trends over the study period as a function of population-type and cumulative impact. I–Non M: geographically isolated in non-marginal habitats; I–M: geographically isolated in marginal habitats; CR–Non M: continuous range in non-marginal habitats; CR–M: continuous range in marginal habitats. L: low-level cumulative impact; M: middle-level cumulative impact; H: high-level cumulative impact.

Figure 1

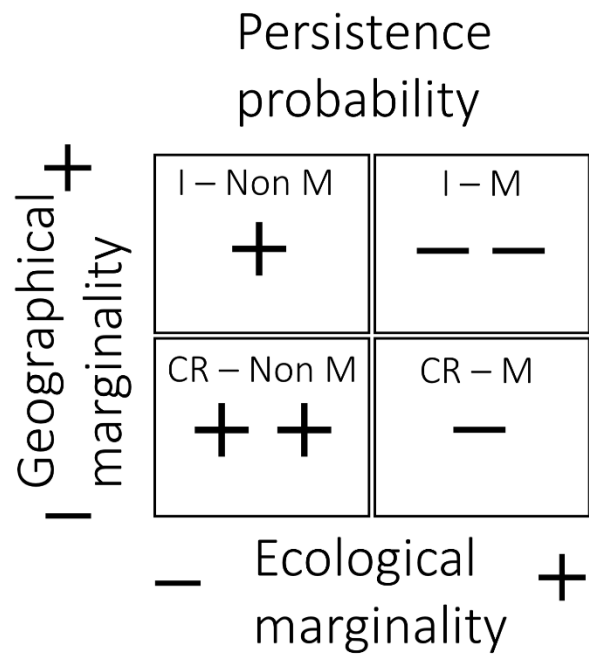
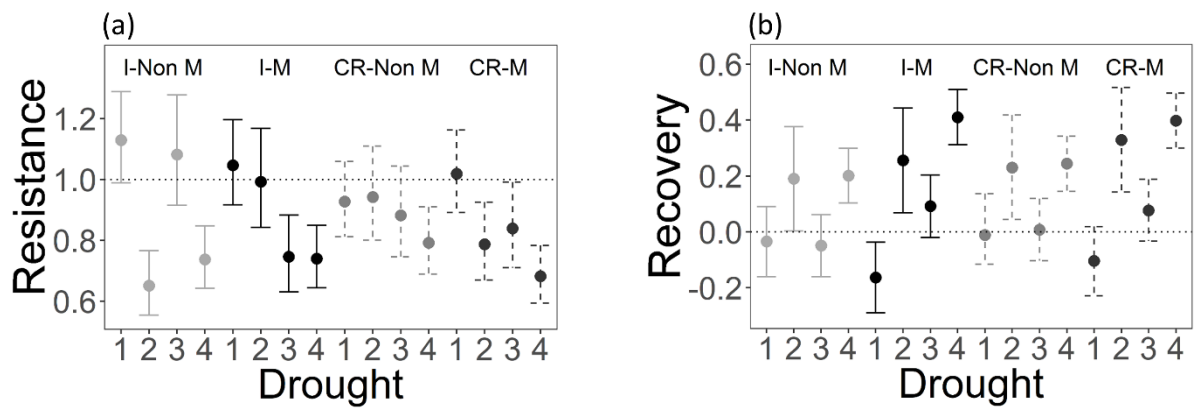
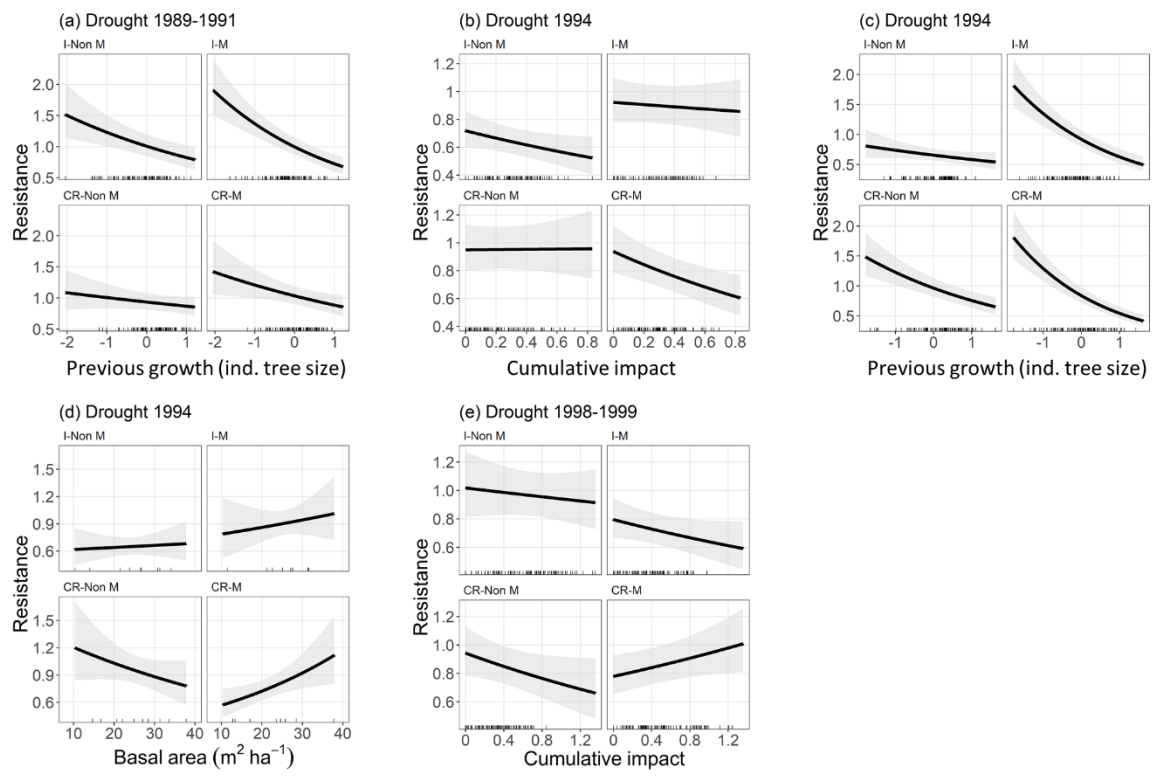


Figure 2



**Figure 3**



**Figure 4**

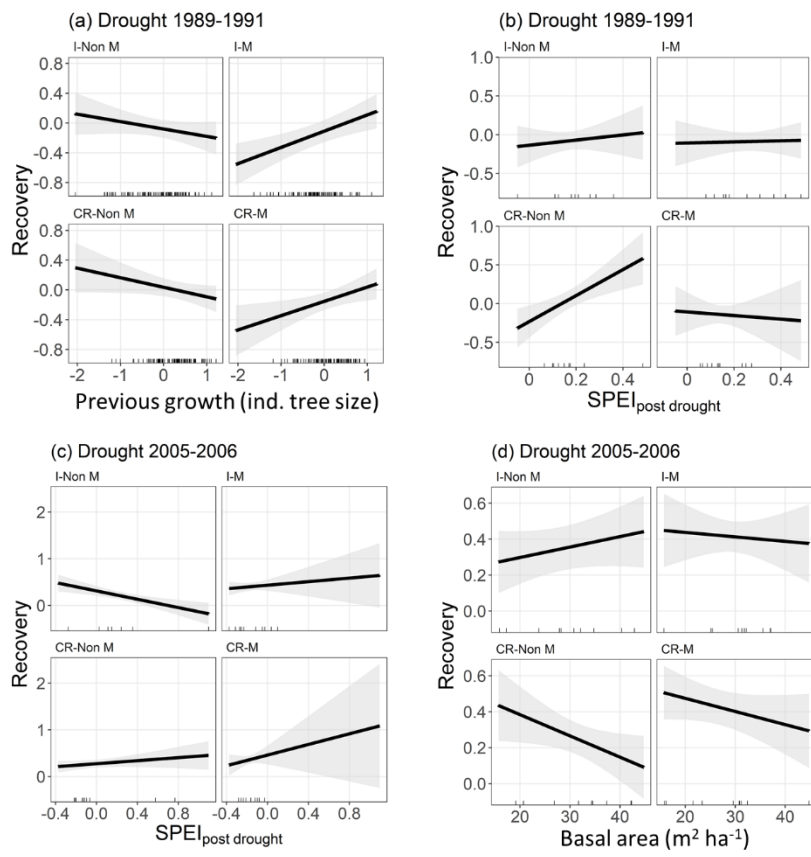




Figure 5

