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**

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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.

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INTRODUCTION

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

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

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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).

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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

Field sampling and measurements

Populations were sampled using a circular sampling plot (12.5 m radius). Within each plot,

we identified species and measured diameter at breast height (dbh) for all adult trees (dbh >=

7.5 cm). We also selected 10 trees (or < 10 individuals if N beech trees within the plot was

lower) and took two wood core samples per tree. We prepared cores and measured ring

widths for the period 1985-2015 using standard dendroecological methods (Text S1). In total,

we used 386 tree chronologies for analyses: 99 CR–M, 95 CR–Non M, 95 I–M and 97 I–Non

M. Finally, we transformed ring width series to basal area increment (BAI) series using

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

the tree for year t and the preceding one, respectively.

161

Selection of drought events

We selected drought events using the standardized precipitation and evapotranspiration index

(SPEI) (Vicente-Serrano *et al.* 2010) (Text S1). We selected four drought events: (i) 1989-

1991–drought characterised by a highest intensity at the beginning and/or end of the period,

(ii) 1994–drought characterised by extreme dry conditions during the growing season, (iii)

1998-1999–drought characterised by moderate but continuous dry conditions, and (iv) 2005-

2006–drought characterized by extreme dry conditions during two consecutive years.

169

Resilience components: resistance and recovery

Here we consider 'resistance' and 'recovery' as complementary components of resilience

(Hodgson *et al.* 2015). Resistance is defined as the individual capacity for maintaining

performance during disturbance, while recovery is defined as the individual ability for

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

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

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

197

198   where $BAI_{drought}$ is the growth during the corresponding drought (averaged across years for

199   multi-year drought periods), while $BAI_{pre\ drought}$ 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 $BAI_{drought} > BAI_{pre\ drought}$ 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_c, 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 [$SPEI_{drought}$] and

221   following drought for recovery [$SPEI_{post\ drought}$]). We included the interaction term 'covariate

222   x population-type' to assess differences in covariate effects on resistance and recovery among

9

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_c. All the best models (lowest AIC_c)

226   within two AIC_c 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 $SPEI_{post\ drought}$ 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, $SPEI_{post\ drought}$ 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

14

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

15

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

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

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

Reducing uncertainty of climate change impacts at the local scale to more accurately predict the pattern and consequence of species range shifts are key challenges for advancing our preparedness for global climate change. While we found regional-scale decline of *F. 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

490

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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) $SPEI_{post drought}$ in 1989-1991–drought, (c) $SPEI_{post drought}$ 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.
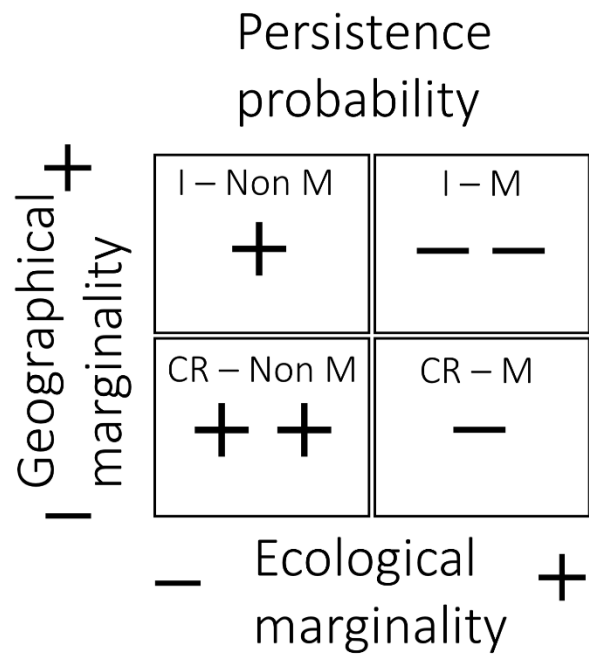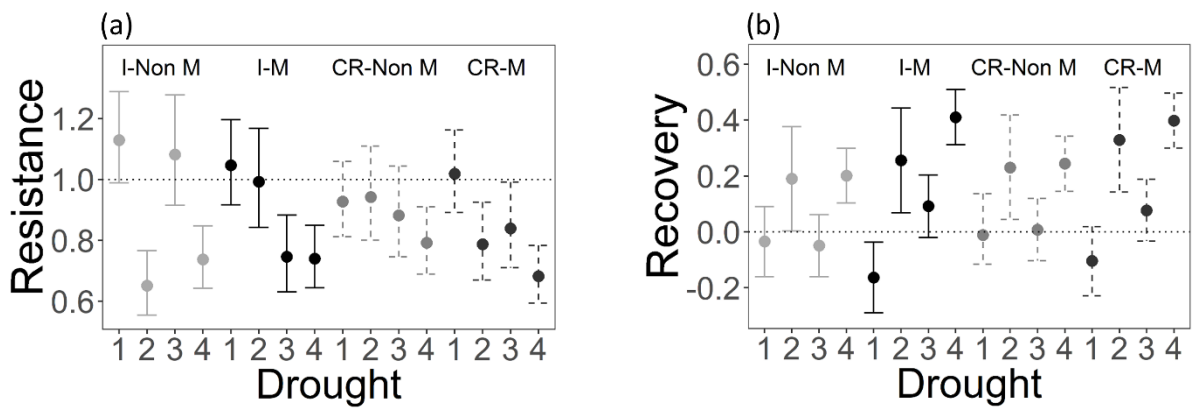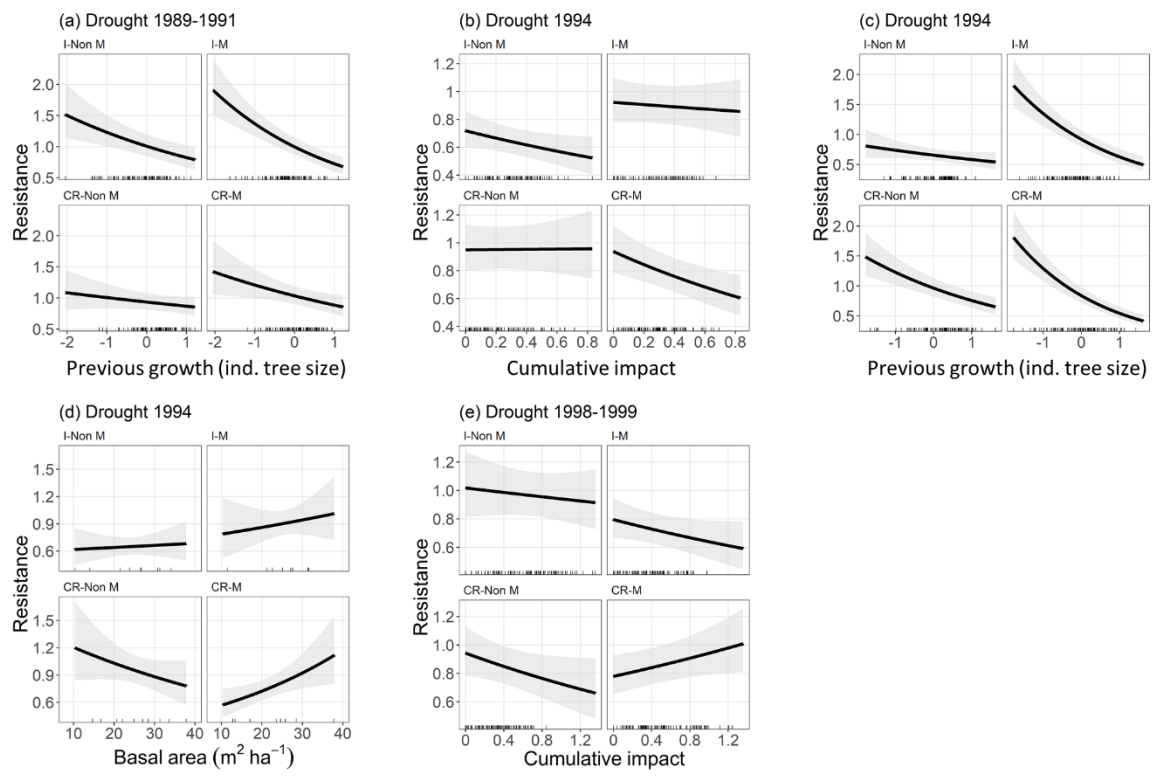
Figure 1

Persistence
probability

Geographical
marginality

	I – Non M	I – M
+	+	– –
–	CR – Non M: + +	CR – M: –

– Ecological +
marginality

Figure 2

Figure 3

Figure 4

(a) Drought 1989-1991

(b) Drought 1989-1991

(c) Drought 2005-2006

(d) Drought 2005-2006

Figure 5