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

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ABSTRACT

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

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 performance rather than consistent decline among rear edge populations is often observed (e.g. Lesica & Crone 2016; Cavin & Jump 2017; Sánchez-Salguero *et al.* 2017).

This disparity between prediction and observation can be linked to oversimplification of the concept of marginality. Climate is a strong determinant of plant distribution (Harper 1977), so we can expect that individual performance decreases with increasing ecological marginality e.g. at the driest edge of a species' range. Predictions of ecological marginality based on climate alone can be improved with biotic patterns. Rear edge populations occur along bioclimatic transition areas (Jump *et al.* 2009), where changes in the composition of communities can occur over small spatial scales, with shifts in habitat quality (Forman 1995). For example, alterations to species coexistence can reflect deteriorating habitat quality even in climatically favourable areas (e.g. middle or high elevations), such that more stress-tolerant species gain a competitive advantage (Galiano *et al.* 2010). We might expect, therefore, that individual performance also depends on the community composition, with higher ecological marginality (and thus lower individual performance) where co-occurring species have a competitive advantage (but see Granda *et al.* 2018b).

Importantly, an incomplete overlap between geographical and ecological range limits can lead to unexpected population persistence at rear edges (e.g. Tegel *et al.* 2014) highlighting that we cannot assume that ecological marginality will drive decreased individual performance with increasing geographical marginality – e.g. where spatial isolation increases at the rear edge. At the same time, however, the fragmented habitat configuration at species' rear edges increases the chance of ecological edge effects and genetic erosion (Cheptou *et al.* 2017). Consequently, we might expect lower individual performance in geographically isolated patches than in large and more continuous ones, under similar ecological conditions.

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

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

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

METHODS

Experimental design

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

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.

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.

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

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

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

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

Individual and plot-level characteristics

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

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

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

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

Data analysis

To test the hypotheses that increased marginality results in (i) lower tree growth resilience to drought and (ii) stronger effects of cumulative drought impacts on resilience, we used mixed-effects models with plot identity as random factor on the intercept. We first modelled resistance and recovery as a function of the interaction term ‘drought x population-type’ to assess resilience patterns across the successive droughts and population-types. Drought was allowed to vary among populations in the random part of the model (lower AIC_c, corrected Akaike information criterion). In a second step, and for each drought event, resistance and recovery were modelled as a function of the fixed effects population-type and its interaction with individual- and plot-level covariates, i.e. cumulative impact, dbh (log-transformed), previous growth, basal area and SPEI (during drought for resistance [$SPEI_{drought}$] and following drought for recovery [$SPEI_{post\ drought}$]). We included the interaction term ‘covariate x population-type’ to assess differences in covariate effects on resistance and recovery among population-types. Starting from the full model that included all interaction terms, we created a set of models differing in the composition of interactions but always maintaining the single fixed terms and ranked them from lowest to highest AIC_c. All the best models (lowest AIC_c) within two AIC_c units were considered equivalent in terms of fit. In case the model selection procedure yielded candidate models with similar Akaike weights, the simplest model was selected. Resistance was log-transformed and covariates were standardised.

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

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

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

RESULTS

Tree resistance

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

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

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

Tree recovery

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

Non M and CR-M) were able to recover performance after drought (Table S1b; Fig. 2b). Similarly, tree recovery was overall similar among population-types after the 1998-99 drought, meaning that trees experiencing the highest impact (especially in I-M populations) recovered performance better (Table S1b; Fig. 2b). Tree recovery after the 2005-06 drought was higher in I-M and CR-M populations (Table S1b; Fig. 2b). Note that the levels of (low) resistance were similar among population-types during this drought (Table S1a; Fig. 2a). Explained variability by fixed effects was 20% and 47% by fixed and random effects together.

Some covariate effects on tree recovery varied among population-types (Table S3; Fig. 4). Tree growth prior to disturbance had a significant positive effect on tree recovery in the 1989-91 drought across I-M and CR-M populations, i.e. higher previous growth rates were related to higher recovery (Table S3; Fig. 4a). Note that trees showing higher previous growth rates displayed the lowest resistance during this drought, and this effect was stronger across I-M population (Table S2; Fig 3a). In contrast, previous growth had a significant negative effect on tree recovery across all population-types in the 1994 and 1998-99 droughts (Table S3). We also found a significant positive effect of $SPEI_{post\ drought}$ in the 1989-91 drought across CR-Non M populations and in the 1994 drought consistently among population-types, i.e. tree recovery was lower under a more negative water balance after the drought (Table S3; Fig. 4b). In contrast, $SPEI_{post\ drought}$ had a significant negative effect on tree recovery across I-Non M populations in the 2005-06 drought (Table S3; Fig. 4c). Basal area was negatively associated with tree recovery only across CR-Non M populations in the 2005-06 drought (Table S3; Fig. 4d). Tree dbh had a significant negative effect in the 1989-91 drought, while cumulative impact was always non-significant (Table S3). Finally, explained variability by fixed effects varied between 8% and 22% among the selected models for each drought, while explained variability by fixed and random effects together varied between 32% and 48% (Table S3).

Tree growth trends

Overall, tree growth slightly declined by a mean of 1.11% per year over the study period (95% CI –1.44%, –0.79%). Among populations, the growth trend was negative in 24 plots (i.e. the upper 95% CI was below 0), while stable in 15 (i.e. 95% CI included 0) and positive in 1 plot (i.e. the lower 95% CI was above 0) (Table S4). The percentage of plots showing significant growth decline was 80% in CR-M, 70% in CR-Non M, 60% I-Non M and 40% in I-M. There was variation in growth trends among population-types and according to the cumulative impact experienced by trees during the successive droughts (Table S5; Fig. 5). Tree growth was more stable in I-M populations than other population-types, while higher decline occurred in the continuous range: –0.89% (95% CI –1.54%, –0.24%) for I-Non M, –0.76% (95% CI –1.42%, –0.11%) for I-M, –1.58% (95% CI –2.23%, –0.92%) for CR-Non M and –1.21% (95% CI –1.85%, –0.56%) for CR-M. Furthermore, the effect of cumulative impact on tree growth decline was stronger across the continuous range (CR-M and CR-Non M) and better-quality habitat (CR-Non M and I-Non M). That is, growth decline change with increasing the level of cumulative impact was steeper in these population-types, reaching mean decline rates between –1.44% and –3.36% under high cumulative impact (Table S5; Fig. 5). In contrast, tree growth trends were more stable in I-M populations when high impact occurred (Table S5; Fig. 5). Explained variability by fixed effects was 6%, while explained variability by fixed and random effects together was 76%. Model diagnoses were satisfactory and predictions unbiased (Fig. S2.6), however, predictions are conservative with slight under-prediction of extreme growth reductions (Fig. S2.6, panel *b*). When accounting for the effects of tree size (final dbh), the best model included the term ‘year x final dbh’ and model fit substantially increased (Table S6a). However, parameter estimates of the target term ‘year x population-type x cumulative impact’ were qualitatively equivalent (Table S6a). Finally, growth decline was steeper with increasing tree size (Table S6b) and consistently negative among dbh classes in the continuous range (Table S6c).

DISCUSSION

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

Other studies have attempted to document regional-scale evidence for species’ rear edge retractions. For example, Lesica & Crone (2016) found evidence for a declining trend for rear edge populations of arctic and boreal plant species in the Rocky Mountains. However, half of the studied populations remained stable or increased in abundance over the study period. Many other study-cases report mixed evidence for rear edge population decline (e.g. Pulido *et al.* 2008; Galiano *et al.* 2010; Craven *et al.* 2013; Matías & Jump 2015; Kolb *et al.* 2016; Granda *et al.* 2018; Rumpf *et al.* 2018; Stojnić *et al.* 2018). This variation in population response agrees with the results reported here. However, our study suggests that variability in individual performance is predictable across the rear edge with a strong dependence on marginality type, itself a measurable characteristic that should not simply be assumed based on population location. To our knowledge, this work is the first study from field observations that explicitly accounts for the complexity of marginality and evidences why range shifts are heralded by declining regional population density, rather than occurring abruptly.

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

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

Small-scale environmental variation due to topography, edaphic factors, vegetation structure and hydrologic processes may result in high-quality habitat within marginal regional environments, where populations have higher persistence probability despite chronic regional drought that exceeding their climatic tolerance limits (Lenoir *et al.* 2017; McLaughlin *et al.* 2017). For example, the tree *Prunus lusitanica* occurs mainly in Macaronesian mountain cloud forests under subtropical conditions, but rear edge populations persist in riparian habitats under a Mediterranean climate in the Iberian peninsula (Pulido *et al.* 2008). Although differential patterns in topographic characteristics among population-types were not evident (Fig. S4), the occurrence of microrefugia is suggested by some subtle differences observed in some topographical factors (e.g. more northern and flatter, more sheltered terrain but lower elevations across I-M populations; Table S7). Within-species variation in hydraulic traits may also contribute to the observed patterns in growth responses. At the continental scale, rear edge populations of the European beech tree show higher resistance to xylem embolism than those occurring in the species range-core (Stojnić *et al.* 2018). Some evidence shows, however, that vulnerability to embolism does not vary with climate across beech populations in the study area, but other hydraulic traits do (Rosas *et al.* 2019) and these might contribute to explain differential growth responses among population-types. Phenotypic variation over small (regional) spatial scales can occur partially as a result of selection of genotypes adapted to resource limitation, thereby contributing to greater than expected individual performance in marginal habitats. For example, experimental work with ponderosa pine (*Pinus ponderosa*) in northern Arizona shows higher biomass allocation to roots while greater survival capacity to extreme drought of seedlings coming from populations inhabiting low-elevation, drier habitats (Kolb *et al.* 2016). In contrast, decreased tree growth stability across better-quality habitats may result from lack of adaptation (or plasticity) and long-term exposure to climatic suitability and thus greater demand of water resources that are not available during drought (Jump *et al.* 2017).

Our results provide evidence of the potential long-term persistence of “relict” populations at the rear edge, resulting from the interaction between environmental microrefugia and adaptation to marginal habitats (Hampe & Petit 2005; Hampe & Jump 2011). Our findings also support a dependence of population decline on individual- and stand-level characteristics in interaction with population-type. For example, although growth rates were lower in marginal habitats we found that slow-growing trees in these habitats showed similar or higher resilience than comparable slow-growing trees in better-quality habitats or the continuous range. However, high-growth rates prior to drought were associated with lower resilience, especially across marginal habitats (Table S2 and S3; Fig. 3a and 3c; Fig. 4c). One possible explanation for this finding is a structural maladaptation to increased disturbance of fast-growing individuals. Higher drought susceptibility of fast-growing trees can be interpreted as 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 populations in marginal habitats. Furthermore, across the continuous range and better-quality habitats growth stability was lower than anticipated. Our findings indicate a patchy, but predictable pattern of population loss and persistence in response to increased climate change-type drought. Understanding the impacts of changing frequency or magnitude of extreme events on tree growth remains a key challenge in part due to the difficulty of their prediction (Jentsch *et al.* 2007) (Fig S2.6). However, the approach demonstrated here can guide future research to better incorporate population-level ecology at broader spatial scales and demonstrates that we should be highly cautious about simply assuming marginality and thereby population decline as a constant property of a species' rear edge.

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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) $\mathrm{SPEI}_{\mathrm{post\ drought}}$ in 1989-1991–drought, (c) $\mathrm{SPEI}_{\mathrm{post\ drought}}$ 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

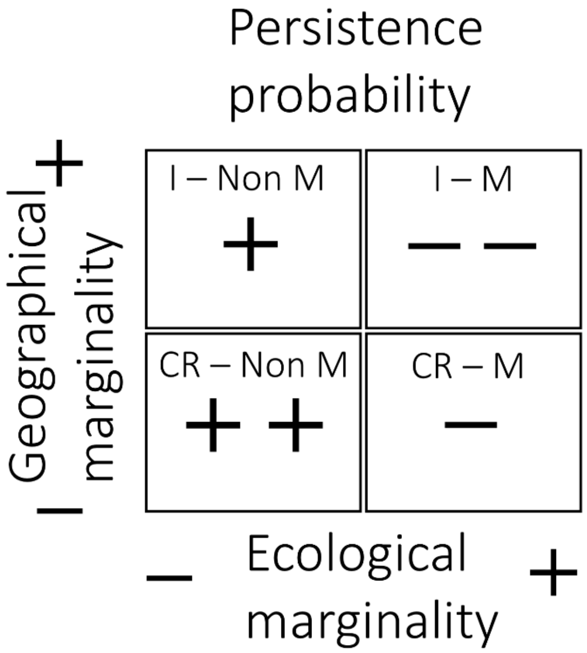

Persistence probability
I – Non M
+
I – M
– –
CR – Non M
+ +
CR – M
–
Geographical marginality
+
–
Ecological marginality
–
+

Figure 2

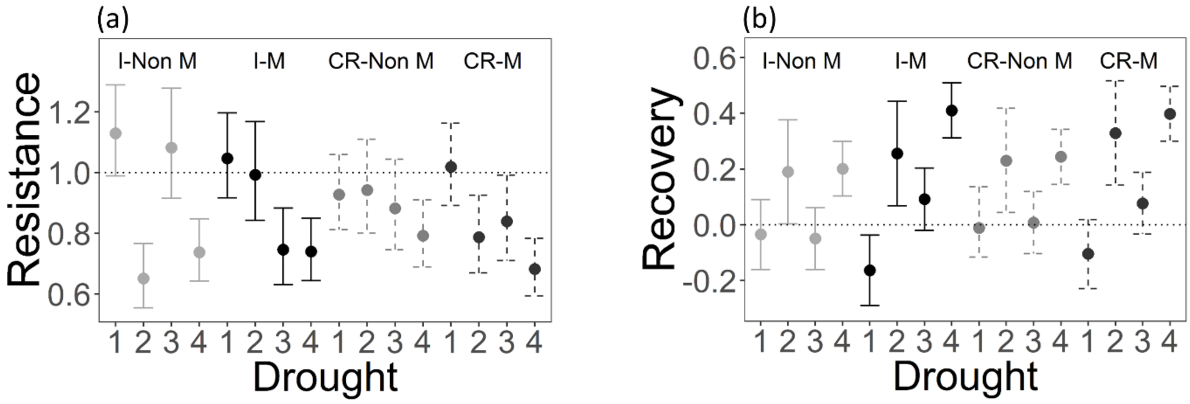

(a)
I-Non M
I-M
CR-Non M
CR-M
Resistance
1.2
1.0
0.8
0.6
1 2 3 4 1 2 3 4 1 2 3 4 1 2 3 4
Drought
(b)
I-Non M
I-M
CR-Non M
CR-M
Recovery
0.6
0.4
0.2
0.0
-0.2
1 2 3 4 1 2 3 4 1 2 3 4 1 2 3 4
Drought

Figure 3

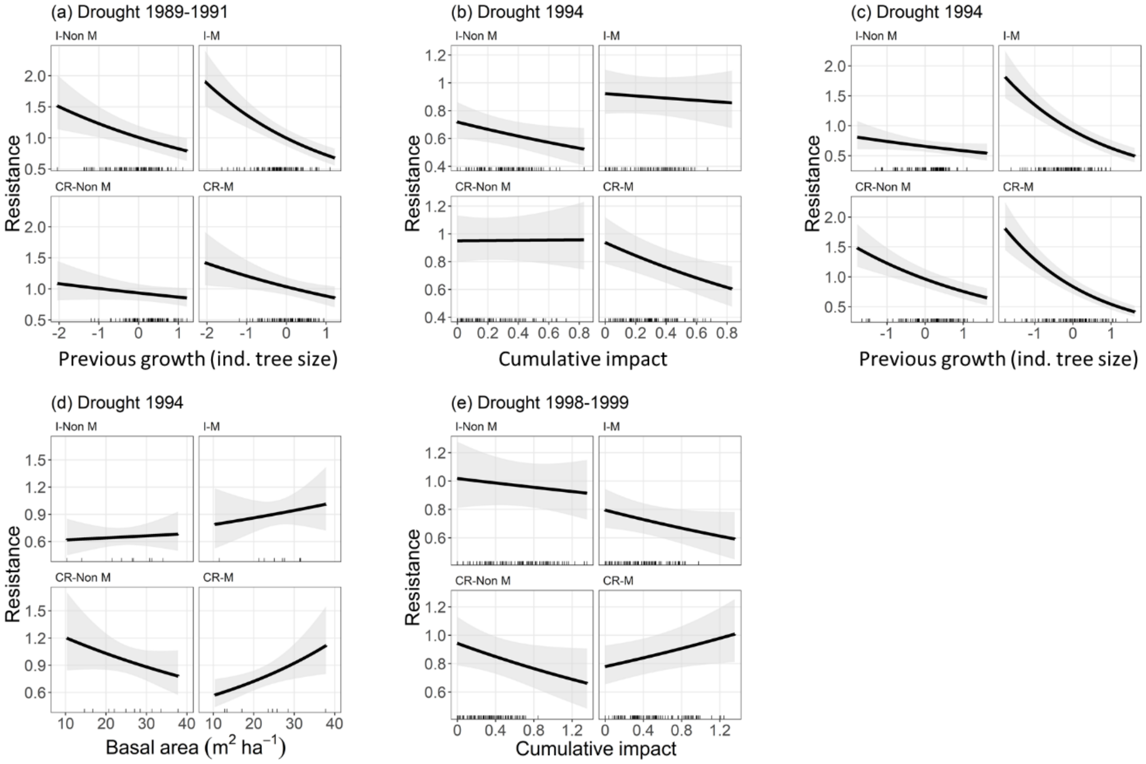

(a) Drought 1989-1991
I-Non M
I-M
CR-Non M
CR-M
Resistance
0.5
1.0
1.5
2.0
-2
-1
0
1
Previous growth (ind. tree size)
(b) Drought 1994
0.4
0.6
0.8
1
1.2
0
0.2
0.4
0.6
0.8
Cumulative impact
(c) Drought 1994
-1
0
1
Previous growth (ind. tree size)
(d) Drought 1994
0.6
0.9
1.2
1.5
10
20
30
40
Basal area (m² ha⁻¹)
(e) Drought 1998-1999
0
0.4
0.8
1.2
Cumulative impact

Figure 4

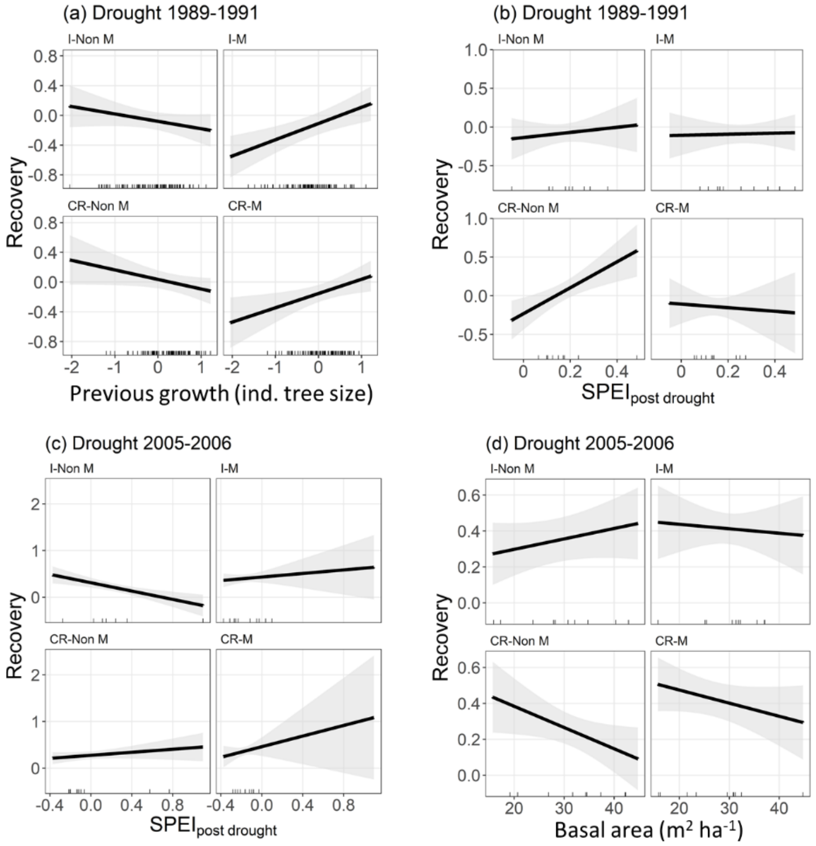
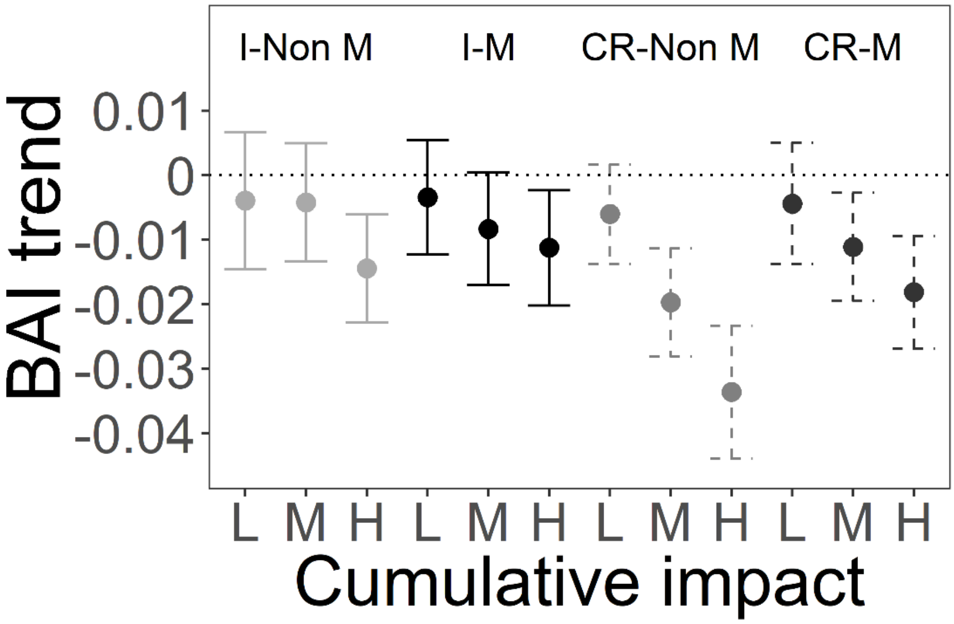

(a) Drought 1989-1991
(b) Drought 1989-1991
(c) Drought 2005-2006
(d) Drought 2005-2006
I-Non M
I-M
CR-Non M
CR-M
Recovery
Previous growth (ind. tree size)
$SPEI_{post\ drought}$
Basal area ($m^2\ ha^{-1}$)
0.8
0.4
0.0
-0.4
-0.8
-2
-1
0
1
1.0
0.5
0.0
-0.5
0.2
0.4
2
1
0
-0.4
0.0
0.4
0.8
0.6
0.4
0.2
0.0
20
30
40

Figure 5


I-Non M
I-M
CR-Non M
CR-M
BAI trend
0.01
0
-0.01
-0.02
-0.03
-0.04
L
M
H
L
M
H
L
M
H
L
M
H
Cumulative impact