Components of tree resilience: effects of successive low-growth episodes in old ponderosa pine forests

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Recent world-wide episodes of tree dieback have been attributed to increasing temperatures and associated drought. Because these events are likely to become more common, improved knowledge of their cumulative effects on resilience and the ability to recover pre-disturbance conditions is important for forest management. Here we propose several indices to examine components of individual tree resilience based on tree ring growth: resistance (inverse of growth reduction during the episode), recovery (growth increase relative to the minimum growth during the episode), resilience (capacity to reach pre-episode growth levels) and relative resilience (resilience weighted by the damage incurred during the episode).

Based on tree ring analyses, we analyzed historical patterns of tree resilience to successive drought-induced low growth periods in ponderosa pine trees growing in unmanaged, remote forests of the Rocky Mountains. Low-growth periods registered in tree rings were related to anomalies in the Palmer drought severity index (PDSI) and were attributed to drought.

Independently of the impact of a specific event, subsequent growth after a single low-growth episode was related to the growth prior to the event. Growth performance differed with tree age: young trees were overall more resistant to low-growth periods, but older trees recovered better from more recent events. Regardless of tree age, recently burned sites exhibited lower post-episode growth and lower resistance and resilience than unburned ones. We found mixed evidence for the cumulative effect of past low-growth episodes: overall, greater impacts of a prior event and greater cumulative effects of past low-growth periods caused a decrease in resistance. However, we did not find a progressive decrease in resilience over time in old trees.

Our results highlight the value of using a combination of estimators to evaluate the different components of resilience. Specifically, while tree responses to disturbance depend on past disturbance episodes, the response is context-specific and depends on the impact the capacity to recover after disturbance. This suggests that recent increases in forest mortality under current climate trends could relate to thresholds on specific components of resilience (resistance, recovery, resilience itself) rather than to an overall loss of resilience over time. Identifying such thresholds and their underlying mechanisms is a promising area of research with important implications for forest management.

Current climate models predict greater climatic variability with increases in the frequency and intensity of extreme episodes such as drought, heavy rains and extreme warm or cold events (IPCC 2007). Higher frequency and/or greater intensity of stressful episodes may push ecosystems to biological thresholds beyond which uncharacteristic responses and ecosystem shifts may occur (Scheffer et al. 2001, Folke et al. 2004). The cumulative effects of recurrent stressful episodes can be assessed by analyzing changes in resilience. Resilience is broadly defined as the capacity of an ecosystem, community or individual to recover after disturbance and regain its pre-disturbance structure and function (Scheffer et al. 2001, Folke et al. 2004). Post-disturbance responses are expected to depend on several factors, including the frequency and intensity of past disturbances (Sousa 1984, Runkle 1985), which in turn affect the abiotic environment and the life cycles and physiological performance of organisms (Zedler et al. 1983).

Analysis of resilience generally involves quantitative estimations based on comparisons between pre- and post-disturbance states (Herbert et al. 1999, Orwin and Wardle 2004, DeClerk et al. 2006), or on the degree to which the values of indicator variables in the disturbed systems approach those of undisturbed control systems (Griffiths et al. 2000, Wardle et al. 2000, Lindberg and Bengtsson 2006, Bee et al. 2007). A potential problem with these estimates, however, is that they usually do not account for the impact inflicted by the disturbance (but see DeClerck et al. 2006), which could underestimate resilience in heavily affected systems. Furthermore, at the individual level, recovery after disturbance is likely a combined response to stochastic extrinsic factors (e.g. competition and mortality of neighbours), and to intrinsic (e.g. physiological and genetic) and microsite factors. For instance, intrinsic factors such as individual age or size, may affect resilience by causing either positive (Lloret et al. 2004) or negative (Mueller et al. 2005, Kolb et al. 2007) responses. If intrinsic or microsite factors dominate, individual performance after the disturbance should positively correlate with that prior to the disturbance.

The recent worldwide increase of drought-related die-back and forest mortality (Allen et al. 2010), which has been attributed to increasing temperatures and associated drought (van Mantgem et al. 2009), may reflect such uncharacteristic responses. Although accumulating evidence suggests that drought events may cause significant ecophysiological memory effects (Peñuelas et al. 2000, Galiano et al. 2011) and delayed tree mortality (Bigler et al 2006, 2007, McDowell et al. 2010, Galiano et al. 2011), our knowledge of the extent to which uncharacteristic forest responses are related to the cumulative effects of recurrent drought events remains limited (but see Lloret et al. 2004, Bigler et al. 2007). In particular, the effect of recurrent stressful episodes at the individual level is poorly documented.

In forests, extreme low-growth periods act as disturbances, due to their episodic nature and potential to induce severe changes in forest structure. Although at the community level resilience after single low-growth periods has been related to diversity (DeClerk et al. 2006) and resource availability (MacGillivray et al. 1995), the effect of recurrent low-growth episodes on resilience at the individual level is poorly documented. A greater frequency of disturbances is expected to reduce the resilience of trees, accelerating environmental change and depleting individual reserves needed to withstand and overcome periods of stress. This prediction is consistent with empirical observations showing slow forest-canopy recovery (Díaz-Delgado et al. 2002) or changes in community structure (Zedler et al. 1983) after increases in fire frequency, and negative responses to the combined effect of successive disturbances of different nature (Payette and Delwaide 2003).

In old trees that established well before the Industrial revolution, tree rings provide a useful record of performance to natural climate variability and disturbance regimes prior to the current conditions of climate change. Severe drought periods often result in canopy defoliation (Lloret et al. 2004, Breda et al. 2006) and subsequent reductions of tree ring growth (Millar et al. 2007). Depending on the impact of drought, subsequent rain events may allow canopy greenness and carbon assimilation to recover, with a corresponding increase in growth and tree ring width. In terms of disturbance theory, this post-drought recovery is a measure of individual-level resilience. Here we use tree rings in old trees as indicators of historical patterns of tree resilience to recurrent stressful periods and to changes in disturbance regimes. To gain insight into the possible mechanisms underlying patterns of resilience, we decompose resilience into several components: resistance (inverse of growth reduction during the episode), recovery (increased growth relative to the minimum growth during the episode), resilience per se (capacity to reach pre-episode growth levels) and relative resilience (resilience weighted by the damage incurred during the episode).

Pure and mixed ponderosa pine *Pinus ponderosa* forests dominate much of the low to mid-elevation mountain forests of western North America, where frequent, low intensity and mixed severity fires regimes were common prior to European settlement (Schoennagel et al. 2004). Active suppression of fires during the twentieth century, however, has significantly reduced fire frequency in much of their range (Arno 1980) and has caused significant increases of density, and changes in community structure and ecosystem function (Keeling et al. 2006, DeLuca and Sala 2006). As a consequence, lack

of fires in these systems is thought to increase competition for resources and alter growth responses of individual trees (Feeney et al. 1998, Stone et al. 1999, Sala et al. 2005; but see Keeling et al. in press), all of which may increase the susceptibility to drought-induced mortality. Indeed, drought-induced mortality in ponderosa pine has recently been documented and has been attributed to increased sensitivity to climate variability and chronic drought (McDowell et al. 2010). However, the extent to which cumulative effects of drought, alteration of fire regimes, and tree age influence tree resilience is not well documented. Such knowledge is critical in the current context of global change, when management practices for ecosystem resilience are imperative. Although old-growth ponderosa pine forests (established prior to Euro-American settlement) are now rare due to historical selective harvesting of valuable old trees (Kolb et al. 2007), remnant stands still exist in remote, unlogged areas, where they provide a unique opportunity to examine resilience to stressful periods both before and after the Industrial revolution.

In this study we use several indices to assess different components of resilience, in relation to the previous history of recurrent stressful episodes, by investigating tree growth performance before and after low-growth periods. We used ring widths to analyze historical patterns of tree resilience to successive low-growth periods over a multi-century time scale in old (>300 years) and young (<200 years) ponderosa pine trees in unmanaged, remote forests in the Rocky Mountains. We predicted that low growth periods are mostly attributable to drought episodes, although interactive, negative effects of surface fires – which tend to occur during dry periods – may also occur. Specifically, we addressed the following questions:

1) is the growth of individual trees after a low-growth episode correlated with the levels present prior to the episode? If so, response to disturbance is dominated by intrinsic and/or microsite factors, but not by disturbance or density-dependent factors (for example, mortality of neighbouring trees);
2) do old trees exhibit lower resilience than younger trees? If age-related constraints compromise the ability of old trees to recover from drought episodes, we expect lower resilience in old trees;
3) is resilience to low-growth episodes influenced by the disruption of recent fire regimes? Specifically, do old-growth trees in stands unburned for most of the twentieth century exhibit lower resilience than trees in stands that continued to experience fire?
4) does the cumulative effect of previous low-growth periods influence resilience to low-growth episodes? A negative correlation between resilience and the cumulative effects of prior events would indicate a memory effect.

Methods

Resilience components

Resilience is often estimated by analyzing the impact of disturbance on ecological properties. However, there is no

standard measure, and comparisons between disturbed and undisturbed systems made using various procedures (Sousa 1980, Kaufman 1982, MacGillvray et al 1995, Griffiths et al. 2000, Wardle et al. 2000, Orwin and Wardle 2004). Although at the individual-level tree rings provide a useful tool to analyze patterns of resilience, this approach has seldom been used (but see DeClerck et al. 2006). Here, we use a set of indices based on changes in tree ring width to estimate several inter-related but complementary, components of resilience. Our indices are conceptually equivalent to some of those used by Pimm (1991) to describe the stability of the trophic structure of communities. The use of several indices to capture different aspects of resilience, allows for a more comprehensive insight than the use of single estimators.

Resistance is considered as reversal of the reduction in ecological performance during disturbance, and it is estimated as the ratio between the performance during and before the disturbance (Kaufman 1982, MacGillvray et al. 1995). In our case it corresponds to the ratio between the growth during the drought (low-growth period) and the growth during the respective pre-drought period (Fig. 1).

Recovery is the ability to recover relative to the damage experienced during disturbance, and it is estimated as the ratio between performance after and during disturbance. In our case it corresponds to the ratio between the post-drought growth and the growth during the respective drought period. This index is positive, with values < 1 indicating a decline in growth after the episode. Note that this index cannot be calculated when the system collapses during disturbance (in our case, when growth is zero during the episode).

Resilience is the capacity to reach pre-disturbance performance levels, and is estimated as the ratio between the performance after and before disturbance (Sousa 1980, Tilman

and Downing 1994). In our case it corresponds to the ratio between post-drought growth and pre-drought growth.

Relative resilience is the resilience weighted by the damage experienced during disturbance, and it is estimated as follows:

$$Relative\ resilience = ((PostDr - Dr)/(PreDr - Dr))$$
$$(1 - (Dr/PreDr))$$
$$= (PostDr - Dr)/PreDr$$

where *PreDr*, *Dr* and *PostDr* indicate performance before, during and after disturbance, respectively.

The rationale for this index is that the ability to achieve the levels of pre-disturbance performance depends on the impact (in our case reduction of growth) during the disturbance. The interpretation of this relationship at the individual level is not unequivocal, however, because high values could reflect either higher buffer capacity to recover (e.g. stored reserves in trees) or compensating positive effects of the impact via increased neighbour mortality and resource availability to surviving trees. Values lower than 1 indicates that the effect of the event persists after disturbance, with lower values indicating decreasing resilience. High resistance to the disturbance (low levels of damage) reduce the relative resilience, while low resistance increases it. Relative resilience may have negative values if post-disturbance performance is lower than performance during the disturbance event.

These resilience indices refer to times relative to when the disturbance occurs. Ecological performance before, during and after disturbance can be calculated as the average or trend during a fixed period of time (in our case, five years). Thus, recovery and resilience refer to a specific time after the end of the disturbance (in our case, the year after the end of the low-growth episode).

These indices of resilience are simple and intuitively related. Resilience is directly related to both resistance and recovery, while resistance has a decreasing effect on relative resilience. Accordingly, if average pre-disturbance ecological performance is standardized as 1, then

$$Resilience = Resistance \times Recovery$$
$$Relative\ resilience = Resilience - Resistance$$

Study area and sites

The study took place in two remote, unlogged, mid-elevation ponderosa pine/Douglas-fir forests in the periphery of the Frank Church River of No Return wilderness of the northern Rocky Mountains (Idaho, USA; DeLuca and Sala 2005, Keeling et al. 2006). Two sites about 40 km apart from each other were chosen: McKay Bar (MB) at elevations of 1535 to 1815 m, and Bullion Ridge (BR) at elevations of 1465 to 1665 m. Control stands had not experienced fire for at least 70 years. During the same time period, burned stands experienced one, two or four wildfires (depending on the site) at intervals ranging from 6–58 years (mean = 34 years) with the most recent fire between 12–17 years before sampling. At each site, sampling took place on a stand that had not experienced fire for at least 70 years ('unburned') and on a nearby stand that experienced

Growth (BAI)

$Rt_a > Rt_b$
$Rc_a < Rc_b$
$Rs_a > Rs_b$
$RRs_a < RRs_b$

Resistance Rt = Dr/PreDr
Recovery Rc = PostDr/Dr
Resilience Rs = PostDr/PreDr
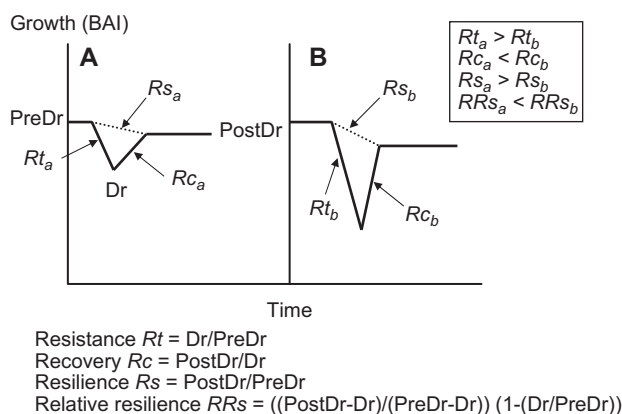Relative resilience RRs = ((PostDr-Dr)/(PreDr-Dr)) (1-(Dr/PreDr))

Figure 1. Resilience indexes in two hypothetical cases: (A) tree with low drought decrease (high resistance) achieving post-drought growth similar to pre-drought growth (high resilience) and (B) tree suffering strong impact but with a fast post-drought growth (high recovery) resulting in high relative resilience. Note that resistance, recovery and resilience correspond with the slopes indicated by the respective arrows (resilience as dashed line); resistance and resilience have a negative slope, so the lower the gradient, the greater the resistance and resilience.

two fires during the last 70 years ('burned'). There was one recorded early 20th century fire at each site that affected both burned and unburned stands (1914 at Mackay Bar, and 1919 at BR). The burned stands of each site experienced two additional fires, 1960 and 1987 at MacKay Bar (MB3), and in 1944 and 1992 at Bullion Ridge (BR3). Fire histories in the twentieth century for all stands were based on US Forest Service fire maps, field reconnaissance, and on-site fire scar analyses (see DeLuca and Sala 2005 and Keeling et al. 2006, 2010 for more detailed methods). Stand density (trees ha^{-1}) was 567 and 183 in the unburned (BR1) and burned (BR3) stands of the BR site, respectively, and 325 and 267 in the unburned (MB1) and burned (MB3) stands of the MB site, respectively. Annual average precipitation for the period 1903–2001 at the nearest weather station (New Meadows, ID) is 581 mm, with average July temperatures of 17.1°C and average December temperatures of –6.0°C.

Individual selection and sampling procedure

Sampling took place in 2004, 2006 and 2007. At least 10 large (>300 years old), canopy-dominant trees of varying diameters and 10 smaller (<200 years old) size ponderosa pine trees were sampled. Trees with fire-scars, rot or insect damage, and trees growing directly adjacent to neighbor trees, were not sampled. For each tree, elevation, aspect, slope, GPS coordinates, and tree diameter at breast height (DBH) were recorded.

Increment borers were used to extract two cores from each tree perpendicular to the direction of the slope at ca 50 cm height. Coring height and diameter was recorded for each tree.

Sample preparation and cross-dating

The two cores from each tree were visually cross-dated, both against each other and against a time-series of reconstructed Palmer drought severity index (< www.ncdc.noaa.gov/paleo/drought/drght_pdsi.html >) for the region. Relatively narrow and wide rings, rings with notable latewood, suspected false or missing rings and years of growth suppression or release, were recorded and used as an aid in the cross-dating of all cores. Rings from all cores were then measured to an accuracy of 0.001 mm using a Velmex measuring station. We used the program COFECHA to verify the dating accuracy and help determine missing and false rings, which were then checked and corrected on the cores (Holmes 1983). Minimum tree age was estimated based on the date of the inner-most ring, after correcting for pith and tree rings to coring height based on ring counts versus height in nearby saplings. The number of trees selected per site for the final analysis are: 9, 21, 8 and 17 old trees (established before 1765 AD) and 17, 23, 11 and 33 young trees (established after 1810 AD), corresponding to the MB1, MB3, BR1 and BR3 sites, respectively.

Calculation of basal area increments (BAI)

Annual radial growth increments were calculated using the proportional method described by Bakker (2005). Based on these basal areas, increments were calculated and averaged for the two cores from each tree.

Selection of the study periods

Based on the averages of the annual basal area increments in all trees, we selected periods with abnormally low growth values when average BAI ≥25% lower than the average of the five previous years (Fig. 2). To ensure that these periods were congruent with regional patterns, and that they were not caused by local drivers such as pest outbreaks, we compared these increments with the information from the reconstructed summer Palmer drought severity index (PDSI) for the area (grid point 69, Cook et al. 1999, <www.ncdc.noaa.gov/paleo/pdsi.html>). Only low growth periods coinciding with PDSI values < –2.5 were selected. In some cases, we selected longer periods than the respective low-value PDSI period because of the existence of consecutive years of low average BAI values. We validated our assumption that low-growth years corresponded with drought events by correlating the reconstructed and instrumentally derived PDSI during the 20th century (years 1900 to 2003; $R = 0.83$, p < 0.001, n = 104). Furthermore, the reconstructed PDSI and average BAI for the 20th century and the whole study period were significantly correlated (partial $R = 0.50$, p < 0.001, n = 104; partial $R = 0.46$, p < 0.001, n = 300, respectively, after multiple regression, including PDSI and year as independent factors and BAI as dependent variable).

Selected low growth periods were: 1756–1757, 1783, 1797–1798, 1846–1849, 1889–1890, 1935–1937 and 1988–1992. Hereafter, we refer to each of these according to the first year: 1756, 1783, 1797, 1846, 1889, 1935 and 1988, respectively. Because fire was a common climate-driven disturbance in these forests (Heyerdahl et al. 2008b), trees during selected low growth periods are likely to have also experienced surface wildfires in addition to drought. For instance, we know that fires occurred at MB in 1782, 1846, 1889 and 1987 (the latter only at MB3; Heyerdahl et al. 2008b). Therefore in some cases low growth periods result from the interaction of drought and surface fire.

We averaged BAI values for the low growth periods (Dr) and for the five years before (PreDr) and after (PostDr). We did not consider a period longer than five years to avoid any overlaps with other low-growth periods. Although environmental factors (i.e. climate) were certainly not identical before and after the episode, we assume that on average this difference is similar for the whole set of trees.

Data analysis

Our first hypothesis was tested by correlating the growth prior to the drought event and that after the growth event. With respect to our second hypothesis, the effect of age in the 20th century on the response to drought episodes was analyzed for the two low-growth events during the twentieth century (1935 and
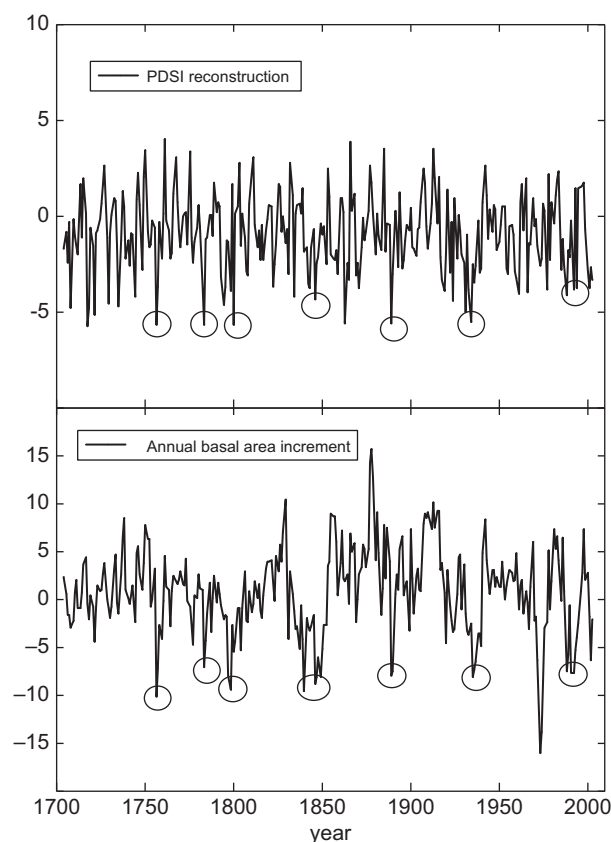
Figure 2. Annual basal area increment (BAI) of old trees and PDSI reconstruction over time (pooled data from the four localities). Data were standardized to the temporal trend by using the residuals of the lineal functions that fit annual BAI and PDSI to year, respectively. Circles indicate the considered low-growth periods.

1988), where we had records from both young trees (established after 1810 AD) and old trees (established before 1765 AD). For our third hypothesis, effects of recent fire history were tested for the 1988 event when fire occurrence during the 20th century differed between stands. To test the second and third hypotheses, we performed general linear models where the dependent variables were growth (log-transformed to meet normality), resistance (log-transformed in the 1935 data), recovery (log-transformed in the 1988 data), resilience (log-transformed in all periods), and relative resilience (log-transformed in the 1935 data). The explanatory factors were age (young and old trees), site (MB and BR) (random factor), fire occurrence (unburned stands –MB1 and BR1- and burned stands –MB3 and BR3-) and the interaction between age and fire occurrence.

For our fourth hypothesis, the effect of past growth performance on the response after a given drought episode was analyzed by general linear models performed for all drought events, except for the first one (dated in 1756). The dependent variables were growth, resistance, recovery, resilience and relative resilience. We performed separated general linear models for each of three estimators of past performance: impact of the previous event, cumulative impact of successive events since 1756 (excluding the considered year) and resilience after the respective previous drought period. The impact of the episodes was estimated as:

$$\text{Impact} = (PreDr - Dr)/PreDr$$

In these analyses we also included growth before the episode and site (random factor) as factors. Data were log-transformed when necessary to meet normality requirements (Table 2). We excluded site MB1 from the analyses of the 1846 and 1988 episodes due to missing rings during the entire drought episode in several trees. We also excluded from the analyses of relative resilience some trees (n = 19) in which the growth during the event was unexpectedly greater than in the previous period, resulting in negative values of this index. The changes in the variables describing the response to drought episodes over time were explored using repeated measures ANOVAs and post hoc Fisher LSD tests to examine differences between events. Independent variables were time and site (random factor) and dependent variables (log-transformed) were growth, resistance, recovery, resilience and relative resilience. As above, we excluded MB1 from the analyses (i.e. the repeated measures ANOVAs only considered the remaining three localities).

Results

Growth after single low-growth episodes was positively correlated to the growth prior to the episode (Fig. 3). In addition, models that analyzed the effect of past growth performance (previous impact, cumulative impact and previous resilience) on growth after a given episode also revealed that growth prior to the episode significantly (p < 0.001) explained growth after a given episode. However, growth prior to an episode very rarely influenced resilience and, in general, the correlation of growth after and prior to the episode was independent of the impact (inverse of resistance) experienced during the episode.

Declines in growth during drought episodes in the 20th century were lower in young trees (higher resistance) than in old trees (Table 1, Fig. 4); recovery after the episode in young trees was not different than recovery in old trees in 1935, but was significantly lower in 1988. As a result, young trees were more resilient than old trees in 1935. However, the ranking between old and young trees for relative resilience, which accounts for the impact of the episode, reversed between the two dates: old trees showed lower values than young trees in 1935 (due to their lower resistance), but higher values in 1988, because of their greater ability to recover after that particular event.

Differences in fire occurrence influenced the post-episode growth and the different estimators of response to drought in 1988: burned sites exhibited lower post-episode growth and lower resistance and resilience than unburned ones (Table 1b). The interaction between age class and fire occurrence was not significant, indicating similar effects of changes in fire occurrence on both old and young trees.

In general, there were no statistically significant differences between the sites, except for post-drought growth (Table 1a).

We found mixed results for the impact of previous events on performance after a low-growth event (growth after the event, resistance, recovery and resilience models; Table 2). In almost all events (except in 1783), resistance was negatively correlated with cumulative impacts, while recovery was positively
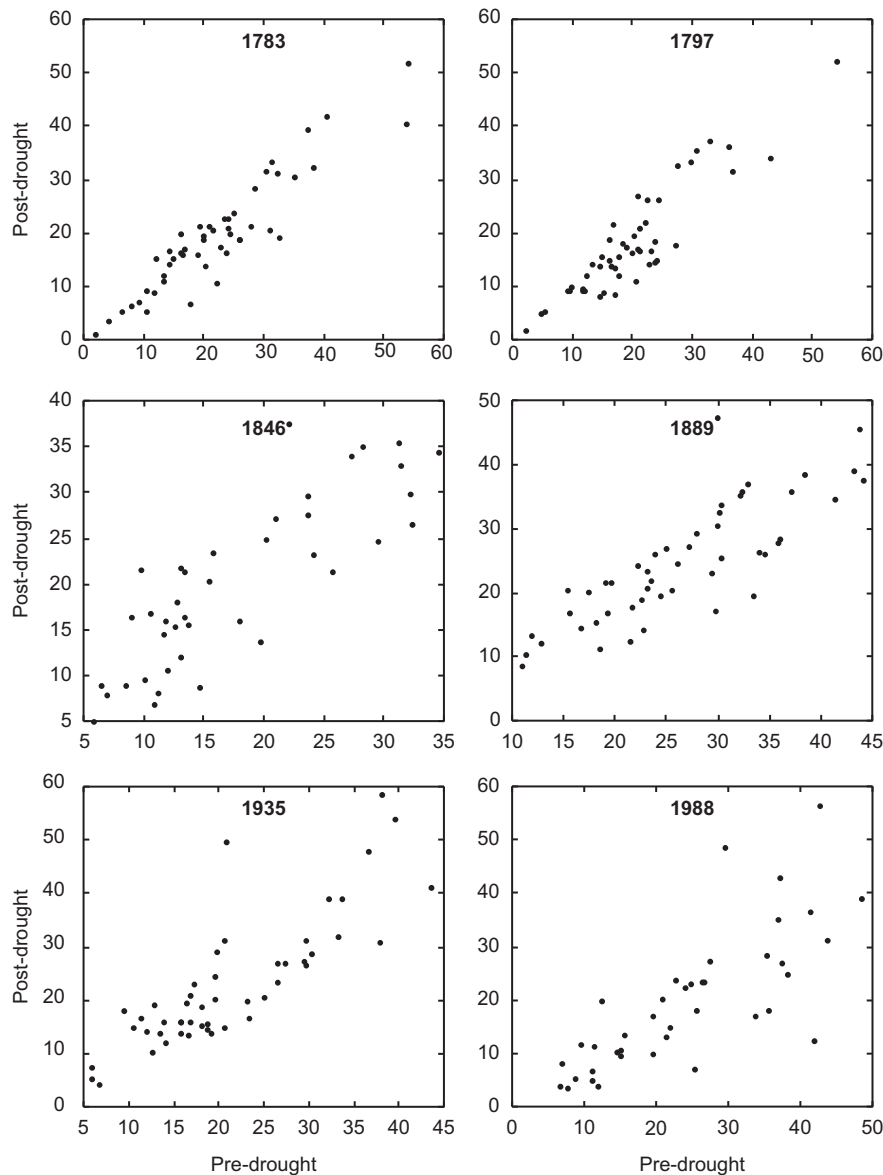
1913

Figure 3. Relationship between the growth (annual BAI, sq cm) after each drought episode and the growth before the respective episode.

correlated in the 1797, 1846 and 1889 episodes. The impact of the previous impact only correlated with recovery in 1846 and with resistance in 1846 and 1988. Relative resilience in 1846 was significantly and positively correlated with the impact of the previous episode and cumulative impacts and, marginally, to cumulative impacts in the 1797 episodes. Resilience was the only parameter that was not correlated to the previous impact. Overall, correlations with cumulative impact were stronger than with impact of only the previous event. The effect of site was only significant in 1797 (recovery), 1846 (recovery, resilience and relative resilience) and 1988 (recovery and resilience). The fires in MB in 1846 and 1989, but not in 1797–1798, do not completely explain this pattern. Analysis using resilience to the previous event as an indicator of impact yielded much weaker effects: only after the 1783 event recovery and relative resilience were positively correlated with the resilience exhibited after the previous event in 1756. The effect of site was only significant in 1783 (resistance and relative resilience), 1846 (resilience and relative resilience) and 1988 (resilience). In all three years, there were wildfires in MB.

were wildfires in MB. Significant interactions were only found for Previous impact × Site in the resistance model of 1988 and Cumulative effect × Pre-drought growth in the recovery model of 1889.

There was a significant interaction between time and site (repeated measures ANOVA, time × site interaction, post-drought growth $F = 4.76$, $p < 0.001$; resistance $F = 1.96$, $p = 0.029$; recovery $F = 1.89$, $p = 0.037$; resilience $F = 2.71$, $p < 0.001$; relative resilience $F = 2.12$, $p = 0.019$) (Fig. 4), indicating that the magnitude and effect of the different episodes varied depending on the site. There was a significant effect of time for all variables (repeated measures ANOVA, post-drought growth $F = 7.27$, $p < 0.001$; resistance $F = 8.06$, $p < 0.001$; recovery $F = 2.09$, $p = 0.055$; resilience $F = 11.12$, $p < 0.001$), except for relative resilience ($F = 1.09$, $p = 0.371$). While the lowest values of recovery, resilience and relative resilience for the whole record were observed in the last episode of 1988, there was no progressive decline in the resilience of old trees, and all the vari-

1914

Table 1. (A) General linear model results of growth (annual BAI, cm^2) and resilience estimators after the 1935 and 1988 events (Fig. 2). Log transformation of data was applied in growth and resilience (1935 and 1988), resistance and relative resilience (1935) and recovery (1988). R^2 corresponds to the respective model (bold numbers indicate significance of the model with $p < 0.05$). (B) Mean (SE) values of growth and resilience estimators in fire managed (unburned) and unmanaged (burned) stands after the 1988 event.

	1935 event			1988 event		
	F	p	R^2	F	p	R^2
(A)						
Growth						
Site	3.03	0.032		20.77	**<0.001**	
Age	1.02	0.315		3.77	0.054	
Fire				5.40	**0.022**	
Fire × Age				0.68	0.412	
Whole model			0.08			0.22
Resistance						
Site	0.36	0.779		2.56	0.112	
Age	26.27	**<0.001**		14.05	**<0.001**	
Fire				11.20	**0.001**	
Fire × Age				0.02	0.883	
Whole model			0.20			0.21
Recovery						
Site	2.55	0.059		1.57	0.213	
Age	1.26	0.265		10.01	**0.002**	
Fire				0.24	0.623	
Fire × Age				0.98	0.324	
Whole model			0.08			0.09
Resilience						
Site	0.35	0.788		0.20	0.659	
Age	21.66	**<0.001**		<0.001	0.966	
Fire				7.95	**0.006**	
Fire × Age				3.23	0.075	
Whole model			0.18			0.08
Relative resilience						
Site	1.13	0.341		0.10	0.747	
Age	7.73	**0.006**		5.40	**0.022**	
Fire				0.80	0.373	
Fire × Age				2.48	0.118	
Whole model			**0.10**			0.05

	Growth	Resistance	Recovery	Resilience	Relative resilience	n
(B)						
Unburned	30.0 (2.67)	0.75 (0.04)	1.33 (0.14)	0.94 (0.09)	0.19 (0.05)	37
Burned	22.1 (1.73)	0.62 (0.02)	1.41 (0.09)	0.77 (0.04)	0.15 (0.03)	87

ables exhibited some peaks in the mid- to late nineteenth century.

Discussion

The response of communities and ecosystems to short-term disturbance has mostly been explored from a theoretical point of view and has resulted in a variety of terminologies and approaches (Holling 1973, Pimm 1991, Peterson et al. 1998, Gunderson 2000, Scheffer et al. 2001, Folke et al. 2004). We use resilience in a broad sense as the ability to retain the structure and function prior to extreme events (Scheffer et al. 2001, Folke et al. 2004), which is equivalent to Holling's engineering resilience (Peterson et al. 1998, Gunderson 2000). We empirically apply this concept to patterns of tree growth, and show the advantages of accounting for various components, which essentially correspond to the ability to minimize change during a disturbance and to then reverse these changes and recover to the pre-disturbance state. The first component (resistance) is estimated by comparing performance during or immediately after the event to performance during the previous (or un-disturbed) state. Post-disturbance response should be considered as a function of the degree of change induced by the event. Recovery from disturbance is a function of the impact of the change induced by the event. Our indices distinguish these effects, since recovery reflects levels of change after disturbance, resilience (sensu stricto) compares post and pre-disturbance states, while relative resilience is a combination of both.

The integrative analysis of the different components of resilience in empirical studies has focused on resistance and resilience, (Sousa 1980, Kaufman 1982, Griffiths et al. 2000, Orwin and Wardle 2004, DeClerk et al. 2006), but their measures often fail to explicitly highlight the tendencies toward recovery in relation to the damage inflicted by disturbance, which is our

Table 2. General linear model results of growth (annual BAI, cm²) and resilience estimators (Fig. 2) after the different events with respect to the impact of the previous event, the cumulative impact of the events since 1756 and the resilience after the previous event (previous resilience). The effect of these variables was analyzed separately in different models, which also included growth before the event and site as explicative variables (results not shown). R^2 corresponds to the respective whole models (bold numbers indicate significance of the whole model with $p < 0.05$). Log transformation of data to attain the normality is indicated as (ln).

|	1783			1797			1846			1889			1935			1988		
	R^2	F	p	R^2	F	p	R^2	F	p	R^2	F	p	R^2	F	p	R^2	F	P
Growth																		
Previous impact	0.87	0.02	0.897	0.73	(ln) 0.04	0.834	0.80	0.40	0.531	0.71	0.01	0.928	0.71	(ln) 0.03	0.863	0.68	(ln) <0.01	0.970
Cumulative impacts				0.73	0.18	0.675	0.81	0.83	0.369	0.72	0.57	0.456	0.80	0.36	0.552	0.68	0.04	0.851
Previous resilience	0.87	1.24	0.271	0.73	0.88	0.352	0.80	<0.001	0.970	0.74	0.43	0.514	0.72	1.49	0.229	0.69	0.73	0.400
Resistance																		
Previous impact	0.17	0.02	0.894	0.15	0.72	0.401	0.31	**10.5**	**0.003**	0.24	2.67	0.111	0.11	(ln) 0.76	0.388	0.29	**8.19**	**0.007**
Cumulative impacts				0.24	**5.52**	**0.023**	0.30	**9.75**	**0.004**	0.46	**18.66**	**<0.001**	0.22	**4.91**	**0.033**	0.23	**4.77**	**0.036**
Previous resilience	0.21	1.82	0.185	0.17	1.57	0.217	0.16	(ln) 2.33	0.136	0.12	0.23	0.630	0.09	0.18	0.673	0.13	0.04	0.834
Recovery																		
Previous impact	0.16	1.10	0.300	0.21	2.92	0.095	0.27	(ln) **8.90**	**0.005**	0.11	(ln) 2.30	0.139	0.07	(ln) 0.56	0.458	0.08	1.04	0.315
Cumulative impacts				0.31	**9.12**	**0.004**	0.37	**15.30**	**<0.001**	0.21	**7.03**	**0.012**	0.12	2.40	0.130	0.06	0.01	0.905
Previous resilience	0.23	**5.03**	**0.030**	0.21	2.65	0.111	0.18	**4.09**	**0.051**	0.10	0.06	0.802	0.08	0.83	0.367	0.12	2.65	0.112
Resilience																		
Previous impact	0.16	0.01	0.917	0.04	0.65	0.424	0.30	(ln) 0.11	0.743	0.08	0.04	0.837	.01	(ln) <0.01	0.988	0.24	(ln) 0.30	0.589
Cumulative impacts				0.02	0.01	0.941	0.30	0.07	0.798	0.11	1.13	0.294	0.05	<0.01	0.947	0.24	0.44	0.513
Previous resilience	0.18	0.97	0.331	0.03	0.46	0.502	0.30	0.06	0.807	0.16	0.01	0.907	0.05	1.54	0.222	0.23	0.11	0.739
Relative resilience																		
Previous impact	0.15	0.06	0.801	0.18	1.10	0.300	0.33	(ln) **7.14**	**0.012**	0.03	0.73	0.399	0.05	0.30	0.588	0.07	0.32	0.575
Cumulative impacts				0.23	3.50	0.068	0.28	**4.16**	**0.049**	0.06	1.83	0.183	0.08	1.54	0.222	0.08	0.46	0.502
Previous resilience	0.26	**6.90**	**0.012**	0.21	2.82	0.100	0.19	0.03	0.854	0.09	0.22	0.641	0.05	0.65	0.423	0.09	0.83	0.370
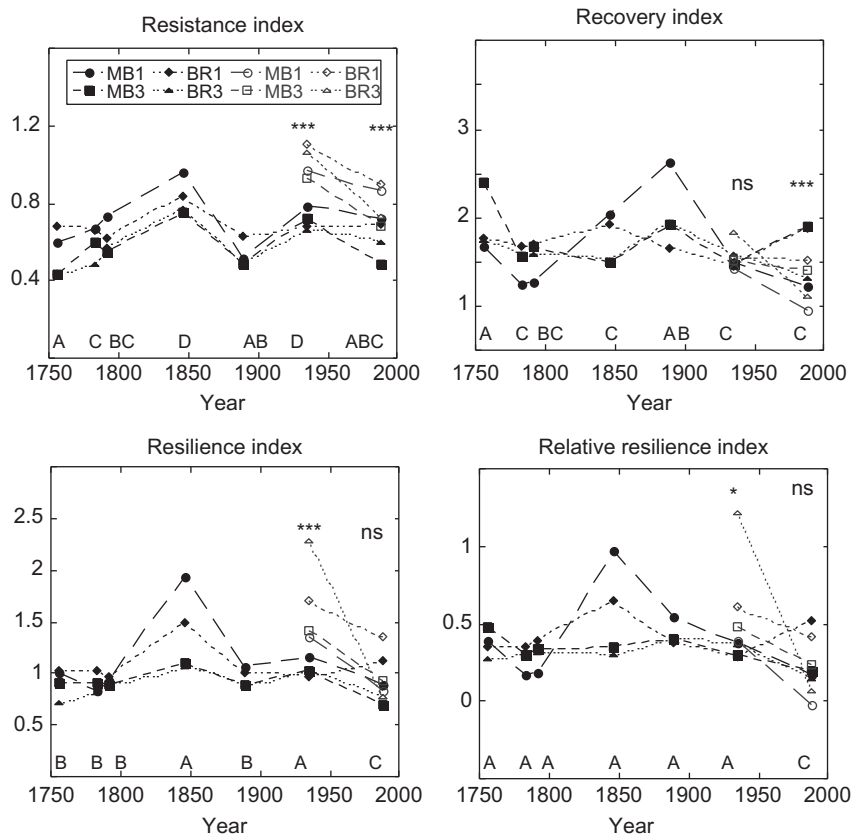
Figure 4. Components of tree response to low-growth periods through time in the studied localities (BR1, BR3, MB1 and MB3). Asterisks indicate significant differences between old (closed symbols) and young (open symbols) trees in the two events in the 20th century (general linear model analysis; ***= $p < 0.001$; *= $p < 0.05$; ns = not significant). Different letters indicate significant differences between years (repeated measures ANOVA, post-hoc Fisher LSD test, $p < 0.05$).

approach. In fact, the mechanisms involved in resistance and post-disturbance performance rates may be different or even exhibit trade-offs. For instance, DeClerk et al (2006) measured productivity in conifer forests after extreme drought and proposed that resistance could be determined by competition for a single resource, while resilience could be more closely related to the partitioning of resources. In plant-herbivore systems, a tradeoff between low resistance (high palatability) and resilience (high growth rates) has been proposed (Bee et al. 2007); this tradeoff is thought to arise due to investment in defence organs or compounds. In forest trees, a tradeoff between resistance and recovery after drought episodes could occur if both resistance and recovery depend in part on the amount of stored reserves (Galiano et al. 2011). Then, high resistance could result in low recovery or vice-versa, but resilience would be the same in both cases, as reflected in our indices. Nevertheless, even if reserve consumption during the stress event result on high impact (low resistance), recovery may occur if it is not exclusively dependent on the reserves remaining in trees, but it benefits from rebuilt canopy photosynthetic tissue (Galiano et al. 2011).

In remote old-growth forests of the Rocky Mountains, we found that fast-growing trees perform better after low-growth periods, and that, overall, young trees are more resistant to low-growth periods than old trees; however, their ability to recover to pre-drought levels is not necessarily greater. This pattern indicates that, at the individual level, resilience

properties may change with age or size. Contrary to our expectations, we did not find any evidence that reduced fire occurrence in the 20th century and the associated increases in forest density, weakened the resilience of trees. We also found conflicting evidence with respect the cumulative effect of previous drought periods on current performance: while increases in the negative cumulative effect of past low-growth periods reduced resistance to low-growth episodes (Table 2), we did not find any decrease in resilience over time (Fig. 4). Note, however, that our retrospective analysis is limited to surviving trees, and we cannot evaluate the performance of trees that eventually died over the course of this sequence of events. Nevertheless, the results clearly show that tree responses to disturbance are highly complex. This raises the possibility that reported increases in forest mortality under current climate conditions may relate to threshold effects on specific components of resilience, rather than to any overall loss of resilience over time.

In addition to climate, other factors including infestation by insects and fires (Schweingruber 1996) may contribute to low-growth periods (at our remote sites, disturbance from logging or active forest management are not a contributing factor; Keeling et al. 2006). Of the factors potentially responsible for low growth on our sites, climate would be expected to have a regional-level impact, while fires and pest outbreaks would be more localized. The correlation

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we consistently found between growth and regional PDSI and between PDSI and instrumental climate data obtained in the 20th century supports the assumption that the low-growth periods we chose were associated with drought. Fire activity in our region is, however, clearly related to climate (Heyerdahl et al. 2008b, Morgan et al. 2008), with greater fire activity during drier years. For instance, in MB, where we have a detailed fire history (Heyerdahl et al. 2008a), the low-growth periods of 1846 and 1889 coincided with fires. However, it is worth noting that the drought-response parameters in these two periods were very different from each other but they were similar to those corresponding to other low-growth events without fire. This is probably because the effects of the low-intensity fires characteristic of our sites (Heyerdahl et al. 2008a) often vary depending on the combined effect of the damage to surviving trees and the release competition after fire (Keeling et al. in press). Without discounting the role of wildfires, the synchrony of low-growth periods between the two sites supports our assumption that climate extremes are major contributors to low-growth events.

The positive correlation between growth after and before a low-growth episode is not surprising and indicates that trees that are more robust (due to a combination of micro-site quality and intrinsic factors such as physiological state and genetics) perform better after a period of stress. The fact that this effect persisted after low-growth episodes, and that several estimators of resilience were weakly correlated with pre-drought growth rates, suggests that micro-site conditions are not significantly altered by the drivers of the episode and/or that trees are able to recover irrespective of the impact of the episode.

Tree age influenced the responses to low-growth periods during the 20th century in complex ways. In general, old trees exhibited greater reductions in growth (lower resistance) compared to younger trees. However, recovery of old trees was similar to that of younger trees after the 1935 episode and even greater in 1988. As a result, old trees were less resilient in 1935 than young ones, but their relative resilience (which accounts for the impact of the episode) was greater in 1988. Because growth recovery in young and old trees was estimated relative to preceding time intervals, the different responses in old and young trees cannot be attributed to within tree age-related effects on ring width (Fritts 1976). The lower resistance of old trees could reflect reduced vigor, which is consistent with the well-documented age-related decline of tree growth (Ryan et al. 1997), and the often disproportionate mortality of old trees (Mueller et al. 2005). Alternatively, it could reflect growth/survival tradeoffs (Bigler and Veblen 2009, Johnson and Abrams 2009) whereby stress-induced growth reductions in old trees reflect a survival strategy. This is consistent with the fact that recovery in old trees was independent of the magnitude of growth decrease (resistance), and that it was similar (1935), or even greater (1988), than in younger trees. Ultimately, if age effects are present, they are clearly not linear, because we did not see any overall decrease in resistance, recovery or resilience in old trees over the study period as a whole.

The greater loss of relative resilience in young trees relative to old trees in 1988 is also complicated because we cannot separate the effects of tree age from those of surface fires (Heyerdahl et al. 2008b, Morgan et al. 2008). For instance,

Keeling (2009) found that recent fires had more negative effects on tree growth relative to earlier 20th-century fires, a finding that was significantly correlated with lower winter precipitation. Thus, it could be the case that the greater overall recovery in older trees in the most recent drought episode (1988) could be driven by a disproportionate negative effect of recent fires on younger trees with thinner barks and less insulation. If this were the case, however, we would expect a significant interaction between age and fire occurrence during the 1988 episode, which was not the case for any of the parameters analysed. It is consistent with the absence of differences between old and young trees in their responses to fire in these forests (Keeling 2009). Differences between fire intervals at the two sites burned in the 20th century and the fact that the fires occurred in different years, could also have contributed to the observed patterns of age-dependent tree resilience components in the 20th century.

In spite of the variability in the response to different episodes, we found that factors that influence individual performance persist through successive episodes. This was supported by the negative relationship between the resistance to a given event and the impact of the previous event. The fact that lower resistance did not influence growth after the episode (i.e. there was no significant relationship between resistance and post-drought growth in any of the episodes) combined with the high positive correlation between pre- and post-drought growth, suggests that micro-site quality often plays a more important role in response to low-growth periods than intrinsic physiological (e.g. resource depletion) or structural (e.g. damage) factors. Micro-site effects would also explain the positive correlations between recovery and the impact of previous episodes. This suggests that as trees regained the same pre-drought growth irrespective of the growth reduction caused by the episode, those that were less resistant were also those with higher levels of recovery (i.e. statistically significant relationship between resistance and recovery in all episodes). This is the expected pattern when resilience (ratio between post and pre-drought growth) remains constant.

If resilience is an individual property resulting from genetic (Meier et al. 2008) or micro-site factors, or to a memory effects (Peñuelas et al. 2000), we would expect such signals to persist and accumulate over time (e.g. some individuals systematically perform better after each episode relative to the average population). Eventually, at the population level some individuals would experience a progressive decline in resilience, while others would gain greater prevalence in the community. As discussed above, we found some relationship between the performance between events close together in time, but our results do not fully support the hypothesis of long-term cumulative effects, as we failed to find a positive relationship between the resilience of successive episodes or a progressive decline in resilience in old trees. It should be noted, however, that we performed our analysis on surviving trees, and so the cumulative effect of successive low-growth events on resilience may have been underestimated in relation to the whole cohort because trees that died were not accounted for. Alternatively, demographic compensation (e.g. competition release due to mortality caused by the previous drought) would result in increasing tree resilience over time during repeated episodes, but we

did not find this either; instead, resilience fluctuated over time, with no clear trend toward either increase or decrease. Such fluctuations are probably more closely related to variability in the intensity of episodes rather than variability between individuals.

Our study provides new a perspective on the analysis of resilience by introducing the performance of different components in a relevant ecological context – forest ecosystems affected by climate change. Several studies have recently documented a relationship between climate change and decline in forest growth during the last decades of the 20th century. Our study introduces resilience and the combination of related parameters as new elements to enhance our understanding of changes in forest behaviour. Such analysis is relevant because today's extreme events will presumably become the average conditions of the future (Battisti and Naylor 2009). Interestingly, resilience to recent 20th century low-growth episodes was not significantly different than resilience to episodes in the past. Similarly, old trees were not necessarily less resilient than younger trees. While these results may initially appear counterintuitive, they illustrate the importance of methods for assessing different components of resilience, which was our approach in this study. Our results show a variable but inherently high capacity of trees to recover from disturbance in these disturbance-prone systems. Furthermore our results suggest that the negative effects of current climate conditions may be related to threshold effects on specific components of resilience such as loss of resistance rather than to a gradual loss of overall resilience over time. There remains the challenge of identifying specific thresholds (i.e. conditions in which trees are no longer able to recover), the degree to which these thresholds are species- or functional type-specific, and ultimately, the mechanisms that enhance over all resilience. Better metrics for assessing resilience in trees will be especially valuable given recent worldwide increases in forest dieback and mortality, and should increase our predictive power for more effective decision-making in forest management.

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