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Differential effects of climate variability on forest dynamics along a precipitation gradient in northern Patagonia

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Summary

1. The understanding of the impacts of climate anomalies on demographic processes involved in forest dynamics is becoming a major global change research objective, as climate-driven demographic changes have the potential to alter ecological processes and change the composition of existing communities.

2. Here, we test whether the effects of climatic variability on *Nothofagus dombeyi* forest dynamics differ along the W–E precipitation gradient of northern Patagonia, Argentina, due to different controlling factors along the gradient.

3. Using a dendroecological approach, we sampled six *N. dombeyi* stands along the gradient. Tree death, growth release and sapling birth dates were obtained and used to reconstruct stand mortality, canopy disturbance and establishment patterns in each stand. Discrete extreme climatic events were obtained by applying thresholds to meteorological time series. Bivariate event analysis was performed to examine the temporal relationships between climate events and forest demographic and canopy disturbance patterns.

4. In the xeric region, forest dynamics is driven by drought/heat and humid events. Following drought/heat events we observed standing-dead tree mortality, releases in growth, and tree establishment episodes. Regional synchrony of these events was coincident with droughts registered for northern Patagonia. However, successful establishment was related to wet periods that occurred after drought events, showing the dependence on favourable periods for growth. For wet regions, demographic patterns showed a temporally uniform pattern but with synchronies at the regional and local scales. Canopy openings produced by fallen trees, and consequent release in growth and establishment, were related to both drought and snowy/windy years. The effect of drought in wet region forests was related mainly to the extreme 1998–99 drought in northern Patagonia.

5. *Synthesis*. Climate in northern Patagonia influences *N. dombeyi* forest dynamics differentially along a precipitation gradient. In xeric forests, strong but relatively short climatic fluctuations impact forest structure through direct effects on tree demography. In wet forests, climatic-induced mechanical disturbance prevails, driving mortality and subsequent growth and establishment. Considering that recent extreme droughts have the strongest negative impact on *N. dombeyi* populations at the eastern distributional limits, a change in distribution of this species as a consequence of projected climate change is expected.

Key-words: drought, establishment rates, extreme climatic events, forest dynamics, *Nothofagus dombeyi,* plant–climate interactions, release events, tree mortality

Introduction

Around the world, the effects of an altered climate on forest ecosystems are becoming more evident (Allen 2009; van Mantgem *et al.* 2009; Allen *et al.* 2010). Therefore, understanding the impacts of climate on demographic processes involved in forest succession, such as regeneration and mortality, is becoming a major global change research objective. Over recent decades, a lot of effort has gone into developing models that help us understand how forests may respond to alterations

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*Correspondence author. E-mail: marialau.suarez@gmail.com in climate. Increasingly sophisticated (e.g. stochastic and spatially explicit approaches) simulations of establishment, growth and mortality are contributing to understand future scenarios of altered climate tree species composition and forest structure (Shugart 1984; Bugmann 1996).

For several forest types, models have been developed, parameterized and validated (e.g. Pacala *et al*. 1996). These models have low capabilities of reflecting the effects of extreme climatic events on terrestrial biota as it is becoming increasingly clear that many processes driving forest dynamics are highly sensitive to changes in climate variability rather than changes in actual climate means (Bugmann & Pfister 2000). However, parameterization of these relationships is still in its infancy mostly because empirical studies are lacking. Recently, demand has been increasing for reconstructing key tree demographic processes under extreme weather conditions in contrasting abiotic conditions (e.g. along environmental gradients) in order to improve our understanding of ecosystems sensitivity to future changes in climate variability rather than of changes in average values alone.

Climatic anomalies evidenced at both inter-annual and decadal time-scales are strong drivers of forest dynamics, having important influences on the landscape that could persist through decades in long-lived forest ecosystems (Allen & Breshears 1998). In this context, extreme climatic events such as droughts, floods, or strong snow storms have the potential to alter ecological processes and change the trajectories of existing communities. Climate directly affects tree structure through favourable or unfavourable conditions for physiological processes to be maintained or not. For example, tree establishment is expected to occur during favourable climatic conditions (e.g. moist periods), whereas tree and seedling mortality are expected to be higher during stressful periods (e.g. droughts) (Villalba & Veblen 1997; Lloret, Peñuelas & Estiarte 2005). Across a species distribution range, direct physiological effects of climate on tree demography are expected to increase towards abiotically determined distribution limits (precipitation or temperature limits) because individuals are living at the edge of their physiological tolerance (Woodward 1987). In addition to climatic effects on tree physiology, 'force-related' climatic events (e.g. snow and wind) often produce mechanical damages to the forest canopy, driving succession by gap forest dynamics. For example, snow storms disturb forests by depositing thick snow layers on tree crowns, breaking branches or uprooting the whole tree. Likewise, wind storms impart a strong physical force above stem resistance threshold, snapping or uprooting the tree. Thus, treefall is one of the direct outcomes of climatic events, allowing successful regeneration and maintaining many forests in compositional equilibrium (Veblen 1989). We propose here that across an entire species distribution, force-related climatic disturbances will be more important in driving forest dynamics in more productive areas away from abiotic limits and where biotic interactions (both intra- and interspecific) become important.

In recent decades, inventories and dendroecological studies, combined with accurate historical climatic records, were significant sources of data for calibrating models of tree mortality (Bigler *et al*. 2007; Wunder 2007; Drobyshev, Dobrovolsky & Neshataev 2009). However, most studies were performed in ecotones, where signs of climate impact on forest ecosystems may be expected (Allen & Breshears 1998) and comparative assessments of climatic effects across dominant tree species or biome distributions are lacking. Thus, broad-scale studies about the influence of past and present climate on forest dynamics may aid understanding how forest vegetation will shift distribution in response to scenarios of future climate changes.

During 1998–99, strong La Niña conditions led to a severe drought in northern Patagonia, Argentina (annual rainfall was the lowest in the last 100 years). During the drought, a massive die-off of *Nothofagus dombeyi* (Mirb.) Blume was triggered near its eastern distributional limit (Suarez, Ghermandi & Kitzberger 2004), whereas a lesser climatic impact was evidenced in westward forests. Knowledge of the predisposing causes of drought-induced regional-scale *Nothofagus* mortality and the presence of possible long-term compositional shifts in mixed *N. dombeyi–Austrocedrus chilensis* (D.Don) Flor. *Et* Boult forests allowed for new conceptual models of forest dynamics that incorporate dieback as a source of potential vegetation shifts (Suarez & Kitzberger 2008). However, a more complete model would be improved by a dynamical integration of mortality processes triggered during past climatic anomalies and subsequent establishment opportunities in canopy gaps. Therefore, the effect of recent climatic events on demographic processes along an environmental gradient may be used to understand processes underlying species distribution shifts. Since extreme climatic events are predicted to increase in magnitude and frequency (IPCC, 2007) and resulting nonlinear effects on forest vegetation are poorly understood, prediction of forest dynamics is complicated without a basic understanding of past versus recent climatic effects on forest composition and structure.

Motivated by possible species distribution shifts due to changed climate, this study provides a retrospective, long-term perspective on extreme events and on their effects on forest dynamics. We used a spatio–temporal sampling framework to test the main hypothesis that the relative contribution of physiological versus force-related effects of climatic variability on *Nothofagus dombeyi* forest dynamics are different along the prevailing W–E precipitation gradient of northern Patagonia, Argentina. The main goal of the study was to quantify *N. dombeyi* mortality, canopy opening and establishment patterns, their variability across the precipitation gradient and their relationship with major past climatic events.

Materials and methods

STUDY AREA

Regionally, the Andes produce a strong rainshadow effect on precipitation (decrease in annual precipitation from *c*. 3000–500 mm year^{-1} over 100 km W–E distance (De Fina 1972). Precipitation is highly seasonal with *c*. 60% falling during May through August (austral winter). Mean annual temperature is 7.9 °C and the maximum temperatures are registered during January and February (austral summer). Locally, northern and western aspects are characterized by high water deficits due to solar radiation and prevalent westerly winds. Decreases in cloudiness determine an eastward increase in mean annual temperature of *c.* 2 °C. A W–E gradient of increasing volcanic soil ages determines decreasing acidity and increasing soil fertility (Garibaldi *et al.* 2010), but productivity is still higher in wet compared to dry forests (Mazía, Kitzberger & Chaneton 2004). At *c.* 800–900 m, altitudinal belt vegetation changes abruptly from temperate rain forests dominated by tall evergreen *N. dombeyi* to semi-arid steppe dominated by cushion shrubs and bunchgrasses (Fig. 1). At the wet extreme, *N. dombeyi* forms pure stands, and low frequency of fires results in extensive old-growth with individuals reaching maximum longevity (*c.* 600 years old) whereas at intermediate precipitation (*c.* 1400 mm year^{-1}), following more frequent stand-devastating fires, *N. dombeyi* and the conifer *A. chilensis* both form even-aged populations.

The study was conducted in Nahuel Huapi National Park (NHNP), Argentina (Fig. 1), where *N. dombeyi* is the dominant low-altitude tree species. To represent *N. dombeyi* wet forests, three *c.* 2-km^2 study areas encompassed by the 2500–3000 mm year^{-1} isohyet (WET1, WET2 and WET3; Fig. 1) were sampled. Three additional areas encompassed by the 1200–1400 mm year^{-1} isohyet were selected to represent more xeric mixed *N. dombeyi–A. chilensis* forests (XER1, XER2 and XER3; Fig. 1). Stands were selected that showed no signs of logging activities or evidence of recent fires. In addition, for stands in wet regions, old-growth mature stands (> 250 years old) were avoided because gap phase processes are dominant and could result in large differences in stand structure and other potential variables that would affect susceptibility to snow, rain and wind events, in comparison with relatively young post-fire *N. dombeyi–A. chilensis* stands growing in xeric regions. Selected stands in xeric and wet regions had similar tree-age and size structures.

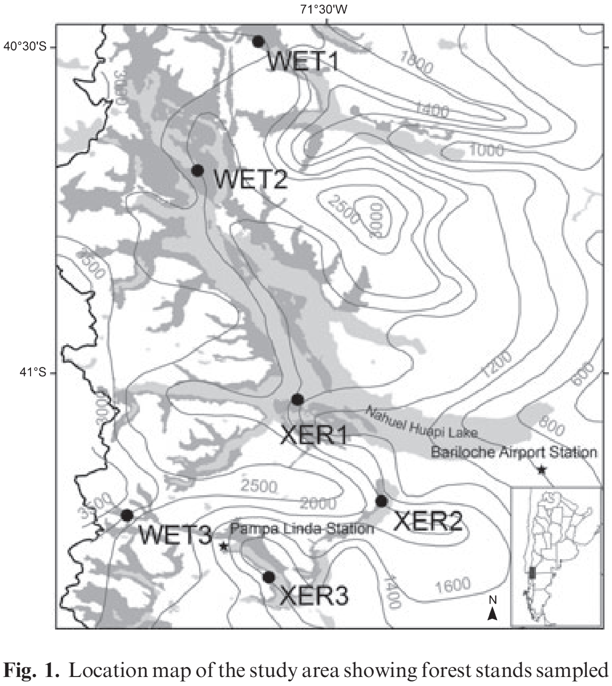

Fig. 1. Location map of the study area showing forest stands sampled in Nahuel Huapi National Park, Argentina. Precipitation gradient is represented by mean annual precipitation isohyets and *Nothofagus dombeyi* distribution is shown in dark grey. XER prefix corresponds to stands growing between 1200 and 1400 mm year^{-1}, and WET prefix to stands growing between 2500 and 3000 mm year^{-1} along the precipitation gradient. Meteorological stations used in this study are indicated with stars.

RECONSTRUCTING TREE MORTALITY, GROWTH RELEASES AND ESTABLISHMENT DATES

Each stand was sampled using six 600-m-long transects located parallel to each other and separated by 150 m. Sampling points were established at 100-m intervals. At each point, we took increment cores of the four nearest trees. Tree selection criteria varied among the mortality, establishment and release studies (see below). We used standard dendrochronological procedures (Stokes & Smiley 1968) for processing all samples. Following Schulman (1956), the date of an annual ring was assigned to the calendar year when growth began (October–November in the Southern Hemisphere). The quality of dating was examined using COFECHA (Holmes 1983) and CrossdateR (Bigler 2006) software. However, when tree-ring series were < 50 years in length, cross-dating was done visually using marker years.

MORTALITY DATES

Snapped, uprooted and dead standing trees that unambiguously showed evidence of being killed by climatic events (wind, snow or drought) were selected. Each dead tree was cored at least twice. The date of the outermost tree ring was defined as the date of death; however, the confidence of the date was influenced by the condition of the wood and by the possibility that trees do not form an annual ring for one or several years before they die (Amoroso & Daniels 2010). Cores were taken only from dead trees with bark or from trees with recently fallen bark in order to avoid the possibility of ring erosion since death. In order to preserve the annual resolution of death dates, we avoided the inclusion of old (rotten) dead trees (Villalba & Veblen 1998). The calendar year of the outermost ring was determined by cross-dating (using COFECHA; Holmes 1983) against master chronologies developed for the region (Suarez 2010). The main problem with cross-dating *N. dombeyi* dead trees was the presence of strong growth declines 20–50 years prior to death, often related to previous drought events (Suarez, Ghermandi & Kitzberger 2004). These periods lowered the correlation against the master chronology and complicated the precise dating of death. The prevailing mortality cause in each region was analysed using chi-squared test.

RELEASE DATES

Focal trees were juvenile (5–20 cm d.b.h.) *N. dombeyi* individuals in subcanopy positions. To assure independence of mortality and release data, juveniles were sampled randomly without forcing the spatial association to focal dead trees. Canopy openings dates were determined as ‘releases’ in tree-ring growth, examining each tree-ring series based on moderate and major release criteria. A growth release was defined as a 50–99% (moderate release) and > 100% (major release) increase in mean ring width where means for consecutive groups of 5 years were compared, and release was sustained for at least 5 years (Nowacki & Abrams 1997). Years were recorded in which growth releases were initiated. Nowacki & Abrams (1997) release criteria were inspected using the JOLTS package from DPL (Holmes 1992) and Ars41_win (Cook & Krusic 2006).

ESTABLISHMENT DATES

Focal trees were saplings (< 5 cm d.b.h., < 2 m high) and juvenile individuals of *N. dombeyi* (four in each category nearest to the sample point). Again, random sampling of saplings assured little spatial association with dead trees. For all sampled trees, we attempted to determine dates of germination at an annual level of precision. Saplings were uprooted and juvenile trees were cored twice as low as possible (*c*. 20 cm above ground). Uprooted saplings were processed according to the size at the root collar. Small saplings (< 2 cm diameter at root collar) were cut using consecutive histological thin sections of the stem in order to identify the transition zone between root and stem tissue (root collar; Telewski 1993). Wood disks were saturated with ethyl alcohol (70%) and a cross-section (30 μm thick) was cut using a manual sliding microtome. Xylem was coloured using fluoroglucinol and rings were counted under a 40× microscope. Germination dates of larger uprooted saplings were determined by taking four consecutive 1-cm-interval cross-sectional disks below and above the potential root collar zone. Tree rings were counted on each finely polished disk and root–shoot tissue transition was used to aid the identification of the root collar zone. Establishment dates for cored juvenile individuals were determined following two procedures. For cores that reached the pith, the calendar year was identified. For cores that did not reach the pith but passed close to it, arcs of the inner rings were used to estimate the number of missing rings needed to reach the pith (Duncan 1989). Cores with > 10 estimated missing rings were discarded. The obtained pith date was corrected by the number of years needed to reach the coring height. This correction was done using the estimation of height growth rates developed, for each study site, from saplings growing beneath the canopy with non-extreme suppression (Suarez 2009).

CLIMATIC DATA SETS

We used the Bariloche Airport station meteorological data (Fig. 1), the only meteorological station nearby providing century-long records for the study area. Despite the sharp climatic gradient, Bariloche Airport data are representative of a regional network of shorter records such as Temuco, Chile (38°44′ S; 72°35′ W), Ea. Collunco (40°00′ S; 71°17′ W) and Esquel (42°54′ S, 71°18′ W). For example, Pearson correlation of annual precipitation and the first principal component of annual precipitation of these three widespread stations (1963–87) is 0.88 ($P < 0.000001$). Wind velocity records were averaged for the windy period in northern Patagonia (November–January). For snow data, we used records from Pampa Linda station (Fig. 1), which holds a data set covering the period 1980–95. Additionally, precipitation data (amount in mm) of days registered as ‘snowy days’ (1973–2006) from Bariloche Airport station, was used to extend snow records for the region. Considered climatic events were: arid growing season (October–March), humid growing season (October–March), low summer precipitation (December–February), high summer temperature (December–February), high spring precipitation (October–November), high winter precipitation (June–August), high snow precipitation (June–August) and high wind velocities (November–January). For determining the arid and humid growing season, we used De Martonne’s (1926) monthly aridity index for the period 1914–2006 which combines precipitation and temperature for building the aridity of a region. Thresholds used were: mean ± 1 SD as moderate event and mean ± 2 SD as extreme event.

RELATING TREE GROWTH RELEASE, MORTALITY AND ESTABLISHMENT PATTERNS WITH CLIMATIC EVENTS

We performed bivariate event analysis (BEA) using K1D software (Gavin 2007). BEA is a temporal variant of spatial analysis based on Ripley’s *K* function; it has been used to examine the temporal relationships (synchrony and lags) between climate events and forest demographic and canopy disturbance patterns. Assuming one-directional processes, where mortality, release or establishment events only match or follow a particular climatic event, we always used forward selection procedures (Bigler *et al*. 2007). For each relationship we obtained first the bivariate *K* function which is transformed into an *L* function as $L_{AB}(t) = K_{AB}(t)/2 - t$, where ‘B’ events co-occur with or follow ‘A’ events (Gavin 2007). The inspection of climatic time series showed that only once or twice there were two consecutives climatic events. Confidence envelopes for each function were calculated by Monte Carlo simulations with 1000 replicates (95% and 99%), based on randomizing climatic records (without replacement). We randomized the causative event because (i) climatic events cause establishment/release/mortality events and (ii) because the resulting event (e.g. establishment) is often clustered and may contain a temporal effect (C. Bigler, pers. comm.). Values above the upper confidence limit indicate synchrony between the two considered records. Values below the lower confidence limit indicate asynchrony, and values between confidence limits indicate independence between records. Although all types of relationships were inspected, focus was put on synchronic relationships. As the individual tests of increasing window sizes are not totally unique tests in BEA, we put caution in the interpretation of single instances of significance, especially when significance is low. Additionally, and for relating *N. dombeyi* establishment and releases in growth as a consequence of canopy opening events, tree mortality events also were used as a predictor variable in BEA. Superposed epoch analysis (SEA) is commonly used to compare average annual climate conditions (e.g. aridity index) before, during and after a set of particular events (e.g. fires) recorded on two or more trees. However, this method is not able to detect whether there are more or fewer events than expected, during and following a climatic event (e.g. drought, Bigler *et al*. 2007).

Results

GROWTH RELEASE, MORTALITY AND ESTABLISHMENT PATTERNS

Tree mortality patterns

The predominant mode of mortality (as standing versus fallen trees) differed between analysed regions. In the xeric region standing death affected up to 74.6% of dead trees ($\chi^2 = 48.76$, d.f. = 1, $P << 0.0001$); whereas tree-fall (uprooted or broken) was the predominant mode of mortality (70.12%) in the wet region ($\chi^2 = 37.44$, d.f. = 1, $P << 0.0001$; Figs 2a and 3a). Because we worked only with dead trees that either had a bark or had no bark but showed no evidence of ring erosion, most mortality dates fell within the past 60 years, limiting our analysis to this period. During this more reliable period, several regional episodes of mortality (> 4 individuals) were evidenced in the xeric stands: 1959, 1962, 1972, 1978, 1985, 1994 and 1998 (Fig. 2a). Except for the 1962 event, all mortality dates were equally distributed between all xeric stands. Tree mortality in the wet region showed a more continuous pattern of mortality dates that were shared by a low number of trees (Fig. 3a). During the last 25 years, several peaks of mortality were identified for the

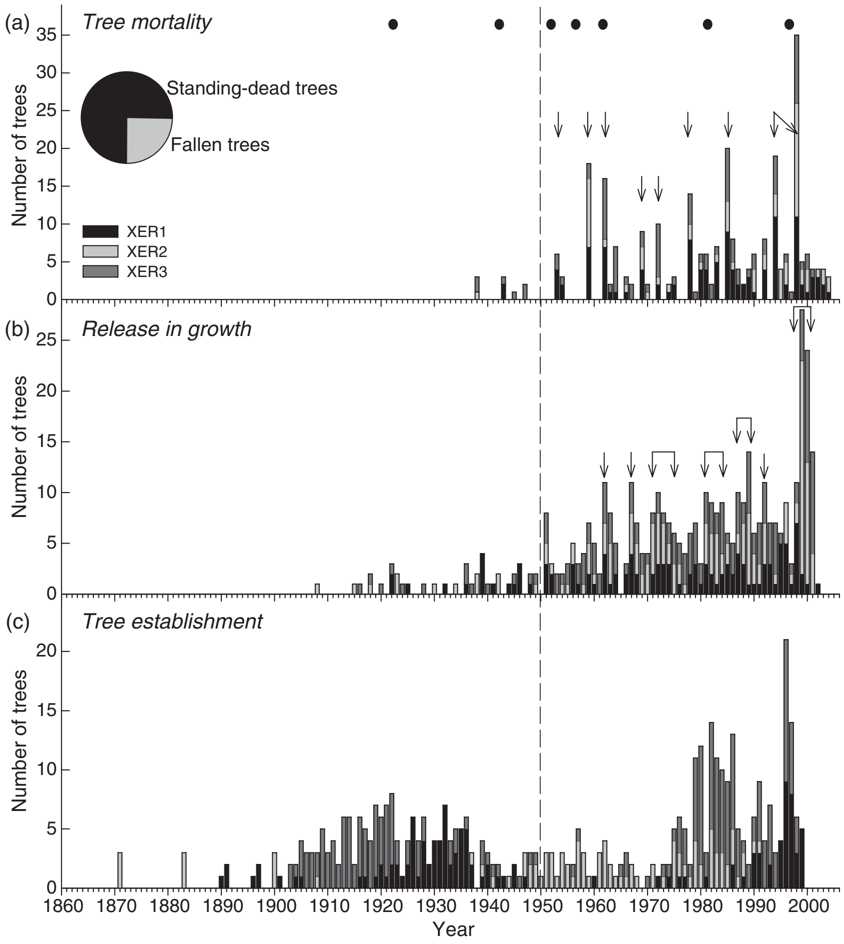

Fig. 2. Xeric forests (a) mortality frequency distribution for *Nothofagus dombeyi* trees, (b) growth release frequency distribution for juveniles *N. dombeyi* trees, (c) establishment frequency distribution for *N. dombeyi* saplings. Dashed vertical line indicates the approximate year since an integrative analysis between found patterns is valid based on the decay of the samples (dead trees) as we go back in time. Filled circles represent extreme droughts recorded in northern Patagonia. The pie chart represents the percentage of dead trees in each studied category (standing dead trees and fallen dead trees). Vertical arrows indicate forest disturbances recorded as peaks in frequency plots.

year/period 1984, 1987, 1993–95 and 2003–04. However, episodes of mortality showed more local signals.

Growth release patterns

In the xeric region, synchrony in release dates was evident for the periods: 1962–63, 1966–68, 1971–74, 1981–85, 1988–93, 1996 and 1998–2000 (Fig. 2b). All detected release periods were characterized by major and moderated releases and were well represented in xeric stands (except 1998–99 release peak in XER 1). In contrast, release patterns were more uniform with some regional and several local synchronies in release dates (Fig. 3b). During the last 30 years, there were four distinctive peaks in growth releases (1984, 1989, 1995 and 2000; Fig. 3b); although the 1984 peak was present exclusively in WET1.

Tree establishment patterns

In the xeric region, the establishment was almost continuous from the beginning of the 20th century, with the exception of a pronounced reduction in establishment episodes observed during the 1940s, 1950s, 1960s and 1970s and almost exclusively confined to XER2 (Fig. 2c). The only period shared by the three stands was the establishment episode recorded during 1970s. The establishment pattern found in the wet region differed, as we expected, from that obtained for the xeric region. Tree establishment was more uniform in this region extending from mid-19th century to the end of the 20th century, and with low frequency of individuals establishing each year (Fig. 3c). In addition, the date of establishment was seldom shared by all sampled stands.

ASSOCIATION BETWEEN FOREST DISTURBANCE AND CLIMATIC EVENTS

Tree mortality

In the xeric region, all stands showed a strong relationship between mortality and dry climatic events (droughts and hot summers). Most peaks observed in the frequency of *N. dombeyi* mortality dates nearly coincided with most of the important droughts registered in northern Patagonia (1922, 1943–44, 1953–57, 1962 and 1998–99). Statistically, at the regional scale, xeric forest mortality events were related to arid events, low summer precipitation and high summer temperature events ($P < 0.05$, Table 1). At the stand scale, this relationship held true and was even strengthened for the case of heat events ($P < 0.01$). Mortality showed also lagged effects with low-summer-precipitation events for lags encompassing 6–9 years after the climatic event (Table 1). Except for 1- to

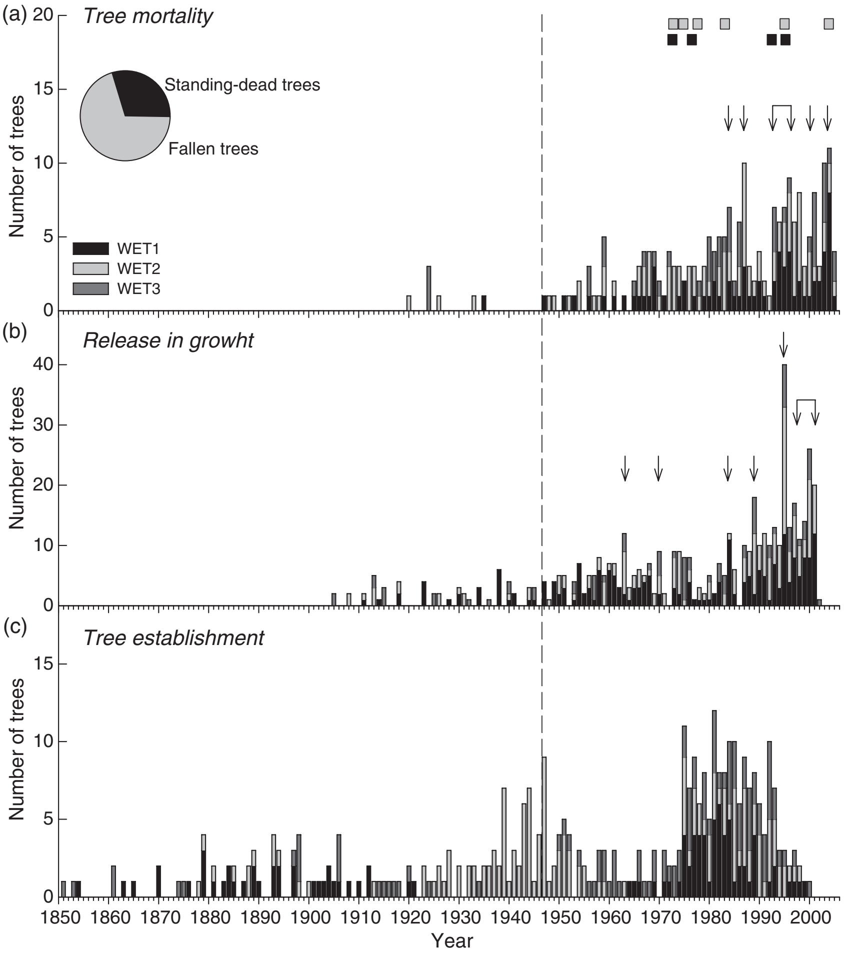

Fig. 3. Wet forests (a) mortality frequency distribution for *Nothofagus dombeyi* trees, (b) growth release frequency distribution for juveniles *N. dombeyi* trees, (c) establishment frequency distribution for *N. dombeyi* saplings. Dashed vertical line indicates the approximate year since an integrative analysis between found patterns is valid based on the decay of the samples (dead trees) as we go back in time. Filled squares indicate extreme snow (grey) and wind (black) storms recorded in northern Patagonia. The pie chart represents the percentage of dead trees in each studied category (standing dead trees and fallen dead trees). Vertical arrows indicate forest disturbances recorded as peaks in frequency plots.

3-year-lagged mortality related to snow events in XER1, no force-related mortality (by rain, snow, wind) was evidenced at either the local or regional scales.

In contrast, the *N. dombeyi* mortality pattern in the wet region had a more mixed origin (probably more physiological and force-related). Regional scale mortality had instantaneous and lagged relationships with low-summer-precipitation events ($P < 0.01$), high-snow-precipitation events ($P < 0.05$) and high spring precipitation events ($P < 0.05$; Table 2). However, other climatic events caused significant tree mortality at the stand scale. For example, high winter precipitation caused instantaneous treefall mortality in WET3 ($P < 0.05$), and high summer temperatures triggered instantaneous mortality in two of the three analysed stands (WET1 and WET3, $P < 0.05$ and $P < 0.01$, respectively) with lagged effects of 1–3 years after the heat year.

Growth release

In the xeric region, growth release events were only related to drought and heat events (low-precipitation and high-temperature summers), with continuing lagged effects up to 9 years after low-summer-precipitation events, and no relationship was found with climatic force events. In addition, release events were significantly and instantaneously associated to mortality events at the regional scale with lagged effects that lasted up to at least 9 years (Table 1). Similarly, at the stand scale low summer precipitation and negative aridity triggered most instantaneous and lagged growth release responses.

Instead, instantaneous releases in wet forests related to high snow precipitation or snow/wind events. Also, as we expected, growth releases were related with tree mortality events with lags of 1–6 years (Table 2). Notably, however, some lagged growth release responses at the regional and stand scale followed low-summer-precipitation events possibly influenced by the strong 1998–99 drought event. However, the most pervasive responses of tree growth releases at the stand level came from instantaneous and lagged responses following high snow precipitation or wind/snow events with lagged effects of 1–5 years depending on the stand (Table 2).

Tree establishment

Nothofagus dombeyi seedling establishment in the xeric region was generally related to drought/heat events and no relationship was found with winter climatic forcing events. Because we predicted that *N. dombeyi* tree establishment in xeric regions could be favoured by the occurrence of moist periods; this drought–establishment association was unexpected. Specifically, seedling establishment events were significantly related

Table 1. Bivariate event analysis, relating frequency (number of individuals year^{-1}) of tree mortality, release and tree establishment dates with climatic event records for xeric region. Synchrony between records are shown from t_0 (year of the event) to t_6 (6 years following the event). Climatic events in the first column correspond to the event inspected as key responsible for the analysed pattern

	XER1							XER2							XER3							Regional						
	t_0	t_1	t_2	t_3	t_4	t_5	t_6	t_0	t_1	t_2	t_3	t_4	t_5	t_6	t_0	t_1	t_2	t_3	t_4	t_5	t_6	t_0	t_1	t_2	t_3	t_4	t_5	t_6
Frequency of mortality																												
Negative aridity index (GS)	¤	–	–	–	–	–	–	¤	¤	–	–	–	–	–	¤	–	–	–	–	–	–	¤	–	–	–	–	–	–
Low summer precipitation (December–February)	¤	¤	¤	¤	¤	¤	¤*	–	¤	–	–	–	–	–	§	¤	¤	¤	¤	¤	¤	¤	–	–	–	–	–	–
High summer temperature (December–February)	§	¤	¤	¤	–	–	–	§	§	¤	¤	¤	¤	–	¤	–	–	¤	–	–	–	¤	–	–	–	–	–	–
Positive aridity index (GS)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
High spring precipitation	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
High winter precipitation	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
High snow precipitation (1)	–	§	¤	¤	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
High wind velocities (2)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Snow + wind (1 plus 2)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Frequency of release																												
Negative aridity index (GS)	§	¤	–	–	–	–	–	¤	¤	–	–	–	–	–	–	–	–	–	–	¤	–	–	¤	–	–	–	–	–
Low summer precipitation (December–February)	¤	–	–	–	–	–	–	–	¤	¤	¤	¤	–	–	–	§	§	¤	¤	¤	¤†	¤	§	§	§	¤	¤	¤†
High summer temperature (December–February)	§	¤	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	§	–	–	–	¤	¤	¤	¤	¤
Positive aridity index (GS)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
High spring precipitation	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
High winter precipitation	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
High snow precipitation (1)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
High wind velocities (2)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Snow + wind (1 plus 2)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Tree mortality dates	–	¤	¤	¤	¤	¤	¤	–	–	–	–	§	§	§†	–	¤	–	–	–	–	–	¤	¤	¤	¤	¤	¤	¤†
Frequency of tree establishment																												
Negative aridity index (GS)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	¤	¤	–	–	–	–
Low summer precipitation (December–February)	–	–	–	–	–	–	–	–	¤	–	–	–	–	–	–	¤	¤	¤	¤	¤	¤	§	§	§	§	¤	¤	–
High summer temperature (December–February)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Positive aridity index (GS)	¤	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
High spring precipitation	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
High winter precipitation	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
High snow precipitation (1)	–	–	–	–	–	–	–	–	¤	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
High wind velocities (2)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Snow + wind (1 plus 2)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

Table 1. (*Continued*)

	XER1							XER2							XER3							Regional						
	t_0	t_1	t_2	t_3	t_4	t_5	t_6	t_0	t_1	t_2	t_3	t_4	t_5	t_6	t_0	t_1	t_2	t_3	t_4	t_5	t_6	t_0	t_1	t_2	t_3	t_4	t_5	t_6
Tree mortality dates	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Pre-1950 (+aridity index)	¤	–	–	–	¤	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	§	¤	¤	¤	–	–	–
Post-1950(+aridity index)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Pre-1950 (droughts)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Post-1950 (droughts)	¤	¤	¤	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	¤	–	–	–	–	–

GS, growing season (October–March).
¤Significance at 95%; –independence; §significance at 99%.
*Relationship remaining significant up to t_{10}.
†Relationship remaining significant up to t_9.

to low-summer-precipitation events with time-lags up to 5 years ($P < 0.05$; Table 1). Notably, however, no relationship was found with tree mortality events. When we partitioned the analysis into pre- versus post-1950, positive aridity events (only for pre1950 events) triggered establishment with lagged effects up to 3 years after the climatic event. In contrast, after the 1950s, *N. dombeyi* establishment was associated with dry growing seasons almost exclusively for the stand XER1 (Table 1).

As expected, heat/drought-related climatic events were unrelated to *N. dombeyi* establishment in the wet forest region as well as in each single wet forest stand. Notably, contrasting with xeric forests, establishment events here were highly synchronous with mortality events with lags of up to 6 years after the event ($P < 0.05$). Instantaneous and lagged responses of regional establishment were associated with high-wind events (year 0, $P < 0.05$), high-snow-precipitation events (1- to 2-year lags, $P < 0.01$ and $P < 0.05$) and snow/wind events (1- to 4-year lags; $P < 0.05$, Table 2). Similar relationships were found at the stand scale (Table 2).

Discussion

Our results show that climatic variation over the last century differentially affected tree mortality, canopy disturbance regimes and tree seedling establishment responses of *N. dombeyi* along a west–east precipitation gradient, with possible important implications on forest dynamics.

As we predicted, at the xeric end of the rainfall gradient (coincident with the eastern distributional limit of *N. dombeyi*), regional and local tree mortality and growth responses of subdominant trees were related to drought and heat-related climatic events inducing instantaneous as well as lagged tree mortality and were unrelated to climatic events that can cause mechanical damage to trees such as extreme winds or snowfalls. Establishment, however, had a more complex response to climatic variability: it responded positively to increased moisture periods but there were other sites or periods in which the response (mostly lagged) was mediated by drought or heat events.

The wet-forest behaviour conformed partially to our predictions. As expected, canopy mortality events as well as growth releases were strongly related to climatic events that can damage trees mechanically, such as heavy snowstorms, winter rains, and/or strong wind events. However, heat- and drought-related climatic disturbances were weakly controlling tree mortality in the wet forest as well. In sharp contrast to dry forests, canopy mortality as a whole (irrespective of cause but represented almost always by treefalls) induced sharp instantaneous and lagged responses in tree establishment.

Drought/heat-induced mortality is increasingly being documented in forests worldwide (Allen *et al.* 2010), and dead standing trees are becoming a common feature of forest structure, especially along xeric distributional limits (Allen 2009). The same process seems to be producing abundant dead standing trees along the eastern boundary of the *N. dombeyi* species distribution in northern Patagonia. Although it may be

Table 2. Bivariate event analysis relating frequency (number of individuals year^{-1}) of tree mortality, release and tree establishment dates with climatic event records for wet region. Synchrony between records are shown from t_0 (year of the event) to t_6 (6 years following the event). Climatic events in the first column correspond to the event inspected as key responsible for the analysed pattern. Underlined symbols indicate synchronies analysed using fallen trees only

	WET1							WET2							WET3							Regional						
	t_0	t_1	t_2	t_3	t_4	t_5	t_6	t_0	t_1	t_2	t_3	t_4	t_5	t_6	t_0	t_1	t_2	t_3	t_4	t_5	t_6	t_0	t_1	t_2	t_3	t_4	t_5	t_6
Frequency of mortality																												
Negative aridity index (GS)	§	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Low summer precipitation (December–February)	¤	–	–	–	–	–	–	§	¤	–	–	–	–	–	–	–	–	–	–	–	–	§	–	–	–	–	–	–
High summer temperature (December–February)	¤	¤	–	–	–	–	–	–	¤	–	¤	–	–	–	§	¤	¤	¤	–	–	–	–	–	–	–	–	–	–
Positive aridity index (GS)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
High spring precipitation	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	¤	¤	¤	¤	¤
High winter precipitation	–	–	–	–	–	–	–	–	–	–	–	–	–	–	¤̲	–	–	–	–	–	–	–	–	–	–	–	–	–
High snow precipitation (1)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	¤̲	–	–	–	–	–	¤	–	–	–	–	–	–
High wind velocities (2)	–	¤	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Snow + wind (1 plus 2)	–	–	–	–	–	–	–	–	–	–	¤̲	¤̲	¤̲	¤̲	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Frequency of release																												
Negative aridity index (GS)	–	–	–	¤	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Low summer precipitation (December–February)	–	–	–	¤	–	–	–	–	–	–	–	–	–	–	–	¤	¤	–	–	–	–	–	¤	¤	¤	¤	¤	–
High summer temperature (December–February)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	¤	–	–	–	–	–	–	–	–	–	–	–
Positive aridity index (GS)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
High spring precipitation	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
High winter precipitation	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
High snow precipitation (1)	¤	–	–	–	–	–	–	¤	–	–	–	–	–	–	–	–	–	–	–	¤	–	¤	–	–	–	–	–	–
High wind velocities (2)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Snow + wind (1 plus 2)	¤	¤	–	–	–	–	–	¤	–	–	–	–	–	–	¤	¤	¤	§	¤	¤	–	¤	¤	–	–	–	–	–
Tree mortality dates	–	–	–	–	–	–	–	–	¤	¤	¤	¤	¤	–	–	–	–	–	–	–	¤	¤	¤	¤	¤	¤	¤	¤
Frequency of tree establishment																												
Negative aridity index (GS)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Low summer precipitation (December–February)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
High summer temperature (December–February)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Positive aridity index (GS)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
High spring precipitation	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
High winter precipitation	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
High snow precipitation (1)	–	–	¤	–	–	–	–	–	¤	¤	¤	–	–	–	§	¤	–	–	–	–	–	–	§	¤	–	–	–	–

Table 2. (*Continued*)

	WET1							WET2							WET3							Regional						
	t_0	t_1	t_2	t_3	t_4	t_5	t_6	t_0	t_1	t_2	t_3	t_4	t_5	t_6	t_0	t_1	t_2	t_3	t_4	t_5	t_6	t_0	t_1	t_2	t_3	t_4	t_5	t_6
High wind velocities (2)	–	–	–	–	–	–	–	¤	¤	¤	¤	–	–	–	¤	¤	¤	–	–	–	–	¤	–	–	–	–	–	–
Snow + wind (1 plus 2)	–	–	–	–	–	–	–	–	–	¤	–	–	–	–	¤	–	¤	–	–	–	–	–	¤	¤	¤	¤	–	–
Tree mortality dates	§	¤	§	§	§	¤	–	–	¤	¤	¤	¤	¤	¤*	–	–	–	¤	¤	¤	¤†	¤	¤	¤	¤	¤	¤	¤

GS, growing season (October–March).
§Significance at 99%; –independence; ¤significance at 95%.
*Relationship remaining significant up to t_{10}.
†Relationship remaining significant up to t_{13}.

tempting to say that these processes are becoming more prevalent under current warming trends (e.g. 1998–99 heat/drought), our data show that drought has recurrently produced (at least during the last century) tree death along the xeric end of the gradient. Furthermore, recurrent droughts may induce additive effects in which trees may spiral into increasing crown dieback, growth suppression followed by eventual death intertwining wet or normal years between droughts (Bigler *et al.* 2007) or as a result of later droughts (Suarez, Ghermandi & Kitzberger 2004).

As in many forests, canopy opening as a consequence of tree mortality represents an opportunity for new establishment and release in growth of understorey components (trees and shrubs; Clinton & Boring 1994). Canopy opening due to *N. dombeyi* drought/heat mortality seems to have triggered strong responses not only of pre-existing individuals of *N. dombeyi* but also probably of the co-dominant conifer *A. chilensis*, as well as many understorey shrubs. If these responses continue, they may induce important changes in the dominance of *Nothofagus*, and could even shift some forest stands to shrublands (Suarez & Kitzberger 2008). The highly variable *N. dombeyi* seedling establishment behaviour we observed seems to suggest that light and water may constitute hierarchically limiting factors, and a single canopy opening is not enough for establishment unless favourable climatic conditions (humid) predominate (Kimmins 1997). In this context, site variability and/or long-term climate trends may play a much greater role in *N. dombeyi* post-drought reestablishment than the mortality event itself. However, it remains unclear whether recruitment pulses could occur in the absence of major mortality events, because the reliable period of the mortality record is too short. These results are similar to those reported by Villalba & Veblen (1997, 1998) for the *A. chilensi* xeric limit along the same gradient. Overall, the vegetation trajectory along the eastern boundary of the species will be controlled by (i) the composition of pre-existing species (Suarez & Kitzberger 2008), (ii) the magnitude of canopy opening as a result of the frequency and severity of drought and/or heat climatic disturbances inducing growth responses of understorey vegetation, and (iii) transient humid periods inducing *N. dombeyi* seedling establishment (but possibly also *Austrocedrus*; Villalba & Veblen 1997; Kitzberger, Steinaker & Veblen 2000).

Although not exclusively, climatic events that inflict mechanical damage to trees (snow, rain or wind storms) were the main agents of tree mortality and/or canopy opening in the wet *N. dombeyi* forests. *Nothofagus dombeyi*, an evergreen species, is subject to larger and heavier snow loads (Armesto & Fuentes 1988) than are deciduous trees with bare branches. In addition, the branch architecture of these trees exhibits horizontal branches that are susceptible to suffering extensive branch breakage or even whole canopy vertical collapses during wet-snow events. *Nothofagus dombeyi* trees are also susceptible to uprooting due to strong winter wind or rain storms especially when rain saturates the soil around the root crown. Our data showed that snow and/or wind events were not important as synchronizers of tree mortality in wet forests, except for extreme events such as the winters of 1984 and 1995.

However, strongly synchronized tree releases and seedling establishment events across the wet region suggest that heavy snow events may still exert important controls on forest dynamics by creating canopy openings through branch breakage in addition to whole tree mortality. Quite surprisingly, heat and drought events were at least as important factors of tree mortality in wet forests as mechanically important climatic events. Both growth releases and new seedling establishment were important responses to these canopy opening events as expected for forests dominated by shade-intolerant species and where light availability is the limiting factor (Lorimer & Frelich 1989).

Numerous analyses of the possible impacts of future climatic changes on tree species composition consider only changes in the average of climatic parameters over time (e.g. VEMAP Members 1995; Shugart & Smith 1996). Specifically, changes in extreme weather events and in duration of time periods exceeding biological thresholds for temperature or precipitation are often neglected in future climate scenarios, but may be crucial components for predicting biological responses (Bugmann & Pfister 2000). This and many other case studies performed show that forest ecosystems (i.e. their turnover rates, compositional changes) are likely more sensitive to climatic extremes rather than to slow, gradual changes in climatic trends. However, detailed studies are needed in order to explain how slow, gradual change combined with nonlinear responses could contribute to the observed patterns. In this case, we show that climatic variability can have different expressions and differential consequences on species in different portions of their ranges, resulting in possible community and ecosystem-level changes. Forest dynamics at range boundaries of dominant trees where water availability is the limiting resource are generally more affected by growing season climatic conditions (rainfall, temperature, water balance) producing lethal events when physiological thresholds are surpassed (Hoffmann & Parsons 1997; Parmesan, Root & Willig 2000). In contrast, in more productive central areas of species distributions, where individuals grow faster, are taller and more limited by light rather than water, forest dynamics are generally more affected by weather events that cause severe mechanical damage when physical (structural) resistance thresholds are exceeded. These physical disturbances become less important towards the dry distributional limit of the species for at least two reasons: climatic events have less force (e.g. lesser amounts of rain and snow) and/or trees grow more slowly and are not as tall as at the wet sites, have less foliage in relation to roots and are thus more resistant to pruning or wind-throw.

Community and ecosystem responses to climatic variability and climatic extremes along the precipitation gradient are different as well. At the xeric end, the relatively high frequency of heat or drought-related *N. dombeyi* mortality events are capable of producing important reductions in the cover of broadleaved evergreen trees, potentially benefiting other co-dominants and shrubs all of which respond vigorously to *N. dombeyi* drought gap opening (Suarez & Kitzberger 2008). Thus, community shifts towards a more open structure with more xeric trees and shrubs, possibly also enhancing fire frequency due to higher fine fuel continuity of these systems, may be expected for the xeric end of this ecosystem. Long-term vegetation changes towards resprouting shrublands will ultimately take place if after drought-mortality events rainfall conditions continue to be dry over extended periods (multi-year periods to decades), restricting recruitment of fire sensitive seeders such as *N. dombeyi* and *A. chilensis* and/or inducing recurrent fires. In contrast, at the centre of the *N. dombeyi* distribution, recurrent severe heat/drought events as well as severe pluvial periods with wet snowy winters related to strong westerly circulation do not produce major community changes but have important consequences for gap turnover rates, rates of tree mortality and establishment and accelerating forest carbon cycling.

Although it is clear that climate controls the distribution of many plants, it is becoming increasingly apparent that extreme climatic events are important drivers of vegetation change and species distributions (Allen & Breshears 1998; Kelly & Goulden 2008). Considering that recent extreme droughts had their strongest negative impact on *N. dombeyi* populations at the eastern distributional limits, a potential redistribution of this species as a consequence of climate change is expected. For eastern populations, we hypothesize that range contractions will occur rapidly, with accelerated mortality and lower recruitment rates that result in shifting towards *A. chilensis*-dominated forest or shrublands. In western wet forests, however, the projected increases in climatic fluctuations may result in a more dynamic forest in which dead standing trees, drought-killed or partially dead trees, and snow-pruned trees would be more commonplace.

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References

Allen, C.D. (2009) Climate-induced forest dieback: an escalating global phenomenon? *Unasylva*, **60**, 43–49.

Allen, C.D. & Breshears, D.D. (1998) Drought-induced shift of a forest-woodland ecotone: rapid landscape response to climate variation. *Proceeding of the National Academy of Sciences of the United States of America*, **95**, 14829–14842.

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

Amoroso, M.M. & Daniels, L.D. (2010) Cambial mortality in declining *Austrocedrus chilensis* forests: implications for stand dynamics. *Canadian Journal of Forest Research*, **40**, 885–893.

Armesto, J.J. & Fuentes, E.R. (1988) Tree species regeneration in a mid-elevation, temperate rain forest in Isla de Chiloé, Chile. *Vegetatio*, **74**, 151–259.

Bigler, C. (2006) *CrossdateR: A Visualization Tool to Assess the Quality of Crossdated Tree-ring Series*. Institute of Terrestrial Ecosystems, ETH Zurich, Zurich.

Bigler, C., Gavin, D.G., Gunning, C. & Veblen, T.T. (2007) Drought induces lagged tree mortality in a subalpine forest in the Rocky Mountains. *Oikos*, **116**, 1983–1994.

Bugmann, H. (1996) A simplified forest model to study species composition along climate gradients. *Ecology*, **77**, 2055–2074.

Bugmann, H. & Pfister, C. (2000) Impacts of interannual climate variability on past and future forest composition. *Regional Environmental Change*, **1**, 112–125.

Clinton, B.D. & Boring, L.R. (1994) Regeneration patterns in canopy gaps of mixed-oak forests of the southern Appalachians: influences of topographic position and evergreen understory. *American Midland Naturalist*, **132**, 308–319.

Cook, E.R. & Krusic, P.J. (2006) *ARSTAN_41: A Tree-Ring Standardization Program Based on Detrending and Autoregressive Time Series Modeling, with Interactive Graphics*. Tree-Ring Laboratory, Lamont Doherty Earth Observatory of Columbia University, New York.

De Fina, A.L. (1972) El clima de la región de los bosques Andino-Patagónicos. *La región de los bosques andino-patagónicos, Sinopsis General* (ed. M.J. Dimitri), pp. 35–58. Instituto Nacional de Tecnología Agropecuaria, Buenos Aires.

De Martonne, E. (1926) Areisme et indices d'aridité. *Academié des Sciences, Comptes Rendus*, **182**, 1395–1398.

Drobyshev, I., Dobrovolsky, A. & Neshataev, V. (2009) Tree mortality in a mixed deciduous forest in Northwestern Russia over 22 years. *Annals of Forest Science*, **66**, 411.

Duncan, R.P. (1989) An evaluation of errors in tree age estimates based on increment cores in kahikatea (*Dacrycarpus dacrydioides*). *New Zealand Natural Science*, **16**, 31–37.

Garibaldi, L., Kitzberger, T., Mazía, C.N. & Chaneton, E.J. (2010) Nutrient supply and bird predation additively control insect herbivory and tree growth in two contrasting forest habitats. *Oikos*, **119**, 337–349.

Gavin, D.G. (2007) *K1D: Multivariate Ripley's K-function for One-dimensional Data*. Department of Geography, University of Oregon, Eugene.

Hoffmann, A.A. & Parsons, P.A. (1997) *Extreme Environmental Change and Evolution*. Cambridge University Press, Cambridge.

Holmes, R.L. (1983) Computer-assisted quality control in tree-ring dating and measurement. *Tree-Ring Bulletin*, **43**, 69–75.

Holmes, R.L. (1992) *Dendrochronology Program Library User's Manual*. Laboratroy of Tree-Ring Research University of Arizona, Tucson.

IPCC (2007) *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Forth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge.

Kelly, A.E. & Goulden, M.L. (2008) Rapid shifts in plant distribution with recent climate change. *Proceeding of the National Academy of Sciences of the United States of America*, **105**, 11823–11826.

Kimmins, J.P. (1997) *Forest Ecology*, 2nd edn. Prentice Hall, Upper Saddle River, NJ.

Kitzberger, T., Steinaker, D.F. & Veblen, T.T. (2000) Effects of climatic variability on facilitation of tree establishment in northern Patagonia. *Ecology*, **81**, 1914–1924.

Lloret, F., Peñuelas, J. & Estiarte, M. (2005) Effects of vegetation canopy and climate on seedling establishment in Mediterranean shrubland. *Journal of Vegetation Science*, **16**, 67–76.

Lorimer, C.G. & Frelich, L.E. (1989) A methodology for estimating canopy disturbance frequency and intensity in dense temperate forests. *Canadian Journal of Forest Research*, **19**, 651–663.

van Mantgem, P.J., Stephenson, N.L., Byrne, J.C., Daniels, L.D., Franklin, J.F., Fulé, P.Z., Harmon, M.E., Larson, A.J., Smith, J.M., Taylor, A.H. & Veblen, T.T. (2009) Widespread increase of tree mortality rates in the Western United States. *Science*, **323**, 521–524.

Mazía, C.M., Kitzberger, T. & Chaneton, E.J. (2004) Interannual changes in folivory and bird insectivory along a natural productivity gradient in northern Patagonian forests. *Ecography*, **27**, 29–40.

Nowacki, G.J. & Abrams, M.D. (1997) Radial-growth averaging criteria for reconstructing disturbance histories from presettlement-origin oaks. *Ecological Monographs*, **67**, 225–249.

Pacala, S.W., Canham, C.D., Saponara, J., Silander., J.A., Jr, Kobe, R.K. & Ribbens, E. (1996) Forest models defined by field measurements: estimation, error analysis and dynamics. *Ecological Monographs*, **66**, 1–43.

Parmesan, C., Root, T.L. & Willig, M.R. (2000) Impacts of extreme weather and climate on terrestrial biota. *Bulletin of the American Meteorological Society*, **81**, 443–450.

Schulman, E. (1956) *Dendroclimatic Changes in Semiarid America*. University of Arizona Press, Tucson.

Shugart, H.H. (1984) *A Theory of Forest Dynamics. The Ecological Implications of Forest Succession Models*. Springer, New York.

Shugart, H.H. & Smith, T.M. (1996) A review of forest patch models and their application to global change research. *Climate Change*, **34**, 131–153.

Stokes, M. & Smiley, T. (1968) *An Introduction to Tree-ring Dating*. University of Chicago Press, Chicago.

Suarez, M.L. (2009) *Efecto de las fluctuaciones climáticas sobre la dinámica de bosques de* Nothofagus dombeyi *a lo largo de un gradiente ambiental, en el norte de la Patagonia, Argentina*. PhD Thesis, Universidad Nacional del Comahue, San Carlos de Bariloche.

Suarez, M.L. (2010) Tree-ring records from *Nothofagus dombeyi*: a preliminary chronology network in Northern Patagonia, Argentina. *Dendrochronologia*, **28**, 65–72.

Suarez, M.L., Ghermandi, L. & Kitzberger, T. (2004) Factors predisposing episodic drought-induced tree mortality in *Nothofagus* – site, climatic sensitivity and growth trends. *Journal of Ecology*, **92**, 954–966.

Suarez, M.L. & Kitzberger, T. (2008) Recruitment patterns following a severe drought: long-term compositional shifts in Patagonian forests. *Canadian Journal of Forest Research*, **38**, 3002–3010.

Telewski, F.W. (1993) Determining the germination date of woody plants: a proposed methods for locating the root/shoot interface. *Tree-Ring Bulletin*, **53**, 13–16.

Veblen, T.T. (1989) *Nothofagus* regeneration in treefall gaps in northern Patagonia. *Canadian Journal of Forest Research*, **19**, 365–371.

VEMAP Members (Melillo, J.M., Borchers, J., Chaney, J., Fisher, H., Fox, S. *et al.*) (1995) Vegetation/Ecosystem Modeling and Analysis Project (VEMAP): comparing biogeography and biogeochemistry models in a continental-scale study of terrestrial ecosystem responses to climate change and CO2 doubling. *Global Biogeochemical Cycles*, **9**, 407–437.

Villalba, R. & Veblen, T.T. (1997) Regional patterns of tree population age structures in northern Patagonia: climate and disturbance influences. *Journal of Ecology*, **85**, 113–124.

Villalba, R. & Veblen, T.T. (1998) Influences of large-scale climatic variability on episodic tree mortality in northern Patagonia. *Ecology*, **79**, 2624–2640.

Woodward, F.I. (1987) *Climate and Plant Distribution*. Cambridge University Press, Cambridge.

Wunder, J. (2007) *Conceptual advancement and ecological applications of tree mortality models based on tree-ring and forest inventory data*. PhD Thesis, ETH, Zurich.

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