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Nothofagus dombeyi regeneration in declining *Austrocedrus chilensis* forests: Effects of overstory mortality and climatic events

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ABSTRACT

This research examines the regeneration dynamics of *Nothofagus dombeyi* and *Austrocedrus chilensis* in *A. chilensis*-dominated forests growing near the eastern limit of *N. dombeyi* where precipitation is limiting. In these forests the widespread decline and mortality of overstory *A. chilensis* trees, known as '*mal del ciprés*' (cypress sickness), generates large canopy gaps in which new individuals establish. Our objective was to study the population dynamics of *N. dombeyi* and *A. chilensis* in these forests to investigate the influences of overstory tree death and climatic variation on establishment. We sampled 6 symptomatic *A. chilensis* stands and used dendrochronological techniques to reconstruct basal area development and regeneration establishment over time. Bivariate event analysis was performed to examine the temporal relationships between tree establishment and mortality events and climatic variation. Overstory *A. chilensis* trees established as post-fire cohorts, with subsequent establishment of *A. chilensis* and *N. dombeyi* during the past 50–60 years. Regeneration in the past two decades was primarily *N. dombeyi*. The establishment of both *A. chilensis* and *N. dombeyi* was synchronous with overstory tree mortality events, but it was more consistent among stands and prolonged for *N. dombeyi*. Establishment of *A. chilensis* was not associated with climatic events but *N. dombeyi* establishment was synchronous with droughts, possibly related to climate-driven mortality creating canopy gaps or reducing competition within gaps. We have demonstrated that *N. dombeyi* has the ability to establish in post-fire *A. chilensis*-dominated forests resulting in mixed-species, uneven-aged forests. The ongoing increase in the abundance of *N. dombeyi* relative to *A. chilensis* represents a shift in composition and increased complexity in stand structure driven by '*mal del ciprés*' and climatic variation.

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Introduction

Increases in gap formation and canopy turnover rates may result as a consequence of climate change. Climatically induced regional-scale tree mortality (Suarez et al., 2004; Bigler et al., 2007; van Mantgem et al., 2009; Allen et al., 2010), forest decline (Beier et al., 2008), and severe insect outbreaks (Stahl et al., 2006; Wermelinger et al., 2008; Axelson et al., 2009) have altered the composition and structure of many forests in recent decades. When these types of disturbances affect overstory trees, they result in a more open canopy structure by causing single and multiple-tree gaps to form, which may facilitate tree species that depend on fine-scale disturbance for successful regeneration. The regeneration dynamics of many species in relation to fine-scale disturbance has been well documented and this process maintains many temperate forests in compositional equilibrium (Veblen, 1989a; Rebertus and Veblen, 1993; Lertzman, 1995). However, if canopy gaps become larger or more frequent and gap turnover rates increase over a short period due to altered climate and its interactions with climate-mediated disturbance regimes, then we would expect regeneration dynamics to change. The end result would be stand-to-landscape level shifts in forest composition.

Austrocedrus chilensis and *Nothofagus dombeyi* are endemic species of the Andean Patagonian forests. Both species establish following stand-replacing fires as even-aged, pure or mixed stands (Veblen and Lorenz, 1987; Dezzotti, 1996). Successful establishment of both species also occurs in the understory of mixed *A. chilensis*–dominated forests in the absence of coarse-scale disturbances (Dezzotti, 1996) and in mixed *N. dombeyi–A. chilensis*

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old-growth stands (Veblen, 1989b; Suarez and Kitzberger, 2008). While the processes of population and regeneration dynamics for *N. dombeyi* have been studied in the western and central part of its distribution where this species requires large gaps to establish (Veblen, 1989b; Dezzotti, 1996; Dezzotti and Sbrancia, 2006), little is known about these processes at the eastern, drier limit of its distribution. These locations include sites with as little as 900 mm of precipitation per year that are dominated by *A. chilensis* forests.

A. chilensis forests in Argentina undergo periodic tree mortality known as 'mal del ciprés' (cypress sickness). Mortality is characterized by dispersed declining and dead trees within stands or aggregations of dead trees forming patches (Rosso et al., 1994; La Manna and Rajchenberg, 2004). Tree decline and death are associated with a species of *Phytophthora* (*P. austrocedrae* Gresl. & E.M. Hansen) (Greslebin et al., 2007) and influenced by climatic variation (Amoroso and Larson, 2010b; Mundo et al., 2010). The widespread mortality of overstory trees in these forests results in gaps where individuals establish in the understory (La Manna et al., 2008; Relva et al., 2009; Amoroso and Larson, 2010b). Furthermore, it appears that the patterns of overstory tree mortality affect subsequent recruitment and the species composition of the new individuals (Amoroso and Larson, 2010a). As it is relatively shade-intolerant, *N. dombeyi* cannot regenerate under a closed canopy (Veblen et al., 1981; Veblen, 1989b). In contrast, *A. chilensis* establishment can occur in small canopy gaps or under a closed canopy, due to the fine-scale, gap-phase regeneration mode of this species (Veblen et al., 1995; Gobbi and Schlichter, 1998; Amoroso and Larson, 2010a). The larger canopy openings resulting from increasing levels of overstory tree mortality due to 'mal del ciprés' might facilitate the recruitment and establishment of *N. dombeyi* and create an opportunity for a shift in species composition (Amoroso and Larson, 2010a).

Climate can also affect tree establishment, as successful recruitment is expected to occur during favourable climatic conditions. In Patagonia, the regional climate is relatively warm and dry and soil moisture is limited in many Argentine forests due to the rainshadow of the Andes mountains. Tree establishment occurs in years of favourable climate when moisture is available due to abundant precipitation or low temperatures (Villalba and Veblen, 1997; Kitzberger et al., 2000; Daniels and Veblen, 2004). Specifically, the timing of successful establishment of *A. chilensis* can be strongly influenced by short-term climatic variability at the regional scale (Villalba and Veblen, 1997; Kitzberger et al., 2000), and strong but relatively short climatic fluctuations have impacted local, stand-level forest structure through direct effects on tree demography in mixed *N. dombeyi–A. chilensis* forests (Suarez and Kitzberger, 2010). Yet, little is known about the effects climatic variation may have on the establishment of *N. dombeyi* and *A. chilensis* when it interacts with disturbances such as the canopy gaps caused by 'mal del ciprés'.

While the establishment of *A. chilensis* and other species in the understory as consequence of canopy tree mortality in declining *A. chilensis* forests is likely to occur (La Manna et al., 2008; Relva et al., 2009; Amoroso and Larson, 2010b), the timing and dynamics of these processes are poorly understood (Amoroso and Larson, 2010b). Moreover, less is known about the establishment of *N. dombeyi* following 'mal del ciprés' and how climate may affect the subsequent recruitment of both species. The objective of this study was to investigate the population dynamics of *N. dombeyi* and *A. chilensis* in declining forests affected by 'mal del ciprés'. Specifically, we reconstructed the establishment of the two species through time and investigated the effects of overstory tree death and climatic variation on timing of successful regeneration.

Methods

Study area

This study was conducted at the Reserva Forestal Loma del Medio, which is managed by the National Institute of Agricultural Technology (INTA) and located near El Bolsón, Rio Negro, Argentina (41°46′S 71°33′W). The study area has a mean annual temperature of 9.3 °C and mean annual precipitation of approximately 900 mm (Cordon et al., 1993). Soils are Andisols with deep profiles containing volcanic ash (Lanciotti and Cremona, 1999). The vegetation is characterized as post-fire *A. chilensis*-dominated forests. Although these forests have been classified as dense and pure *A. chilensis* forests (Seibert, 1982; Dezzotti and Sancholuz, 1991), the landscape in the sampling area is a mosaic of pure *A. chilensis* and mixed *A. chilensis–N. dombeyi* stands. Other species such as *Lomatia hirsuta* (Lam.) Diels and *Maytenus boaria* Mol can also be part of the overstory but in co-dominant or intermediate canopy positions.

Sampling

In each of six stands we established a 1000 m² plot. Plots were square (31.63 m × 31.63 m) or rectangular (40.0 m × 25.0 m), depending on the local topography. In each plot, all living trees, snags and logs with a diameter at breast height (DBH) larger than 5 cm were tagged and we recorded species and DBH (cm). All living and dead *A. chilensis* and *N. dombeyi* trees were cored to reconstruct basal area increments and to determine year of death. Cores were taken perpendicular to the slope and approximately 30 cm above the ground. More than one core was taken from each tree to ensure that the cores included the pith and sound sapwood and bark to guarantee that the outer-most ring was present (Amoroso and Daniels, 2010). Transverse cross-sections were taken from 42 individuals where a good quality core could not be extracted because the bark and wood were decayed.

Within each plot, nine circular 30 m² subplots (radius = 3.09 m) were established 10 m apart in a grid to assess the composition of the tree regeneration. In each subplot, the species of all seedlings and saplings taller than 10 cm in height and with a DBH smaller than 5 cm was recorded. All seedlings and saplings taller than 50 cm in height were cut at the root collar to obtain cross-sections for age determination.

Dendrochronological methods

We mounted all cores and glued cross-sections to wooden boards and sanded them following standard dendrochronological methods (Stokes and Smiley, 1996). From each cross-section we selected two radii to be measured. To ensure comparability with the increment cores we used the following criteria: the two radii were (a) perpendicular to the slope to avoid compression wood and (b) included sound sapwood and bark. All cores and radii were visually cross-dated and ring-width series were measured on a Velmex bench to the nearest 0.01 mm. All ring-width series were statistically cross-dated using the program COFECHA (Grissino-Mayer, 2001) and an existing master chronology for *A. chilensis* (R. Villalba: International Tree-Ring Data Bank, NOAA, ftp://ftp.ncdc.noaa.gov/pub/data/paleo/treering/measurements/southamerica/arge080.rwl). Ring-width series that did not cross-date statistically or presented low correlation coefficient values were visually cross-dated only. Mortality dates were the calendar year of the outermost ring of the cross-dated ring-width series from snags and logs. For individual trees, snags and logs, the ring-width series were converted to cumulative basal area (BA).

At the stand level, we reconstructed living BA per hectare for each species per year.

At the stand level, we calculated the mean ($\pm$ standard deviation) abundance of regeneration of each species and compared the means using the Mann–Whitney–Wilcoxon test for pair-wise comparisons. The cross-sections from the subset of seedlings and saplings taller than 50 cm were sanded. For each individual, the rings were counted using a microscope to determine the year of establishment corresponding to the calendar year of the pith. The resulting establishment dates were combined by stand into frequency distributions to examine tree recruitment in each year.

Climate and tree demography

We performed bivariate event analysis (BEA) using K1D software (Gavin, 2007) to test for temporal relationships between regeneration establishment and (a) climatic variation and (b) overstory tree mortality. BEA is a temporal variant of spatial analysis based on Ripley's K function, and has been used to examine the temporal relationships (synchrony and lags) between climate events and forest demography and disturbance (Gavin et al., 2006; Bigler et al., 2007). In this study, the climatic records were from Bariloche, Rio Negro, Argentina and included mean monthly temperature and total monthly precipitation for the last 100 years (Bariloche Airport station, 41°07′55″S 71°18′27″W). From these records we calculated total summer precipitation (sum of December through February monthly values), mean summer temperature (average of December through February monthly values), and monthly values of De Martonne's (1926) aridity index for 1914–2006 from which we derived a mean growing season aridity index (the average of the October through March monthly values). For each of these three climatic variables, we identified climatic events, defined as the years in which calculated values were at least ± 1 standard deviation (SD) from the mean of the full record. Six sets of climatic events were considered: wet/dry summers, hot/cool summers and arid/humid growing seasons. The mortality records, derived from the reconstructed years of death, were the year overstory *A. chilensis* trees died in each stand. The forest demography data were the number of seedlings and saplings of each species that established in each year in each stand.

Assuming a one-directional process in which regeneration establishment co-occurs with or follows a particular climatic or overstory mortality event, we used the forward selection procedure of the K1D software (Bigler et al., 2007). For each relationship, we calculated the L function which is derived from the bivariate K function as follows: $L_{AB}(t) = K_{AB}(t)/2 - t$, where the 'B' regeneration events co-occur or follow the 'A' climatic or mortality events, and t is the 'temporal window' (Gavin, 2007). Confidence envelopes (95%) for each function were calculated by Monte Carlo simulations with 1000 replicates that were randomly selected without replacement from the climatic or mortality records. Calculated L function values above the upper confidence limit indicated synchrony between the climatic/mortality events and regeneration establishment; values below the lower confidence limit indicate asynchrony of the events; and, values between the confidence limits indicate the events occur independently of each other.

Results

Overstory composition and establishment

The reconstruction of the cumulative basal area of living trees depicted differences in establishment times of the overstory species in all six study stands (Fig. 1). The dominant *A. chilensis*

Table 1

Associations between stand-level *A. chilensis* and *N. dombeyi* establishment (number of individuals year^{-1}) and overstory tree mortality events determined using bivariate event analysis (BEA). Synchronous associations were significant but independent associations were not significant ($\alpha = 0.05$); asynchronous associations were not detected. Temporal window encompass the mortality event (t_0) and 14 subsequent years, where t_1 = the first year after the event, t_2 = second year after the event, etc.

Species	Plot	Type of association	Temporal window
A. chilensis	CE2	Independent	None
A. chilensis	K1	Synchronous	$t_1 - t_9$
A. chilensis	EU1	Synchronous	t_0
A. chilensis	EU2	Independent	None
A. chilensis	RQ1	Synchronous	$t_4 - t_9$
A. chilensis	RQ2	Synchronous	$t_0 - t_1 - t_3 - t_4$
N. dombeyi	CE2	Synchronous	$t_3 - t_{14}$
N. dombeyi	K1	Synchronous	$t_0 - t_2 - t_{14}$
N. dombeyi	EU1	Synchronous	$t_0 - t_{12}$
N. dombeyi	EU2	Synchronous	$t_0 - t_{14}$
N. dombeyi	RQ1	Synchronous	$t_2 - t_{14}$
N. dombeyi	RQ2	Synchronous	$t_9 - t_{14}$

in the overstory were fast-growing trees that likely established following stand-replacing fires. Overstory *N. dombeyi* trees established after the *A. chilensis* cohort in all stands. *N. dombeyi* trees exhibited the same diameter ranges as *A. chilensis* (not shown), but *N. dombeyi* accounted for a smaller proportion of the total basal area given its lower density at all sites, except stand EU2. In stand EU2, *N. dombeyi* trees were present only in the smallest and largest diameter classes (not shown). All other species, *L. hirsuta*, *Schinus patagonicus* and *Aristotelia chilensis* Stunt, formed a minor component of the stands, were limited to small diameter classes, and were not competing with *A. chilensis* and *N. dombeyi* in the upper canopy.

In addition to differences in establishment, the basal area reconstructions depicted the increasing proportion of *N. dombeyi* relative to *A. chilensis* as overstory *A. chilensis* trees began to die (Fig. 1). In most stands, the relative basal area of *A. chilensis* became more variable and started to decrease around the 1950–1960s as trees died. Concurrently, the relative basal area of *N. dombeyi* increased over time to an average of 21% (range of 2–35%) of the total basal area of living trees in the stands at the time of sampling in 2005.

Understory composition and establishment

The abundance of regeneration in the understory was variable among the studied stands (Fig. 2). Overall, *A. chilensis* seedlings and saplings were more abundant than *N. dombeyi* regeneration in most stands, but the differences were significant in stand K1 only ($P = 0.0002$). In stands EU2 and RQ1 the abundance of *N. dombeyi* regeneration was comparable to that of *A. chilensis*.

After the establishment of the current *Austrocedrus*-dominated overstory, both *A. chilensis* and *N. dombeyi* have been successfully establishing in the understory during the last 50–60 years (Fig. 3). While the initial establishment in the understory of all stands was purely *A. chilensis*, most of the establishment during the last 20–25 years was primarily *N. dombeyi*. While variable among stands, successful establishment has been relatively continuous with observations in most years in all stands. Successful establishment during the most recent years is underestimated as only individuals taller than 50 cm were included in the analysis.

Association between understory establishment and death of overstory trees

Within stands, the establishment of both *A. chilensis* and *N. dombeyi* was synchronous with or followed the death of *A. chilensis* overstory trees (Table 1). In the case of *A. chilensis* regeneration, mortality events in the overstory triggered instantaneous (EU1;
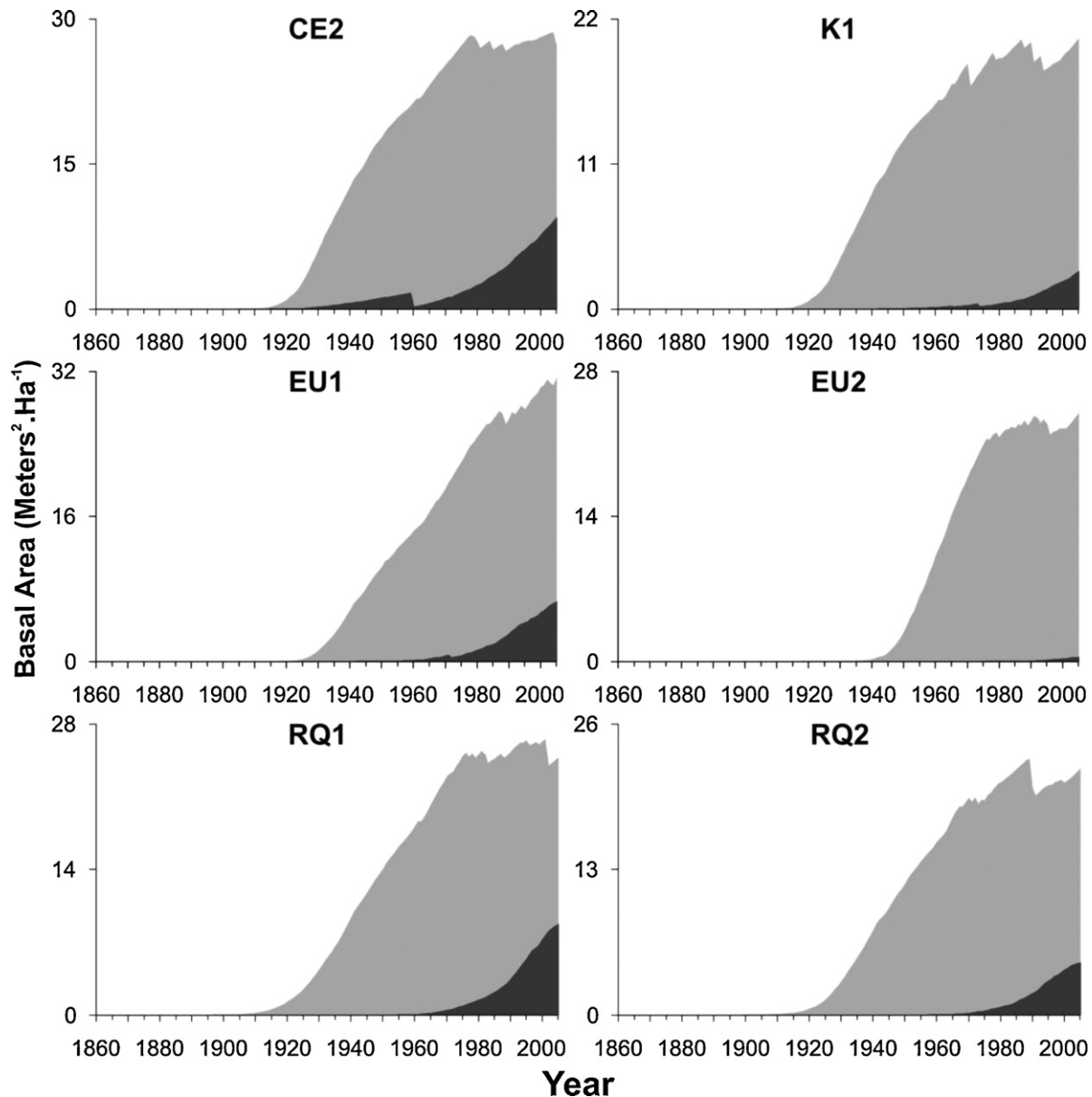
Fig. 1. Living basal area reconstruction of the overstory *N. dombeyi* (black) and *A. chilensis* (grey) trees (>5 cm in DBH) for six *Austrocedrus*-dominated stands.

$P < 0.05$) and lagged (K1, RQ1, RQ2; $P < 0.05$) establishment in the understory. Some establishment occurred up to 9 years after the mortality event. In stands CE2 and EU2, establishment was neither greater nor less than expected during and following mortality of *A. chilensis* overstory trees.

In contrast with *A. chilensis*, the establishment of *N. dombeyi* in the understory consistently showed greater establishment than expected during and following the mortality of *A. chilensis* overstory trees in all stands (Table 1). Elevated rates of *N. dombeyi* establishment continued for up to 30–40 years in individual stands (data not shown; $P < 0.05$).

Association between understory establishment and climatic events

Associations between seedling and sapling establishment and climatic events were more evident for *N. dombeyi* than *A. chilensis*; however, the type of climatic events, direction of associations, and lag times varied among plots (Table 2). Drought events,

indicated by low summer precipitation, high summer temperature and/or high growing season aridity indices were associated with greater than expected *N. dombeyi* establishment (Table 2). For *N. dombeyi* associations with low summer precipitation, we found instantaneous establishment and lags of up to 13 years ($P < 0.05$). In some stands for which this association was not significant, it was close to the upper confidence limit during the first 1–4 years after drought events. For high summer temperature, we found instantaneous establishment and lags of up to 8 years in stand RQ2 ($P < 0.05$). Similarly, for arid growing season, establishment was lagged 1–3 years after drought events in stand (RQ1) ($P < 0.05$).

We found no synchronous associations between *A. chilensis* and *N. dombeyi* establishment and wet, cool summers or humid growing seasons, those with high summer precipitation or low summer temperature (Table 2). Conversely, we found asynchronous associations or less establishment than expected following events with high summer precipitation (stands EU1, RQ1 and RQ2, $P < 0.05$) and humid growing seasons (stand K1, EU1 and RQ1, $P < 0.05$) (Table 2).

Table 2

Significant associations between stand-level *A. chilensis* and *N. dombeyi* establishment (number of individuals year^{-1}) and regional climatic events determined using bivariate event analysis (BEA). Climatic events were years of relatively low/high precipitation or temperature in summer (December to February) and arid/humid growing seasons (October to March). Temporal window encompass the climatic event (t_0) and 14 subsequent years, where t_1 = the first year after the event, t_2 = second year after the event, etc. (α = 0.05).

| Species	Plot	Climatic event	Type of association	Temporal window
A. chilensis	EU1	Low summer precipitation	Synchronous	t_3
A. chilensis	EU1	High summer temperature	Synchronous	t_0
A. chilensis	EU1	High summer precipitation	Asynchronous	t_3-t_{10}
N. dombeyi	CE2	Low summer precipitation	Synchronous	t_3-t_4
N. dombeyi	K1	Arid growing season	Synchronous	t_5
N. dombeyi	K1	Humid growing season	Asynchronous	t_4-t_8
N. dombeyi	K1	Low summer precipitation	Synchronous	t_4-t_{13}
N. dombeyi	EU1	Humid growing season	Asynchronous	t_5-t_6
N. dombeyi	EU1	Low summer precipitation	Synchronous	t_4
N. dombeyi	EU1	High summer precipitation	Asynchronous	t_3-t_{14}
N. dombeyi	EU2	Low summer precipitation	Synchronous	t_0-t_1, t_4
N. dombeyi	RQ1	Arid growing season	Synchronous	t_1, t_3
N. dombeyi	RQ1	Humid growing season	Asynchronous	t_1-t_7
N. dombeyi	RQ1	Low summer precipitation	Synchronous	t_1, t_4, t_9, t_{11}
N. dombeyi	RQ1	High summer precipitation	Asynchronous	t_1-t_{12}
N. dombeyi	RQ2	Low summer precipitation	Synchronous	t_0-t_4
N. dombeyi	RQ2	High summer temperature	Synchronous	t_0-t_8
N. dombeyi	RQ2	High summer precipitation	Asynchronous	$t_{13}-t_{14}$
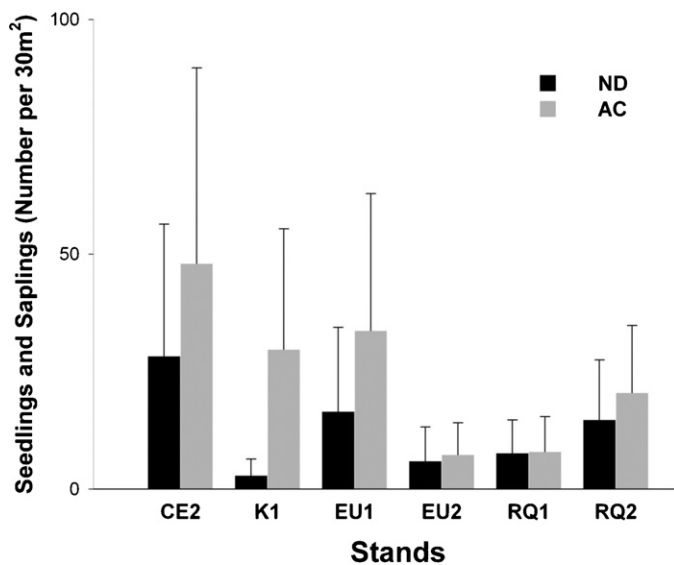
Fig. 2. Total number of *N. dombeyi* (ND) and *A. chilensis* (AC) seedlings and saplings (>10 cm in height and <5 cm in DBH) in the regeneration subplots for six *Austrocedrus*-dominated stands. Vertical bars are mean values and vertical lines are standard deviations.

Discussion

'Mal del ciprés' and stand dynamics

Past research has shown that mortality of overstory trees in *A. chilensis* forests known as 'mal del ciprés' often results in the establishment of new *A. chilensis* in the understory (La Manna et al., 2008; Relva et al., 2009; Amoroso and Larson, 2010b). Our study has demonstrated that the death of overstory trees in *A. chilensis* forests alters the structure of the canopy and generates conditions suitable for the establishment of *N. dombeyi*, in addition to dominant *A. chilensis*. Moreover, based on the increasing mortality rates of overstory *A. chilensis* trees and the successful establishment and survival of *N. dombeyi* after recent droughts, we anticipate a shift in species composition of the forests that we studied.

Based on the reconstruction of canopy-tree basal areas at our study sites, we determined that following stand-replacing fires *A. chilensis* cohorts established and initially dominated the canopy. With the death of overstory trees 50–60 years later, *N. dombeyi* trees established and grew rapidly so that they are similar in size and are currently represented in the same range of diameter classes as the older *A. chilensis* (Amoroso and Larson, 2010b). Additionally, we found substantive recruitment of both *A. chilensis* and *N. dombeyi* seedlings and saplings in the understory. While the proportion of understory *A. chilensis* was greater than that of *N. dombeyi*, this difference appeared to be a result of the timing of successful establishment and subsequent survival of the two species, which we interpreted from the age structure of the understory. Early establishment and survival of seedlings and saplings included only *A. chilensis* while most successful establishment over the last 20–25 years has been *N. dombeyi*. Evidently, as mortality of overstory trees has increased in time resulting in larger canopy gaps and a more open canopy, conditions have become more favourable for the recruitment and establishment of *N. dombeyi* in the understory.

In mesic Andean forests, successful establishment of *A. chilensis* and *N. dombeyi* occurs following stand-replacing fires, resulting in even-aged, stratified stands (Veblen and Lorenz, 1987; Dezzotti, 1996). Both species regenerate successfully in the understory of these mixed forests. In the absence of large-scale disturbances, *N. dombeyi* recruits in both mixed *A. chilensis*-dominated forests (Dezzotti, 1996) and in mixed *N. dombeyi–A. chilensis* old-growth stands (Veblen, 1989b; Suarez and Kitzberger, 2008). In drier forests, the successful establishment of *A. chilensis* in post-fire, pure *A. chilensis* stands is likely to occur in small canopy openings or under a closed canopy (Veblen et al., 1995; Gobbi and Schlichter, 1998; Amoroso and Larson, 2010a). *N. dombeyi*, alternatively, cannot regenerate under a closed canopy (Veblen et al., 1981; Veblen, 1989b) but will establish in small or large gaps in the canopy due to its low shade-tolerance (Veblen et al., 1995; Dezzotti, 1996; Gobbi and Schlichter, 1998; Suarez and Kitzberger, 2008; Amoroso and Larson, 2010a). Establishment of *N. dombeyi* in the understory of pure *A. chilensis* forests near the eastern limit of the forests in Argentina where precipitation is limiting (mean annual precipitation = 900–1200 mm), has not been reported previously.

As we hypothesized, large gaps caused by 'mal del ciprés' developed through time and facilitated the recruitment of *N. dombeyi*. The on-going recruitment of *N. dombeyi* in *A. chilensis*-dominated forests affected by 'mal del cipres' will probably lead to important compositional and structural shifts. To understand this change and anticipate future patterns of stand development in these mixed
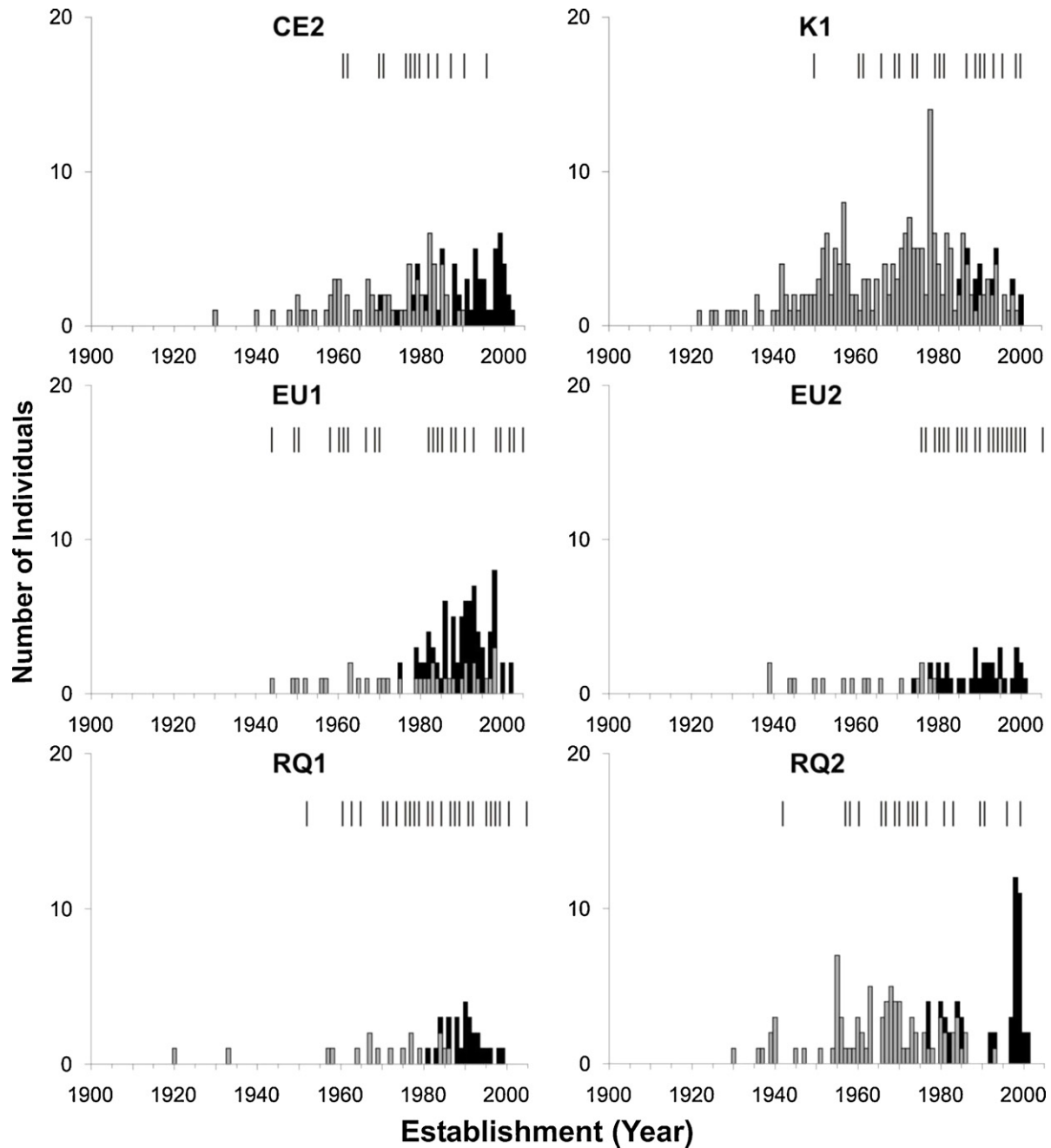
Fig. 3. Establishment dates of *N. dombeyi* (black) and *A. chilensis* (grey) seedlings and saplings (height > 50 cm) in the understory by species for six *Austrocedrus*-dominated stands. Vertical lines indicate dates of overstory tree mortality events.

forests, several aspects regarding the ecology of these two species need to be considered. Due to its high growth rates compared to *A. chilensis* (Dezzotti, 1996), the recruitment of *N. dombeyi* could result in the suppression of *A. chilensis* regeneration and, eventually, overstory trees. Since *N. dombeyi* requires large gaps to establish (Veblen, 1989b; Dezzotti, 1996; Dezzotti and Sbrancia, 2006), the ongoing forest decline and future mortality of overstory trees will generate more suitable conditions for its successful establishment increasing its proportion and dominance in the stands. As *N. dombeyi* continues to grow and recruit into the upper canopy, the forest will become more structurally complex as they will shift from pure even-aged *A. chilensis* forests to uneven-aged mixed-species forests. Increased complexity will include vertical stratification of the canopy. Stratification develops naturally in mixed-species

stands as the result of growth and inter-specific competition (Kelty, 1992; Oliver and Larson, 1996) and depends on the differences in shade tolerance, height growth rates and maximum heights among species (Larson, 1992; Menalled et al., 1998). Moreover, stand development will be influenced by density and the proportion of the component species (Garber and Maguire, 2004; Amoroso and Turnblom, 2006), attributes that vary among forests affected by '*mal del ciprés*' (Amoroso and Larson, 2010b).

Regeneration dynamics

While tree regeneration generally follows the mortality of *A. chilensis* canopy trees affected by '*mal del ciprés*' (La Manna et al., 2008; Relva et al., 2009; Amoroso and Larson, 2010b), the

specific timing of establishment relative to tree death is less well understood (Amoroso and Larson, 2010b). Amoroso and Larson (2010b) found no consistent pattern between the occurrence of mortality events and the timing of establishment of new individuals in the understory. At some sites, understory establishment was significantly related to overstory tree mortality but at other sites it was independent of and even asynchronous relative to tree deaths; however, they did not differentiate between species. In this study, we investigated the regeneration dynamics of the dominant tree species independently and found that the establishment of *N. dombeyi* coincided with or followed the death of overstory trees in all stands, while *A. chilensis* establishment coincided with or exhibited a short lag following the death of overstory trees in only four stands. Our species-specific results are consistent with well-documented patterns of establishment of *A. chilensis* and *N. dombeyi* in relation to disturbance and stand development. *A. chilensis* establishment occurred during the early stages of stand development, at the onset of the overstory tree mortality when tree death was more sporadic and resulted in a minimal degree of canopy disturbance. Furthermore, the establishment of *A. chilensis* can occur in the absence of discrete mortality events and may have preceded the onset of '*mal del cipres*' at some sites (Amoroso and Larson, 2010b). In contrast, most *N. dombeyi* established later following the onset of '*mal del cipres*' when canopy openings were larger, coinciding with the light requirements of this species (Read and Hill, 1985).

The examination of the establishment patterns in relation to climatic events depicted dissimilar results between species. While we did not detect a significant influence of climatic events on *A. chilensis* establishment, the establishment of *N. dombeyi* exhibited some degree of synchrony with climatic variables related to drought. This result was unexpected, given the location of our study sites near the distributional limit of *N. dombeyi*, where precipitation is limiting. For example, recent extreme droughts had strong negative impacts on *N. dombeyi* populations located further north in Patagonia (Suarez and Kitzberger, 2010). Subsequent recruitment and survival of *N. dombeyi* also appears to depend on the occurrence of humid periods following establishment (Suarez and Kitzberger, 2010), a pattern we did not detect in our study area. Our paradoxical results indicate that climatic influences are complex and likely mediated by processes acting at a range of spatial and temporal scales.

In our stand-level study, the observed patterns of *N. dombeyi* establishment coincident with or following droughts was more likely an indirect than direct climatic effect. Specifically, it could be related to three potential mechanisms acting on different processes involved with gap creation and filling: (i) an indirect effect of drought-induced mortality of overstory trees producing canopy gaps available for new regeneration, (ii) an indirect effect of differential drought-induced sapling and shrub mortality reducing competition for new regeneration within gaps, and (iii) a direct effect of higher seed input due to masting events resulting from drought years. Support for the first two mechanisms is from search on *N. dombeyi* in xeric forests in northern Patagonia. In these forests, frequent droughts generate a continuous source of canopy openings in which new regeneration occurs and established vegetation can fill the gap owing to higher growth rates (Suarez and Kitzberger, 2010). In addition, high levels of sapling mortality after severe drought, which reduced competition for water and light, has been documented as a mechanism favouring new recruitment in xeric mixed *N. dombeyi*–*A. chilensis* forests (Suarez and Kitzberger, 2008). Although seed production of some species is stimulated by drought or other forms of stress (Heinemann, 2007), data on seed production are not available for *N. dombeyi* forests to test the third potential mechanism. Therefore, the potential relationships between climate and recruitment mediated by masting are not possible at this time. To fully understand the ongoing changes we have documented in the *A. chilensis* forests will require additional research on the effects of extreme events and long-term climatic variation and their interactions with stand-level processes.

Conclusion

This study shows that *N. dombeyi* has the ability to establish in post-fire *A. chilensis*-dominated forests following the death of overstory trees known as '*mal del ciprés*'. For *N. dombeyi*, regeneration in these forests appears to be the result of a synchrony between mortality events that coincide with drought conditions. Although drought is often considered adverse for successful seeding establishment, in these forests it potentially facilitates regeneration by contributing to canopy gaps and decreasing competition from shrubs and advance regeneration. The observed increase in establishment of *N. dombeyi* during the last two decades probably resulted from larger gaps generated by increased mortality of overstory trees due to '*mal del ciprés*'. Current evidence supports an increase in the abundance of *N. dombeyi* relative to *A. chilensis*, indicating an important compositional shift in these stands over the 100 years since they established. Future development in these mixed-species stands will likely include stratification of the canopy resulting in complex structural patterns.

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