

Self-replacement after small-scale partial crown dieback in austral *Nothofagus dombeyi* forests affected by an extreme drought

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Abstract: The spectrum of structural response in drought-induced mortality (degree of partial crown mortality) could play a key role in pervasive changes in plant composition, as individual openings could reset self-replacement dynamics or trigger shifts in vegetation. Here we capture the community pattern 17 years after a drought episode over a range of canopy responses in *Nothofagus dombeyi* forests. We applied a widespread demographic approach to address evidence of species shifts vs. self-replacement and to relate partial dieback to understory structure and composition. Assuming that the outcome of growth release of the understory components can be observed 17 years after canopy loss, this study reveals evidence of self-replacement in *N. dombeyi* forests heavily affected by drought. Alternatively, when the co-dominant species *A. chilensis* is widely present in the understory and large gaps are opened, a compositional shift may be possible, with a potential change in forest functionality. Individual partial openings do not favor more shrubby communities or a shift toward a new community. Thus, partial crown dieback contributes to self-replacement mechanisms by hampering strong growth release in understory shrubs, as evident in plots with high mortality, and by facilitating the growth of dominant tree species.

Key words: mixed forest, Patagonia, community trend, understory structure, vegetation shifts.

Résumé : L'ampleur de la réaction structurale à la suite de la mortalité causée par la sécheresse (degré de mortalité partielle de la cime) pourrait jouer un rôle dans les modifications généralisées de la composition végétale, étant donné que chaque ouverture pourrait réenclencher la dynamique d'auto-remplacement ou déclencher des modifications de la végétation. Dans cet article, nous cernons le patron de la communauté 17 ans après un épisode de sécheresse pour une gamme de réactions du couvert dominant dans des forêts de *Nothofagus dombeyi*. Nous avons utilisé une approche démographique très répandue pour déceler les indices de modification vs d'auto-remplacement des espèces et pour relier le dépérissement partiel à la structure et à la composition du sous-étage. Prenant pour acquis que le résultat d'une reprise de croissance des composantes du sous-bois peut être observé après la perte du couvert dominant, cette étude révèle des indices d'auto-remplacement dans les forêts de *N. dombeyi* sévèrement touchées par la sécheresse. Alternativement, lorsque l'espèce codominante *Austrocedrus chilensis* est largement présente en sous-étage et que de grandes trouées sont ouvertes, il peut y avoir une modification de la composition accompagnée d'un changement dans la fonction de la forêt. Les ouvertures partielles individuelles ne favorisent pas les communautés qui sont davantage arbustives ni une évolution vers une nouvelle communauté. Par conséquent, le dépérissement partiel de la cime contribue au mécanisme d'auto-remplacement en empêchant une forte reprise de croissance des arbustes en sous-étage, comme cela est évident dans les places échantillons où la mortalité est élevée, et en favorisant la croissance des espèces arborescentes dominantes. [Traduit par la Rédaction]

Mots-clés : forêt mixte, Patagonie, tendance communautaire, structure du sous-étage, modifications de la végétation.

Introduction

Episodes of drought-induced tree mortality have been reported globally for a variety of forest communities (Allen et al. 2010; Greenwood et al. 2017), with great effort devoted in recent years to understanding the mechanism underlying this phenomenon. This growing research area has made important contributions to the interplay between tree carbon and water economies during extreme climatic events and the role of extreme carbon depletion, as well as failures in water and carbohydrate transportation (McDowell et al. 2011; Mencuccini et al. 2015; Pellizzari et al. 2016). Meanwhile, other research revealed a contribution to climate-induced forest die-off by biotic factors (i.e., pest outbreaks, mistletoe), disturbance regime, and previous management practices at both tree and forest community levels (Galiano et al. 2010;

Vilà-Cabrera et al. 2013; Anderegg et al. 2015; Sangüesa-Barreda et al. 2015). As the frequency and intensity of severe droughts are expected to increase in many regions under the ongoing climate change (Intergovernmental Panel on Climate Change (IPCC) 2014), the research agenda has broadened to study the demographic mechanism counteracting the mortality of these events, which can eventually determine thresholds that would trigger vegetation shifts (Lloret et al. 2012).

The loss of dominant overstory species has knock-on effects on the structure and dynamics of affected forests (Ellison et al. 2005). Following tree mortality, a long-term alteration in radiation flux, as well as in chemical and physical soil properties, takes place, with consequences on the associated plant communities (Kane et al. 2011; Royer et al. 2011; Anderegg et al. 2013; Štursová et al. 2014). Increasing near-ground solar radiation increases soil evap-

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oration and understory transpiration, influencing the understory microclimate and potentially regulating the growth and recruitment of understory species (Suarez and Kitzberger 2008; Anderegg et al. 2012). Leaf drop and reduced competition due to mortality can also trigger the release of resources and change nutrient dynamics (Kane et al. 2011; Royer et al. 2011). In austral *Nothofagus dombeyi* forests, these potential modifications to the forest floor happened after a substantial loss of overstory canopy following extreme droughts (Suarez and Kitzberger 2008; Suarez and Sasal 2012); however, the loss of canopy associated with drought-induced episodes reveals a wide range of structural responses, from total loss of leaves to partial crown dieback (sometimes occurring simultaneously), likely reflecting a mismatch between water demand and water availability (Jump et al. 2017). Partial crown dieback seems to be conceivably species-specific and frequent in *Fagaceas* and *Nothofagaceas* (Suarez et al. 2004; Galiano et al. 2010; Rodríguez-Catón et al. 2016). Thus, partial crown dieback, if present, could trigger knock-on mortality effects through the forest understory.

If recovery after drought-induced partial crown dieback occurs or partial crown dieback is low, no major changes can be expected in the understory environment (Lloret et al. 2012; Saura-Mas et al. 2015; Jump et al. 2017); however, when partial crown dieback is high (>50% of crown), an array of physiological and demographic processes can come into play in the understory. A significant growth increase of the woody and (or) herb component of the community underneath (Kane et al. 2011; Anderegg et al. 2012; Suarez and Sasal 2012; Saura-Mas et al. 2015) causes alterations in competitive relationships and produces a decrease in shade-tolerant species below the opened canopy (Olano and Palmer 2003; Suarez and Sasal 2012). Alternatively, the recruitment opportunities for light-demanding species can be jeopardized by dense shrub cover. The overall outcome of all of these interactions resulting from drought-induced forest dieback remains largely unexplored, although it is relevant for determining future vegetation shifts (Beckage et al. 2000; Suarez and Kitzberger 2008). The existence of strong stabilizing processes (i.e., facilitation, competition release, species interaction) acting at different spatiotemporal scales and the pervasive inertia exhibited by long-lived forest systems (Lloret et al. 2012) can compensate for the negative effect of drought mortality by maintaining the composition of vegetation; however, the evidence for drought-induced vegetation shifts is still limited (but see Martínez-Vilalta and Lloret 2016).

Nothofagus dombeyi – *Austrocedrus chilensis* in austral South America is a long-lived forest system that has experienced drought-induced tree mortality in recent decades (particularly in 1998–1999 (Suarez et al. 2004; Suarez and Kitzberger 2010) and in 2014–2015). Drought mortality proved to be species-specific, only affecting the less shade-tolerant and relatively moisture-demanding perennial broadleaf *N. dombeyi*, but fewer effects were observed in the highly shade-tolerant and drought-avoidant conifer *A. chilensis*. Although drought affected large areas, tree mortality was extremely patchy, and there was often a wide spectrum of responses from partial crown defoliation to whole-tree mortality. As a further consequence, lower recruitment and survival rates of *N. dombeyi* were observed in heavily affected patches (Suarez and Kitzberger 2008), possibly due to shrub layer release (Suarez and Sasal 2012); however, partial crown openings may not be large enough to produce shrub release, in contrast with the changes in plant composition previously observed.

Here, we address the response of the understory community (potential replacement by trees and shrubs) to a drought occurring in 1998–1999 in northern Patagonia, Argentina, that affected

mixed *N. dombeyi* – *A. chilensis* forests. We capture the community pattern 17 years after the drought episode in a wide range of canopy responses from healthy canopy to partial crown dieback and gap opening after tree mortality. More specifically, we investigated the following questions to find evidence of species shifts vs. self-replacement in the *N. dombeyi* forests. (Q1) Do canopy conditions determine understory species' replacement? (Q2) Are there any differences in species' ability to achieve canopy after partial crown dieback? (Q3) Does shrub presence influence the ability of dominant tree species to achieve canopy? (Q4) Do understory communities differ according to the degree of dieback? We hypothesize that a wide-ranging demographic approach assessing understory vegetation provides a valuable framework for examining whether partial crown dieback openings reset the self-replacement dynamic or trigger a change in species composition.

Materials and methods

Study area

The study area encompasses the Nahuel Huapi National Park (NHNP) in northern Patagonia, Argentina (Fig. 1). Precipitation in the NHNP is seasonally variable, with approximately 60% falling in May through August (austral autumn–winter). Due to the rain shadow produced by the Andes, mean precipitation decreases from approx. 3000 mm·year⁻¹ on the Andes divide to less than 500 mm·year⁻¹ 100 km away, in a west to east direction (Villalba et al. 2003). Along this environmental gradient, the evergreen broadleaf *N. dombeyi* tree occurs in a variety of environments. On the western slopes of the Andes, mixed rainforests (with *Fitzroya cupressoides* in the moister stands) and pure *N. dombeyi* forests predominate. Eastward — with total annual precipitation ranging from 1200 to 1800 mm — *N. dombeyi* co-occurs with the conifer *Austrocedrus chilensis*. In these forests, the understory commonly includes shrub species (*Maytenus chubutensis*, *Schinus patagonicus*, and *Aristotelia chilensis*), saplings of understory trees (*Luma apiculata* and *Lomatia hirsuta*), and small individuals of the exotics *Pseudotsuga menziesii*, *Rosa rubiginosa*, and *Retama sphaerocarpa*, mostly in sites near urban areas (i.e., houses, campsites).

We conducted the research across the eastward *N. dombeyi* populations, where the broadleaf *N. dombeyi* coexists with the conifer *A. chilensis* and where the effect of drought was high (Bran et al. 2001). The most important mortality event occurred during strong La Niña conditions in 1998–1999, although other less severe events, as well partial crown dieback and scattered mortality, occurred in the subsequent years (Suarez and Kitzberger 2010). For this study, target trees were those that exhibited a variety of tree-level responses, ranging from healthy trees to trees displaying partial dieback to dead trees likely resulting from the 1998–1999 drought. To avoid trees that died recently or a long time before such date, we selected trees depicting branches with no bark but still bearing twigs.

Data collection

We sampled a total of 527 points corresponding to focal *N. dombeyi* trees located along six sites in NHNP (Fig. 1). The site and stand characteristics are available from previous studies (Suarez and Kitzberger 2008; Suarez and Sasal 2012) and covered a range of different environmental conditions and degrees of affectation after the drought episode; we present a brief description of the sites' characteristics in Table 1. In each site, we regularly sampled focal trees every 20–30 m along a transect established in an area with no sign of recent disturbance (i.e., fire, logging). We characterized each focal tree according to its height and degree of partial crown dieback (0, healthy crown; 1, <25% dead crown; 3, 25%–50% dead

Fig. 1. Map of the study area in northern Patagonia, Argentina. Vertical gray lines determine the area affected by drought in the studied austral forests, specifically showing the *N. dombeyi* (gray) and *A. chilensis* (black) species distribution in the area. Panels on the right depict a detailed area and the location of sampled transect of each stand.

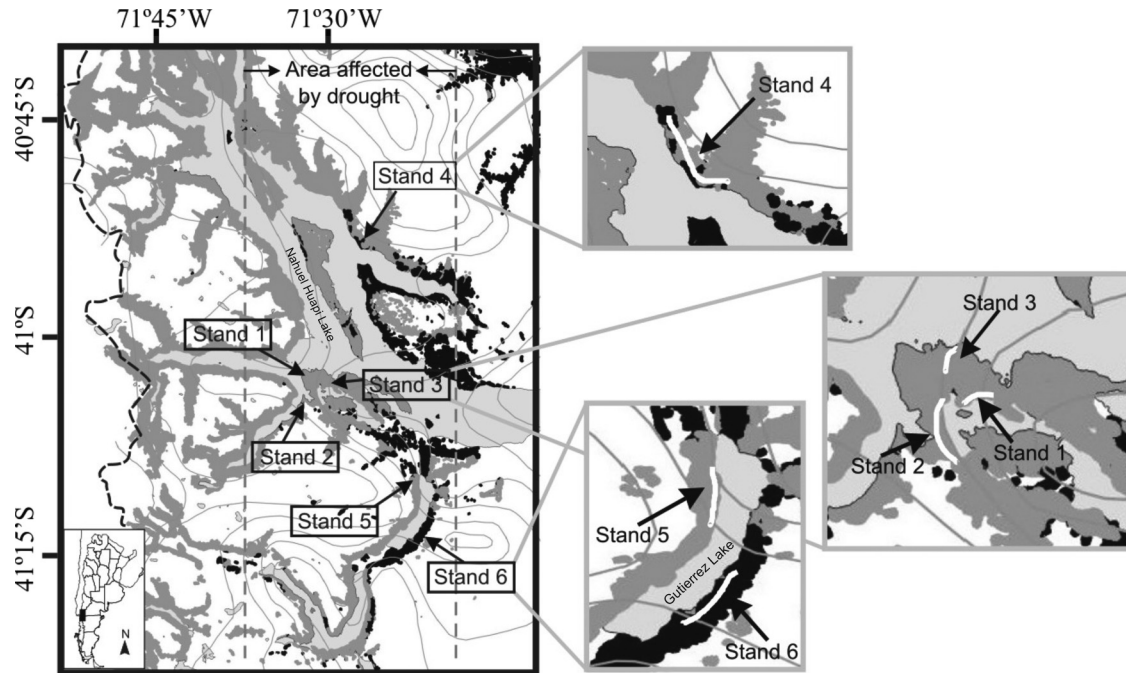


Table 1. Stand and topographic characteristics of sampled stands in NHNP.

Stand	Location	Elevation (m a.s.l.)	Stand density (trees-ha ⁻¹)	<i>A. chilensis</i> (% in canopy)	Canopy height (m)	No. of trees	Drought-induced mortality (%)	Precipitation (mm)
Stand 1	41°0.3'S, 71°32'W	830	396	17	27.8 (±5.1)c	89	Isolated trees	147
Stand 2	41°0.3'S, 71°33'W	850	363	25	17.2 (±1.6)a,b	52	Isolated trees to <25	167
Stand 3	41°0.2'S, 71°33'W	840	355	37	19.7 (±3.9)a	29	<25 to 25–50	139
Stand 4	40°52'S, 71°30'W	795	300	29	21.4 (±3.9)a,e	66	25–50	125
Stand 5	41°10'S, 71°24'W	855	386	37	23.6 (±4.5)e	166	25–50 to 50–75	118
Stand 6	41°12'S, 71°24'W	820	325	50	14.7 (±5.5)d	124	50–75	116

Note: Stand density: data from Suarez and Kitzberger (2008) and Suarez (2009). Percentage of *A. chilensis* in the canopy: data from Suarez and Kitzberger (2008) and Suarez (2009). Lowercase letters following canopy height indicate post-hoc pairwise comparisons using Bonferroni adjustment. Drought-induced tree mortality degree is according to the map of the area affected by drought in NahuelHuapi National Park by Bran et al. (2001) and further assessed visual estimation of mortality by Suarez (2009). Precipitation: data from WorldClim 1.4 database, BIO18 = precipitation of warmest quarter.

crown; 4, 50%–75% dead crown; 5, >75% dead crown; 6, fully defoliated crown). Focal trees served as the center of a 3 m radius plot, always confined to the canopy projection at each focal tree. In each plot, we registered species identity, height, and number of all trees, saplings (diameter at breast height < 0.05 m and height < 3 m), and large shrubs. Because we focused on the understory component with the potential ability to interfere with the canopy ascension of dominant trees (*N. dombeyi* and *A. chilensis*), we only registered shrub or small trees capable of forming dense layers underneath the canopy. Moreover, we registered the degree of partial dieback of the trees closest to the neighborhood of focal trees to describe the “mortality context”, thus expanding the spatial scale of mortality. We estimated neighboring mortality as the mean value of the degree of partial crown dieback of the nearest trees (with crowns in direct contact with the focal tree’s crown; Mölder and Leuschner 2014), considering the midpoint of the range of each category of partial dieback. Note that we assumed that plant-to-plant replacement is mainly driven by plants growing underneath the focal tree and not by lateral growth from neighboring canopies. This assumption is consistent with most forest gap models (Veblen 1989a) and is supported by the relatively low tree density.

Data analysis

We tested if canopy dieback extent can predict which, if any, tree species is best poised to replace the focal tree (Q1). For this purpose, we built a multinomial model in which the dependent variable was the identity of the highest plant (*N. dombeyi*, *A. chilensis*, shrubs) currently achieving dominance underneath the crown of the focal *N. dombeyi* tree, as well as the lack of replacement (no understory species). The independent variables were partial crown dieback (categories of partial dieback, ordinal variable), canopy height (metres, continuous variable), and neighbor mortality (percentage, continuous variable) corresponding to focal *N. dombeyi* trees. As we recorded consistent differences between sampled stands representing a gradient of affectionation by the drought episode at the landscape scale, correlated with abundance of *A. chilensis* (Table 1), we included them in the model as a fixed factor. This stand factor was ordinal, ranging from 1 to 6 (following the same percentage categories as in partial dieback) according to the degree of canopy area affected by the 1998–1999 drought and coincident with the percentage of *A. chilensis* in the overstory (Table 1). Effect displays were used to inspect the interaction of stand vs. predictor variables.

To assess species' ability to achieve canopy (Q2), we focused on the two dominant species (*N. dombeyi* and *A. chilensis*). Consequently, we only analyzed cases with these two species in the understory of living focal trees. We included focal healthy trees (level 1) and focal trees with evident partial dieback (levels 2 to 5). We expected that no conditions for growth release prevailed underneath healthy trees. Dead trees were excluded from the analysis because the distance to remaining green canopy was considered zero, as the highest species considered in the resulting gap was the one already replacing the focal trees. Also, we used the height to the green canopy (mid-height of green crown) of the focal tree instead of tree height, because in several cases, dead branches were located exclusively in the upper part of the tree, so measurement of the maximum height of branches would overestimate the actual canopy. We applied a general linear model (GLM) in which the dependent variable was distance from the top of the understory species to the green canopy of the focal tree (log-transformed). The independent variables were the same as in the multinomial models.

In the studied forests, shrub species are important in developing a dense layer that may inhibit the establishment and early growth of broadleaf species (Suarez and Sasal 2012). Thus, we used a shrub layer descriptor to test if shrub presence influences the possibility to achieve canopy (Q3). The independent variable (presence or absence of shrub layer) was included in the GLM described previously.

Finally, we analyzed if understory communities differ according to the degree of dieback (Q4). First, we inspected the relationship between species richness and the above-mentioned independent variable by generalized linear models (GLZMs) using Poisson distribution with a log-link function. Second, we applied nonmetric multidimensional scaling (NMDS) analysis to assess species composition associated with *N. dombeyi* partial crown dieback. This method generates a set of orthogonal synthetic axes for plotting cases in a species space where proximity reflects understory similarity. For the analysis, we used a full taxon matrix built with abundance (number of individuals) data registered underneath each focal tree. We determined whether the community composition of the ordination obtained by NMDS was related to the crown variables measured in each focal tree (degree of partial crown dieback, canopy height, neighbor's mortality). The role of external environmental variables in the resultant ordination was established by fitting the environmental vector determined by these crown variables onto the ordination. Differences in the group means were examined by running permutational multivariate ANOVA based on dissimilarities (adonis function; Oksanen et al. 2007). NMDS was performed with multiple random starts (100) to find the best overall solution and with specifications of three dimensions to reduce stress level. Lastly, species that were commonly associated with a given sampled stand and partial crown dieback level were identified on the basis of an indicator species analysis (Dufrene and Legendre 1997). This method assesses the degree to which a species fulfills the criteria of specificity (component A) and fidelity (component B).

For all analyses, we used R software (v.3.1; R Core Team 2014), mainly the nnet package (Ripley and Venables 2016) and the vegan package (Oksanen et al. 2007) for multinomial and ordination analysis. For the indicator value method, we used the indicspecies package (De Caceres et al. 2016).

Results

Canopy conditions and understory species' replacement

Degree of partial crown dieback, percentage of neighbor mortality, canopy height, and stand factor were related at different degrees to the identity of the understory component (i.e., highest plant or no understory) underneath *N. dombeyi* trees (Fig. 2; Table 2; Appendix Table A1). As partial dieback decreased in one category (i.e., increasing remaining canopy), the probability of no understory vs. *N. dombeyi* or shrubs increased by a factor of 1.15 (Table 2) and 1.20 (Table 2, CI of 0.72–0.95), respectively. Consequently, the probability of finding conditions without vegetation in the understory increases as long as the focal tree is alive. This pattern was more evident in more affected and *A. chilensis* mixed stands in which the probability of no vegetation rapidly declined underneath a high level of partial dieback, while there was an increase in the probability of finding *N. dombeyi* and (or) *A. chilensis* as a potential replacement species (Fig. 2a). In less affected and less mixed stands (levels 1–2), the probability that *A. chilensis* would be the potential replacement species rapidly decreased with higher levels of partial crown dieback (Fig. 2a).

However, neighbor mortality increased the probability of the main understory component (highest plant) being *A. chilensis* (vs. *N. dombeyi*) by a factor of 1.28 when the neighbor mortality increased by a quarter (25%, Table 2). As expected, this relationship was evident in all of the sampled stands but became stronger towards more mixed ones. Moreover, in those stands with higher mortality levels in the neighborhood of focal trees, the probability of *A. chilensis* increased as the probability of *N. dombeyi* decreased. Shrubs and no understory conditions showed a weak relationship with neighbor mortality.

The model also showed that the probability of finding no understory (vs. *N. dombeyi*) decreased by a factor of ~1.10 when the focal tree height increased by 1 m (Table 2). This pattern was more evident towards less affected and mixed stands where the incidence of shrub and *A. chilensis* increased under taller trees. On the contrary, an increase in the probability of *N. dombeyi* underneath taller trees was more evident in more affected stands and was related to the decline in the incidence of shrubs (Fig. 2c).

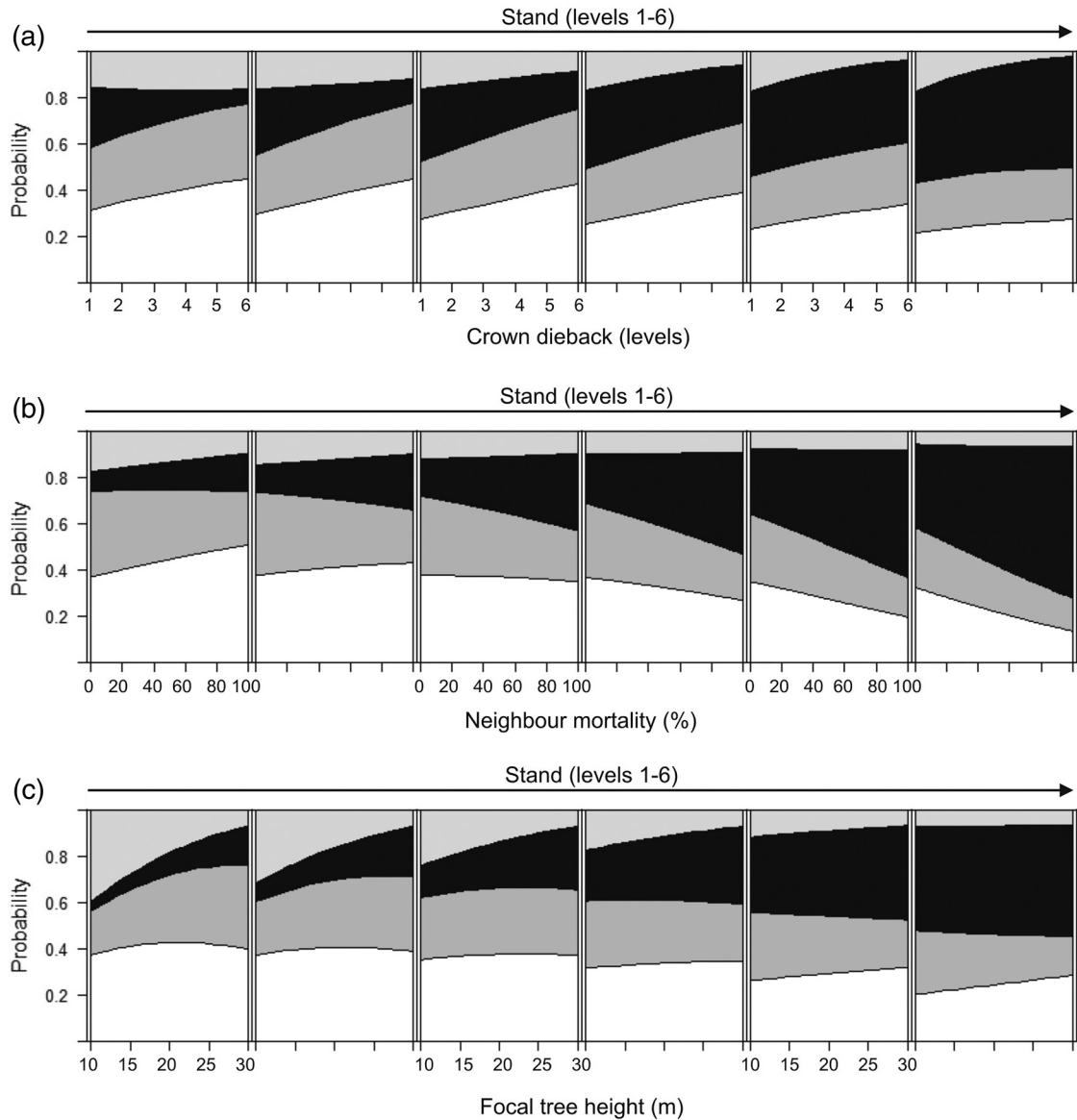
Likelihood of achieving canopy and shrub influence

Seventeen years after the die-off episode, *N. dombeyi* and *A. chilensis* displayed different probabilities of achieving canopy in relation to the level of partial dieback (Table 3; Fig. 3). *Nothofagus dombeyi* plants were closer to the green canopy beneath more defoliated *N. dombeyi* trees, supporting a replacement by this species, while the opposite pattern was observed for *A. chilensis*, thereby endorsing the dynamics of self-replacement rather than shift. These differences were not related to the presence or absence of a shrub layer (Table 3). In general, when a shrub layer was present above the replacing plant, there was a greater distance between the green canopy and the highest plant, irrespective of the identity of the potential replacement species.

Understory community composition under focal trees

We identified a total of 12 medium-sized woody species growing underneath *N. dombeyi* crowns. Species richness was similar for all focal trees, with no differences with regards to level of partial crown dieback, tree height, level of mortality in the neighborhood, or stand factor (Table 4). Moreover, NMDS reduced to two axes the composition of the understory plant community (Fig. 4). The ordination did not present any strong grouping in understory species composition in any of the sampled stands (adonis, $r^2 = 0.03$). Axes 1 and 2 showed a very low correlation with partial

Fig. 2. Effect plot for the three interaction terms of the multinomial model: (a) stand × partial crown dieback, (b) stand × neighbor mortality, and (c) stand × focal tree height. To simplify the interaction display, probabilities are represented as stacked areas in the plots, with shading depicting the four different possibilities of the highest plant underneath focal tree: no shading, *N. dombeyi*; medium grey shading, shrub; black, *A. chilensis*; light grey shading, no understory.



dieback level (axis 1, $r = 0.014$; axis 2, $r = -0.08$). Neighbor mortality was negatively correlated with axis 1 ($r = -0.19$) and positively correlated with axis 2 ($r = 0.17$). Height of the focal tree showed a low positive correlation with axis 1 ($r = 0.08$) and a negative correlation with axis 2 ($r = -0.12$). Finally, the indicator species analyses showed that *N. dombeyi* was the main species under level 5 (50%–75%) of crown dieback. Although the specificity of *N. dombeyi* was quite low ($A = 0.28$, $P = 0.03$), the fidelity of the species to the level was high ($B = 0.60$), highlighting the role of *N. dombeyi* as a replacement species when there were higher levels of partial crown mortality. On the contrary, the specificity and fidelity of *A. chilensis* was high ($A = 0.83$, $B = 0.55$, $P = 0.001$) in those stands that depicted higher levels of trees affected by drought and percentage of *A. chilensis* in the overstory (more mixed stands). The rest of recorded species did show high specificity with either canopy structural variables considered or stand factor.

Discussion

This study reveals evidence of self-replacement in austral *N. dombeyi* forests heavily affected by drought-induced partial crown dieback. A recent review highlighted the great uncertainties remaining in forest dynamics resulting from widespread episodes of tree mortality associated with drought events and reported some cases of potential self-replacement (Martínez-Vilalta and Lloret 2016). However, to our knowledge, only one previous study (Saura-Mas et al. 2015) reported the effects of partial crown dieback on understory vegetation, although this kind of canopy damage is not infrequent in forests affected by drought, particularly in Fagaceae (Galiano et al. 2011) and Nothofagaceae (Suarez et al. 2004; Rodríguez-Catón et al. 2016).

In this study, we considered that the potential replacement tree was the highest individual established underneath a *N. dombeyi* crown, thus assuming that the outcome of a growth release of the

Table 2. Model-averaged parameter estimates (*b*), standard errors (SE), and odds ratios and their 90% confidence intervals (CI) from multinomial regression models predicting whether the potential successor underneath *N. dombeyi* dead canopy could be *N. dombeyi* (reference taxon), *A. chilensis*, shrubs, or no understory.

Parameter	<i>b</i> ± SE	Odds ratio	Odds ratio CI
<i>Austrocedrus chilensis</i>			
Crown dieback (levels 1–6)	–0.09±0.06	0.92	0.82–1.01
Neighbor mortality (%)	0.011±0.005	1.01	1.01–1.02
Target tree height (m)	–0.008±0.02	1.00	0.97–1.04
Stand (levels 1–6)	0.37±0.08	1.57	1.29–1.67
Shrubs			
Crown dieback (levels 1–6)	–0.04±0.06	0.95	0.86–1.06
Neighbor mortality (%)	–0.001±0.006	0.99	0.98–1.00
Target tree height (m)	–0.01±0.02	0.98	0.95–1.02
Stand (levels 1–6)	0.02±0.07	1.02	0.90–1.14
No understory			
Crown dieback (levels 1–6)	–0.26±0.09	0.77	0.66–0.88
Neighbor mortality (%)	0.003±0.008	1.00	0.99–1.01
Target tree height (m)	–0.05±0.03	0.95	0.90–0.99
Stand (levels 1–6)	–0.08±0.09	0.92	0.78–1.08

Note: Parameters in bold have odds ratios with 90% CIs that do not overlap values equal to 1. Odds ratios above or below 1 indicate a positive or negative relationship, respectively, between the predictor variable and the probability of the potential successor belonging to the respective group or species (vs. *N. dombeyi*). Odds ratios between any two group or species can be calculated by dividing the odds ratios provided here for each group.

Table 3. Species' ability to achieve canopy after partial crown dieback measured as the distance of underneath species (*N. dombeyi* and *A. chilensis*, reference taxon) for reaching the green canopy of focal *N. dombeyi* trees.

Independent variable	Estimated effect	SE	<i>t</i>	<i>P</i> value
Shrub layer (PSH)	0.66	0.36	1.82	0.06
Partial dieback (PD)	0.22	0.14	1.58	0.11
Neighbor mortality (NM)	–0.006	0.007	–0.76	0.45
Species (SP)	0.94	0.93	1.01	0.31
Stand (S)	–0.21	0.13	–1.60	0.11
PD × SP	–0.54	0.18	–2.89	0.004
NM × SP	0.01	0.01	1.02	0.31
S × SP	0.27	0.16	1.68	0.09
PSH × SP	–0.32	0.50	–0.63	0.52

Note: Predictors in the general linear model depict understory, focal, and neighborhood tree conditions. Shrub layer (PSH) refers to the presence or absence (reference) of a shrub layer underneath the focal tree.

understory components can be observed 17 years after canopy loss. Previous results suggested that both *N. dombeyi* and *A. chilensis* behave similarly as a consequence of canopy openings, with equal possibilities of reaching the canopy when growing above a shrub layer (Suarez and Sasal 2012); however, the response to canopy opening may vary according to understory conditions. In austral forests, the shrub layer potentially plays a major role in the differential recruitment and establishment of these species (Veblen 1989b; Suarez and Kitzberger 2008). Previous monitoring, supported by manipulative experiments, showed a lower recruitment and survival of *N. dombeyi* than *A. chilensis* in the shadier understory environment after drought mortality (Suarez and Kitzberger 2008). Here, both canopy species were furthest from the canopy when shrubs were present, and there was no evidence of differential behavior in favor of *N. dombeyi*. These results could imply that the presence of shrubs potentially hampers understory tree growth or that tree species were merely lower in height than the shrub species, probably due to recent establishment.

Fig. 3. Effect of species on the distance to achieve green canopy in relation to the level of partial crown dieback (species × partial dieback interaction). The solid lines (grey, *N. dombeyi*; black, *A. chilensis*) show the GLM fitting lines with confidence bands. Dots (same color as lines) depict partial residuals.

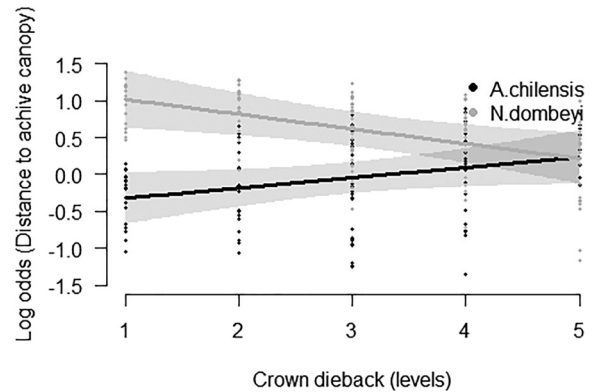


Table 4. Results of general linear model on species richness underneath *N. dombeyi* trees according to predictors of focal and neighborhood conditions.

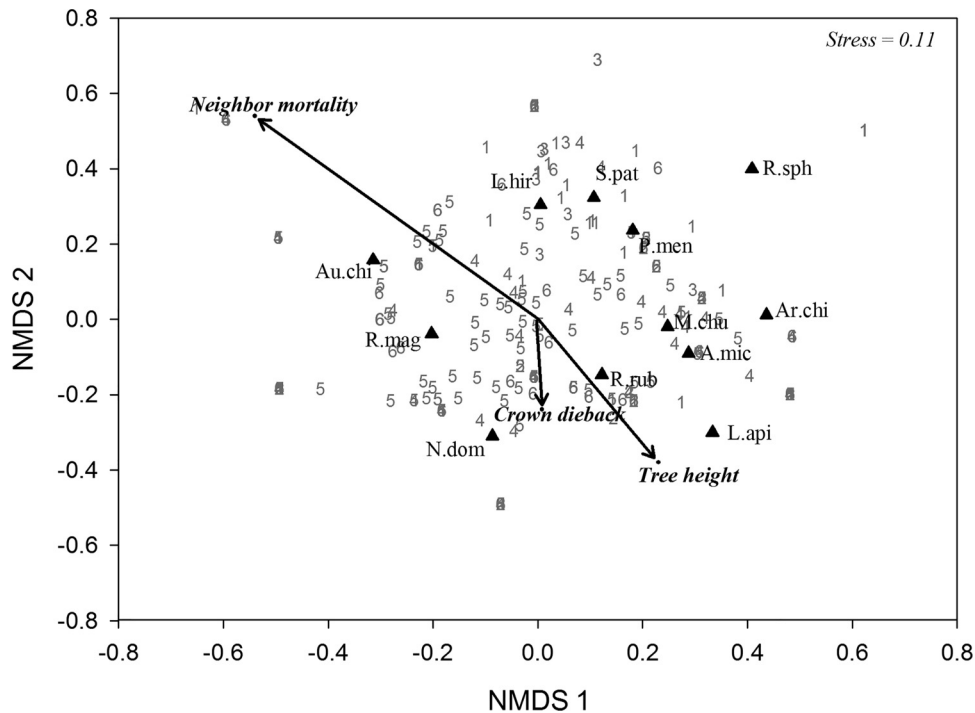
Independent variable	Estimated effect	SE	<i>t</i>	<i>P</i> value
Partial dieback	–0.018	0.021	–0.87	0.38
Focal tree height	0.12	0.007	1.79	0.07
Neighbor mortality	–0.0005	0.002	–0.28	0.78
Stand	0.034	0.024	1.41	0.16

Note: Residual deviance 139.32 on 470 degrees of freedom (df).

However, *N. dombeyi* may effectively reach the canopy layer thanks to saplings growing above the shrub layer; it has the ability to occupy medium- to large-sized tree fall openings (Veblen 1989a) in accordance with its light requirements for growth (Piper et al. 2009). Here, we show that this species also has the ability to cope with small openings (higher levels of partial dieback in a context of low neighbor mortality) and take on the role of the successor. This result concurs with the reported eightfold increase in the growth of *N. dombeyi* as a result of canopy openings of 50 to 225 m² (Suarez and Sasal 2012). These changes probably responded, at least in part, to changes in the microclimate after overstory mortality that involved increases in diffuse and direct light and nutrients from dropped leaves (Suarez and Kitzberger 2008; Anderegg et al. 2013).

Hence, the fact that the distance needed by *N. dombeyi* to reach the canopy level is always lower than that of *A. chilensis* under higher degrees of partial dieback suggests that less shade tolerant species could monopolize available resources (i.e., light, water, and nutrients). However, growth release and then differences in canopy ascension also depend on other tree-level and local-level variables (Stan and Daniels 2010, 2014). For example, prior growth, tree diameter, and age helped to predict the magnitude of growth release of understory species following fine-scale canopy gaps in *Thuja plicata* – *Tsuga heterophylla* old forests from coastal British Columbia, Canada (Stan and Daniels 2010). This relationship would also apply for *N. dombeyi*, as individuals growing under closer canopy evidenced lower growth rates during the previous 5 years and major release abilities (Suarez and Sasal 2012). Alternatively, when the co-dominant species *A. chilensis* is widely present in the understory, a possible compositional shift cannot be ruled out, particularly if large gaps are opened. Our results indicated that the shade-tolerant conifer was the main potential suc-

Fig. 4. NMDS ordination biplot of understory plant community composition (based on species abundance) according to the six levels of stand factor. Arrows indicate the correlation between the ordination axes and structural variables at plot level: partial crown dieback (levels 1 to 6), neighbor mortality (%), and tree height (m). The length of the arrow indicates the strength of the correlation.



cessor when *A. chilensis* were more present in the overstory and when canopy openings were larger, as evidenced by the enhancement of *A. chilensis* in the understory as a result of neighbor mortality. This evidence of a shift in canopy composition may result in changes in forest functionality because of the differences in the functional traits of these species. *Nothofagus dombeyi* is a broadleaf evergreen tree, whereas *A. chilensis* is a needle-leaf evergreen tree with low wood density, low leaf nitrogen concentration, and higher specific leaf area, which implies photosynthetic differences and potential differences in forest productivity (Lusk et al. 2003).

In natural mixed forests, *A. chilensis* may form dense sapling banks that could persist for several years and regenerate effectively under dense shrub layers (Gobbi 2007). Moreover, *A. chilensis* is considered a drought-avoidant species (Gyenge et al. 2005), and this results in higher postdrought survival rates compared with *N. dombeyi* (Suarez and Kitzberger 2008). Thus, our results were not incompatible with the requirements of the conifer, and the main distinction between these species may respond to differences in the ontogeny stage, as well as their different demands for light and water. In favorable sites (see Suarez et al. 2004), the mortality rate of *N. dombeyi* saplings is expected to be relatively low (Suarez and Kitzberger 2008), with no reduction in its dominance in favor of the drought-tolerant *A. chilensis*. Therefore, *N. dombeyi*, with its great demand for light, improves its growth as higher degrees in partial dieback provide an opportunity to reach the canopy. However, in spots where the drought episode reduces the density of potential *N. dombeyi* replacements, as well as adult individuals (here indicated by a high percentage of neighbor mortality), the *A. chilensis* replacements have a higher chance of surviving in the understory, as this species can maintain potential water levels during drought beyond its hydraulic functional limit (Scholz et al. 2014). Consequently, a possible change in the future composition of the canopy in favor of the conifer *A. chilensis* could be expected.

Note, however, that our approach is mainly descriptive and we cannot distinguish whether the observed pattern is caused by the distinct establishment of *N. dombeyi* and *A. chilensis* populations in the understory prior to the drought-induced gap opening or to the effect of environmental conditions associated with canopy opening (Suarez and Kitzberger 2008). Further research is needed to disentangle the extent to which the degree of partial defoliation affects differences in species recruitment and drives the balance between competitive and facilitative processes (Mueller et al. 2005; Stultz et al. 2007), which ultimately determines which species occupies the newly available space.

Changes in the whole understory community are also expected to occur as a result of environmental changes induced by canopy loss. In fact, there are numerous indications in forests worldwide of understory community change associated to canopy loss by drought mortality (Olano and Palmer 2003; Kane et al. 2011; Anderegg et al. 2012; Saura-Mas et al. 2015). Thus, a new understory community (measured as increase in shrub cover and volume) was detected in dying *Populus tremuloides* stands, suggesting shrub expansion and changes in understory plant communities with the decline of these forests (Anderegg et al. 2012). Likewise, in a *Juniperus monosperma* woodland, Kane et al. (2011) found a positive effect of mortality on understory plants, with a change in community composition. However, our study, which considered a wide spatial representation several years after the mortality episode, showed that isolated partial openings do not favor either more shrubby communities or a shift toward a new community in terms of composition or richness. This result contrasts with the previous study in this area that depicted growth release of the understory component and presence of particular species as the clearest biotic response in patches marked by drought-induced tree mortality (Suarez and Sasal 2012), though partial drought induced openings seem not to be enough to trigger the recruitment of generalist heliophilous species (i.e., *Schinus patagonicus*

and *Lomatia hirsute*; Damascos and Rapoport 2002) or species that show high phenotypic plasticity to light such as *Aristotelia chilensis* (Lusk and del Pozo 2002). The small size of the partial opening should not be the only reason for these different results, as other factors can influence understory new colonization and growth. Thus, further research analyzing structure and composition of the seed bank, distance from colonization sites, and resilience of the understory is needed to disentangle the mechanisms influencing regeneration strategies underneath partial dieback. In general, the observed set of understory species was typical of this type of forest (Veblen 1989a; Suarez and Sasal 2012), while two exotic species — *Pseudotsuga menziesii* and *Rosa rubiginosa* — were also present. In a previous study (Suarez and Sasal 2012), these non-native species were found only under canopy dead from drought. Further research is needed to study their invasive potential, particularly in the case of the exotic conifer *P. menziesii*.

The frequency and severity of drought in Patagonia is projected to increase (Villalba et al. 2003), and *N. dombeyi* is expected to be affected over all of its distributional range (M.L. Suarez, personal records of new mortality events). The range of tree-level responses (from partial crown dieback to whole-plant mortality), as well as the variety of stand-level responses (from slight to severe effects) in the mortality process, may determine the impact of ecological processes that operate to compensate for the loss of *N. dombeyi*. Previous studies have suggested that in places with extended mortality, environmental changes in the understory facilitated drought and (or) shade-tolerant species, encouraging the grouping of new species and hampering the maintenance of predrought populations (Suarez and Sasal 2012; Suarez and Kitzberger 2008). Nevertheless, when we considered the full range of canopy loss, compensatory processes (i.e., higher survival and growth release of dominant understory species, without any enhanced shrubby layer) can come into play, favoring the resilience of austral *N. dombeyi* forests. Thus, accurate knowledge of the extent to which canopies are affected by drought episodes and the consequences for the demographic and functional processes of both native and non-native species is needed to develop compensatory measures against potential shifts in temperate forests subject to great climatic variability.

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Appendix A

Table A1. Model-averaged parameter estimates (*b*), standard errors (SE), and odds ratios and their 90% confidence intervals (CI) from multinomial regression models predicting whether the potential successor underneath *N. dombeyi* dead canopy could be *A. chilensis*, *N. dombeyi*, shrubs, or no understorey.

Parameter	<i>b</i> ± SE	Odds ratio	Odds ratio CI
Reference taxon: <i>A. chilensis</i>			
<i>Nothofagus dombeyi</i>			
Partial dieback (levels 1–6)	0.09±0.06	1.09	0.98–1.21
Neighbor mortality (%)	−0.011±0.005	0.98	0.98–0.99
Target tree height (m)	−0.008±0.02	0.99	0.95–1.02
Stand (levels 1–6)	−0.38±0.08	0.68	0.59–0.77
Shrubs			
Partial dieback (levels 1–6)	0.04±0.07	1.04	0.93–1.16
Neighbor mortality (%)	−0.01±0.005	0.98	0.97–0.99
Target tree height (m)	−0.02±0.02	0.98	0.94–1.01
Stand (levels 1–6)	0.37±0.08	0.69	0.60–0.79
No understorey			
Partial dieback (levels 1–6)	−0.17±0.09	0.84	0.72–0.97
Neighbor mortality (%)	−0.008±0.007	0.99	0.98–1.00
Target tree height (m)	−0.06±0.03	0.94	0.89–0.98
Stand (levels 1–6)	−0.46±0.10	0.63	0.52–0.74
Reference taxon: Shrubs			
<i>Nothofagus dombeyi</i>			
Partial dieback (levels 1–6)	0.04±0.06	1.04	0.94–1.16
Neighbor mortality (%)	0.001±0.005	1.00	0.99–1.01
Target tree height (m)	0.01±0.02	1.01	0.97–1.04
Stand (levels 1–6)	−0.02±0.07	0.98	0.87–1.10
<i>A. chilensis</i>			
Partial dieback (levels 1–6)	−0.04±0.06	0.96	0.85–1.06
Neighbor mortality (%)	0.01±0.005	1.01	1.00–1.02
Target tree height (m)	0.02±0.02	1.02	0.98–1.05
Stand (levels 1–6)	0.37±0.08	1.44	1.26–1.65
No understorey			
Partial dieback (levels 1–6)	−0.22±0.09	0.80	0.69–0.93
Neighbor mortality (%)	0.004±0.007	1.00	0.99–1.01
Target tree height (m)	−0.04±0.03	0.96	0.91–1.00
Stand (levels 1–6)	−0.09±0.098	0.91	0.77–1.07
Reference taxon: No understorey			
<i>Nothofagus dombeyi</i>			
Partial dieback (levels 1–6)	0.26±0.09	1.30	1.12–1.50
Neighbor mortality (%)	−0.003±0.007	0.99	0.98–1.00
Target tree height (m)	0.05±0.03	1.05	1.00–1.10
Stand (levels 1–6)	0.08±0.09	1.08	0.92–1.26
<i>A. chilensis</i>			
Partial dieback (levels 1–6)	0.17±0.09	1.19	1.03–1.40
Neighbor mortality (%)	0.007±0.007	1.01	0.99–1.02
Target tree height (m)	0.06±0.03	1.06	1.01–1.11
Stand (levels 1–6)	0.46±0.10	1.59	1.33–1.89
Shrubs			
Partial dieback (levels 1–6)	0.17±0.09	1.25	1.07–1.44
Neighbor mortality (%)	−0.004±0.008	0.99	0.98–1.00
Target tree height (m)	0.04±0.03	1.04	0.99–1.09
Stand (levels 1–6)	0.09±0.09	1.10	0.93–1.29

Note: Parameters in bold have odds ratios with 90% confidence intervals that do not overlap values equal to 1. Odds ratios above or below 1 indicate a positive or negative relationship, respectively, between the predictor variable and the probability of the potential successor belonging to the respective group or species (vs. *A. chilensis*). Odds ratios between any two group or species can be calculated by dividing the odds ratios provided here for each group.