

Episodic bamboo die-off, neighbourhood interactions and tree seedling performance in a Patagonian mixed forest

Fernando D. Caccia^{1*}, Thomas Kitzberger² and Enrique J. Chaneton³

¹Departamento de Producción Vegetal, Facultad de Agronomía, Universidad de Buenos Aires, Av. San Martín 4453, 1417 Buenos Aires, Argentina; ²INIBIOMA-CONICET and Laboratorio Ecotono, Universidad Nacional del Comahue, Quintral 1250, 8400 Bariloche, Argentina; and ³IFEVA-CONICET and Facultad de Agronomía, Universidad de Buenos Aires, Av. San Martín 4453, 1417 Buenos Aires, Argentina

Summary

1. Episodic mass flowering and subsequent die-off of bamboo understories may generate rare opportunities for tree regeneration by altering consumer–seedling interactions as much as by increasing light availability to seedlings. We hypothesized that bamboo dieback interacts with canopy neighbourhood composition in creating recruitment microsites for tree seedling species with varied shade tolerance and susceptibility to herbivory.

2. We conducted a 2-year experiment in a Patagonian mixed forest altered by extensive, but patchy dieback of the bamboo *Chusquea culeou*. Newly emerged seedlings of *Nothofagus alpina* (more shade-tolerant) and *Nothofagus dombeyi* (less shade-tolerant) were planted in conspecific and hetero-specific canopy neighbourhoods, with either a flowered (dead) or non-flowered (live) bamboo understory. Seedlings were placed inside and outside mesh cages to assess mortality from vertebrate or invertebrate consumers.

3. Vertebrate exclusion increased seedling survival regardless of bamboo condition. Seedling loss to invertebrates decreased with bamboo die-off, resulting in higher survival of *N. alpina* in dead than in live patches. In contrast, bamboo die-off increased *N. dombeyi* mortality by wilting, which counteracted the benefits of seedling release from consumers. Bamboo die-off increased light availability and enhanced seedling growth for both species.

4. *Nothofagus alpina* seedlings were less damaged or killed by invertebrates under heterospecific canopies than under conspecifics (associational resistance), whereas *N. dombeyi* performance was unaffected by neighbourhood composition. Bamboo die-off did not change seedling performance patterns observed across canopy neighbourhoods with live bamboo understories.

5. *Synthesis.* Gaps created by bamboo die-off can exert both positive and negative, species-specific effects on the likelihood of tree seedling establishment. We conclude that infrequent understory disturbances coupled with canopy neighbourhood effects mediated by seedling herbivores may drive gap-phase succession within old-growth forests.

Key-words: associational effects, disturbance, herbivory, plant population and community dynamics, recruitment, succession, temperate forest, understory

Introduction

Tree recruitment microsites are shaped by the juxtaposition of overstorey and understory plant layers, which can exert negative or positive effects on seedling performance (Caccia & Ballaré 1998; Massey *et al.* 2006; Comita & Hubbell 2009).

A large body of research has focused on how treefall gaps alleviate competition and favour niche partitioning among seedling species with contrasting life histories (Christie & Armesto 2003; Schnitzer, Mascaro & Carson 2008; Clark, Poulsen & Levey 2012). Conversely, the role of understory gaps in driving regeneration within closed-canopy forests has received less attention (Connell, Lowman & Noble 1997; Caccia, Chaneton & Kitzberger 2009). This is particularly true with regard to the effects of understory plants on

*Correspondence author. E-mail: fcaccia@agro.uba.ar

seedling–herbivore interactions across a mosaic of tree neighbourhoods (Pearson *et al.* 2003; Norghauer, Malcolm & Zimmerman 2008).

Tree recruitment is often limited by dense understorey layers interfering with seedling growth and survival (George & Bazzaz 1999; Royo & Carson 2006). Long-lived, monocarpic, bamboos (Poaceae, Bambusoideae) dominate the understorey of many temperate and tropical forests (Janzen 1976; Veblen 1982; Nakashizuka 1988; Taylor & Qin 1992; Griscom & Ashton 2003; Montti *et al.* 2011). Bamboo thickets may impede tree establishment through direct competition for light (Veblen 1982; Taylor & Qin 1992) or soil resources (Griscom & Ashton 2003), and through indirect effects mediated by pathogens (Nakashizuka 1988) or seed/seedling consumers (Abe, Miguchi & Nakashizuka 2001; Caccia, Chanton & Kitzberger 2006, 2009). Bamboo species undergo gregarious flowering episodes followed by mass seeding and die-off (Janzen 1976). Bamboo blooms are synchronized over extensive areas, creating large-scale, endogenous forest disturbances (Veblen 1992), which drastically alter microclimate conditions (Marchesini, Sala & Austin 2009; Montti *et al.* 2011) and may generate windows of opportunity for tree recruitment (Griscom & Ashton 2003; Holz & Veblen 2006; Giordano, Sánchez & Austin 2009). Bamboo seed crops may lead to satiation of resident granivores, allowing canopy tree seeds to escape predation (Janzen 1976; Kitzberger, Chanton & Caccia 2007). In addition, bamboo dieback creates understorey gaps that might be exploited by tree seedling species with varying degrees of shade tolerance (Taylor & Qin 1992; González *et al.* 2002; Holz & Veblen 2006). However, the extent to which seedling consumers differentially affect tree species recruitment after bamboo die-off events remains largely untested.

Bamboo die-off may alter the understorey habitat for vertebrate and invertebrate consumers through its transient effects on light, moisture and temperature conditions (Abe *et al.* 2005). If bamboo dieback reduces understorey habitat quality for consumers, for instance, through reduced cover and increased abiotic stress (Pigot & Leather 2008) or predation risk (Stoepler & Lill 2013), then seedling establishment could be facilitated not only by greater light penetration to the forest floor (Marchesini, Sala & Austin 2009), but also through seedling release from herbivory (Abe *et al.* 2005). Previous work suggests that the consequences of bamboo–herbivore interactions for seedling demography will depend on the consumer guild (rodents, insects) and focal tree species (Caccia, Chanton & Kitzberger 2009). Thus, species-specific differences in susceptibility to herbivory and abiotic stresses (Norghauer, Malcolm & Zimmerman 2008; Norghauer & Newbery 2014) may affect the chances of successful seedling recruitment into the sapling stage after bamboo die-off events.

Tree seedling dynamics are influenced by the spatial arrangement of canopy trees (Catovsky & Bazzaz 2002; Schnurr *et al.* 2004; Massey *et al.* 2006). Growing evidence shows that density- and distance-dependent mortality may drive seedling establishment in both tropical and temperate

forests (Comita & Hubbell 2009; Comita *et al.* 2014). Negative effects from resource competition or fungal pathogens may decrease seedling survival under/near conspecifics (Alvarez-Loayza & Terborgh 2011; McCarthy-Neumann & Ibañez 2013). Also, seedlings may have greater chances of establishing away from conspecifics because of the aggregation of herbivorous consumers under parent trees (Humphrey & Swaine 1997; Wada, Murakami & Yoshida 2000; Terborgh 2012). In a mixed-species context, seedling performance may be thus increased under heterospecific, relative to conspecific canopy neighbourhoods (Massey *et al.* 2006; Comita & Hubbell 2009). Such associational effects can be mediated by vertebrate or invertebrate consumers acting at various spatial scales (Barbosa *et al.* 2009; Underwood, Inouye & Hambäck 2014). Yet canopy–seedling interactions would be also modulated by understorey effects on microclimate, resources and consumer activity (Royo & Carson 2006; Norghauer, Malcolm & Zimmerman 2008; Norghauer & Newbery 2014). Hence, there is ample scope for understorey disturbances, like bamboo mass dieback, to interact with canopy composition in creating recruitment opportunities for tree seedlings.

We tested the hypothesis that gregarious bamboo die-off alleviates consumer pressure on newly emerged tree seedlings, increasing the chances for canopy species recruitment in an old-growth Patagonian forest. We focused on an extensive flowering/die-off event of the native bamboo *Chusquea cu-leou* that swept through northern Patagonian forests in Argentina during 2000–2001 (Kitzberger, Chanton & Caccia 2007; Marchesini, Sala & Austin 2009). The study forest comprises a mosaic of canopy patches dominated by two *Nothofagus* species (*N. dombeyi* and *N. alpina*) with a dense bamboo understorey. Tree seedling recruitment is scarce and mostly limited to canopy gaps and bamboo-free microsites (Veblen 1982, 1989; Veblen *et al.* 1996). In a 2-year experiment, we planted seedlings of both *Nothofagus* species under conspecific and heterospecific canopies. The patchy nature of the flowering event allowed us to compare seedling performance in nearby flowered (dead) and non-flowered (live) bamboo patches, with either a *N. dombeyi* or *N. alpina* overstorey. We expected seedlings to experience reduced loss to consumers and higher overall survival in dead than in live bamboo patches. Further, we expected that seedling establishment within live bamboo patches would be increased in heterospecific, relative to conspecific canopy neighbourhoods. We also predicted that relaxation of consumer pressure after bamboo dieback would overwhelm differences in seedling performance across canopy neighbourhoods.

Specifically, we asked (i) How does bamboo die-off affect tree seedling survival and growth? (ii) What are the main sources of seedling mortality in flowered vs. non-flowered bamboo patches? (iii) Does seedling survival vary consistently between heterospecific and conspecific canopy neighbourhoods for these *Nothofagus* species? If so, is consumer-mediated seedling mortality higher under conspecific than heterospecific canopies? (iv) Could bamboo die-off override or reinforce seedling establishment patterns across canopy neighbourhoods?

Materials and methods

STUDY AREA

The study was conducted between December 2002 and April 2004 in a mixed evergreen-deciduous forest located near Lake Curruhué, 40 km northwest of Junín de los Andes, Lanín National Park, Neuquén, Argentina (39°50'S, 71°31' W; 1080 m a.s.l.). Mean temperatures range between 3.2 °C in July and 14.4 °C in January. Mean annual precipitation is c.1800 mm; the November–March growing season is typically dry, with c.15% of the total precipitation. Soils are poorly developed Andisols derived from volcanic deposits. The site is dominated by the evergreen *Nothofagus dombeyi* (Mirb.) Blume and the deciduous *N. alpina* (Popp. & Endl.) Oerst. (synon. *N. nervosa*), which form a mosaic of stands (c.1–5 ha) ranging between 60% and 80% in canopy cover. These forests can reach densities of nearly 200 trees ha⁻¹ and a total basal area of 55 m² ha⁻¹ (Dezzotti *et al.* 2003). Mature trees within stands are spaced 5–10 m apart. There are no conspicuous differences in topography and soil conditions between *Nothofagus* spp stands (Lusk & Ortega 2003; Vivanco & Austin 2008). The canopy mosaic would reflect long-term recruitment dynamics driven by stochastic gap formation and spatio-temporal variation in seed availability (Veblen 1989; Veblen *et al.* 1996; Dezzotti *et al.* 2003). The understorey is dominated by the bamboo *Chusquea culeou* Desvaux, a common element throughout the region. *Chusquea culeou* culms grow up to 5–6 m tall, reaching densities of 30–60 culms m⁻² and c.3500 g m⁻² of above-ground biomass (Veblen 1982; Marchesini, Sala & Austin 2009). Other species include the shrubs *Azara lanceolata*, *Berberis* spp, *Gautheria phillyreifolia* and *Maytenus chubutensis*, and several ground herbs. Understorey structure is similar between *Nothofagus* canopy patches (Lusk & Ortega 2003). The site is characteristic of old-growth, mixed, cool-temperate forests on the eastern foothills of the northern Patagonian Andes (Veblen *et al.* 1996).

NATURAL HISTORY AND STUDY SPECIES

In summer 1997–1998, isolated patches of *C. culeou* began flowering in Lanín National Park after a non-flowering period of nearly 60 years (Sanguinetti & García 2001). In spring (November) 2000, bamboo understoreys flowered across 200 000 ha between 39° and 40° S in the Andes of Argentina and adjacent areas of Chile. Bamboo flowering was followed by mass seeding and extensive dieback in autumn (March–April) 2001. Bamboo seeds were released at c.2–5 × 10⁵ seed m⁻², which generated a large resource subsidy preceding a short-lived rodent outbreak; rodent populations crashed in spring 2001 (Kitzberger, Chaneton & Caccia 2007). Many bamboo thickets remained green (unflowered) across the study area, which created a mosaic of dead and live bamboo patches of varying size (Kitzberger, Chaneton & Caccia 2007). Flowered and non-flowered patches alternated in areas with either a *N. alpina* or *N. dombeyi* overstorey.

For both study species, seed dispersal occurs between March and May; germination takes place during November–December. Average dispersal distances imply that most seeds fall beneath parent trees (Burschel *et al.* 1976; Veblen *et al.* 1996). However, dispersal kernels for individual temperate trees may overlap broadly, increasing the chances that seedlings emerge in heterospecific canopy neighbourhoods (Schnurr *et al.* 2004). Thus, for both *Nothofagus* species, seedlings emerging after bamboo flowering could face conditions created by any combination of bamboo condition (live or dead) and canopy neighbourhood (*N. alpina* or *N. dombeyi*). *Nothofagus* seedling

establishment is favoured by moderate to elevated light levels (Read & Hill 1985; Weinberger & Ramírez 2001). Canopy gaps provide recruitment microsites for South American *Nothofagus* (Veblen 1989; Donoso *et al.* 2013), but effective regeneration is reduced within bamboo thickets (Veblen 1982; Holz & Veblen 2006). Whilst *Nothofagus* spp are regarded as being relatively intolerant to shade (Veblen *et al.* 1996), *N. alpina* seedlings exhibit greater shade tolerance than *N. dombeyi* ones, according to their photosynthetic behaviour, growth rate and survival under varying shade levels (Read & Hill 1985; Weinberger & Ramírez 2001; Peyrou 2002). This allows *N. alpina* to regenerate in smaller canopy gaps (Dezzotti *et al.* 2003; Donoso *et al.* 2013). Seedling fate also depends on soil moisture, *N. alpina* being more drought-resistant than *N. dombeyi* (Varela *et al.* 2010).

Both vertebrate and invertebrate consumers represent a major source of seedling mortality in Andean forests. Tree seedlings may be damaged or killed by rodents (del-Val *et al.* 2007), ground-dwelling birds (Burschel *et al.* 1976) or insect herbivores (Chacón & Armesto 2006; Simonetti *et al.* 2007). Consumer impacts can vary widely between gap and closed-canopy microsites, as well as among tree species (Chacón & Armesto 2006; Caccia, Chaneton & Kitzberger 2009). *Nothofagus alpina* produces larger and softer leaves, with a higher nutrient (N, P) content, lower C:N ratio and lower phenol levels than *N. dombeyi* leaves (Diehl *et al.* 2003; Vivanco & Austin 2008). These foliar traits may render *N. alpina* seedlings more susceptible to herbivory, but direct evidence for this is missing.

EXPERIMENTAL DESIGN

We performed a transplant experiment using newly germinated *N. alpina* and *N. dombeyi* seedlings about 1–2 cm height and with two expanded cotyledons. *Nothofagus alpina* seedlings were obtained from the nursery at the Instituto Nacional de Tecnología Agropecuaria (Bariloche, Río Negro). Seedlings were grown in a glasshouse from wet-stratified (4 °C) seeds sown in plug-in containers with native forest soil. *Nothofagus dombeyi* seedlings were obtained in November 2002 from stands located within 5 km of the study site. Lack of sufficient viable seeds prevented us from growing *N. dombeyi* seedlings in the glasshouse. *Nothofagus dombeyi* seedlings were transferred to trays with local soil and kept in the glasshouse for 20 days. At the time of transplant, seedlings had no signs of herbivore or pathogen damage.

For each seedling species, the experiment comprised eight treatments from the factorial combination of (i) canopy neighbourhood (*N. alpina* or *N. dombeyi*), (ii) bamboo condition (flowered/dead or non-flowered/live) and (iii) vertebrate exclusion (cage enclosure or open control). In December 2002, 2 years after the bamboo bloom, we selected five forest stands for each combination of canopy neighbourhood and bamboo condition (total = 20 stands). Stands were interspersed along a 3 km east–west transect. Canopy neighbourhoods 2–3 ha in size were chosen with the constraint that the overstorey should be clearly dominated by either *N. dombeyi* or *N. alpina*. Areas where bamboo flowering was too extensive (>1 ha) or where flowered and non-flowered patches were too small (clumps < 0.2 ha) were avoided. In flowered patches, dead bamboo culms remained standing throughout the experiment.

In each stand, we planted eight pairs of seedlings, each comprising one *N. alpina* and one *N. dombeyi* plant. This yielded a total of 20 stands × 8 plants × 2 species = 320 seedlings. Four seedling pairs within each stand were covered with a cage enclosure to prevent access by small vertebrates; the other four pairs remained uncaged (open). Thus, for each species, the full design comprised five replicate

stands, each with four planting locations per cage/open treatment (=160 plants). Cage enclosures were made of 1-cm-mesh galvanized wire [$15 \times 15 \times 15$ cm (height)] and were pushed 3 cm into the ground. The enclosures protected seedlings from rodents and birds but did not exclude invertebrate herbivores (insects, slugs). Cages had only a minor effect on light levels (PPFD reduction < 15%, relative to sub-canopy ambient light, in dead bamboo patches) and had no measurable impact on soil temperature (data not shown). A treatment excluding all consumers was disregarded as being impractical. The use of fine-mesh cages to exclude insects would have altered microclimatic conditions for seedlings, while insecticide use was unfeasible given the length of the study and small size of the seedlings. Seedling pairs (caged/open) were randomly interspersed between 5 and 8 m apart within each stand; distance to the nearest adult tree was 1–3 m. Seedlings were taken to the field in early December 2002 (spring) and planted with a 7-cm-deep soil core, leaving 5 cm between paired seedlings. The litter layer was replaced around the seedlings after planting; ground vegetation was sparse and left undisturbed. Each pair of seedlings received 250 mL of water to reduce transplant shock; no additional watering was supplied. After 2 weeks, 16 plants (5%) were assumed dead by transplant and replaced.

Seedlings were monitored over two growing seasons (16 months) in January, April, October and December 2003, and again in April 2004. On each census date, we recorded the status of each seedling (alive or dead), apparent cause of death and leaf number and damage by folivorous insects (see below). Leaf number was used as a measure of seedling growth; we only report data for plants surviving at the end of the experiment (April 2004).

SOURCES OF SEEDLING MORTALITY

Seedling mortality was attributed to either consumers or wilting stress according to prior work in the system (Caccia, Chanton & Kitzberger 2009). Seedlings labelled as dead by wilting could have been killed by desiccation, direct sunlight or shading, depending on microsite exposure (Weinberger & Ramírez 2001; Peyrou 2002). Wilting may be also induced by fungal pathogens (Nakashizuka 1988; Alvarez-Loayza & Terborgh 2011), but we did not find obvious symptoms of pathogen attack (leaf spots, moulds, damping off) in this study. Wilting seedlings were found both outside and inside cage enclosures. In the consumer category, we included seedlings with a clean cut of the hypocotyl (Ct), those with the leaf area removed but the stem left intact (Si), seedlings that were uprooted (Up) and missing seedlings (Mi). Seedlings in categories Ct, Si and Mi occurred both inside and outside the cage enclosures, whereas Up seedlings were found only outside the cages, indicating that they were probably disturbed by small vertebrates (Burschel *et al.* 1976). We distinguished seedlings killed by vertebrate or invertebrate consumers by assuming that caging effectively impeded vertebrate access to seedlings (Caccia, Chanton & Kitzberger 2009). Hence, to estimate invertebrate mortality, we considered only seedlings killed inside cages (Ct+Si+Mi). Seedling loss to vertebrates was estimated as the difference between the number of plants killed outside and inside cages (assuming effects from both consumer guilds were additive). Because caged and uncaged treatments were not paired, mortality attributed to vertebrates was estimated by subtracting from each uncaged replicate the mean number of seedlings lost to consumers inside cages for a given stand type defined by bamboo condition and canopy neighbourhood.

To characterize the level of consumer activity, we assessed the amount of leaf area removed by folivorous insects. The percentage

area missing or damaged was scored for each individual leaf (or cotyledon) in all surviving seedlings, using the scale: 1 = 5%, 2 = 5.1–25%, 3 = 25.1–50%, 4 = 50.1–75% and 5 = 75.1–100%. Leaf damage scores were averaged over each seedling; all measurements were performed by the same observer. Herbivory was monitored throughout the experiment yet only final measures for surviving seedlings are reported here. At this stage, average leaf sizes were about 35 mm² (*N. alpina*) and 16 mm² (*N. dombeyi*). To evaluate habitat use by small mammals, we laid out 160 live-capture Sherman traps ($7.5 \times 9 \times 22.5$ cm) during three nights; traps were baited with an oat–grease mixture. Trapping was conducted in autumn (April 2004), the season of peak rodent abundance in the area (Kitzberger, Chanton & Caccia 2007). We randomly selected four stands of each canopy–bamboo combination, and in each of them, we placed 40 traps at a regular distance of 10 m along four transects (10 traps per transect). Total capture effort was 120 traps-night per treatment, and 480 traps-night for the whole study. Traps were inspected every morning; rodents were identified to species, marked and released.

MICROENVIRONMENTAL MEASUREMENTS

In February 2004 (midsummer), we measured light intensity, soil moisture, soil temperature and litter depth for each canopy–bamboo treatment combination. We assumed that conditions measured towards the end of the study were representative, since bamboo did not recover in flowered patches, and live bamboo patches remained so throughout the experiment. At this stage, the canopy foliage of both *Nothofagus* species was fully expanded. Photosynthetic photon flux density (PPFD) was recorded at 5 cm height above the soil level using a quantum sensor (Li-Cor Q 24122) attached to a LI-1000 radiometer (Li-Cor, Nebraska). Measurements were taken over two consecutive sunny days, between 10:00 and 17:00 hs, in 2–3 stands per patch type ($n = 12$ –15 readings per stand). Volumetric soil water content (%) was measured to 7-cm depth ($n = 12$ –15 per stand) using a Theta Probe sensor (Delta-T Devices, Cambridge). Ground-level temperatures were recorded for 2–4 stands per patch type ($n = 10$ –15 per stand) using a digital thermometer, with the sensor inserted 2 cm into the litter layer and 2 cm into the mineral soil. Litter depth was measured to the nearest 0.5 cm using a ruler ($n = 6$ –8 readings per stand).

STATISTICAL ANALYSES

Data for seedling survival and source of mortality were analysed separately for each *Nothofagus* species using generalized linear models with a binomial error structure and a logit-link function (proc genmod, SAS Institute 1996). Analyses considered five replicates per treatment after pooling over four planting microsites per stand. For each species, the number of seedlings placed inside or outside cages within a stand (four plants) was used as the binomial denominator. We report mean probability values for seedling survival (or mortality) at the stand scale, with binomial standard errors (Agresti & Finlay 2009). The effects of canopy neighbourhood, bamboo condition and cage enclosure on cumulative seedling survival and source of mortality were tested through deviance analysis. Maximal models including all interactions were reduced until all parameters were significant (likelihood ratio tests, $P = 0.05$). Models were adjusted for overdispersion (dscale procedure, SAS Institute 1996).

Treatment effects on insect damage and seedling growth (leaf no.) were initially analysed through three-way ANOVA, with canopy neighbourhood, bamboo condition and cage enclosure as main effects (proc

glm, SAS Institute 1996). The cage treatment had no significant ($P < 0.10$) single or interactive effects on seedling damage or growth and was removed from final models (two-way ANOVAS). Because many seedlings were killed by biotic or abiotic agents, the final design for surviving plants was unbalanced. No seedlings were found alive in some stands for certain treatments after 2 years of field exposure (27.5% for *N. alpina*, and 57.5% for *N. dombeyi*). Therefore, individual plants rather than stands were used as replicates in these analyses (*N. alpina*, $n = 3-22$; *N. dombeyi*, $n = 2-9$). Leaf damage (%) data were arcsin-square-root transformed to reduce variance heterogeneity. We also used two-way ANOVA for microenvironmental variables, with canopy species and bamboo condition as main effects. Light data were rank-transformed before analysis.

Results

OVERALL PATTERN OF SEEDLING SURVIVAL

After 2 years, overall seedling survival was 29% and 16% for *N. alpina* and *N. dombeyi*, respectively. Cage exclosures significantly enhanced seedling survivorship for both species, irrespective of bamboo condition and canopy neighbourhood (Table 1). Excluding small vertebrates increased survival by almost twofold (21–36%) for *N. alpina*, and by threefold (7–25%) for *N. dombeyi*. In addition, *N. alpina* seedlings survived nearly twice as much in heterospecific (*N. dombeyi*) as in conspecific canopy patches (Table 1, Fig. 1a). Bamboo die-off increased *N. alpina* survival, and this effect was similar in conspecific and heterospecific neighbourhoods (Table 1, Fig. 1a). Survival of *N. alpina* seedlings was lowest under conspecific canopies with live bamboo, and increased up to 60% under *N. dombeyi* canopies with a dead bamboo understorey. Conversely, *N. dombeyi* survival was generally low and only marginally affected by bamboo die-back and neighbourhood composition (Table 1). On average, seedling survival for *N. dombeyi* increased to 20% with bamboo die-off under heterospecific canopies ($P = 0.083$, Fig. 1b).

SOURCES OF SEEDLING MORTALITY

Nothofagus seedlings experienced higher mortality attributable to consumers (56%) than to wilting stress (21%). Seedling mortality associated with consumers was similar between seedling species (*N. alpina* = 55%, *N. dombeyi* = 58%). Cage exclosures reduced seedling loss to consumers by nearly 25% for both species, regardless of bamboo condition or canopy neighbourhood (Table 1, Fig. 2a,c). Overall, bamboo die-off significantly reduced consumer-related seedling mortality. For *N. alpina*, this effect appeared to be greater under heterospecific (*N. dombeyi*) canopies, but the bamboo $\times$ canopy interaction was not significant (Table 1, Fig. 2a). Still, the likelihood of *N. alpina* seedlings being lost to consumers was significantly lower in heterospecific than in conspecific neighbourhoods (Fig. 2a). In contrast, neighbourhood composition did not consistently affect total seedling mortality by consumers in *N. dombeyi* (Fig. 2c).

Patterns of mortality attributed to wilting stress depended on the seedling species (Fig. 2). Bamboo die-off significantly increased *N. dombeyi* wilting mortality ($F_{1,38} = 9.19$, $P = 0.0044$, Fig. 2d), whereas *N. alpina* mortality by wilting stress was not affected by bamboo condition ($F_{1,38} = 0.13$, $P = 0.72$, Fig. 2b). Cage exclosure and canopy neighbourhood did not significantly influence the chance of seedling loss through wilting stress (all P values > 0.10).

When consumer-related mortality was compared between caged and uncaged plants, it became clear that *Nothofagus* seedlings were more likely to be killed by invertebrates (44%) than by vertebrates (27%). *Nothofagus alpina* seedlings suffered significantly higher mortality by invertebrate consumers in conspecific than in heterospecific neighbourhoods ($F_{1,17} = 8.76$, $P = 0.0088$, Fig. 3a). Bamboo dieback decreased *N. alpina* seedling loss to invertebrates ($F_{1,17} = 8.76$, $P = 0.0088$), and although differences between live and dead bamboo patches were greater under *N. dombeyi* canopies (Fig. 3a), the bamboo $\times$ neighbourhood interaction

Table 1. Effects of vertebrate exclusion (cage vs. open), bamboo condition (live vs. dead) and canopy neighbourhood (conspecific vs. heterospecific) on cumulative survival and overall loss to consumers after two growing seasons, for *Nothofagus alpina* and *Nothofagus dombeyi* seedlings, in a mixed temperate forest, northern Patagonia, Argentina. Data were analysed through generalized linear models with binomial errors and a logit-link function ($n = 5$). Parameters with a significant effect ($P = 0.05$) on the final, reduced model are shown in bold

Parameter	d.f.	Overall survival				Loss to consumers			
		<i>N. alpina</i>		<i>N. dombeyi</i>		<i>N. alpina</i>		<i>N. dombeyi</i>	
		<i>F</i>	<i>P</i> <	<i>F</i>	<i>P</i> <	<i>F</i>	<i>P</i> <	<i>F</i>	<i>P</i> <
Cage exclosure	1	7.33	0.011	9.85	0.004	7.61	0.010	19.13	0.001
Bamboo condition	1	19.56	0.001	3.52	0.069	11.11	0.003	25.59	0.001
Canopy	1	16.02	0.001	0.89	0.36	13.05	0.001	1.04	0.32
Cage $\times$ Bamboo	1	0.15	0.71	1.39	0.25	0.54	0.47	3.24	0.09
Cage $\times$ Canopy	1	0.44	0.52	1.07	0.31	0.28	0.61	1.33	0.26
Bamboo $\times$ Canopy	1	0.19	0.67	3.20	0.083	1.91	0.18	0.67	0.42
Cage $\times$ Bamboo $\times$ Canopy	1	2.83	0.11	0.21	0.65	0.44	0.52	0.38	0.55

For each species, maximal models including all interaction terms were reduced through deviance analysis; thus, residual d.f. for the final models differed slightly. *Nothofagus alpina* d.f. = 36, for both analyses; *N. dombeyi* d.f. = 38 and 37, for overall survival and loss to consumers, respectively.

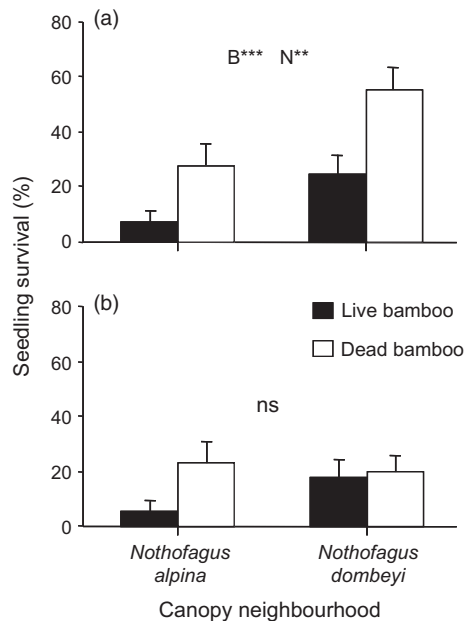


Fig. 1. Effects of bamboo die-off and canopy neighbourhood on (a) *Nothofagus alpina* and (b) *Nothofagus dombeyi* seedling survival. Two cotyledon seedlings were planted in live and dead bamboo (*Chusquea culeou*) patches under conspecific and heterospecific canopies, in an old-growth forest in northern Patagonia, Argentina. Bars show mean survival ± 1 SE ($n = 5$ stands) after 2 years. Asterisks denote effects of bamboo condition (B) and neighbourhood (N): *** $P < 0.001$, ** $P < 0.01$, ns = non-significant.

was not significant ($F_{1,16} = 3.10$, $P = 0.097$). *Nothofagus dombeyi* also experienced lower mortality by invertebrates in dead than in live bamboo patches ($F_{1,18} = 7.42$, $P = 0.014$, Fig. 3c), irrespective of canopy neighbourhood (bamboo $\times$ canopy $F_{1,16} = 1.57$, $P = 0.23$).

Mortality of *N. alpina* seedlings attributed to vertebrate consumers was not affected by bamboo condition or canopy neighbourhood (all P values > 0.10 , Fig. 3b). In contrast, bamboo die-off significantly decreased *N. dombeyi* mortality by vertebrate consumers under conspecific canopies (bamboo $\times$ canopy $F_{1,16} = 5.91$, $P = 0.027$, Fig. 3d).

CONSUMER ACTIVITY

Leaf area loss to insects ranged between 1% and 35%, depending on the seedling species and treatment. Insect damage on *N. alpina* plants was higher under conspecific than under heterospecific canopies ($F_{1,42} = 6.67$, $P = 0.013$, Fig. 4a), but was not affected by bamboo die-off ($F_{1,42} = 2.72$, $P = 0.11$, bamboo $\times$ canopy $F_{1,42} = 1.79$, $P = 0.19$). Conversely, herbivory on *N. dombeyi* was higher under heterospecific (*N. alpina*) than conspecific canopies ($F_{1,22} = 20.14$, $P = 0.0002$) with a live bamboo understorey (Fig. 4b). Bamboo die-off significantly reduced herbivore damage on *N. dombeyi* seedlings under *N. alpina* canopies (bamboo $\times$ canopy $F_{1,22} = 14.2$, $P = 0.0011$, bamboo $F_{1,22} = 29$, $P = 0.0001$).

Rodent trapping yielded 42 individuals (0.0875 rodent trap $^{-1}$ night $^{-1}$) from six species. The most common one was the omnivore *Abrothrix longipilis*, which accounted for 55% of all captures. Rodent numbers were, on average, higher in *N. dombeyi* patches with a live bamboo understorey (0.15 rodents trap $^{-1}$ night $^{-1}$) than in either *N. alpina* or bamboo die-off patches (0.067 rodents trap $^{-1}$ night $^{-1}$). Yet rodent distribution across stands did not significantly deviate from that expected by chance alone ($\chi^2 = 2.29$, $P = 0.13$, d.f. = 1).

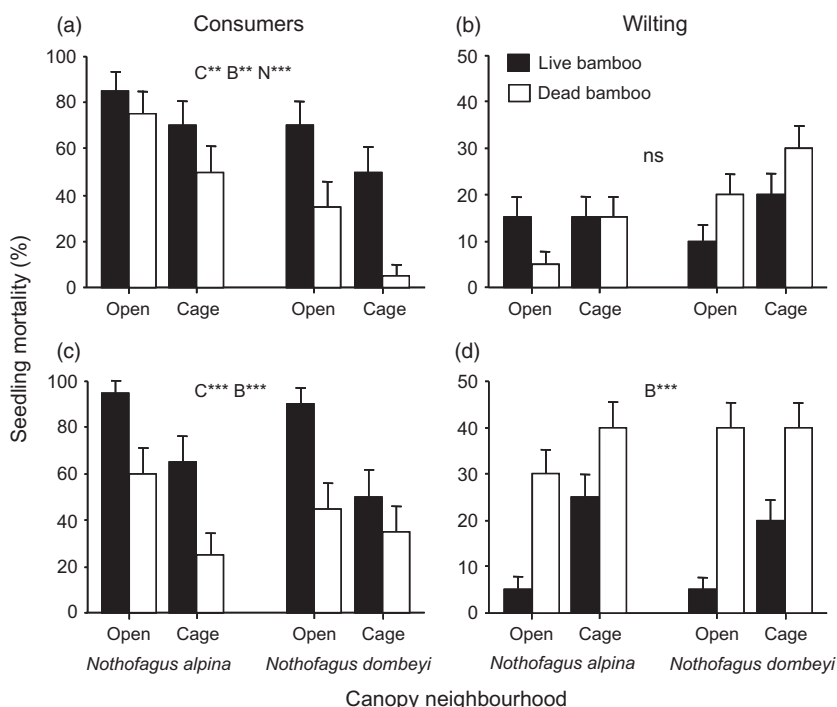


Fig. 2. Effects of cage closure, bamboo die-off and canopy neighbourhood on *Nothofagus alpina* (a, b) and *Nothofagus dombeyi* (c, d) seedling mortality attributed to resident consumers (a, c) and wilting stress (b, d). Seedling loss to consumers comprised plants killed by either vertebrates or invertebrates. Bars show mean mortality rates ± 1 SE ($n = 5$ stands) after 2 years. Asterisks denote effects of cage closure (C), bamboo condition (B) and neighbourhood (N): *** $P < 0.001$, ** $P < 0.01$, ns = non-significant.

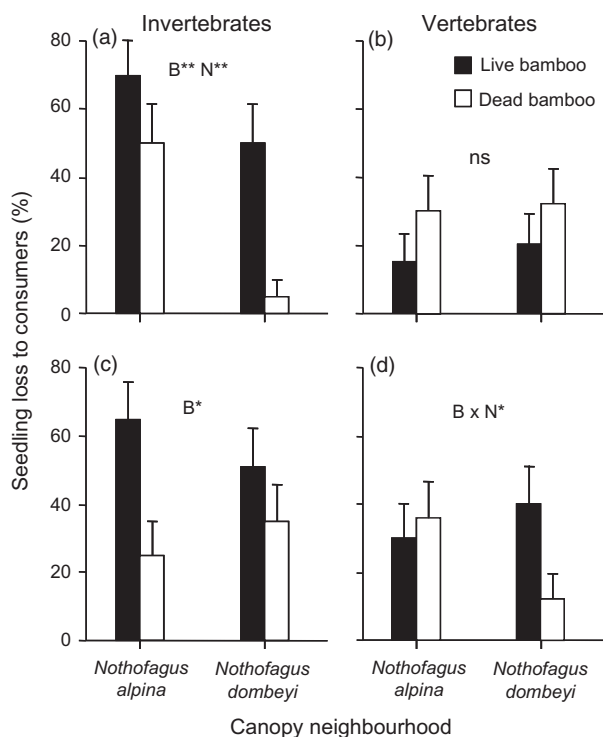


Fig. 3. Effects of bamboo die-off and canopy neighbourhood on *Nothofagus alpina* (a, b) and *Nothofagus dombeyi* (c, d) seedling mortality attributed to invertebrate (a, c) or vertebrate (b, d) consumers. Loss to invertebrates was estimated from seedlings planted inside cage enclosures. Vertebrate losses were derived from differences in consumer-induced mortality outside vs. inside cage enclosures. Bars show mean mortality rates $\pm$ 1 SE ($n = 5$ stands) after 2 years. Asterisks denote effects of bamboo condition (B) and neighbourhood (N): ** $P < 0.01$, * $P < 0.05$, ns = non-significant.

TREE SEEDLING GROWTH

The cage treatment had no significant effect on the final leaf number per plant ($P > 0.10$). Tree seedlings grew larger in dead than in live bamboo patches for both study species (Fig. 5), although this effect was more pronounced for the less shade-tolerant *N. dombeyi* than for *N. alpina* ($F_{1,22} = 11.85$, $P = 0.0023$ and $F_{1,42} = 7.38$, $P = 0.01$, respectively). *Nothofagus alpina* seedling growth was significantly enhanced in heterospecific canopy neighbourhoods, compared to conspecific ones ($F_{1,42} = 9.01$, $P = 0.0045$, Fig. 5a), regardless of bamboo condition (bamboo $\times$ canopy $F_{1,42} = 1.86$, $P = 0.18$). Conversely, *N. dombeyi* seedling growth did not vary with canopy neighbourhoods ($F_{1,22} = 1.82$, $P = 0.19$, bamboo $\times$ canopy $P = 0.98$, Fig. 5b).

MICROENVIRONMENTAL CONDITIONS

Light availability beneath live bamboo thickets was less than 5% that recorded in dead bamboo patches (5.2 vs. 180 $\mu\text{mol m}^{-2} \text{s}^{-1}$, $F_{1,152} = 396.5$, $P < 0.0001$, Fig. 6a). Bamboo dieback increased mean temperatures of the mineral soil (12.9 vs. 12 $^{\circ}\text{C}$, $F_{1,102} = 72.6$, $P < 0.0001$) and litter layer (16.4 vs. 13.7 $^{\circ}\text{C}$, $F_{1,137} = 79.3$, $P < 0.0001$), compared

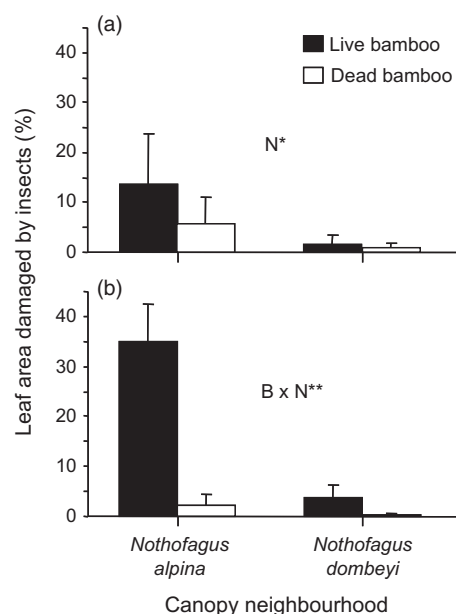


Fig. 4. Effects of bamboo die-off and canopy neighbourhood on percentage leaf area removed by folivorous insects in *Nothofagus alpina* (a) and *Nothofagus dombeyi* (b) seedlings. Bars show means $\pm$ 1 SE ($n = 2$ –22 plants), for seedling transplants surviving 2 years in the field. Asterisks denote significant effects of bamboo condition (B) and neighbourhood (N): ** $P < 0.01$, * $P < 0.05$.

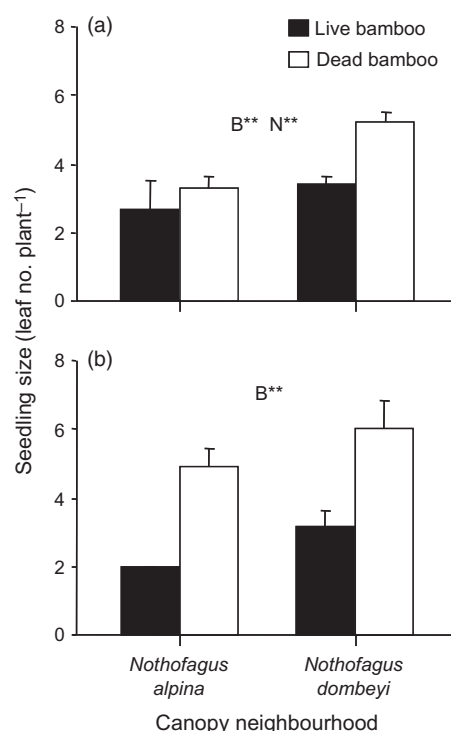


Fig. 5. Effects of bamboo die-off and canopy neighbourhood on *Nothofagus alpina* (a) and *Nothofagus dombeyi* (b) seedling size (no. of leaves per plant). Bars show means $\pm$ 1 SE ($n = 2$ –22 plants), for seedling transplants surviving 2 years in the field. Asterisks denote significant effects of bamboo condition (B) and neighbourhood (N): ** $P < 0.01$.

to live bamboo patches (Fig. 6b). Soil and litter temperatures were higher in *N. dombeyi* than in *N. alpina* neighbourhoods (soil $F_{1,102} = 13.3$, $P < 0.001$; litter $F_{1,137} = 5.2$, $P = 0.024$; Fig. 6b). As a result, soil moisture was significantly higher in live than in dead bamboo patches ($F_{1,154} = 17.2$, $P < 0.0001$), and in *N. alpina* than in *N. dombeyi* neighbourhoods ($F_{1,154} = 5.7$, $P = 0.019$, Fig. 6c). Effects of bamboo dieback and canopy neighbourhood on abiotic conditions were independent (all interactions $P > 0.10$). Litter depth decreased with bamboo die-off under *N. alpina* canopies (bamboo $\times$ canopy $F_{1,74} = 14.82$, $P < 0.001$), although the litter layer was still thicker in *N. alpina* than in *N. dombeyi* neighbourhoods (Fig. 6d).

Discussion

The synchronous flowering and subsequent die-off of monocarpic bamboos has long been thought to create opportunities for canopy species regeneration (Taylor & Qin 1992; Griscom & Ashton 2003; Giordano, Sánchez & Austin 2009). Yet mechanisms driving tree seedling dynamics after bamboo blooms have remained unclear. Our study shows that dieback of bamboo understories may not only enhance tree seedling survival and growth via changes in light conditions (Abe *et al.* 2005; Marchesini, Sala & Austin 2009), but also by disrupting seedling–consumer interactions under closed canopies. We found that light availability to *Nothofagus* seedlings increased, and consumer pressure decreased in flowered/dead bamboo patches. As a result, bamboo die-off increased the chances of successful recruitment into the sapling stage for *N. alpina*, and had similar, yet non-significant effects on the survival of *N. dombeyi* seedlings (Table 1, Figs 1 and 2). In addition, neighbourhood composition induced species-specific

associational effects (Norghauer & Newbery 2011; Underwood, Inouye & Hambäck 2014) on seedling performance that were largely independent of bamboo condition. Thus, in this Patagonian mixed forest, widespread bamboo die-off modified the magnitude, but not the direction of canopy–seedling interactions.

BAMBOO DIE-OFF EFFECTS ON TREE SEEDLING PERFORMANCE

Consumers were a major agent of seedling mortality in this forest community. Bamboo dieback reduced seedling loss to invertebrate herbivores for both *Nothofagus* species, although release from consumers only translated into higher survival for the most palatable species (*N. alpina*, Figs 1–3). The decrease in seedling mortality could reflect reduced invertebrate abundance in dead bamboo patches. This idea is consistent with the greater leaf damage experienced by *Nothofagus* seedlings surviving in live bamboo patches (Fig. 4). Flowered bamboo patches had reduced above-ground biomass and litter cover (Marchesini, Sala & Austin 2009), which led to greater light penetration, higher temperatures and less moisture at ground level, relative to non-flowered patches (Fig. 6). Such microclimate conditions may increase exposure of invertebrate herbivores to physical stresses (Pigot & Leather 2008) as well as to natural enemies (Stoepler & Lill 2013). Live bamboo patches might retain herbivores by providing sheltered habitat and oviposition sites (Pigot & Leather 2008), thus increasing the risk of attack on emerging seedlings. Our results reassert that apparent competition can be a major mechanism whereby dense understories suppress seedling recruitment (Caccia, Chaneton & Kitzberger 2006, 2009; Royo & Carson 2008).

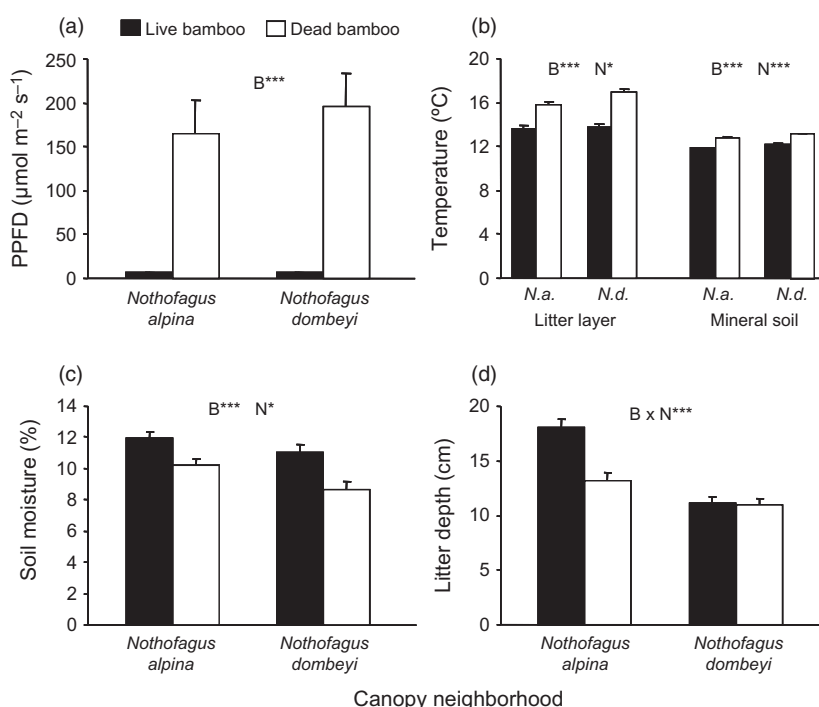


Fig. 6. Microhabitat conditions as affected by bamboo die-off and canopy neighbourhood in a mixed Patagonian forest. (a) Photosynthetic photon flux density (PPFD) at ground level; (b) temperature of the litter and topsoil layers; (c) volumetric soil moisture content (%); (d) litter depth. Bars show means $\pm$ 1 SE, for February 2004 (summer). *N.a.* = *Nothofagus alpina*; and *N.d.* = *Nothofagus dombeyi*. Asterisks denote significant effects of bamboo condition (B) and neighbourhood (N): *** $P < 0.001$, * $P < 0.05$.

Studies performed in *Fagus crenata* forests (Japan) have shown that release from soil pathogens (damping off) facilitated tree seedling survival after dieback of dwarf bamboo understories (Nakashizuka 1988; Abe, Miguchi & Nakashizuka 2001). In this experiment, we found no symptoms of *Nothofagus* seedlings being killed by damping off. Furthermore, seedling mortality by wilting stress, which is often taken as evidence of pathogen attack (Fricke, Tewksbury & Rogers 2014), actually increased (not decreased) in the more insolated and drier microsites beneath dead bamboo (Figs 2 and 6). Still, we cannot fully discard that a decrease in pathogen incidence played a role in the positive impact that bamboo die-back had on seedling survivorship.

Tree seedlings planted beneath live and dead bamboo experienced contrasting microclimatic conditions (Fig. 6), which could affect their vulnerability to invertebrate consumers (Dudt & Shure 1994; Stoepler & Lill 2013) or fungal pathogens (Nakashizuka 1988). Even low levels of tissue loss may alter early seedling growth (Clark & Clark 1985), so that herbivory would be particularly lethal to seedlings in shaded microsites (Pearson *et al.* 2003; Norghauer, Malcolm & Zimmerman 2008). *Nothofagus* seedlings in live bamboo patches may be inherently more susceptible to folivory and/or less able to recover from damage, compared to those in gaps created by bamboo die-off. Increased light availability in die-back patches may enhance seedling growth rates (Holz & Veblen 2006; Marchesini, Sala & Austin 2009; see Fig. 5), allowing new seedlings to better withstand herbivory (Chacón & Armesto 2006; Norghauer, Malcolm & Zimmerman 2008). Our study was not designed to distinguish the effects of consumers and abiotic factors during seedling establishment. It is then possible that the larger size of *Nothofagus* plants surviving beneath dead bamboo reflected a synergism between reduced herbivory and increased light levels.

Our results are consistent with previous work in Patagonia that emphasized the role of increased light levels in facilitating the growth of seedlings or saplings established prior to a bamboo-flowering event (González *et al.* 2002; Holz & Veblen 2006; Raffaele, Kitzberger & Veblen 2007; Marchesini, Sala & Austin 2009). It has been suggested that bamboo die-back may not encourage recruitment from newly emerged seedlings (Raffaele, Kitzberger & Veblen 2007; Muñoz *et al.* 2012). However, field experiments have shown that increased red: far-red light ratios beneath dead bamboo may enhance seed germination of *N. obliqua* (Giordano, Sánchez & Austin 2009). Our study adds a plausible mechanism, namely, reduced loss to invertebrate herbivores, whereby young seedlings have better chances of establishing after bamboo die-off.

Exclusion of vertebrate consumers increased overall seedling survival for both *Nothofagus* species (Fig. 2). However, bamboo die-off did not substantially decrease *Nothofagus* seedling mortality attributed to vertebrates (Fig. 3; cf. Abe *et al.* 2005). Seed and seedling predation by rodents often decreases in exposed microhabitats, such as large natural gaps in bamboo understories (Caccia, Chaneton & Kitzberger 2006, 2009). The lack of inter-patch differences in rodent activity observed in this study suggests that dead bamboo

thickets still provided effective habitat for rodents (Kitzberger, Chaneton & Caccia 2007). Although *N. dombeyi* mortality by vertebrates decreased after bamboo die-off, this only occurred under conspecific canopies (Fig. 3d) and had no impact on final survivorship. Indeed, *N. dombeyi* seedlings escaping from vertebrate predation in dieback patches were nevertheless killed by wilting stress (Figs 1b and 2c,d).

We expected that bamboo die-off would increase the likelihood of tree seedlings becoming established under close-canopy conditions. Yet we found that the outcome of bamboo–seedling interactions was species-specific. For *N. dombeyi*, the species less vulnerable to herbivory, wilting mortality counteracted the benefits of seedling release from consumers after bamboo die-off (Figs 1 and 2). While *N. dombeyi* exhibits low shade tolerance (Read & Hill 1985), a live bamboo cover appeared to create less stressful conditions for early survival than those faced by seedlings in dead bamboo patches with higher temperatures and lower soil moisture (Fig. 6). In contrast, bamboo dieback enhanced *N. alpina* survival, presumably because of its greater tolerance to water stress (Varela *et al.* 2010). These results suggest that interspecific differences in seedling tolerance to herbivory and drought may influence recruitment dynamics after bamboo blooms. Our findings show that understorey disturbances may affect tree recruitment patterns by modifying the relative strength of direct (resource-mediated) and indirect (consumer-mediated) interactions at the early seedling stage (Abe *et al.* 2005; Royo & Carson 2008; Caccia, Chaneton & Kitzberger 2009).

ASSOCIATIONAL EFFECTS WITHIN CANOPY NEIGHBOURHOODS

We found that effects of bamboo die-off and canopy neighbourhood were largely independent. Although bamboo die-off reduced herbivory on *N. dombeyi* seedlings under *N. alpina* canopies, this had no net effect on seedling survival (Figs 1b and 4b). Nonetheless, we did find patterns of seedling loss to invertebrates that depended on canopy composition (Fig. 3). Notably, these associational effects (Underwood, Inouye & Hambäck 2014) influenced seedling dynamics despite widespread understorey disturbance from bamboo dieback. We predicted that seedling species' performance would be increased in heterospecific canopy neighbourhoods. Instead, the impact of consumer-mediated associational effects varied with the focal tree species. The more palatable *N. alpina* experienced associational resistance (Barbosa *et al.* 2009), being less frequently damaged or killed by invertebrates under heterospecific than conspecific canopies. Conversely, while insect herbivory on the less vulnerable *N. dombeyi* increased under *N. alpina* canopies (i.e. associational susceptibility), total consumer-related mortality for *N. dombeyi* did not differ with canopy neighbourhood (Figs 2 and 4). Such asymmetries in associational effects between co-occurring species may be expected when they differ markedly as host plants to polyphagous herbivores (Norghauer & Newbery 2011; Underwood, Inouye & Hambäck 2014). The observed neighbourhood effects imply that *N. alpina* would have greater chances of

establishing in adjacent *N. dombeyi* stands, but not *vice versa*, and that bamboo dieback events may reinforce this asymmetrical interaction (see Fig. 1).

Canopy neighbourhoods may differ not only with regard to consumer density (Humphrey & Swaine 1997; Wada, Murakami & Yoshida 2000), but also microhabitat conditions affecting seedling performance (Catovsky & Bazzaz 2002). Indeed, both litter depth and soil microclimate differed between *Nothofagus* neighbourhoods (Fig. 6). The thick litter deposited by *N. alpina* canopies could provide habitat for ground-dwelling herbivores, thus contributing to explain why *N. alpina* seedlings performed better in hetero-specific neighbourhoods. Other biotic factors including canopy–seedling competition and negative plant–soil feedbacks via fungal pathogens might also contribute to seedling mortality under conspecifics (Alvarez-Loayza & Terborgh 2011; McCarthy-Neumann & Ibañez 2013), and deserve more investigation in Patagonian forests. Additional studies are also needed to assess the influence of microhabitat factors on density-dependent patterns of seedling survival at the canopy neighbourhood scale (Catovsky & Bazzaz 2002; Piao *et al.* 2013).

BAMBOO DIE-OFF AND FOREST DYNAMICS

In old-growth, Andean *Nothofagus* forests, background rates of seedling establishment are typically low, except when masting episodes overlap with coarse-scale disturbances (Pollmann & Veblen 2004). Seedling-to-sapling recruitment may occur in treefall gaps of varying sizes, and less frequently in closed-canopy microsites (Veblen 1989; Dezzotti *et al.* 2003; Pollmann & Veblen 2004). This is partly true because the presence of dense bamboo understories strongly inhibits seedling survival and growth (Veblen 1982; Holz & Veblen 2006; Raffaele, Kitzberger & Veblen 2007). Our experiment helps to explain the scarcity of *Nothofagus* recruits in undisturbed forests as a result of heavy seedling mortality from both vertebrate and invertebrate consumers, as reported in other temperate (Clark, Poulsen & Levey 2012) and tropical forests (Norghauer & Newbery 2011; Fricke, Tewksbury & Rogers 2014). Overall, the combined effects of seed removal by rodents (Kitzberger, Chaneton & Caccia 2007), low germination (Giordano, Sánchez & Austin 2009), early seedling predation (this study) and light competition (Veblen 1982) create a multiple barrier to *Nothofagus* recruitment in old-growth forests.

In this context, understorey disturbances from bamboo dieback may increase the chances that *Nothofagus* seedlings recruit into the sapling stage (Holz & Veblen 2006; Marchesini, Sala & Austin 2009; Muñoz *et al.* 2012). However, we stress that the lack of extended monitoring of tree seedling fates after bamboo blooms precludes drawing definite conclusions. Re-establishment of bamboo dominance after dieback events can be a slow process (>10 years; Marchesini, Sala & Austin 2009) in closed-canopy stands like those studied here. Our results suggest that microsite conditions in dead bamboo patches may foster seedling recruitment of shade-tolerant species like *N. alpina*, which form sparse seedling/sapling

banks (Weinberger & Ramírez 2001; González *et al.* 2002). In contrast, early seedling survival of the less shade-tolerant species *N. dombeyi*, which is a common colonizer of larger canopy gaps (Veblen 1989; Pollmann & Veblen 2004; Donoso *et al.* 2013), did not appear to be facilitated by bamboo dieback (Fig. 1; cf. Holz & Veblen 2006). We have also shown that the likelihood of *Nothofagus* seedling survival differs across canopy neighbourhoods, because of specific canopy–seedling interactions (Figs 1–3). Yet, in the absence of spatial data on natural seed dispersal and seedling/sapling densities (Schnurr *et al.* 2004; Comita & Hubbell 2009), the relevance of this finding to forest community dynamics remains to be determined.

Our results may help to refine successional models for mixed deciduous-evergreen forests in northern Patagonia. It has been posited that in the absence of catastrophic disturbances (e.g. fires, landslides), forest succession proceeds by the slow recruitment of shade-tolerant species into small treefall gaps (Veblen 1989, 1992). On the other hand, large-scale disturbances would promote widespread establishment and dominance by the less shade-tolerant *N. dombeyi* (Veblen *et al.* 1996; Pollmann & Veblen 2004). The present work suggests that bamboo die-off events may accelerate gap-phase succession by increasing the chances that *N. alpina* seedlings escape from consumers and colonize understorey gaps beneath *N. dombeyi* canopies. We conclude that bamboo die-off events create transient, species-specific recruitment opportunities, which coupled with associational effects from neighbourhood composition and stochastic canopy disturbances, may influence the pattern and rate of forest succession.

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Data accessibility

Data available from the Dryad Digital Repository (Caccia, Kitzberger & Chaneton 2014).

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