Masting has different effects on seed predation by insects and birds in antarctic beech forests with no influence of forest management

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ABSTRACT

Mast seeding is characteristic of many long-lived tree species and widely proposed as a mechanism to reduce seed predation. However, whether the efficiency of this reproductive response may vary depending on type of seed predator (e.g., invertebrates vs. vertebrates) or depending on local characteristics, remains seldom explored. We evaluated for 8 yrs the patterns of seed production in antarctic beech (*Nothofagus antarctica*) forests related to management and its influence on insect and bird pre-dispersal seed predation. Along the study, mature seed production was highly variable across years (the population-level coefficient of variation, CVp: 0.98–1.14) and spatially synchronized (Pearson correlation coefficient: 0.83–0.86). Forest type (primary unmanaged, secondary-growth and managed stands) did not influence the amount of seed production nor masting patterns. Mean yearly seed predation by insects was higher than by birds, and their relationship with seeding patterns differed: i.e., while the proportion of seeds predated by insects increased during non-mast years maximum bird predation occurred in mast years. Therefore, predation by insects and birds showed a strong negative relationship. Our results suggest that effectiveness of masting to escape seed predators may be highly depend on the type of predator. We address whether this effect may be due to differences in life history traits among the seed predators involved (i.e., degree of host specificity, dispersal ability or the duration of the life-cycle) and whether an "imperfect" control of avian seed predation may partially be advantageous for the dynamics of the masting species to enhance seed dispersal.

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1. Introduction

High supra-annual variability in seed production ("masting") has been extensively described in many long-lived tree species (e.g., Silvertown, 1980; Kelly, 1994; Kelly and Sork, 2002). This high variation in the reproductive output has been claimed to have important consequences for regulating plant populations dynamics (Espelta et al., 2009), but the extreme resource abundance fluctuation may have relevant effects on the entire trophic web of the forest system (Silvertown, 1980; Ostfeld and Keesing, 2000; Kon et al., 2005). In fact masting has been interpreted as a reproductive strategy potentially evolved to dampen seed predation by exerting some control on predator populations by satiating/starving seed consumers through variable seed production (Janzen, 1971; Kelly, 1994; Yasaka et al., 2003; Kon et al., 2005; Espelta et al., 2008; Fletcher et al., 2010; Fukumoto and Kajimura, 2011). The effectiveness of this strategy has been suggested to vary depending on seed predator life history traits such as host-specificity, dispersal ability or duration of the life-cycle (Ims, 1990). Thus, masting has been suggested to be specially effective to control seed predation by insects because they usually have a short life cycle intimately related with the period of seed production, a high host specificity and, in some cases low dispersal ability (e.g., coleoptera of the *Curculio* genus that predate upon acorns, hazelnuts and chestnuts, see Bonal et al., 2007; Espelta et al., 2009). In comparison, although vertebrates predating upon seeds are also affected by masting (see Bergeron et al., 2011; Bogdziewicz et al., 2015), the impact would be less intense, owing to their lower host specificity and higher mobility (Curran and Leighton, 2000; García et al., 2011; Bell and Clark, 2016). Thus, treating insect and vertebrate

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seed predators separately is necessary to elucidate the role of masting in reducing seed predation (Bell and Clark, 2016).

Even though it is acknowledged that seeds are often predated by a diverse guild of insects and vertebrates, most studies addressing the consequences of masting have focused on a single group like insect seed predators (Yasaka et al., 2003; Espelta et al., 2008; Fukumoto and Kajimura, 2011), or seed-eating rodents (Clotfelter et al., 2007; Bergeron et al., 2011; Sunyer et al., 2013, 2015). Insects and vertebrates may not only differ in the above mentioned life-history traits relevant for the impact of masting but they may interact having different effects upon seed predation rates: i.e., a neutralizing effect, as vertebrates may contribute to control insects by consuming infested seeds (Herrera, 1998; Bonal et al., 2007; Peguero and Espelta, 2013), or a cumulative effect on the number of seeds destroyed (Traveset, 1994) due to avoidance of infested seeds by vertebrates. According to (Christensen and Whitham, 1993) birds not only ignore damaged seeds within a tree; sometimes they avoid trees and entire stands with low-quality fruits or those affected by insects. Moreover, the presence of these two groups may largely vary with habitat conditions such as vegetation structure and landscape attributes. Different levels of canopy cover determine changes in microenvironment conditions (e.g., solar radiation, surface soil temperature, or soil moisture), which may influence insect development and abundance, and ultimately insect damage to seeds (Bonal et al., 2012). Different forest structures may also modify habitat suitability for vertebrates (e.g., perching branches and snags for birds, understory cover for rodents), influencing their feeding behavior (see Sunyer et al., 2013, 2015 for rodents; García et al., 2011 for birds). Therefore, altering forest structure through management practices might ultimately influence the effects of masting in seed predation in these two groups.

In the temperate forests of Southern hemisphere, birds and insect are among the most sensitive organisms to human-caused canopy alterations such as forest harvesting (Lencinas et al., 2009, 2012, 2014). Such response in birds, somewhat more generalists and high mobile organisms, could be reflected in lower seed predation (at canopy level) occurring in managed forests, while insects with a more restricted action range heavily depend on the number of seeds produced in a small scale. The main goal of this study was to explore the patterns of masting in antarctic beech (Nothofagus antarctica) forests differing in their structure, and the influence of this pattern on insect and bird predation. These forests offer an interesting opportunity to investigate this ecological processes because: (i) Nothofagus species show large inter-annual variability in seed production (Kelly, 1994; Kelly and Sork, 2002; Allen et al., 2012), (ii) seeds of southern beech are consumed by insects (e.g., Lepidoptera and weevils, or beetles larvae) and vertebrates (e.g., birds like Carduelis magellanica), and (3) southern beech forests in Tierra del Fuego have been subjected to different anthropogenic disturbances (i.e., fire, livestock, clear-cutting) which shaped a mosaic of forests conditions (i.e., different stages of forest development and heterogeneous canopy cover; Soler et al., 2012) that may influence seed production, masting patterns and the predation rates by insects or birds.

The objective of this study was to assess the temporal variability in seed production of antarctic beech forests in southern Patagonia forests (Argentina), and the consequences on pre-dispersal seed predation by insects and birds. Specifically, we hypothesize that (1) differences in forest structure, represented by different forest types (i.e., primary unmanaged, secondary and grazed by livestock) influence the amount of seeds produced and its inter-annual variability patterns; (2) variable seed production has a strong effect on predation by insects (i.e., organisms with bounded mobility) than by birds (i.e., generalist organisms and with great mobility); and (3) there is a cumulative effect on the number of seeds pre-

dated (Traveset, 1994) due to avoidance of larvae-infested seeds by birds.

2. Materials and methods

2.1. Forest species and study site

The antarctic beech Nothofagus antarctica (G. Forster) Oerst., is a representative species of sub-Antarctic forests. It is a monoecious species, with pollination mediated by wind. Budburst occurs in spring and fruits (a nut) develop in early summer. Nuts have three seeds per cupule that ripen and fall in early autumn (March). Seeds are subject to pre-dispersal predation by insects such as Lepidoptera and Coleoptera, and birds such as passerines and parrots. Both insect larvae and bird consumption produce the loss of the whole seed due to the small seed size (3 mm length) and the total consumption of cotyledons. In example, McGehee and Eitniear (2007) described the method of feeding used by Phrygilus patagonicus which consists of thoroughly grinding and crushing all food items before swallowing. There are no evidences that Patagonian bird species play a significant role as dispersers of Nothofagus seeds, as most of these seed eating birds consume the seeds at the canopies during autumn as energy resource for migrations. N. antarctica forests in southern Patagonia occur naturally in different habitats such as poorly drained sites at low elevations, exposed windy areas with shallow soils, depressions under cold air influence, or in drier eastern sites near the Patagonian steppe (Veblen et al., 1996).

This study was conducted in a forest where the canopy was dominated exclusively by N. antarctica located at Los Cerros Ranch (54°22′16″S, 67°51′11″W) in central Tierra del Fuego Island, Argentina. Climate is strongly influenced by oceanic current, Antarctica proximity, and the insular characteristic (high rate of sea mass/-landmass) determines a uniform climate regime with low range of annual temperature (7–10 °C of annual difference). Average annual precipitation is 400–600 mm, and the mean monthly temperature range from −1.7 °C mid-winter to 10.2 °C during summer inside forests (Soler et al., 2013).

2.2. Sampling design of seed production

In 2008 we established 12 sampling sites considering three forest types: (i) primary unmanaged forests (PF): mature old-growth without signs of anthropic disturbance; (ii) secondary-growth forests (SF): young stands originated by intentional fires; and (iii) forests under silvopastoral use (SILVO): mature stands that had been thinned 5 yrs before the onset of this study, and currently are being used for cattle grazing. According to dendrochronological analysis of these sites (Ivancich et al., 2011), mature forests (PF and SILVO) were 150–200 years old, while second-growth forests (SF) were 70–80 years old (see Soler et al., 2013 for more details about forest structure of the study sites).

To monitor seed production we established 10 seed traps at each sampling site (n = 120 in total). The traps (plastic buckets of 0.06 m² area and 30 cm deep) were placed along a 10 m transect to better represent the whole canopy structure of each site. Each trap were separated 1 m from each other and elevated 1.8 m above the ground to avoid damage by big herbivores. From 2008 to 2015 we collected the fallen seeds once at year (mid to late May). The seeds were manually classified into one of three categories: (1) insect predated (e.g., characterized by 0.5- to 1-mm circular exit wounds, or by deformation of the normal shape of fruits caused by larvae infestation), (2) bird predated (characterized by damage to the shell and complete consumption of the seed inside) or (3) sound (e.g., attaining mature seed size and good formation).

Mature seed production per trap was obtained adding sound seeds to insect and bird predated seeds for each, and relativized to the area of each trap to obtain mature seed production per hectare (millions.ha^{-1}). The proportion of seed predation (total, insect or birds) was obtained in relation to mature seed production per trap.

2.3. Data analysis

According to previous studies aimed to describe masting patterns in trees (see among others Herrera, 1998; Koenig et al., 2003; Espelta et al., 2008), annual variability in mature seed production for each sampling site was examined using the coefficient of variation at population-level (CVp), calculated as the ratio between standard deviation and mean of yearly average seed production among traps, for each sampling site. Synchrony in the pattern of seed production was determined by calculating the Pearson's coefficient of correlation (r) of all possible pairs of traps in each site and then calculating the mean of those correlation coefficients per site per year. We are aware that this variable does not totally represent synchrony among trees, as according to our sampling design two traps may contain seed from the same individual. Yet considering the intermingling of branches among trees and the possibility that these light seed are partially dispersed by wind, we still consider that it may be considered a proxy of the synchrony in the overall pattern of reproduction among trees at the stand level: i.e. a low r would indicate that reproduction only occurs in some particular trees or sites in the plot in different years while a high r would suggest an overall similar pattern in reproduction among the different trees.

We assessed the effect of forest type and year-to-year variation on seed production and predation proportions by using repeated measures ANOVAs (p < 0.05). For this, we used data for seed production recorded along the eight year period and data for seed predation recorded along seven year period, because data were missing for 2014. Data of seed production was log transformed while proportion of seed predations was arcsin transformed to accomplish normality and homoscedasticity assumptions. Differences in CVp and synchrony among forest types were tested using Kruskall-Wallis test (p < 0.05).

Potential effects of variable seed production in the reduction of seed predation by satiation and starvation of seed predators were analyzed by the standard methods used in masting studies (see Kelly and Sullivan, 1997; Shibata et al., 1998; Satake et al., 2004). To examine whether predation satiation occurred in years with high seed production, we analyzed the yearly proportion of seeds suffering insect or bird predation as a function of the number of mature seeds produced annually per site. To assess a possible satiation/starvation effect by annual fluctuation of seed production on predators, we used Pearson correlation to measure how yearly percentage of predated seeds (total) correlated with the ratio of seed production in year t to that in year (t-1) per plot. For all these analyses, plot values were calculated as the sum of the seed production per site.

To check whether bird seed predation could be higher or less intense during those years with high insect predation, we tested the relationship between the proportion of seeds predated by insects and those predated by birds. We used the Spearman correlation coefficient instead of Pearson correlation because this variables did not meet normality and homoscedasticity assumptions (Dollar et al., 2014).

Finally, as proposed by Satake et al. (2004), we also tested the ultimate influence of variability in seed production on overall seed survival by examining the relationship between the mean proportions of seeds of *N. antarctica* predated per sampling site accumulated throughout the seven-year study as a function of the temporal variability in seed production (CVp) per plot.

3. Results

3.1. Temporal variability

Along this 8-year study, *N. antarctica* showed strong among-year variation in mature seed production (Fig. 1). We observed a seeding failure in 2011, two extremely poor seeding events in 2014 and 2015 and two maximum peaks of seed production in 2010 and 2012 (Fig. 1). Comparing seed production among the three forest types we detected significant differences in the year-to-year seed production but not among forest types (Fig. 1 and Table 1). Mean number of seeds produced ranged from 0.3–10.1 millions.ha^{-1} in PF, 0.5–8.2 millions.ha^{-1} in SF, and 0.9–6.7 millions.ha^{-1} in SILVO (Fig. 2). Similarly, the three forest types did not differ in the inter-annual variability of seed production (measured as the coefficient of variation at the population level; CVp, H = 1.38; p = 0.501) or in the synchrony in the spatial distribution of seeds in the plots (measured as r-Pearson coefficient among traps, H = 0.73; p = 0.694) (Table 2).

As shown in Table 1, seed predation (total, by insects or by birds) was also strongly influenced by years but not by forest type (Fig. 2), with the exception of year 2008 when seeds in SF suffered significant higher predation by birds than in other forest types, which explain the interaction in bird predation showed in Table 1. Mean yearly seed predation by insects (9.5%) was higher than by birds (2.2%; F = 53.81; p < 0.001). On a yearly basis, the proportion of seeds predated by insects was higher than for birds in six (2008, 2009, 2010, 2011, 2013, 2015) out of the eight sampled years (Fig. 1). Interestingly, while insect predation increased during small seeding years (e.g., 2011), maximum bird predation was higher in one of the largest seeding years (e.g., 2010).

3.2. Effects of variability in seed production on seed predation

We observed a negative relationship between total seed predation and the ratio (log-proportion) of mature seed production in t than in t-1 (Fig. 3), indicating the potential satiation-starvation effect of predators due to fluctuating seed production among years. This effect was clearly significant for both mature PF and SILVO forests, but yet less pronounced (marginal) for SF (Fig. 3). Concerning the identity of the seed predator, mean percentage of seeds predated by birds showed a strong negative relationship with the proportion of seeds predated by insects (Fig. 4). This was mainly evident in years when insect predation reached the highest levels (20–40% of total seed production) and when bird predation occurred at very low rates. Concerning the influence of forest type, this strong negative relationship was significant for PF and SF forests while for SILVO only a slight non-significant trend was observed. Finally, the proportion of total seeds predated during the 8-year period decreased when increased the CVp in all forest types (Fig. 5A). This pattern was observed for total predation and the proportion of insect predation (Fig. 5B). Contrary, bird predation showed no correlation with CVp (Fig. 5C). This indicates that high variability in seed production may help trees to escape from insect predation, while no effects were observed for bird consumption.

4. Discussion

Seed production in *N. antarctica* in southern Patagonia was highly variable across years and was spatially synchronized, testifying to conspicuous masting. These results are in accordance with those reported by Bahamonde et al. (2016) for *N. antarctica* in continental Patagonia, and by Kelly et al. (2001, 2013) for other *Nothofagus* species in the New Zealand where CVp has shown sim-
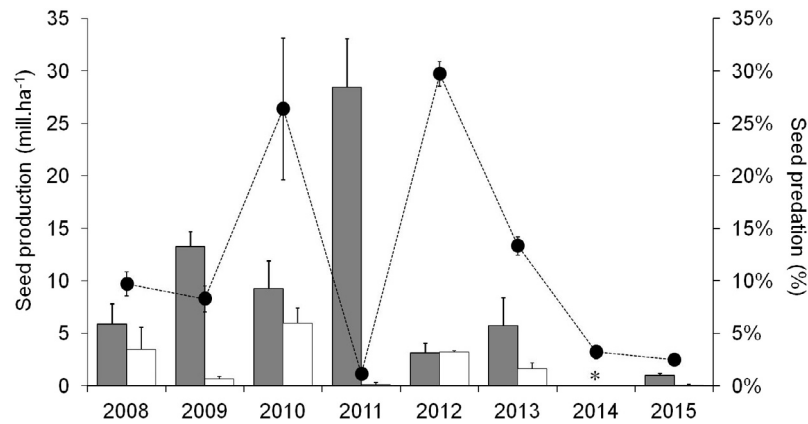
Fig. 1. Mean (+SE) yearly seed production of *Nothofagus antarctica* (solid black dots), and proportion of seeds predated by insects (grey bars) and birds (white bars) in the period 2008–2015. Data of seed predation were missing for 2014 (*).

Table 1
Repeated-measures ANOVAs for the effects of *Nothofagus antarctica* forest type (PF = primary unmanaged forests, SF = secondary-growth forests, and SILVO = forests under silvopastoral use), and years (2008–2015) on the yearly seed production and the proportion of seed predation (total, by insects and by birds).

Effect	Seed production		Total predation		Insect predation		Bird predation	
	F	p	F	p	F	p	F	p
Between subject								
Forest types	0.43	0.660	0.09	0.914	0.21	0.814	0.53	0.605
Within subject								
Years	23.93	<0.001	21.76	<0.001	25.88	<0.001	12.70	<0.001
Interaction	1.50	0.135	1.42	0.184	1.73	0.086	2.60	0.008

Seed production was log transformed while proportion of seed predations was arcsin transformed.
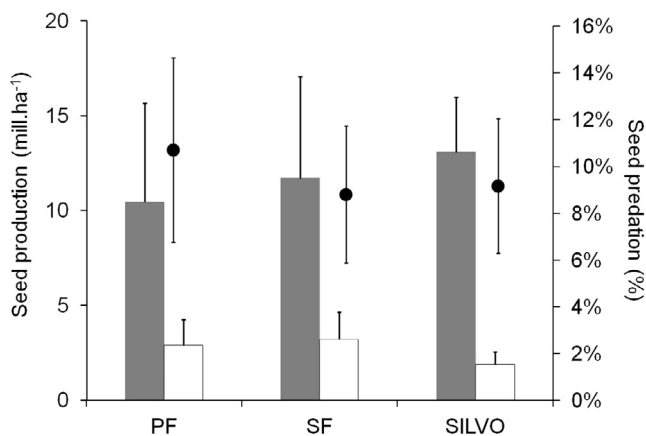

Fig. 2. Mean (+SE) yearly seed production of *Nothofagus antarctica* (solid black dots), and the proportion of seeds predated by insects (grey bars) and birds (white bars) in primary unmanaged forests (PF), secondary-growth forests (SF) and forests under silvopastoral use (SILVO).

ilar values (1.2–2.2). Population-level synchronicity in seed production, as found in our study, has been widely attributed to the

Table 2
Variability in yearly seed production at population level (CVp) and synchrony (r) in different *Nothofagus antarctica* forest types (PF = primary unmanaged forests, SF = secondary-growth forests, SILVO = forests under silvopastoral use).

Forest type	CVp	r
PF	1.14 ± 0.08	0.83 ± 0.05
SF	1.08 ± 0.05	0.86 ± 0.07
SILVO	0.98 ± 0.06	0.86 ± 0.09

N = 12 plots. Data are mean ± SE.

effect of inter-annual variation in some limiting resource (Smaill et al., 2011), environmental cues (Richardson et al., 2005; Allen et al., 2012; Kelly et al., 2013), pollination efficiency (Kelly, 1994; Kelly et al., 2001) or a combination of these proximate mechanisms (Pearse et al., 2016; Pesendorfer et al., 2016) resulting in a fitness advantage for masting plant species (e.g., predator satiation hypothesis). In addition, and contrary to the generalized seeding cycles stated for the South American *Nothofagus* trees (e.g., periods of 6–7 years according to Donoso et al., 2006), we found evidence for multiple period lengths between seeding events for all forest types (i.e., 2 years between 2010 and 2012, but more than 3 years after 2012) reflecting an imperfect periodicity pattern (Satake and Iwasa, 2000). Because mast seeding has a major influence on trophic web of the forest system it is important to understand such interactions and the potential influence of site condition (e.g., stand age, canopy cover).

4.1. Null effect of forest type on seed production

Contrary to what could be expected there were no effects of different forest structures of each forest type on the amount of seed production and the pattern of inter-annual variability. Some authors have suggested that mean reproductive effort per unit area may decrease with reduced plant density (e.g., through thinning) by lower pollen availability (Kelly and Sullivan, 1997; Kelly et al., 2001) although other studies have observed a marked increase (Sánchez-Humanes and Espelta, 2011). For this study area, other authors reported a negative impact of forest management (e.g., harvesting) on *N. pumilio* seed production (Martínez Pastur et al., 2013; Torres et al., 2015) after reducing to 30% canopy cover. However, such reduction is strongest than the thinning intervention in silvopastoral (managed) stands included here. The lack of effect of forest type could be understood as a compensating effect between
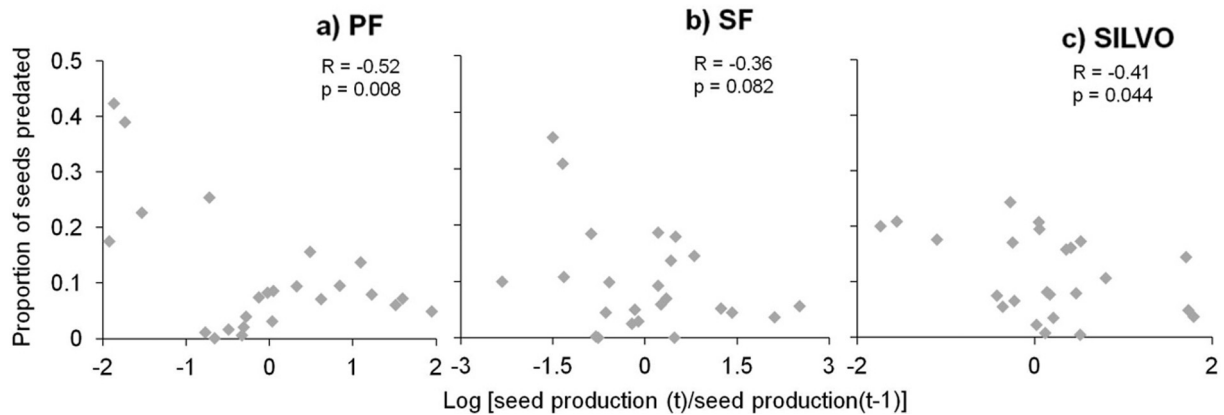
Fig. 3. Correlation between proportion of total seed predation and logarithm of the ratio between seed production in year *t* and seed production in year *t-1*, in (A) primary unmanaged forests (PF), (B) secondary-growth forests (SF), and C) forests under silvopastoral use (SILVO). Log transformed variables were used for calculation. R = Pearson correlation coefficient; p = probability.
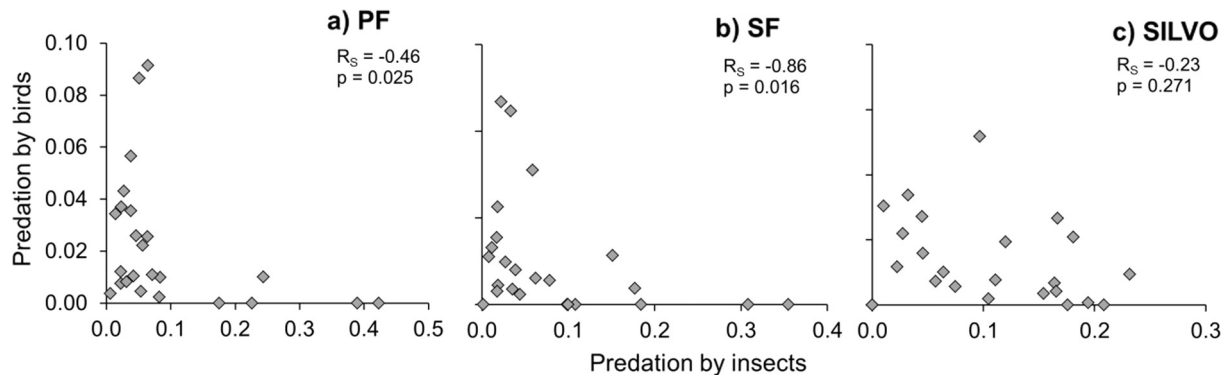

Fig. 4. Correlation between bird predation and insect predation on seeds, in (A) primary unmanaged forests (PF), (B) secondary-growth forests (SF), and C) forests under silvopastoral use (SILVO). RS = Spearman correlation coefficient, p = probability.

tree density and vigor at the stand (population) level. Mature sites with low tree density but large individual trees (with high diameter at breast height) could be more vigorous than high-density sites (secondary forest) where small young trees are less vigorous due to high intra- individual competition by light, water and nutrients availability (Frangi et al., 2005).

The effect of thinning on tree reproduction might disappear few years after the treatment application (Sánchez-Humanes and Espelta, 2011) likely due to a quick expansion of the canopy in the retained stems (Peri et al., 2016) as result of above- and below-ground biomass partitioning. Sánchez-Humanes and Espelta (2011) reported the short and transient effects of this type of thinning on Mediterranean oak reproduction. In our case, as thinning was applied about 5 years before the onset of this study we could not detect an evident reproductive response to canopy modification. Because seed production is one of the most critical component of tree regeneration and it is the least amenable to control by silvicultural management, understanding the variability in seed production among years and among trees will allow better planning of silvicultural interventions or seed collection for seedling production and natural regeneration. Seed production by a particular species is usually determined by observing individual trees (Espelta et al., 2008; Fukumoto and Kajimura, 2011; Żywiec et al., 2012; Perea et al., 2013). Limitations of our study include assessing seed production at stand level, wherewith tree individual variations might have been masked. There is much opportunity to investigate further the causes and consequences of individual variation in synchrony, and individual lags in seed production, with a

view to increasing our understanding of seeding patterns within *Nothofagus* species populations.

4.2. Seed predation

Nothofagus antarctica suffered a noticeable pre-dispersal seed predation, with similar values than those reported for other larger-seeded *Nothofagus* species (5–13% of insect predation and 7–9% of bird predation, Martínez Pastur et al., 2013). However, in the present study we agree with the hypothesis that fluctuations in seed production may satiate/starve seed predators and thereby allow a proportion of individuals to escape predation. This evidence is coincident with other studies dealing with the benefits of masting in trees for escaping predation (see Kelly et al., 2001; Koenig et al., 2003; Canham et al., 2014 for *Nothofagus*; see Espelta et al., 2008 for *Quercus*, see Yasaka et al., 2003 for *Fagus*). Our results indicated that predation decreased with high values of CVp for total predation and insect predation, while bird predation showed no relationship with CVp.

The negative correlation observed in *N. antarctica* between seed production at *t-1* and the proportion of seed predation, suggests that a poor seed year for this species reduced insect predator populations in the following year, producing high seed survival in the following good seed year. In addition, the number of seeds predated by insects was variable among years. This indicates that year-to-year variation in total seed production could play a role in controlling the density of these seed predators as was informed by recent studies in other forest systems (Bogdziewicz et al., 2017).
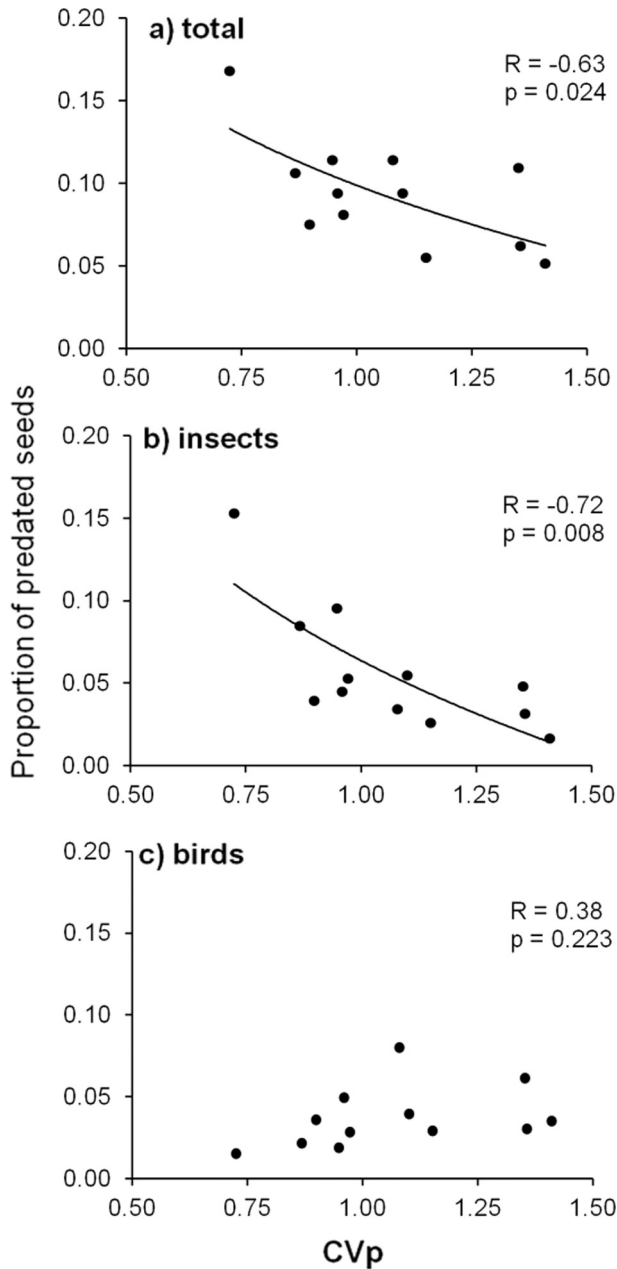
Fig. 5. Relationship between the coefficient of variation (CVp) of yearly seed production per site and (a) total proportion of seed predation, (b) proportion of seeds predated by insects, and (c) proportion of seeds predated by birds. R = Pearson correlation coefficient, p = probability.

Insect are less mobile organism and thus have more restricted dispersion compared to birds. Unfortunately, we do not know the species of insects predating specifically on southern *N. antarctica* trees. However, most insect species in southern Patagonia forests are small-sized organisms with reduced dispersal abilities (Lencinas et al., 2012, 2014), and thus very susceptible to local changes of food availability as seeds. For example, a recent review study (Quinteros et al., 2014) revealed at least five orders of gall inducer insects associated with *Nothofagus* trees (Chile and Argentina), of which Homoptera, Lepidoptera, and Diptera attacked mainly buds and seeds (Díaz and Peris, 2011; Quinteros et al., 2014). However, knowledge regarding taxonomy and specificity of insect seed predators and their linkage with masting is at this time extremely limited, but also guarantees a fruitful new area of research.

Regarding the bird seed consumers, mainly passerine birds (*Carduelis barbata* (Fringillidae), *Curaeus cuareus* (Icteridae), *Phrygilus patagonicus* (Thraupidae)) have been observed feeding on *Nothofagus* seed (pers. obs.) but also the austral parakeet (*Enicognathus ferrugineus*, Psittacidae) (Díaz and Peris, 2011). However, the avifauna of these austral forests is mainly generalist species (Lencinas et al., 2009) and there is no evidence of bird species restricted to seed consumption. Probably because these temperate forests had marked seasonal shortages of food some bird species occupy a broader dietary niche than similar avifauna at lower latitudes (Díaz and Peris, 2011). For this, we assume that no relationship exist between the inter-annual variability of seed production and bird seed predation likely as result of overall higher mobility of birds, which may allow them to move freely among habitats looking for resources (Lencinas et al., 2009). While massive seeding events offer an attractive nutrient-rich food source for local avifauna (Clotfelter et al., 2007; Bogdziewicz et al., 2015), in lean years birds would be able to reach other sources of food or perform small-scale migrations (e.g., in Dipterocarpaceae forests, Curran and Leighton, 2000; in oak forests Pesendorfer and Koenig, 2017) showing a circumstantial use of the tree seeds.

Coexisting species exploiting the same resources commonly use it in different ways. Vertebrates that consume the seeds that are being exploited by different species of insect predators, add another dimension to such coexistence. For example, the consumption of larvae-infected seeds by mammal herbivores may affect the populations of seed-feeding insects through incidental digestion of infected seeds and thus reducing insect seed predation (Bonal and Muñoz, 2007; Peguero and Espelta, 2013). On the other hand, some birds of austral temperate forests select larvae-infected seeds to maximize exploitation of ephemeral protein sources during periods of high nutritional demand (Díaz and Peris, 2011). However, we found the higher is the insect predation rate, the lower the probability of being predated by birds. This reasoning suggests that the presence of larvae-infected seeds reduce *N. antarctica* seed predation by birds, likely due to altered fruit characteristics (deformation of the pericarp) deter birds consuming unappealing fruits. In addition, larvae infestation usually causes total destruction of seed content (pers. obs.) and thereby it would be less palatable to birds especially in years with high proportion of insect predation. Because plant defenses at individual (tree) level play a key role determining the infection rate in *Nothofagus* species (Quinteros et al., 2014), birds could avoid entire tree canopies because of high insect infestation in a given individual tree, as has been seen in other systems (Christensen and Whitham, 1993). Although seed predation rate is considered a minor loss factor within the entire regeneration cycle (flowers-fruits-seedlings) of these forests (Soler et al., 2013), it is necessary to assess the intra-individual variation of seed production and the significance of seed-predator trade-off. Clearly, a longer series of data in *N. antarctica* forests, as well as new experiments combining a wider range of thinning levels under livestock grazing, would help to elucidate the potential trade-off with tree recruitment and forest continuity.

In conclusion, we found enough evidence to assume a masting behavior, strong local synchrony in total seed production, and an imperfect periodicity pattern occurring in antarctic beech forests. Based on the 8 years of our study, and considering the lack of quantitative information on southern hemisphere, this study improves the understanding of inter-annual variability in seed production and masting processes occurring in temperate broadleaved forests. Masting was not affected by changes in forest structures due to management or stand age, showing a negligible impact of tree density. Moreover, we believe that compensating effect between tree density and vigor at the population level may boost this generalized masting pattern. However, evidence for changes in masting driven by more intense management practices or large-scale envi-

ronmental changes will potentially require long-term data to detect. Finally, our results warn about generalizing the impact of masting for all type of seed predators. The type of predator functional response is of crucial importance to the relative success of synchronously and asynchronously reproducing individuals (Ims, 1990). Our results suggest that antarctic beech primarily benefits from masting through insect satiation, while bird predation was totally unresponsive to such pulses. The logic of the classical predation-swamping hypothesis supported by numerous authors is often based on the assumption that the predators behave as specialist predators. However, many aspects of animal ecology (e.g., specific insect seed predator-tree species relationships) may be influenced by highly dynamic processes such as mast seeding.

Author contribution statement

RS and GMP conceived and designed the experiment. RS, GMP and MVL conducted fieldwork. RS and JME analyzed the data, made all tables and figures, and wrote the first draft of the manuscript. PP contributed to revisions. All authors provided editorial advice.

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