

Ecological consequences of an unusual simultaneous masting of *Araucaria araucana* and *Chusquea culeou* in North-West Patagonia, Argentina

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ABSTRACT

A simultaneous masting of two abundant species in the temperate forests of North-West Argentinean Patagonia occurred in 2013 for the first time ever recorded: the semelparous bamboo grass *Chusquea culeou* (colihue), dominating the understory, flowered and set seed across 1100 km² while pehuén (*Araucaria araucana*), an endemic conifer co-dominating the tree layer had the highest regionally-synchronised mast event in the last 30 years. Strong trophic effects were expected as a consequence of this extraordinary amount of seed, such as rodent outbreaks (*ratadas*) that followed previous *Chusquea* spp. mast events and included *Oligoryzomys longicaudatus*, the main reservoir of the Andes virus causing the Hantavirus Pulmonar Syndrome. From March 2013 to May 2014 we sampled relative abundance and activity of seed-eaters and carnivores at four study sites with different proportions of both masting species. Surprisingly, total rodent capture rates never exceeded 14% in wild habitats and 8% in peridomestic areas showing low overall density in spite of some heavy *O. longicaudatus* males extending their reproductive activity into winter. Total abundance and relative proportion of granivorous birds peaked at the four sites in winter or spring, when they are usually scarce. Other surveyed organisms (native and exotic seed-eaters, ungulates and carnivores) showed moderate responses at most, probably through aggregation from surrounding areas rather than reproduction. Seed removal from experimental seed stations varied in time and space though never peaked. The clearest pattern of community responses, though much subtler than expected, occurred at the site where colihue was abundant and pehuén scarce. This is the first systematic study that reports such a simultaneous double masting and our surveys revealed no widespread community consequences. We propose that either contingent events, such as an unprecedented drought, or permanent environmental features or contextual characteristics may explain the lack of a rodent outbreak in this area.

Key words: mast event, bamboo, pehuén, caña colihue, ratada, rodent outbreak, bottom-up

INTRODUCTION

Many terrestrial ecosystems are characterised by infrequent ecological events such as dramatic pulsed increases in the availability of resources (Ostfeld & Keesing 2000; Meserve et al. 2003). Examples include mast fruiting by trees and herbs in tropical, temperate and arid ecosystems varying in scale and predictability (Kelly 1994; Guerreiro 2014). Community interactions usually change in response to these regional perturbations occurring during relatively short term periods (Schmidt & Ostfeld 2008). Determining how the effects of pulsed resources permeate through food webs is still a major challenge for community ecology as it reveals the integration of both bottom-up and top-down forces (Ostfeld & Keesing 2000; Meserve et al. 2003; Prevedello et al. 2013).

Pehuén (*Araucaria araucana*) is an endemic conifer of the austral South American Andes that co-dominates temperate forests in Northern Patagonia along with several *Nothofagus* species. *A. araucana* has a notorious, highly regionally synchronised reproduction system with mast events every 3–7 years in which seed production increases >20-fold (Sanguinetti & Kitzberger 2008; Sanguinetti 2014). The bamboo grass *Chusquea culeou* (caña colihue) dominates the understory in these temperate forests east of the Andes and exhibits a semelparous reproductive strategy where most plants within a region flower simultaneously every ~60 years and die off (Pearson et al. 1994; Marchesini et al. 2009; Guerreiro 2014, 2016). Several native species of rodents and birds are able to consume seeds of *A. araucana* and *C. culeou*, including four species of sigmodontine rodents, several finches and sparrows and the austral parakeet *Enicognathus ferrugineus*, as well as introduced mammals such as wild boar *Sus scrofa*, rats *Rattus norvegicus* and *R. rattus*, and domestic ungulates (Shepherd & Ditgen 2005, 2012; Sage et al. 2007; Shepherd et al. 2008; Sanguinetti & Kitzberger 2010; Díaz et al. 2012; Tella et al. 2016). The survival and germination of seeds produced during mast events are critical for the population dynamics of both pehuén (Sanguinetti & Kitzberger, 2009) and colihue (Pearson et al. 1994) and, in consequence, for the long term survival of the forests they dominate.

Previous events of massive seed production by *Chusquea* spp. elicited pronounced community effects, beginning with population outbreaks of mice (*ratadas*) and followed by high abundance of rats

and other predators such as foxes and raptors (Jaksic & Lima 2003; Sage et al. 2007; Piudo et al. 2012). Rodent outbreaks mainly involve the long-tailed colilargo *Oligoryzomys longicaudatus*, a species with eruptive populations that respond rapidly to local food availability (Kelt 1994). This species is the main reservoir of the Andes virus causing the Hantavirus Pulmonar Syndrome (HPS), so an increase in abundance and mobility of *O. longicaudatus* increases the probability of virus transmission in local human communities (Piudo et al. 2005, 2011; Piudo & Monteverde 2016). The community effects of mast events in *Araucaria* have not been evaluated yet. Several studies did analyse the role of mammalian and bird species as seed dispersers and predators on *A. araucana*, and on its congeneric *A. angustifolia* in Brazil, and reported changes at the local scale in microhabitat use and seed predation rates according to seed availability (Shepherd & Ditgen 2005, 2012; Shepherd et al. 2008; Sanguinetti & Kitzberger 2010; Vieira et al. 2011; Ribeiro & Vieira 2014). Some numerical and functional responses to *Araucaria* mast events were also described at the patch scale (Sanguinetti & Kitzberger 2010; Díaz et al. 2012; Shepherd & Ditgen 2016; Prevedello et al. 2016), but no regional patterns have been ever reported.

In 2013 the simultaneous masting of *A. araucana* and *C. culeou* occurred for the first time ever recorded in North-West Argentinean Patagonia. Colihue flowered and set seed across a 1100 km² area while pehuén had the highest regionally-synchronised mast event in the last 30 years, at least (Sanguinetti 2014). This simultaneous masting generated an extraordinary amount of seed of markedly different, complementary characteristics: the abundant and widespread availability of the relatively small and short-lived grass seed of colihue (0.009 g) together with the spatially aggregated offer of rich, large and hoardable seeds of pehuén (3.5 g). We therefore expected this unusually high availability of seeds to have an intense, synergistic effect through the trophic chain of these temperate forests, starting with a rodent outbreak in the austral autumn-winter of 2013. A huge increase in rodent populations in the wild is expected to lead to a *ratada* some weeks later when mice, particularly *O. longicaudatus*, invade human structures in peridomestic areas, with important sanitary consequences (Piudo & Monteverde 2016). These outbreaks could then be able to defer or avoid the population

collapse that usually follows by exploiting the longer-term resource of pehuén. We set up a multiple, simultaneous sampling strategy aiming to detect and evaluate the impact of the massive simultaneous flowering of *Araucaria* and *Chusquea* on the relative abundance and activity of rodents, ungulates, birds and their predators at sites with different relative abundance of the two masting plant species.

METHODS

The study was conducted in northern Lanín National Park, Neuquén Province, Argentina (39°09'–39°34' S; 71°13'–71°27' W; Fig. 1). Vegetation typically consists of southern beech (*Nothofagus* spp.) and *A. araucana* forests with an understory dominated by *C. culeou*. The climate is temperate with a drier summer season. Average winter temperature is 7–8 °C and 17–19 °C in summer. Precipitation falls mostly in winter as snow and ranges 1500–2600 mm/year following a strong gradient decreasing from the west (De Fina 1972).

We selected four study sites with different masting conditions within the 1100 km² area where the double-masting phenomenon was recorded in summer 2013. Site selection followed a pseudo-factorial design based on the relative cover of the two species: (1) Malleo: *A. araucana* forest with no *C. culeou* in the sampling area, (2) Tromen: dense *A. araucana* forest with isolated patches of *C. culeou* in the understory, (3) Ñorquinco: mixed *A. araucana*–*Nothofagus* spp. forest with *C. culeou*, and (4) Quillén: dense *C. culeou* patches under a *Nothofagus* dominated forest with no *A. araucana* in the sampling area (Figure 1). Proximity to local human communities at potential health risk and logistic limitations (winter accessibility, equipment and personnel) also influenced the decision on the actual position and number of study sites to sample. Altitude of sampled areas was 970–1240 masl.

Fieldwork was conducted every 2-3 months (~seasonal) at each study site from March 2013 (after most primary seed dispersal) to April 2014. A widespread wildfire in Ñorquinco at the end of December 2013 prevented the following summer and autumn surveys there. At each site we estimated the horizontal cover and seed production of the focal species *A. araucana* and *C. culeou*, we evaluated

postdispersal removal of their seeds and we captured rodents and estimated activity level of birds, ungulates and carnivores.

Vegetation cover and seed production. In March-April 2013 we sampled *A. araucana* and *C. culeou* horizontal cover using a line-interception technique along six 100 m long transects in each study site. We estimated seed production by the two species to compare study sites and associate their characteristics with different patterns of responses along the trophic chain. To quantify *Chusquea* seed production we counted the number of culms intercepting the transect for each bamboo plant, which were visually categorised according to the density of spikes produced, from 0 (no spikes) to 4 (many spikes). We obtained a surrogate of *C. culeou* relative seed production per transect by adding the number of culms in each plant multiplied by its categorical value (0–4 abundance of spikes). To quantify relative *A. araucana* seed production per area, we counted the number of cones produced by 15 female trees >50 m apart per site and compared mean number among sites with ANOVA on log scale.

Rodents. We live-trapped rodents in a 5×10 grid at each site using 50 Sherman traps set 10 m apart, baited with a mix of whole oats, cow fat and artificial vanilla essence. We also set five cage traps (30×13×13 cm) in each grid baited with carrot and cow meat to capture rats. Simultaneously, we set 30 Sherman and 3–5 cage traps around houses and sheds of local residents <3 km from the trapping grids in Tromen, Ñorquinco and Quillén (no residents lived within that range around the Malleo sampling area). Each seasonal trapping session lasted for three consecutive nights. Captured rodents were ear-tagged, sexed, weighed, measured, and classified as juvenile, subadult and adult based on the combination of reproductive condition (males: testes scrotal or abdominal; females: non-perforated, perforated vagina, pregnant, and/or lactating), body size, and body mass at first capture (Meserve & Le Boulenger 1987; Guthmann et al. 1997). Mice trapped in the grid were released at the site of capture; rats and rodents captured in peridomestic settings were euthanised according to international guidelines on animal handling procedures (Animal Care and Use Committee 1998; American Veterinary Medical Association 2013). Relative abundance of rodents was estimated from trap success

(%), calculated by dividing the number of individuals captured over the total trap-nights per season and site and multiplying by 100. Fat *O. longicaudatus* individuals were characteristic of previous *ratadas* in the area (Sage et al. 2007). We compared body size of *O. longicaudatus* adult males (total body weight and body length excluding tail) with reference distributions from two local studies conducted in this region in non-masting years following the same field protocol (same traps, baits, habitats, age and reproductive classification criteria, measuring equipment): (1) “El Contra” (Lago Huechulafquen) and “Villa La Angostura” sites (Neuquén) during 2003–2004 (Piudo 2011) and (2) “El Contra” site during 2007–2010 (Monteverde 2014). The reference data set was larger for body weights ($n = 492$) than for body lengths ($n = 157$), so we compared weights and lengths separately with two-sample t-tests after log transformations (following Welch approximation to the degrees of freedom for variances not assumed homogeneous). Body weight and body length relationships for adult *O. longicaudatus* males captured in this study and in Piudo (2011) were modelled with power functions using nonlinear least squares (function *nls* in R; R Core Team 2013). Model selection was based on difference in Akaike's information criterion (ΔAIC) between a “full” model with different parameters for each group ($y = a_i * x^{b_i}$) and a “reduced” model with the same parameters estimated for both groups ($y = a * x^b$).

Birds. We counted the number of individuals per species of all birds observed or heard at six 50 m radius permanent points placed >100 m apart in each site throughout the study. Seasonal samplings were conducted by 1–2 researchers during three consecutive mornings (8:00–11:00 h) for 10 min after arriving at each point. Records from consecutive mornings were averaged per site and season to calculate mean relative abundance reported as individuals per sampling point. Abundance and proportion of granivorous birds were estimated by aggregating species able to feed on seed of any of the focal plant species, following Becerra Serial & Grigera (2005) and Díaz et al. (2005). Species assemblages were compared among sites to evaluate if their similarity was more associated with distance among sites or with abundance of each of the masting plant species. Similarities among all pairs of sites were estimated by Spearman rank correlations (r_s) on the abundances of the 22 most

common bird species (i.e., on 22×2 data matrices with species as rows and the pair of focal sites as columns).

Ungulates and carnivores. We counted signs (tracks, faeces, uprooted ground) along 10 transects of 300×2 m in each site in order to estimate activity of ungulates and carnivores throughout the study. Transects were >300 m apart from each other, four of them along dirt roads and trails, aiming at carnivore signs, and six within the forests to increase the chance of detecting ungulate signs (though we registered all signs in every transect). The number of signs of each species (or group of species) per seasonal sampling and site was normalised by calculating its standard score (Z-value using mean and variation calculated for all seasons and sites) for comparison among sites throughout the study period.

Seed removal. We estimated intensity of post-dispersal seed predation on seeds of *A. araucana* and *C. culeou* through seed removal field experiments at each site. We selected 15 *A. araucana* female trees with cones, separated >50 m from each other, in Tromen, Malleo and Ñorquinco, and 15 *Nothofagus* trees >50 m apart at Quillén (where no *A. araucana* trees occur). We installed three seed stations on the ground in different microhabitats around each tree: (1) under tree canopy, 5 m from the trunk with no understory vegetation, (2) 15 m from tree trunk with no understory vegetation, and (3) 15 m from tree trunk, in another direction, with dense understory vegetation, usually *C. culeou* where available. Microhabitats differed in availability of naturally dispersed *A. araucana* seeds (high around stations under tree canopy except under *Nothofagus* trees at Quillén and nil far from the tree trunks) and density of understory vegetation. At each seed station we offered 20 *C. culeou* seeds on a plastic Petri dish on the ground and 20 marked seeds of *A. araucana* around (dispersed directly on the ground in a ~0.5–1 m diameter area). The Petri dish was covered with a plastic translucent tray on four tall wire legs (>20 cm) to prevent bamboo seed displacement by water and snow. Each seasonal trial lasted for three consecutive days, recording and replacing the number and identity of removed seeds every day. We calculated the average proportion of removed seeds of each species per site and season.

RESULTS

Our estimations of horizontal cover and seed production of the two focal plant species confirmed the intended selection of study sites to provide different scenarios of exceptional seed resources (Fig. 1). Horizontal cover, number of culms and estimated seed production were all highly correlated for *C. culeou* (Pearson correlations: $r > 0.95$). Bamboo cover and seed production was high in Quillén, moderate in Ñorquinco, very low in Tromen and nil in Malleo (though no bamboo was recorded on the transects, some small plants grew near a stream nearby). For *A. araucana*, horizontal cover was high in Tromen, moderate in Ñorquinco and Malleo, and nil in Quillén. Seed production of *A. araucana* was much lower in Ñorquinco (mean number of cones per seeding female tree \pm SE = 29 ± 7) than in Tromen and Malleo (88 ± 19 and 65 ± 7 , respectively; $F_{2,41} = 11$, $P < 0.001$). By integrating tree density, production and seed weight per cone according to long-term studies (Sanguinetti & Kitzberger 2008; Sanguinetti 2014) estimated gross seed production was 1230 kg/ha in Tromen, 911 kg/ha in Malleo and 490 kg/ha in Ñorquinco. In consequence, in one extreme Malleo was a pure masting site for pehuén and in the other Quillén was a pure masting site for colihue, with Tromen and Ñorquinco with both masting species present, though the former with a higher amount and proportion of *Araucaria* seed.

We captured a total of 191 individuals of 10 rodent species with an effort of 3630 Trap Nights (TN) in wild habitats (trap success = 5.6 ind/100TN) and 66 individuals of 8 rodent species with 1464 TN in peridomestic habitats (4.5 ind/100TN) at the four sites throughout the study (Table 1). *Abrothrix hirta*, *A. olivaceus*, *Chelemys macronyx*, *Geoxus valdivianus*, *Loxodontomys micropus*, *Oligoryzomys longicaudatus*, and two exotic murids *Rattus rattus* and *R. norvegicus*, were all captured in both habitat types, while *Eligmodontia morgani* and *Phyllotis darwini* were only captured in wild habitats and *Reithrodon auritus* only in peridomestic areas. The most frequently captured species in the wild was *A. hirta* (50% of captures in wild habitats), followed by *O. longicaudatus* (25%), which was the most captured species around houses and sheds (34% of captures in peridomestic habitats). In wild habitats of Tromen and Malleo, where *C. culeou* cover was low or nil, rodent relative abundance showed an

autumn peak in June (Fig. 2). In Quillén, with the highest *C. culeou* cover and seed production, a second peak was recorded in spring (Fig. 2). Ñorquinco, with intermediate bamboo cover, followed a similar though attenuated temporal pattern. In peridomestic habitats we also observed an increase in rodent abundance in autumn and spring (Fig. 2). Still, even at those peaks trapping success for all rodents never exceeded 13.3% in wild habitats and 7.6% in peridomestic areas (overall trap success = 5.0%).

Captured adult males of *O. longicaudatus* were 43% heavier in average than in previous local studies during non-masting years (mean weight \pm SD: 44.1 ± 9.8 g, $n = 29$, reference values in non-masting years from Piudo (2011) and Monteverde (2014): 30.8 ± 6.8 g, $n = 492$; $t_{31} = 8.25$, $P < 0.001$, Fig. 3a) and 17% heavier than the mean body weight reported by Pearson (1983) for adult males in Nahuel Huapi National Park (37.7 ± 8.5 g, $n = 54$). The average body length (\pm SD: 10.6 ± 0.7 cm, $n = 29$) was slightly longer than those measured by Piudo (2011) (10.0 ± 0.8 cm, $n = 157$; $t_{48} = 4.61$, $P < 0.001$) or reported by Pearson (10.1 ± 0.7 cm, $n = 45$). Still, *O. longicaudatus* adult males captured in 2013-2014 ($n = 29$) were heavier than expected for its length during a non-masting year ($n = 152$; “full” vs “reduced” power-law models: Δ AIC = 66.92; Fig. 3b). Other unusual observations were a high proportion of captured individuals in reproductive condition during winter in Tromen (9 out of 14 mice), and an important increase of exotic rats after spring in Quillén (Table 1).

A range of 22–29 bird species were observed at each site. Pooling all records, the most common species in the region were *Phrygilus patagonicus*, *Carduelis barbatus*, *Aphrastura spinicauda*, *Enicognathus ferrugineus*, *Zonotrichia capensis*, *Scelorchilus rubecula*, *Eleania albiceps*, *Pygarrhichas albobularis*, *Tachycineta leucophyga* and *Troglodytes aedon*. Closest sites shared similar bird species assemblages (Quillén–Ñorquinco: $r_s = 0.63$, Malleo–Tromen: $r_s = 0.59$; other paired comparisons: $r_s < 0.44$), with Quillén the most, and Tromen the least, diverse sites. Total abundance and relative proportion of granivorous birds peaked at the four sites during their winter or spring seasonal samples (Fig. 4). *Carduelis barbatus* and *P. patagonicus* were the most abundant granivorous birds at Quillén and Ñorquinco, whereas *Z. capensis*, *P. patagonicus* and *C. barbatus*, or the first two

and *E. ferrugineus* (the only bird species that can eat *A. araucana* seed), were the three most abundant at Malleo and Tromen sites, respectively.

Transect surveys revealed the presence of several introduced and domestic herbivores and omnivores (*Cervus elaphus*, *Sus scrofa*, *Bos taurus*, *Equus caballus*, *Oryctolagus cuniculus*, *Lepus europaeus*) and carnivores (*Lycalopex culpaeus*, *Puma concolor*, *Conepatus chinga*, *Canis lupus familiaris*, *Felis/Leopardus spp.*). Variation in local activity of domestic species reflected management decisions of the National Park and livestock owners. *Cervus elaphus* increased its activity in winter-spring in Tromen and *S. scrofa* in winter-spring in Tromen and Malleo, while domestic ungulates decreased or were practically absent in both sites (Fig. 5). Exotic *C. elaphus* and *S. scrofa* populations have not reached Ñorquinco and Quillén sites, respectively, yet. Lagomorphs increased its winter activity in Quillén (same as rodents: Fig. 2), where *L. culpaeus* was most frequently recorded in winter-spring (Fig. 5). Wild carnivores increased their activity in spring in Ñorquinco (Fig. 5) also in accordance with the second relative peak of rodents in this site (Fig. 2).

We identified murid and sigmodontine rodents, *S. scrofa*, *Enicognathus ferrugineus* and cattle among the species that removed seeds from the experimental seed stations. Seed removal of *A. araucana* was higher than of *C. culeou* in all sites throughout the study, though we did not observe a peak or any steep increase associated with variation in seed-eaters activity at any particular date (Fig. 6). Instead, a general trend of increasing *A. araucana* seed removal through time was observed in all sites. Higher seed removal occurred always at the microhabitat station with understory vegetation (43–100% of removed seeds) than in open microhabitats (0–37% and 0–42% in close and far open microhabitats, respectively) in all study sites throughout the study period.

DISCUSSION

This is the first systematic study of community consequences of a simultaneous masting of *C. culeou* and *A. araucana*, two species that dominate or co-dominate the temperate forests in Northwestern Patagonia. Simultaneous masting of these species have not been previously reported, and

our surveys revealed unexpected results on the relative abundance and activity of seed-eaters and their predators in this region. Primarily, no rodent outbreak was recorded in response to the *C. culeou* masting. This was surprising as we expected an even higher or more extended response due to the added surplus of the large and highly nutritious seeds of *A. araucana*, which the rodents hoard and consume. Secondly, there was a notorious lack of marked and ubiquitous responses for seed-eaters of *A. araucana* following the largest mast event for at least the last 30 years (Sanguinetti & Kitzberger, 2008; Sanguinetti 2014). Although we did observe some increase in abundance, activity or other features of particular species or groups of species at particular seasons and sites, no widespread community consequences were recorded in this area after a probably unprecedented peak of seed availability.

According to previous studies, reports and informal accounts, massive flowering of *Chusquea* in southern temperate forests of Argentina and Chile should have led to rodent population outbreaks (Gallardo & Mercado 1999; González et al. 2000; Jaksic & Lima 2003; Murúa et al. 2003; Sage et al. 2007; Piudo et al. 2012). Similar records of rodent outbreaks following massive bamboo flowering in Asia are well known for their dramatic effects on food production and public health (Singleton et al. 2010a, 2010b). Even when food is recognised as a necessary but not sufficient factor to trigger outbreaks of mice in anthropogenic environments (Ylönen et al. 2003; Brown et al. 2010), this repeated pattern in the wild has led researchers to consider that masting of *Chusquea* (or other bamboo species) is a key variable to forecast rodent outbreaks (Murúa et al. 2003, Smith et al. 2015). In fact, a simultaneous event of *Chusquea* flowering ~350 km south of our study region (within Los Alerces National Park, Chubut province, Argentina) led to the predictable rodent outbreak in 2013, with its expected symptoms and consequences (Izquierdo M., National Parks Administration, pers. comm.). Unexpectedly, we did not record a rodent outbreak even in our study site with high bamboo density (Quillén). Maximum capture rate during our study was 13.3% (8% in peridomestic areas) but were $\geq 50\%$ during previous rodent outbreaks following bamboo mastings in this region (Sage et al. 2007; Piudo et al. 2012), with short-term trap success even higher in outbreaks elsewhere (e.g., 80–125%:

Gallardo & Mercado 1999; 100%: Izquierdo M., pers. comm.). Not only were rodent abundances rather normal, but other prominent features of rodent outbreaks such as odd diurnal mice activity, drowned rodents in lakes and rivers, widespread autumn-winter reproduction, and sudden rodent invasions of human houses and peridomestic structures (Gallardo & Mercado 1999; Pearson 2002; Sage et al. 2007; Piudo et al. 2012), were not observed during our surveys nor reported by local inhabitants or visitors. We only observed a weak, isolated increase in the number of rodent captures (e.g. in spring in Quillén or in winter in Tromen) in association with some unusual features which are expected during a *ratada*, such as heavy adult mice, scattered records of reproductive rodents in winter (reported reproductive period is from late spring to autumn: Pearson 1983, Kelt 1994), some dead mice on trails and dirt roads and culpeo fox *L. culpaeus* faeces notoriously composed by sigmodontine rodents remains (particularly in Quillén). Summer visitors to the Park occasionally commented on more exotic rats than usual at some campsites (e.g., around Quillén, Ñorquinco and Paimún lakes) during the following (2013-2014) summer. A simultaneous survey of rodent abundance was carried out 45 km further north from our study area, around Moquehue Lake, on the northeastern limit of the area where *C. culeou* flowered in 2013, with similar results (i.e. no rodent outbreak; see Piudo et al. 2014). To our knowledge, there are no previous formal reports of a massive bamboo masting without a rodent outbreak following it.

We propose two alternative hypotheses to understand these unexpected results. The first is a hypothesis of ecological contingency: particular conditions in one or more variables affecting rodent populations at the time of the 2013 bamboo masting could explain the lack of a strong response to an explosive surplus of food. The most prolonged and intense drought in the last 1000 years, according to climate reconstruction from tree rings, was recorded in the Andean region within 34–39°S during 2010–2015 (Bustos et al. 2015). These conditions could have diminished rodent abundance to extremely low levels impeding their widespread and exponential increase in abundance. Capture rates of small mammals tend to vary widely with environmental factors (e.g., plant cover, food availability, season) and trapping and reporting protocols (e.g., grids, lines or webs; area covered and trapping

effort; trap and bait characteristics; density, MNKA or trap success) (e.g., Lawrence 1992; Weihong et al. 1999; Pocock et al. 2004). We have no previous data on estimated rodent abundance following our field protocol at these particular sites but our overall trap success during the year following the double mast event of *Chusquea* and *Araucaria* (average[range] = 5.0% [0–13.3%]; Fig. 2) seems rather low even compared to those reported in studies of the small mammal communities in these temperate Andean forests under “normal” (non-masting) conditions (though obtained with different techniques, trapping schemes and time frames). E.g., in *Araucaria* forests: 7.5% [0.3–14.5%] (Shepherd & Ditgen 2005), 12.8% [7.9–19.9%] (Shepherd & Ditgen 2016); in *Nothofagus* forests in Argentina: 6.6% [2.7–90.7%] (Cantoni et al. 2001); 5.9% [0.7–18%] (Piudo et al. 2005), 5% [1.7–27%] (Piudo et al. 2011); and in Valdivian forests in Chile: 9.4% [6.5–12.2%] (Meserve et al. 1982), 18.5% [7–30.7%] (Kelt 1996), 16% [6.2–46.6%] (Kelt 2000), 10.7% [6.3–17.3%] (Murúa et al. 2003). Under this hypothesis, rodent outbreaks should have happened in the past and are to be expected after the next *C. culeou* masting in this area (i.e., in ~60 years), with the typical, explosive population response only occasionally prevented by contingencies such as a previous drought (though a previous stressful period may be involved in triggering the mast event; Guerreiro 2016).

Alternatively, some environmental or contextual characteristics in this region may prevent or reduce the probability of a rodent outbreak following *C. culeou* masting. Climate, soil, disturbances or other landscape features in this region may differ from areas in Argentina and Chile where rodent populations have responded to *Chusquea* flowering. This relatively dryer region, supporting the eastern *A. araucana* forests in the Andes, encompasses the northern distribution of *Nothofagus* forests with *C. culeou* understory. Though *Chusquea* flowered in patches of various sizes in this area, previous mast events in southern areas occurred in forests with understories more continuously and homogeneously dominated by *Chusquea* (1938 and 2001 in southern Lanín National Park, 1939 and 2011 in Nahuel Huapi National Park, 1940 and 2013 in Los Alerces National Park; Pearson et al. 1994; DRP 2010; Piudo et al. 2012). Though rodent communities are similar to those in regions that did respond, local populations of some key species may differ in social, spatial or genetic structure that

prevent their outbreak (e.g., haplotype loss at the local scale in *O. longicaudatus*: Boric-Bargetto et al. 2012). Under this group of hypotheses, no rodent outbreak would be expected after *C. culeou* mastings in this northern region, in the future nor in the past. In support, we found no previous record of rodent outbreaks in this particular area (from Lake Tromen to Villa Pehuenia, Neuquén province) either in formal reviews (Jaksic & Lima 2003), grey literature from local-regional agencies nor in interviews to local indigenous mapuche families (Pra I. & Delgado J., pers. comm.). Local residents of old age did mention large flocks of doves (presumably *Columba araucana*) in response to a previous bamboo flowering in this region (probably around 1950), but no *ratada* (Pra I. & Delgado J., pers. comm.).

Other surveyed organisms showed moderate responses, at most, to high availability of seeds, more probably through aggregation from surrounding areas rather than reproduction. Our sampling design and field effort aimed at the temporal description of an expected general, massive response at the regional level, and assumed a strong association of trophic groups' responses to the relative abundances of the two masting species. In consequence, though we collected conclusive evidence on the lack of a regional response of relevant magnitude, our results do not allow for a clear distinction between signal and error in each seasonal survey at each site. The only notable exception were granivorous birds that increased in abundance and proportion in all sites (also where bamboo was scarce) during winter-spring, reaching similar post-mast winter and summer abundances than those recorded in the 2001 *Chusquea* mast event around Yuco (Lanín National Park), south of this area (Lanín National Park 2003, unpublished data). During usual, inter-mast periods, insectivorous or frugivorous bird species (such as *A. spinicauda*, *Elaenia albiceps*, *Tachycineta spp.* and *Scelorchilus rubecula*) dominate bird assemblages in temperate *Nothofagus spp.* or mixed *Nothofagus–Araucaria* forests in Patagonia (Becerra Serial & Grigera 2005; Díaz et al. 2005; Ibarra et al. 2010), while most granivorous species, except for the Austral parakeet *E. ferrugineus*, decrease their abundance 2-3 fold during autumn-winter; for example, *C. barbatus* and *P. patagonicus* descend every winter to lower altitudes and almost disappear from *Nothofagus* forests above 1100 masl (Becerra Serial & Grigera 2005). Our results showed the association between the mast event and the predominance of

granivorous species, which probably suspended their altitudinal displacement because of the extraordinary abundant seed crop. Long-term bird censuses involving five pre-mast years and two post-mast years in the *Nothofagus* forests around Yuco showed a similar transition from an insectivorous-dominated to a granivorous-dominated bird community after the mast event, and switched back one year after (Lanín National Park 2003, unpublished data). Some mammals showed variations in activity at the local scale though with no general, regional patterns to infer a clear response to the masting events. Lagomorphs increased their activity in Quillén (the site with more bamboo but no *Araucaria* trees) in winter. A slight trophic response can be inferred from an increase in relative abundance and activity of larger mammals, particularly the increase of foxes (*L. culpaeus*) following the abundance peaks of rodents in Quillén. Visual inspection of the numerous fox faeces found in Quillén in spring supported the idea that sigmodontine rodents were their main dietary item in that site and season (though rodents are ordinary prey for foxes, in no other site nor season we did find so many faeces and so conspicuously composed of rodent remains).

The clearest signal of a community response, though still much subtler than expected, occurred in Quillén in association with high bamboo cover and with no *Araucaria* forests within a 10 km radius. We were not able to detect any clear regional response to the largest *Araucaria* mast event formally recorded in the last 30 years (Sanguinetti & Kitzberger 2008; Sanguinetti 2014). Various species in Patagonian forests such as rodents, parrots and exotic mammals normally consume seeds of *A. araucana* (Shepherd & Ditgen 2005, 2012; Shepherd et al. 2008; Sanguinetti & Kitzberger 2010) and there are previous reports of their local responses to an *Araucaria* mast event in 2007 (Sanguinetti & Kitzberger, 2010; Diaz et al. 2012; Shepherd & Ditgen, 2016). Rodents such as *A. hirta* and *O. longicaudatus*, which are usually more abundant in autumn especially during the mast event (Sanguinetti & Kitzberger 2010, Piudo et al. 2012), showed significant associations with current or previous cone productions and decreased their body weight during an inter-mast year (Shepherd & Ditgen 2016). More directly dependent on *Araucaria* seed crops, a population of Austral parakeet, *E. ferrugineus*, improved its reproduction success during the mast year and increased its abundance the

following year (Díaz et al. 2012). *Araucaria* reproductive strategy may have been effective for deterring the evolution of big populations of native granivores by providing a nutritious but unpredictable seed crop, alternatively satiating and starving seed predators, and recruiting by pulses of seedling establishment after every mast event (Sanguinetti & Kitzberger 2008, 2009, 2010). Seedling counts in Tromen and Malleo in 2014, following the same long-term protocols in references above, proved the 2013 masting event to be no exception (Tromen: 0.15 vs. 0.10–0.17 seedlings/m² in previous mast events; Malleo: 0.06 vs. 0.02–0.03 seedlings/m²) (Sanguinetti J., unpublished data). Although colihue was scarce at those two sites and recruitment at Ñorquinco was affected by wildfire, we have no evidence that numerical or functional responses of seed-eaters to the bamboo mast event had a negative effect on *Araucaria* recruitment (i.e., no evidence of apparent competition; Kitzberger et al. 2007).

The main present threat to *Araucaria* reproduction are exotic generalist mammals exploiting their autumn-winter crops, which associate negatively with *Araucaria* seedling density in Chile and Argentina and had clear detrimental effects at a regional scale (Sanguinetti 2008; Sanguinetti & Kitzberger 2010; Zamorano-Elgueta et al. 2012; Tella et al. 2016). Increased activity of *C. elaphus* and *S. scrofa* in winter-spring in Tromen and Malleo could reveal their aggregative responses to *Araucaria* seeds; *Araucaria* seed was a major item of *S. scrofa* winter diet in our study (observations of white faeces) and elsewhere (Gallo et al. 2004). Still, our systematic field experiment did not show a steep increase in seed removal at any season or site. Seed removal seemed more associated with microhabitat use than with non-experimental seed density or variations in local herbivore assemblage or plant composition at the habitat scale. Seed removal was always higher under microhabitat cover than closer to seed-producing *Araucaria* trees, suggesting that most removal was by seed-hoarding rodents near their burrows (Shepherd & Ditzgen 2005; Sanguinetti & Kitzberger 2009, 2010) rather than from big patch-selecting mammals. This may have been favoured by our short-term offer (three days) not measuring adequately the impact of animals wandering at larger scales. In any case, none of the microhabitats, even in open patches, showed a peak of extreme seed removal at any site. The

increasing trend of seed removal along the study, everywhere, could be related to a dilution effect, as natural seed offer surrounding the focal seeds decreased towards the end of the study. Similar results were obtained in Brazil, where increased rodent consumption of experimentally added *Araucaria* seeds outside the seed production season was explained in terms of the predator-satiation hypothesis (Vieira et al. 2011).

In conclusion, we set up a group of replicate, simultaneous field protocols to detect and describe the expected community signal in response to a huge pulse of seed abundance at the regional scale: the rare, probably unprecedented, simultaneous mast event of two dominant plant species in Northern Patagonia: *A. araucana* and *C. culeou*. Our results were more surprising than the expected response itself: there were, at most, subtle reverberations along the trophic chain. This not only adds a relevant case to current discussions on bottom-up vs. top-down forces and the effects of food supply on small mammal populations and subsequent resource pulses in natural communities (Pearson 2002; Jaksic & Lima 2003; Schmidt & Ostfeld 2008; Prevedello et al. 2013; Smith et al. 2015) but it may also be the first systematic record of an unreported, locally known phenomenon of dissociation between bamboo masting (*floración*) and rodent response (*ratada*). Its potential association with regional climate or landscape features deserves future studies, which are obviously complicated by the longevity of this semelparous bamboo.

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Table 1. Number of individuals of all rodent species captured in wild and peridomestic (Peri) habitats at the four study sites between April 2013 and April 2014 (Total effort: 3630 and 1464 Trap Nights in wild and peridomestic habitats, respectively). No peridomestic habitats were close enough (<3 km) to the trapping grid in Malleo. †: exotic murids.

Species	Quillén		Ñorquinco		Tromen		Malleo
	Wild	Peri	Wild	Peri	Wild	Peri	Wild
<i>Abrothrix hirta</i>	25	10	12	1	41	6	23
<i>Abrothrix olivaceus</i>	-	2	1	5	1	3	4
<i>Chelemys macronyx</i>	-	-	-	-	-	2	1
<i>Eligmodontia morgani</i>	-	-	-	-	-	-	26
<i>Geoxus valdivianus</i>	4	2	-	-	2	2	-
<i>Loxodontomys micropus</i>	1	2	-	-	-	1	-
<i>Oligoryzomys longicaudatus</i>	21	3	7	8	16	4	15
<i>Phyllotis darwini</i>	-	-	-	-	-	-	1
<i>Reithrodon auritus</i>	-	2	-	-	-	-	-
<i>Rattus norvegicus</i> †	2	-	-	-	1	5	6
<i>Rattus rattus</i> †	5	2	6	2	3	4	1
Total effort (trap-nights)	990	630	660	204	990	630	990

Figure 1. Study area in Northern Patagonia (Province of Neuquén, Argentina) where the simultaneous masting of colihue (*Chusquea culeou*) and pehuén (*Araucaria araucana*) occurred in 2013. Our four study sites are indicated (empty squares), with mean (\pm SE) percentage horizontal cover of pehuén (light gray) and flowered colihue (dark gray) estimated from six 100-m transects per site. Plant layers by PN Lanín; base layer modified from OpenStreetMap (URL: <http://www.openstreetmap.org/>).

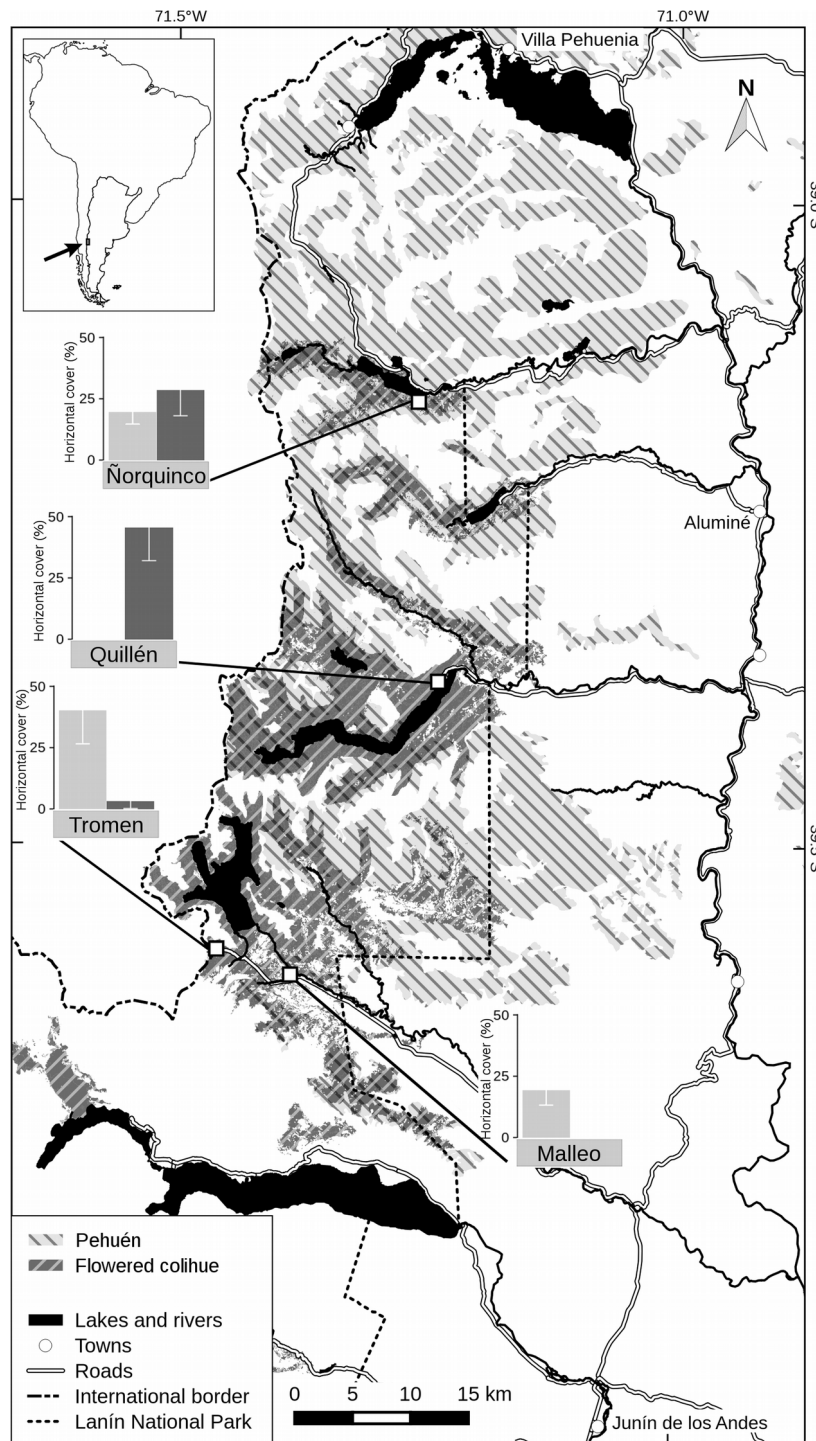


Figure 2. Temporal variation of rodent relative abundance expressed as trap success (percentage of captured individuals over total trap-nights per season and site) in wild (black) and peridomestic (grey) habitats in the four study sites (Quillén: full circle, continuous line; Ñorquínco: full square, dashed; Tromen: open circle, dot-dashed; Malleo: open square, dotted) throughout the study period (April 2013–April 2014). Sampling dates correspond to the position of circles and squares; lines were added to help the interpretation of temporal patterns. Table 1 shows actual number of rodents per species captured at each site.

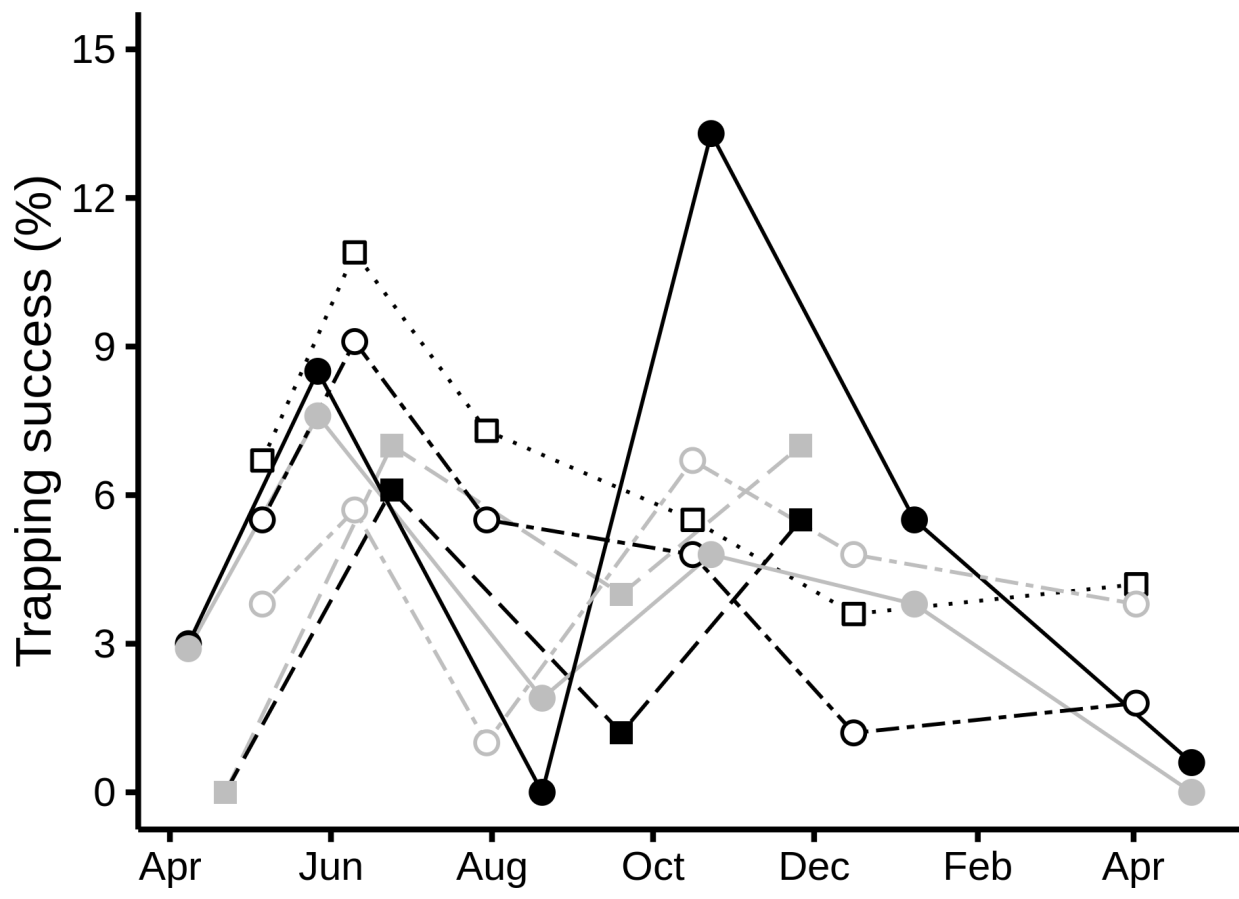


Figure 3. (a) Horizontal box-plots for body weight of *O. longicaudatus* adult males captured in the four sites throughout the 2013–2014 study period (open, n = 29) against reference data from two previous studies in non-masting years (light grey: “El Contra” site during 2007–2010 in Monteverde 2014, n = 195; dark grey: “El Contra” and “Villa La Angostura” sites during 2003–2004 in Piudo 2011, n = 297). Boxes extend between the first and third quartiles (IQR) of each sample, with the black thicker vertical line for the median; notches extend to $\pm 1.58 \text{ IQR}/\sqrt{n}$, roughly a 95% confidence interval for the difference in two medians; whiskers represent data ranges except for outliers (dots) more than 1.5 IQR away from the box. (b) Body weight – body length relationship for *O. longicaudatus* adult males captured in this study (open, dashed, n = 29) and those captured, weighted and measured following the same protocols in “El Contra” and “Villa La Angostura” sites during 2003–2004 by Piudo 2011 (full, n = 152). Regression lines are power functions estimated for each group (weight = a_i * length b ; see text).

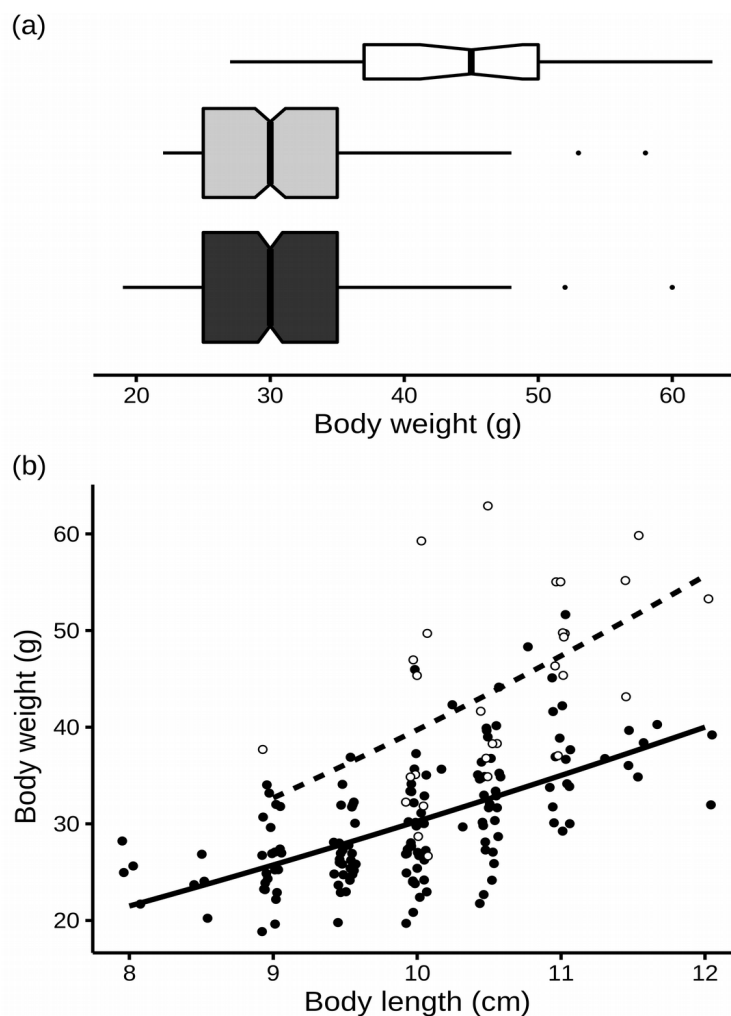


Figure 4. (a) Temporal variation in mean relative abundance (\pm SE; individuals per census point, $n = 6$) of all granivorous birds observed in the four study sites (Quillén: full circle, continuous line; Ñorquinco: full square, dashed; Tromen: open circle, dot-dashed; Malleo: open square, dotted). (b) Percentage of individuals of granivorous species over all bird individuals observed. Sampling dates correspond to the position of circles and squares; lines were added to help the interpretation of temporal patterns.

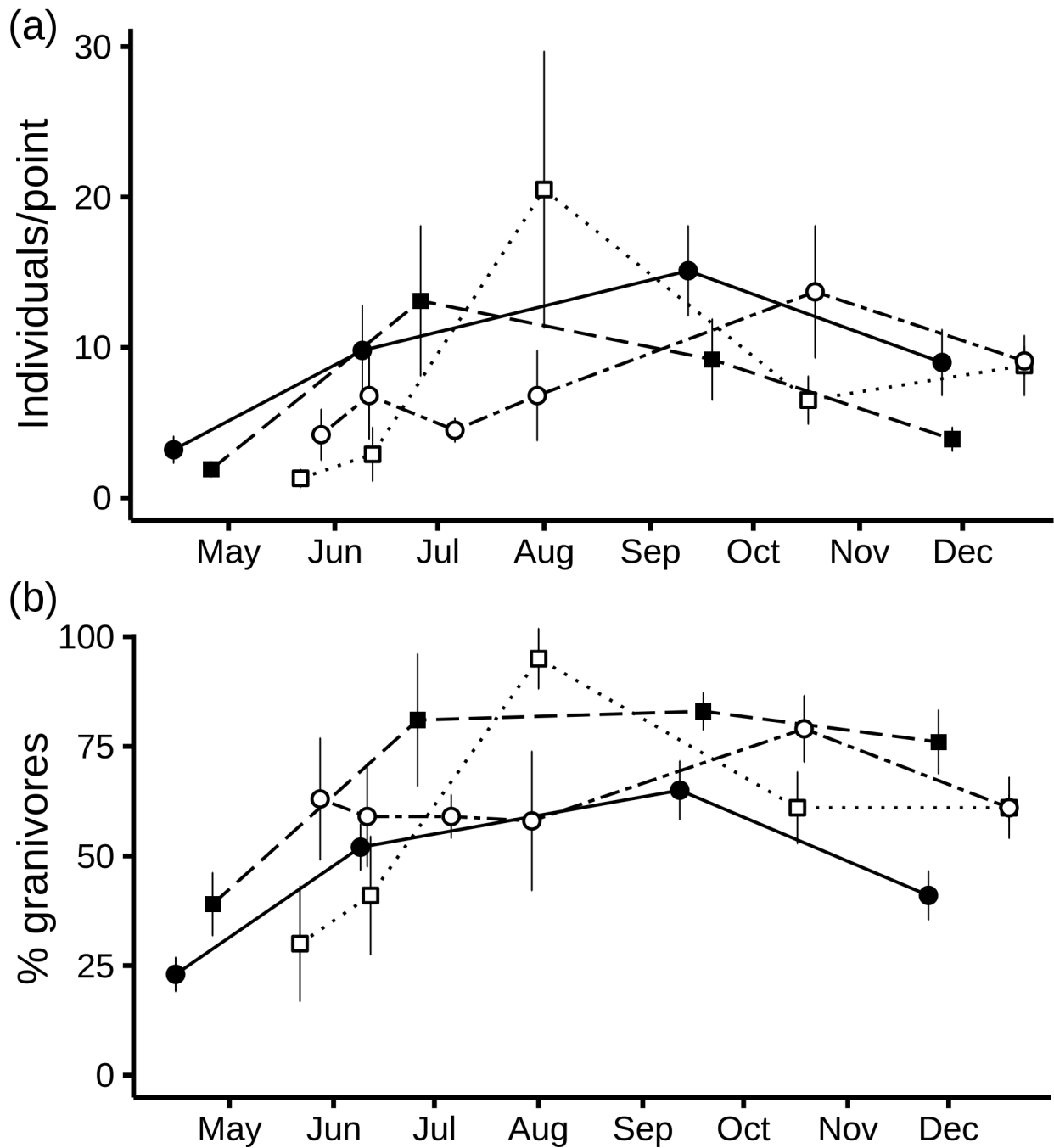


Figure 5. Relative abundance (z-value) of activity signs (footprints and faeces) of (a) *Cervus elaphus*, (b) *Sus scrofa*, (c) Lagomorphs, (d) domestic ungulates, (e) *Lycalopex culpaeus*, and (f) other wild carnivores, along 10 300-m transects per study site (Quillén: full circle, continuous line; Ñorquinco: full square, dashed; Tromen: open circle, dot-dashed; Malleo: open square, dotted) throughout the study period (April 2013–April 2014). Sampling dates correspond to the position of circles and squares; lines were added to help the interpretation of temporal patterns.

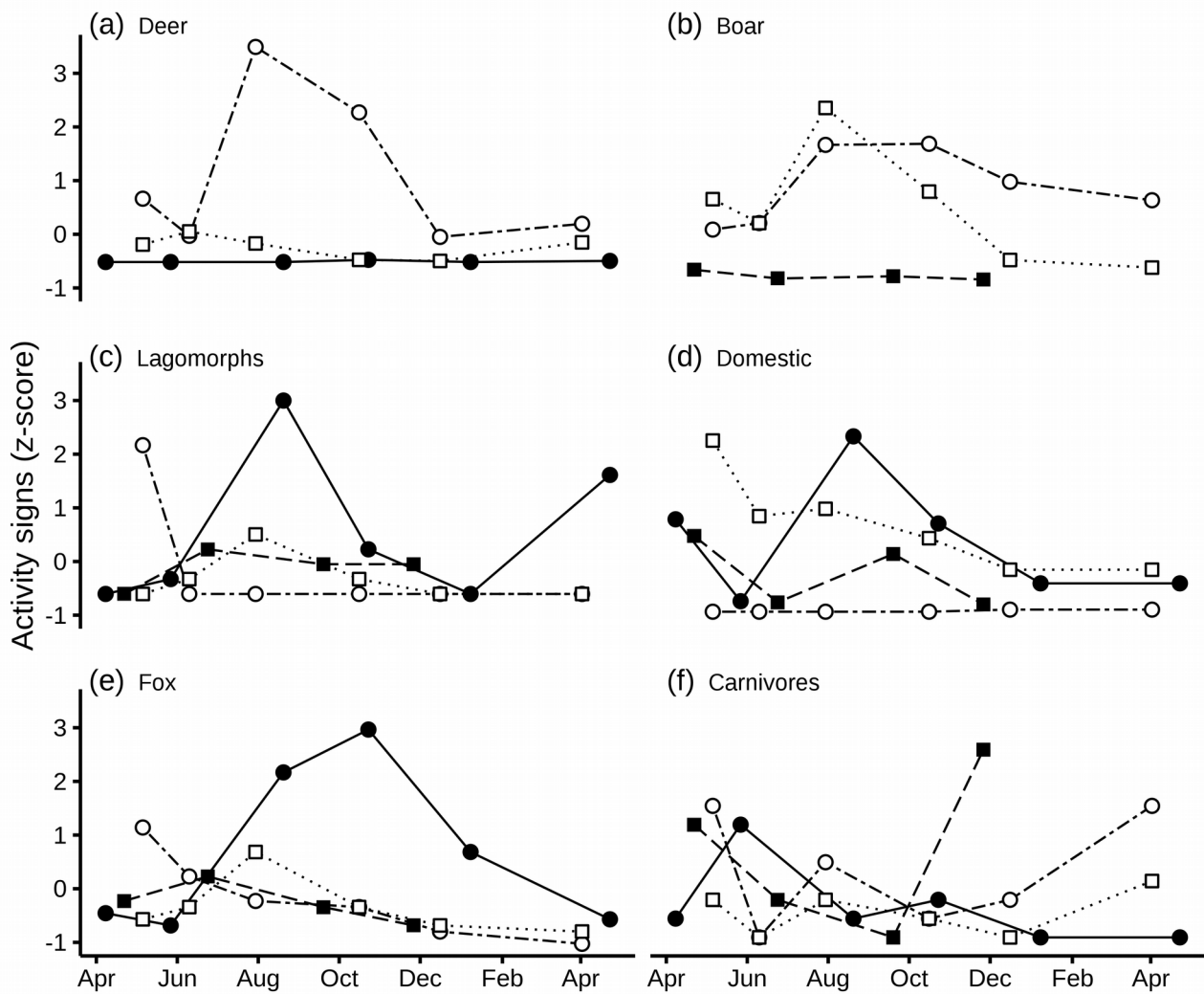


Figure 6. (a) *Araucaria araucana* and (b) *Chusquea culeou* mean percentage seed removal (\pm SE, $n = 15$) during field experiments offering 20 seeds of each species in three microhabitats for three consecutive days in each of 15 seed stations per season and study site (Quillén: full circle, continuous line; Ñorquinco: full square, dashed; Tromen: open circle, dot-dashed; Malleo: open square, dotted) throughout the study period (April 2013–April 2014). Sampling dates correspond to the position of circles and squares; lines were added to help the interpretation of temporal patterns.

