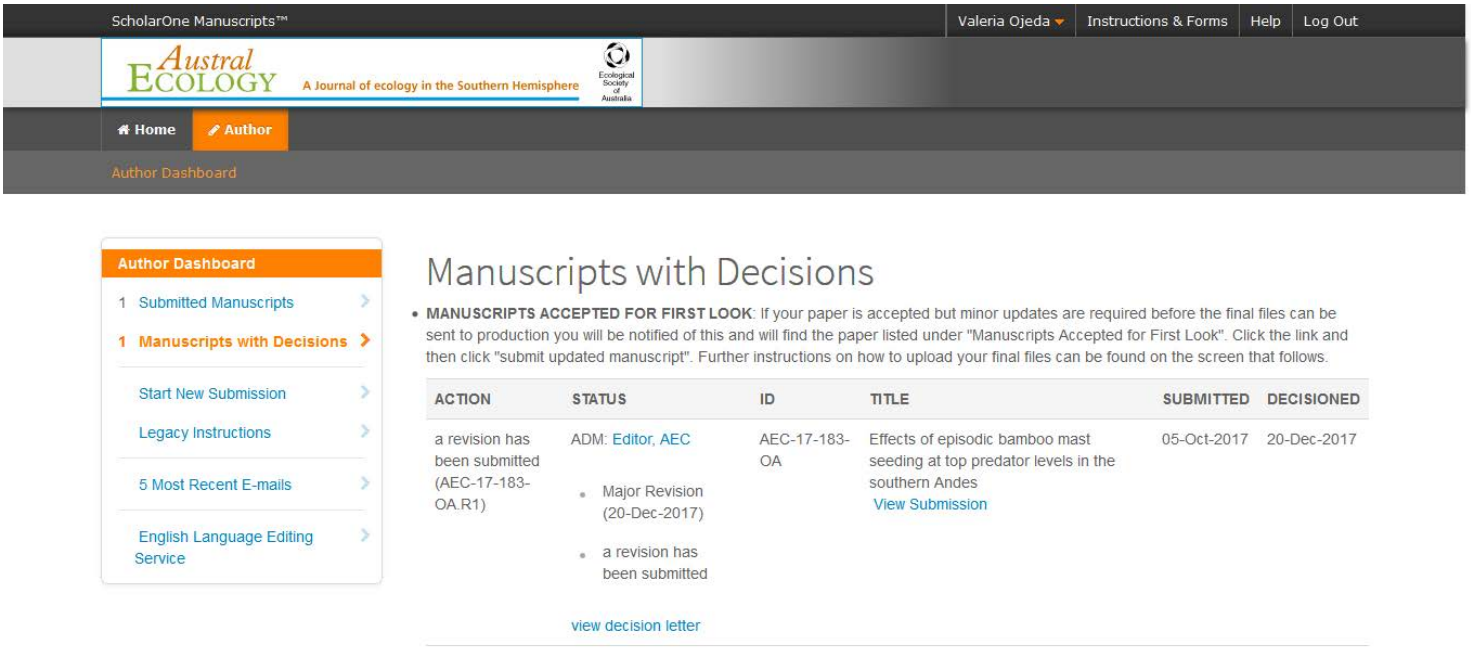

Manuscripts with Decisions

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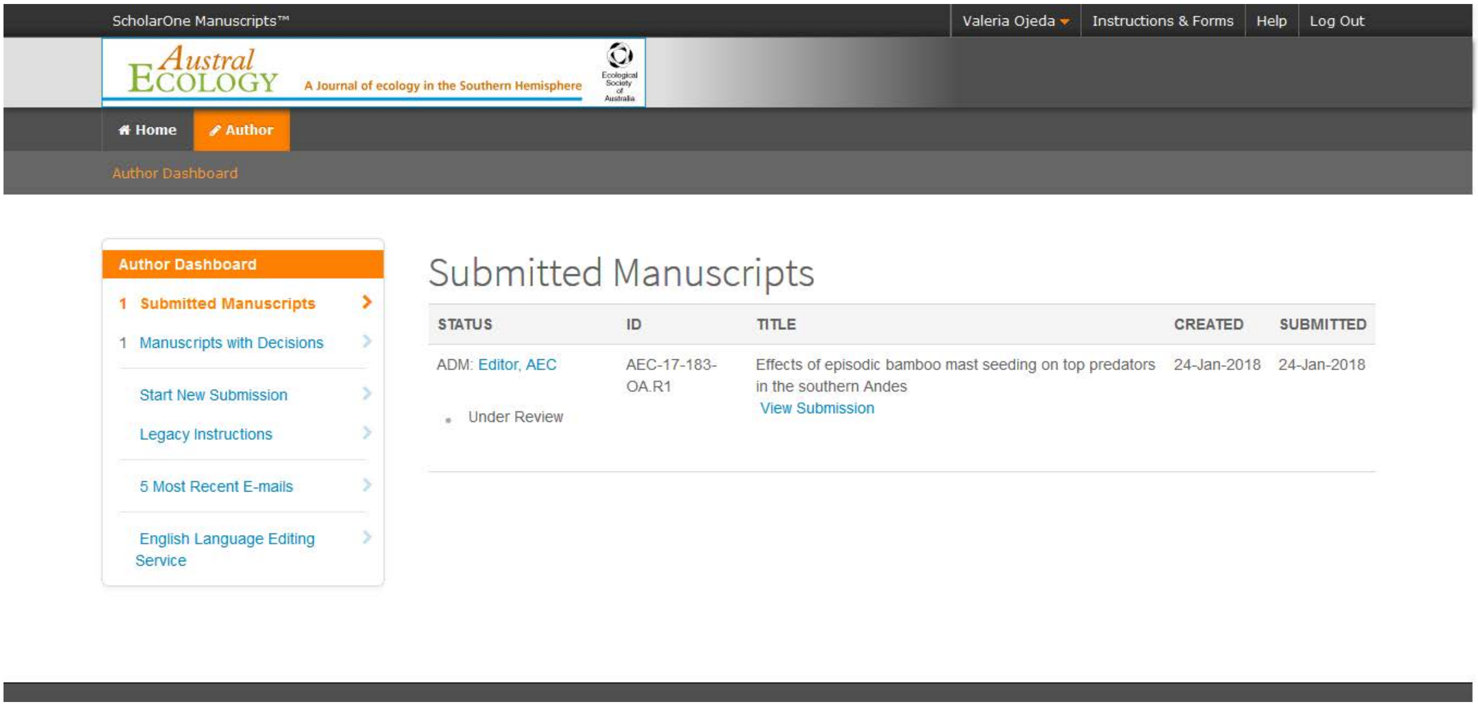
ACTION	STATUS	ID	TITLE	SUBMITTED	DECISIONED
a revision has been submitted (AEC-17-183-OA.R1)	ADM: Editor, AEC • Major Revision (20-Dec-2017) • a revision has been submitted view decision letter	AEC-17-183-OA	Effects of episodic bamboo mast seeding at top predator levels in the southern Andes View Submission	05-Oct-2017	20-Dec-2017



Submitted Manuscripts

STATUS	ID	TITLE	CREATED	SUBMITTED
ADM: Editor, AEC • Under Review	AEC-17-183-OA.R1	Effects of episodic bamboo mast seeding on top predators in the southern Andes View Submission	24-Jan-2018	24-Jan-2018

Austral Ecology
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Effects of episodic bamboo mast seeding on top predators in the southern Andes

Journal:	*Austral Ecology*
Manuscript ID	AEC-17-183-OA.R1
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Keywords:	owl, predator-prey system, pulsed resource, rodent outbreak, strigiform

Effects of episodic bamboo mast seeding ~~at~~ on top predators ~~levels~~ in the southern Andes

Comment [L1]: Title changed following R1

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Field Code Changed

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ABSTRACT. Woody bamboos that undergo masting on a cyclic basis constitute large-scale endogenous disturbances in forests of America, Africa, and Asia, driving long and short-term effects on community structure and dynamics. Among the transient effects of these nonequilibrial phenomena are rodent outbreaks whose potential bottom-up consequences on top predators have never been explored. We investigated the effects of unpredictable rodent outbreaks on the assemblage of nocturnal raptors of the southern Andes after a large-scale (>140.000 ha), spatially heterogeneous, *Chusquea culeou* masting event in north Argentine Patagonia. We compared owl numbers and behaviours between pre-masting (2009) and post-masting (2011) at subsidised (outbreaking rodents) and unsubsidised (normal rodents) contiguous sites. Both generalist (opportunistic forest resident) and rodent-specialist (forest-facultative) owls were monitored, with emphasis on the resident territorial Rufous-legged owl (*Strix rufipes*). The resident owls behaved as predicted, perceiving the rodent increases soon and gathering at subsidised sites, while apparently relaxing territoriality. Contrary to our predictions, later at the rodent outbreak phase, resident territorial owls turned inconspicuous, coinciding -causally or not- with an irruption of forest-facultative Barn owls (*Tyto alba tuidara*), and influx of some open country Short-eared owls (*Asio flammeus suinda*, some of which took a chance to breed in the woods). Considering the whole rodent outbreak period, besides significant changes in owls' numbers, we recorded a notable adjustment in owls' foraging modes in ~~front of~~ response to food surplus (consuming prey heads only), and null interference behaviours among all observed species. This study provides a first quantitative assessment of the effects of bamboo episodic masting on top carnivores globally, and contributes novel data on the indirect effects of these events in forests of South America.

Comment [L1]: R1

Key words: owl, predator–prey system, pulsed resource, rodent outbreak, strigiform

Infrequent large-magnitude events such as climatic extremes (e.g., droughts) and pulses in resource availability (e.g., prey outbreak) are acknowledged as part of long-term ecosystem dynamics, and may sustain key ecological functions in nature (Curran & Leighton 2000; Lima 2002; Ojeda *et al.* 2007). Yet because extreme events are generally short and rare, only occasionally ecological research captures them in action, and rather focuses on the actual consequence of past extreme events (Kitzberger 2013).

Pulsed resources (brief and infrequent events of resource superabundance) have been described for a wide range of natural systems, and may entail tremendous bottom-up effects on consumer communities at multiple trophic levels (Anderson *et al.* 2008; Holt 2008; Yang *et al.* 2008, Holmgren *et al.* 2017). Woody bamboos (Poaceae: Bambusoideae) are semelparous plants that typically generate conspicuous resource pulses in several parts of the Neotropics, Africa and Asia (Janzen 1974). Their life cycles include a long vegetative phase on asexual reproduction, and a short period in sexual reproduction (seeding), followed by death. These phenomena are usually synchronised over hundreds of square kilometres (Janzen 1974). Given the magnitude of these flowering episodes and long intervals between them, these nonequilibrial phenomena provide unique opportunities to observe community structure and dynamics both through transient and long-term consequences.

Comment [L2]: R1

Woody bamboos of the *Chusquea* genus dominate the understory in the northern (warmer) half of the cool temperate southern beech (Nothofagaceae) forests that stretch along the southern Andes, in Chile and Argentina. These plants undergo large-scale blooming and massive seeding events on a cyclic basis (every 10-75 yrs., depending on the species). Environmental triggers like droughts and floods concerning El Niño Southern Oscillation, natural fire cycle, and genetic factors, affect their cycles. Thus, although cyclic, these flowering episodes are unpredictable at any locality. More, not all individuals in a stand may flower at the same interval, which eventually generates patchy blooming (Veblen 1982).

These large-scale endogenous disturbances have been shown to substantially affect these austral temperate forests in various ways, like influencing tree regeneration dynamics in gaps (Veblen 1982; Caccia *et al.* 2015), generating enormous loads of fuels that favour large fire events (Kitzberger 2013), and through more sophisticated (indirect) interactions (e.g., Kitzberger *et al.* 2007).

Comment [L3]: R1

Among the most conspicuous short-term effects are the rodent outbreaks promoted by the enormous nutritional input of protein-rich bamboo seeds (Gallardo & Mercado 1999; Sage *et al.* 2007). These events, locally known as ratadas (Jaksic & Lima 2003), are of great public concern in southern Chile and Argentina (Appendix S1), mainly because some of the commonest rodent species in the outbreaks are the natural reservoirs of an Andes virus that causes hantavirus pulmonary syndrome in humans, an emerging infectious deadly disease. The temporal course of the ratadas is well known: an abrupt population build-up based on increased reproduction, followed by approximately half-year of rodent superabundance, and a breakdown phase due to food depletion, about one year after the bamboo blooming (González *et al.* 2000; Sage *et al.* 2007) (Appendix S2). The food depletion phase is usually accompanied by conspicuous rodent movements outside the forest areas (Jaksic & Lima 2003). This way, ratadas differ greatly from the cyclic inter-annual or multiannual variations in rodent numbers due to population regulatory mechanisms typical of the local species (e.g., Murúa & González 1986).

In turn, cyclic prey outbreaks are substantial perturbations for consumers in a wide range of communities (Hanski *et al.* 2001; Korpimäki *et al.* 2004; Newton 2006; Yang *et al.* 2008, Letnic *et al.* 2011). Despite an extensive accumulation of knowledge on predator-prey systems (South American communities included, as per Lima 2002; Meserve *et al.* 2003), the bottom-up consequences of bamboo masting at top predator levels remain unexplored, and only preliminary evidence is available: 1) a qualitative assessment of Barn owl (*Tyto alba*

Comment [L4]: R1

tuidara, 322-485 mm total length) numerical increase paralleling a *C. culeou*-triggered ratada in Argentina (Sage *et al.* 2007), and 2) a dietary shift of Rufous-legged owls (*Strix rufipes*, 330-429 total length) towards the most abundant rodent species during a *C. valdiviensis*–triggered ratada in Chile (Figueroa *et al.* 2015: 241).

Comment [L5]: R2

Comment [L6]: R2

In recent years (2000 onwards), several ratadas were triggered by masting of *C. culeou* (coligüe) on the eastern (Argentinean) slope of the Patagonian Andes; coligüe blooms every ca. 60-75 yrs. in extended areas (Veblen 1982; Núñez *et al.* 2013). The preliminary antecedent of Barn owl as –apparently- the only strigiform responding to one of these ratadas in Lanín National Park (LNP, Sage *et al.* 2007) was intriguing, for these owls are not abundant in the Austral temperate forests, as compared to the forest-dwelling Rufous-legged owl, and the partially diurnal Austral pygmy-owl (*Glaucidium nana*, a forest facultative, 150-220 total length), commonest Patagonian forest strigiforms (Trejo *et al.* 2006; Ibarra *et al.* 2014). But these species are cryptic in colouration and highly territorial, traits that may mask their potential responses to ratadas unless specific survey methods (e.g., Trejo *et al.* 2011; Ibarra *et al.* 2014) are used.

Comment [L7]: R2

These antecedents stimulated us to investigate the bottom-up consequences of bamboo-triggered ratadas on the assemblage of nocturnal raptors from the southern Andes, with emphasis on Rufous-legged owls, the only endemic forest specialists (Trejo *et al.* 2006). These owls have experienced range retraction and population decline due to habitat loss, and are currently a conservation target in South American temperate forests. They are territorial year round, and forage mostly on nocturnal small-mammals (Figueroa *et al.* 2015). Their current status and life history profile, along with a paucity of antecedents on their ability to respond to ratadas, turned Rufous-legged owls into interesting models to evaluate how a highly-territorial predator may behave in ~~front of~~response to unpredictable food superabundance subsidising some owl territories, but not all (i.e., patchily distributed).

Comment [L8]: R1

Comment [L9]: R1

Events under scrutiny and hypotheses

In 2010, an extensive (>140.000 ha), spatially heterogeneous, blooming of *C. culeou* in south Nahuel Huapi National Park (NHNP) created a natural experiment that allowed as to undertake a direct assessment of numerical and behavioural responses of Rufous-legged owls (and secondarily, other nocturnal raptors) to the rodent outbreaks. The patchiness of the blooming (i.e., several ha in bloom, mixed with similar-sized non-flowered patches, Núñez *et al.* 2013), and regional owl surveys conducted one year before (Trejo *et al*. 2011), permitted us designing an experiment to compare owl responses at unsubsidised (no ratada) and subsidised (ratada) forest sites, using our pre-blooming surveys as baseline reference for contrasting owl numbers at different times after the initiation of the rodent outbreak.

In front of the upcoming 2011 ratada in NHNP, we hypothesised that Rufous-legged owls (opportunistic resident consumers) would move from territories with no extra rodents to nearby subsidised territories, gathering progressively as prey increased. Based on this hypothesis, and on the temporal course of previous ratadas (Sage *et al.* 2007, Appendix S2), some of our predictions for Rufous-legged owls were: (1) to detect moderate increases in their numbers at subsidised patches during the autumn 2011, (2) along with decreases in their numbers at unsubsidised sites, and (3) more individuals at subsidised patches during the plague phase (late 2011), than at the population build-up phase (early 2011). Also based on Sage *et al*. (2007), we expected increases in Barn owl numbers in subsidised sites, but specific (scheduled) predictions were not risked due to the low abundance and uncertain status (i.e., degree of territorial residence) of Barn owls in South American temperate forests (see Table 14 in Figueroa *et al*. 2015:204).

Our structured research at NHNP was complemented with pertinent data from a second massive coligüe blooming/masting occurred in 2012, 100 km southwards, in Los

Alerces National Park (LANP, Argentina). The course of the bamboo cycle, as well as rodent numbers, were closely monitored by the national park staff, and semi-quantitative data on owl numbers and behaviours were collected, which were granted to us.

METHODS

Study area

The study was conducted on the eastern slopes of the Patagonian Andes, in Argentina. The NHNP, epicentre of our systematic owl surveys, extends about 700,000 ha (40º8'-41º35' S and 71º2-71º57' W); the LANP ~~extends~~ covers about 260,000 ha (42º33'-43º11' S and 71º34-72º10' W).

Comment [L10]: R1

From west to east, north Patagonia includes the Andean cordillera (>2000 m elevation), the lower foothills intersected by glacial lakes and valleys, and the Patagonian plains at ca. 700 masl. Because of the rain shadow effect of the Andes on the westerlies, mean annual precipitation declines from ca. 3000 mm at the continental divide to less than 500 mm only 70–80 km to the east in the steppe. The strong west-to-east decline in precipitation is paralleled by a vegetation gradient, with cool moist mountain forests composed by *Nothofagus* spp. (and bamboo) at western sites, and the conifer *Austrocedrus chilensis*, with increasing aridity. The vegetation of both national parks is fairly similar, with evergreen lowland coihue *N. dombeyi*, and deciduous alpine (on slopes over 900 masl) lenga *N. pumilio*, dominating the forest landscape. Discrete stands of deciduous ñire (*N. antarctica*) are spread through the landscape, and *A. chilensis* characterize the forest-steppe ecotone.

Forests surveyed and experiment rationale

The forests surveyed for owl activity in NHNP were tall (20-35 m high) stands of *N. dombeyi*, and low (5-20 m high) stands of *N. antactica* with continuous dense understories dominated by *C. culeou*. Both forest types were identified as occupied habitat by Rufous-legged, Barn and Austral pygmy-owls in our previous research (Trejo *et al.* 2011).

The NHNP blooming event covered almost 150,000 ha (Núñez *et al.* 2013), south and west of Nahuel Huapi lake, affecting different forest communities. The area that underwent blooming in 2010 overlapped with regional owl surveys that we had conducted the year before; in 2009, Rufous-legged owls and other strigiforms were quantified in > 400 GPS-georeferenced survey stations established every 1 km on existing roads, all-over north Andean Patagonia (Trejo *et al.* 2011). About 180 of these stations were located in forest areas later affected by the blooming (e.g., Pampa Linda valley, Circuito Chico scenery road).

The great spatial overlap between the 2010 blooming/masting event, and our 2009 owl counts (hereafter, baseline surveys, BS09) allowed for pre- and post-masting (i.e., ratada) comparisons of the owl assemblage and behaviours, by repeating the owl survey protocol at different stages of the ratada evolution. For the purposes of this study, we set eight sampling sites at the BS09-blooming overlap zone (Table 1, Appendix S3), where owl numbers and behaviours were assessed twice on the course of 2011: in autumn (autumn surveys, AS11), with moderate rodent increases, and in spring (spring surveys, SS11), at the peak of the rodent outbreak.

Because the blooming was patchy (i.e., tenths to hundreds of ha in blooming mixed with similarly large non-flowered patches, Núñez *et al.* 2013), first we assessed the condition of potential survey sites within the BS09-blooming overlap zone. Taking advantage of the conspicuousness of the bamboo dieback, during march 2011 (late summer) we checked the condition of most 2009 owl survey stations located in south NHNP. These evaluations allowed defining tracts of at least four adjacent survey stations that were homogeneous in their treatment (i.e., masting or no masting), to be contrasted against nearby (2-5 km) survey transects under the opposite treatment, while not differing in most other attributes, such as forest type, bamboo cover (minimum threshold 60%, visual estimation), or altitude. We excluded areas where blooming patterns were not net at the stand level (i.e., only isolated thickets showing dieback, while others remained green).

Along with the above considerations, we checked the results of the first (autumn 2011) rodent monitoring by public health institutions and by mammal specialists (see next section), before finally setting our sampling sites. The survey stations set this way totaled 48. These stations were grouped in eight survey transects (of at least four stations each), with four replicates for each treatment (ratada *vs.* no ratada) (Table 1, Appendix S3). These replicates were then used for comparisons of the owl numbers between ratada (2011) and baseline (2009) counts, and also between sites with and without ratada during 2011.

Rodent increments

The ratadas here analysed (2011 in NHNP, and 2013 in LANP) were widespread (>100,000 ha) and catastrophic, with invasion of the national parks' infrastructures and closure of recreational areas during months. Previous ratadas in these parks had taken place 60-70 yrs. before (1938-1939 in NHNP, and 1942 in LANP). Ratadas in south Argentina and Chile are characterized by invasion of human settlements by numerous rodents (Appendix S1). Because these outbreaks drastically increase the risk of emergence of the hantaviral disease for people living in or around the bamboo forest, sanitary authorities monitor the rodent populations during the outbreaks, in both countries. Besides, for their negative impacts on public health, tourism, and other important economic activities, these events are closely covered by the local media (Appendix S1).

Due to sanitary risk, trapping of wild rodents in Andean Patagonia needs be conducted under specific equipment and safety techniques, by specialist (3rd. video, in Appendix S1). Hence, we used the results of systematic rodent monitorings conducted by sanitary agents and mammal specialists in different masting areas of south NHNP, to refine our selection of the ratada and no-ratada sampling sites. Against normal rodent numbers (i.e., capture rates 5-20%) (Pearson 2002; Piudo *et al.* 2005; Sage *et al.* 2007), the capture rates obtained in 2011 at any masting site monitored in NHNP were >50% (Sage 2011; Piudo *et al.* 2012). At an extreme, masting areas in LANP approached 100% capture rate (Piudo *et al*. 2014). Adding to the numbers provided by systematic trappings, 300-500 rodents were caught per night at the peak of rodent outbreaks in water ditches constructed in peridomestic settlements. In LANP, over 30,000 rodents were captured this way between April-November 2013 (Piudo *et al.* 2014). Since these data are only available in Spanish, in institutional reports, the evolution of rodent populations at one of our sampling sites (Circuito Chico) was translated to English, and is shown as an example (Appendix S4).

Comment [L11]: R1

Direct evidence of the r~~a~~ises in rodent abundance during 2011 at out sampling sites in masting areas consisted of increased night and daytime rodent activity, and a growing number of dead mice on roads and trails. In our last surveys (late October), the rodents were so many, and so fearless, that we avoided leaving the main roads for the sanitary risk through bites or other direct contact with animals nervously moving among the vegetation, as described for ratadas elsewhere (Sage *et al.* 2007).

Comment [L12]: R1

In sum, masting areas of south NHNP (the epicentre of our systematic surveys) exhibited moderate increases in rodent populations during the first half of 2011; rodents reached plague numbers in the spring, and their populations crashed after a few weeks (Sage 2011; Piudo *et al.* 2012), more or less following a classic ratada cycle (Sage *et al*. 2007). Instead, the ratada in LANP was much prolonged, with capture rates approaching 100% from March 2013 to February 2014 (Piudo et al. 2014).

Owl surveys

Elicited responses are considered a good proxy for relative abundance in *Strix* owls. Further, from our baseline surveys (2009), we knew that few Rufous-legged owls would not be detected based solely on spontaneous calls (see conclusions by Trejo *et al.* 2011); on the contrary, when acoustic lure was used, these owls turned highly reactive, usually approaching the emission source while responding from nearby spots.

The survey protocol is explained in great detail by Trejo *et al.* (2011): an acoustic lure (recordings of contact and territorial calls broadcast by using a car digital audio system) was used to attract Rufous-legged owls, always at night. We spent around 20 min at each survey station, with an initial 2 min silent period (scheduled for spontaneous calls recording), and three playback emissions. At each station, we recorded the exact number of individual owls in each species that were detected aurally and/or visually. In SS11, we had to add a “five or more” category for owl counts, and adjustment that was improvised as owl numbers overpassed our counting capacity beyond a handful of individuals of the same species.

Comment [L13]: With regard to R1 comment (“I think “and” should be “an”): This is correct, meaning either aurally, visually, or both ways at the same time (or sequentially).

Although our protocol was designed to survey Rufous-legged owls, during the 2009 surveys we also detected other owls that inhabit Andean Patagonia. Several Austral pygmy-owls, which are small-size spontaneous loud vocalizers (Jiménez & Jaksic 1989), were recorded aurally most of the times. Also Barn owls were recorded, either by their hissings or visually, as they are almost white (i.e. visually conspicuous). Based on these experiences, we were confident to detect individuals of these species in the 2011 surveys, ~~wherever~~ ~~present~~with the same potential bias than during our baseline surveys .

Comment [L14]: R2 (validity of the survey techniques as for non-Strix spp).

Owl pellets

After finding several beheaded prey that were left unconsumed, w~~W~~e decided to collect and inspect owl pellets to look for potential relationships with such remains. We collected fresh pellets (n=72) at our sampling sites (details in Table 1) early in the morning, to ensure

Comment [L15]: This was added after a commentary by R1.

nocturnal raptors had just produced them. Pellets were brought to the laboratory, and the material was disassembled under light and magnifier for preliminary assessments of prey remains. Our aim was to recognize main parts of skeletons that were present, so skulls were not identified to species level.

Analytical procedures

We compared the relative abundance of each owl species between sites under different treatments (unsubsidised *vs.* subsidised) across the three surveyed seasons: before (BS09) and after (AS11, SS11) the masting event. We used generalised linear mixed effect models with a Poisson error structure (using the package 'lme4' in the R statistical language, Bates *et al.* 2008) to assess potential ratada effects on the relative abundance of owls and how these effects might interact. Analyses were carried out separately for different owl species. The ratada or no-ratada conditions constituted the states of the treatment. Owl abundance was used as the dependent (outcome) variable in all models, with survey seasons and treatment being incorporated as fixed factors, and survey sites as random effects, to control for potential bias associated with each replicate. Because we included the same survey stations throughout the years, the survey seasons (BS09, AS11, and SS11) were incorporated in the model as repeated measurements. In all models, we assessed the interactions between combinations of treatment and survey seasons. The interaction may arise because the response in owl abundance at subsidised and unsubsidised patches depends on the ratada occurrence, but also on the time after the initiation of the ratada. Then, we needed to assess how the specific interaction effect conditions differ to one another, and thus we ran multiple comparisons for generalised linear mixed effects models using the 'multcomp' package from R software.

Comment [L16]: R1

All subsets of models were compared and ranked according to the Akaike information criterion (Akaike 1973) corrected for small sample sizes (AICc) (Hurvich & Tsai 1989), and the model with the lowest AICc value was chosen.

RESULTS

Forest owls

As the rodent outbreak evolved, forest owls triplicated their numbers (all sampling sites combined). Analysed by stage (Fig. 1), forest owls in the sampled stations raised from 60 in BS09 (51 Rufous-legged, one Barn, and eight Austral pygmy owls), to 105 in AS11 (67 Rufous-legged, 19 Barn, and 19 Austral pygmy), to >150 in SS11 (15 Rufous-legged, > 120 Barn, and 18 Austral pygmy owls). These increments were mostly due to the late irruption of forest-facultative Barn owls; because exact counts of these owls were not feasible beyond five individuals (i.e., at the peak of the rodent outbreak), the threefold increase of total owl numbers is a minimum estimation.

As derived from the best model (Appendix S5), Rufous-legged owls significantly increased in numbers at subsidised sites, and decreased at unsubsidised sites, early in the ratada cycle (AS11) (~~uns.AS11-sub.AS11~~ Z=-5.038, P<0.001; Fig. 1). These owls remained strictly nocturnal through the studied period, responding mostly (*ca.* 78% of all individuals) from just around the broadcast emission spot, and much rarely from the distance. On the contrary, these owls were hardly recorded at any survey station late in the ratada cycle (SS11), decreasing significantly (ubiquitously with respect to ratada distribution in the landscape) with respect to both their autumn (AS11; Z=-4.755, P<0.001) and baseline (BS09; Z=-3.608, P=0.003) numbers ~~(sub.SS11-sub.AS11 Z=-4.755, P<0.001; sub.SS11-sub.BS09 Z=-3.608, P=0.003)~~ (Fig. 1).

Comment [L17]: R 1 "..informe on the model comparison…"

Comment [L18]: R1 "…change format of these results…"

During the rodent population build-up (AS11), Barn owl numbers increased only slightly (non-significantly with respect to baseline numbers) at both subsidised and unsubsidised sites (Z=-0.025, P=1.0 for the uns.BS09-sub.AS11 comparison). Barn owls increased exponentially during the rodent plague phase, appearing in supernumerary numbers in subsidised areas, as compared to their abundance in 2009 (Z=4.777; P<0.001; Fig. 1); their numbers were much higher at subsidized areas than at those with no rodent outbreak (Z=-6.037; P<0.001; Fig. 1). Several individuals (usually overpassing our counting capacity) were observed hunting together at the survey stations, flying and perching around, without noticeable mutual interference. Lots of these owls were also sighted within reach of the vehicle lights during our short trips between survey points. Supernumerary Barn owls were also recorded on route during the rodent irruptions in LANP, where over 120 individual owls were counted one night by park staff while driving ca. 30 km through continuous *N. dombeyi* forest. In both NHNP and LANP, the conspicuous increase of Barn owl numbers was followed by an also notable decline of sightings across the study areas, soon after the rodent population crash.

Comment [L19]: R1 "…change format of these results…"

Austral pygmy owls were recorded in small numbers, steadily through 2011, both during night surveys and daylight visits to our sampling sites. Responses to changes in rodent abundance by these small owls were similar than those of Rufous-legged owls (i.e., apparently moving to subsidised sites, Fig. 1), but in non-significant magnitudes.

Open country owls

Late in 2011 (SS11), we opportunistically recorded nine Short-eared owls (*Asio flammeus suinda*, 330-430 total length) in forests showing bamboo dieback around Bariloche, always during daylight hours; a few more of these owls were recorded by colleagues. Sightings of these open country owls also occurred at the peak of the ratada in LANP, with up to four individuals seen together at a forest spot exibiting ratada. Rarer still, ground nests of Short-

Comment [L20]: R2

eared owls were found within forest areas at both ratada episodes (at 41°2'40.36"S, 71°34'17.42"O in NHNP, and at 42°53'39.80"S, 71°36'42.40"O in LANP).

Behavioural observations

Aggressive interactions (including intensified callings, vocal duels, or other such territorial vocalizations we usually record for the species involved), were never recorded during this study, even at high owl densities. For Rufous-legged owls, unsolicited responses (i.e., spontaneous calls during the first two minutes of the survey protocol) were almost absent (with only one case), and only weak and short elicited responses were obtained during AS11, when rarely the same bird vocalised more than once. With this, responses were notoriously much less intense and persistent than we expected based on experience (BS09 own data, and literature).

Carcasses and pellets

We found numerous dead rodents (*ca.* 0.30/m) on roads and trails in the ratada sampling sites during SS11, of which about one quarter were headless. Rapid analyses of the carcasses in the field revealed that dismemberment of the head had been apparently by tearing, not by cutting (i.e., biting). Decapitated rodents also occurred in LANP during the weeks coinciding with the rodent peak, being found on a regular basis across the ratada epicentre by the national park staff and rural inhabitants. At both ratada events, most headless carcasses (>80%) belonged to *Oligorizomys longicaudatus*, as recognised by its diagnostic long tail.

Laboratory analyses of the fresh pellets collected in proximity of the carcasses in NHNP revealed that most (83%) contained only one, sometimes two, rodent heads, with no other bones; accordingly, these pellets were rounded and small size, shorter than those usually found for owls in these forests (Trejo & Ojeda 2004). Because of the rounded shape and small size of the pellets, the owl species that had produced them could not be identified.

Comment [L21]: Derived from comment by R1

DISCUSSION

This study provides a first quantitative assessment of the effects of bamboo episodic masting on top carnivores globally, and contributes novel data on the indirect effects of these events in forests of South America. The main short-term effects (although with potential multi-year consequences) on the strigiform assemblage were: (1) movements of the resident (territorial) Rufous-legged owl towards the pulsed resource, as derived from rapid (i.e., first autumn after the masting) rises in their numbers wherever rodents were increasing, and the opposite at nearby sites where rodents were not increasing, (2) Barn owls (facultative forest inhabitants) progressively dominating in numbers among the owl assemblage, (3) late influx of open country Short-eared owls into forest areas (with opportunistic forest breeding), (4) notable adaptations of owls ‘foraging behaviour in front of food surplus (consuming prey heads only), and (5) weakened interference behaviour for all observed species, notably the resident, highly territorial, Rufous-legged owl.

Both opportunistic resident and mobile specialist consumers represent two common strategies among animals that take profit of pulsed resources (e.g., Yang *et al.* 2008). Since the predator-prey system here analysed contains at least one of each, our results are discussed under the theory on how these two predator types respond to disproportionate spatio-temporal variations in resource availability, including the perception mechanisms likely involved.

Comment [L22]: R1

Responses by forest owls

While the three species that typically inhabit the bamboo-covered native forests of Patagonia, Rufous-legged, Barn and Austral pygmy owls (Trejo *et al.* 2006), contributed to the increase in total owl numbers, their response differed in magnitude and timing, according to their distinctive life histories, especially their degree of forest attachment, territoriality, and foraging behaviour (Figueroa *et al.* 2015).

As predicted by theory for opportunistic resident predators (Yang *et al.* 2008), Rufous-legged owls soon perceived the rodent increases (or some proxy, like the bamboo dieback), ~~duplicating~~ doubling their numbers at subsidised areas, while deserting sites not benefitted by the rodent increments. Their response was rapid but not massive (i.e., low numbers clumped at subsidised patches during the rodent population build-up), as compared to the invasion numbers that were later observed for the less territorial, highly nomadic Barn owls. Accounting for their moderate numerical response, most extra Rufous-legged owls that were counted at the subsidised sites during AS11 seem to have travelled short-distances, possibly from unsubsidised nearby forest areas (Appendix ~~S5~~S6).

Comment [L23]: R1

What was the triggering signal for the movements of these resident owls at the onset of the ratadas here studied? Flexman & Lou (2009) named top predators that track the gradient of the primary resource (from the prey's perspective) "resource trackers"; instead, predators that track prey directly were named "prey trackers". For Rufous-legged (and Austral pygmy) owls, the actual mechanism cannot be ascertained, for both the primary resource (bamboo seeds, with dieback as a proxy), and increasing rodent prey, were at hand to neighbouring resident owls. Whichever was the signal, their rapid response implies an ability to relax interference competition while moving to subsidised sites already occupied by congeners. In normal conditions (i.e., our baseline surveys), these owls would exhibit a vigorous approach followed by persistent singing "against" playback emissions, and frequent disputes between neighbouring pairs (Trejo *et al.* 2011). Instead, our broadcast emissions in the present study produced only weak and short responses, and null aggressive interactions were recorded during the surveys.

Rufous-legged owls are highly attached to their home-range areas year-round, which include valuable possessions such as roosting and nesting large cavities that may deserve guarding (Beaudoin & Ojeda 2011). Hence, while flexible enough as to allow neighbours coexistence, territorial behaviour in Rufous-legged owls may still limit their movements towards locations with increasing prey, in both distance and duration (i.e., performed on a daily basis), in virtue of the risks of unguarding territorial possessions in the mean time.

An almost absence of Rufous-legged owls at subsidised areas in the spring (at the peak of the rodent outbreak) was unexpected, and may be explained by different, not mutually exclusive factors. First, from previous work (Trejo *et al.* 2011; Beaudoin & Ojeda 2011), we knew that pairs engaged in breeding were elusive and reacted weakly to playbacks of conspecific calls, as compared to their own non-reproductive responses. Probably most Rufous-legged owls in our study area were engaged in breeding activities in the spring of 2011, after the bonanzas of the preceding autumn and winter, not reacting to our survey emissions. Second, the irruption of similar-sized Barn owls in large numbers just before spring may have been inhibitory for Rufous-legged owls. Although the co-occurrence interactions between these owls have not been explored (less with supernumerary forest-facultative Barn owls), interspecific interference among owls has been extensively documented (Mikkola 1983), specifically between forest-specialist owls invaded by forest-facultative ones (Sovern *et al.* 2014). Either concentration on reproduction with little vocal exposure, or avoiding encounters with invading Barn owls, would suffice to explain the null response by the Rufous-legged owl.

Austral pygmy owls apparently behaved like Rufous-legged owls at the onset of the rodent increases, but the lack of statistical significance of their numerical changes through 2011 limits discussion. It may, in deed, reflect a weaker response, for they are versatile owls, showing much diurnal activity and large proportions of non-rodent food in their diet (Jiménez & Jaksic 1989). Their actual response behaviours to ratadas should be tested in future ratada events by means of specific survey methods (e.g., both diurnal and nocturnal surveys); dietary shifts towards rodents, as well as increased nocturnal activity, are expectable predictions.

Also in line with theory (Yang *et al.* 2008), mobile specialist consumers in our system (Barn owls) clumped in large numbers wherever rodents were plague (SS11). Barn owls are cosmopolitan small-mammal predators with high versatility in habitat, movement, and migratory behaviour (Newton 2006). In South America, although present in almost all habitats, Barn owls have only been studied in open landscapes, mostly with regard to diet. There's almost no information on their behaviour in the austral forests of America, where even their degree of residence is uncertain (Figueroa *et al.* 2015); in fact, we are aware of only one breeding record (unpublished data) pertaining to undisturbed forests of the southern Andes (Appendix ~~S6~~S7). Despite their unclear forest affininities in regular conditions (i.e., no ratada interpulses), three different events (LNP, NHNP, and LANP) now confirm the irruptive nature (*sensu* Newton 2006) of the southernmost Barn owl populations with regard to bamboo-triggered rodent outbreaks. A Southern Hemisphere close relative, the Eastern Barn owl (*T. a. javanica*), is also essentially irruptive in Australia, gathering where plagues of rodents occur, breeding as long as conditions are good, and dispersing when the prey numbers collapse (Pavey *et al.* 2008). In contrast, Northern Hemisphere Barn owls are much sedentary and spatially less opportunistic; although not irruptive, some show nomadic wandering in certain areas (Newton 2006).

As said, Barn owls are not normally abundant within the austral forests, and although some pairs may be resident, their supernumerary numbers in the three events here analysed may only be reached by the influx of individuals from distant places (i.e., ecotone or steppe owls outside the masting area) (Appendix ~~S5~~S6). How do long-distance mobile consumers become aware of the rodent outbreaks within the forest? Since bamboo masting (the primary resource, or its proxy, the dieback) occurs in discrete units within a finite area, not reaching distant environments, owls at distant locations obviously require a prey (i.e., mobile organism) gradient as a trigger for displacements. The rodent exodus characteristic of ratadas when seeds are depleted (Gallardo & Mercado 1999; Sage *et al.* 2007) are likely the trigger for the movements of distant prey-tracking consumers. Empirical data on such prey-gradients were obtained in LANP: (1) a mouse marked in the ratada epicentre was recaptured 7 km east of the sampling grid, in almost steppe habitat, and (2) unmarked *O. longicaudatus* were caught 12-16 km east of the species' border (the matorral-steppe edge) in regular (no ratada) periods. The time needed for the rodents to outbreak and generate the prey-gradient would explain the retarded (i.e., later stages of the outbreak) irruption of forest-facultative (and some open country) owls at the ratada areas, in all three cases (NHNP, LNP and LANP).

Open country visitors

Not only Short-eared owls came into the ratada epicentre in both NHNP and LANP events, but some individuals took a chance to breed in association with southern beech forests, which constitute a very unusual breeding habitat for this species. Short-eared owls are widely distributed birds characteristic of treeless areas, where they are highly nomadic during food searches and juvenile dispersal (Mikkola 2013). The subspecies here studied is recognised as spatially opportunistic, as birds from south-central Chile are nomadic and partially migratory (Figueroa *et al.* 2015: 227), while the southernmost populations are fully migratory (e.g., Jaramillo 2003). Besides, Housse (1945: 270) reported an irruption of these owls from neighbouring areas in response to a ratada (triggering factor unknown) in the 1930'. Thus, despite sightings of Short-eared owls in natural forests (and less, forest breeding) were unprecedented, our records add to previous evidence on their ecological opportunism with regard to food availability in the southern Andes.

Foraging in times of plenty

Although we didn't witness owls pulling rodents' heads apart, the presence of only heads in much of the pellets analysed is a strong evidence of such behaviour among the local owls. Most adult owls swallow small prey whole. In fact, pellets of Patagonian owls regularly contain pieces of entire small-mammal skeletons (scapulas, etc.), along with skulls and jaw bones (Trejo & Ojeda 2004). This way, the widespread consumption of only rodent heads (discarding headless bodies) by local owls is a notable departure from their usual foraging behaviour. Faced with prey superabundance, owls in NHNP and LANP were obviously only interested in the brains, which concentrate protein and essential fats. Avoiding swallowing whole prey also shortens the pellet formation time, which increases the prey consumption rate.

On the other hand, prey were consumed according to their availability, as *O. longicaudatus* was both the most abundant beheaded species, and the dominant rodent in the systematic trappings at all surveyed sites (Sage 2011; Piudo *et al.* 2012; Piudo *et al,* 2014), same as in previous bamboo-triggered ratadas (Gallardo & Mercado 1999; Sage *et al*. 2007). In short, not only the best meals were consumed by the "beheaders", but these were ingested at higher rates, with low costs (i.e., predators flooded with potential prey). This way, the head-consuming behaviour here documented combines tactics of time minimisers and energy maximisers (Schoener 1971).

Although we revealed an extraordinary adaptation of the predators' foraging behaviour, future research is needed for a better understanding of this behaviour. For example, is it widespread among the local raptors? As the dismemberments were not by biting, mammalian carnivores are ruled out, but some diurnal raptors may have contributed to produce such prey remnants, along with owls.

Conclusions and perspectives

The negligible role of predation ~~on~~ in controlling outbreak rodent populations triggered by bamboo masting is widely accepted, as confirmed by the typical rafts of dead mice in the lakes and beaches during these ratadas (Pearson 2002). On the contrary, knowledge on the bottom-up consequences of ratadas on mice predators is very poor, and there's still much to learn. Because our surveys were limited to the first year after the bamboo masting, the magnitude and temporal extent of the changes for nocturnal avian top predators cannot be established beyond the immediate numerical and behavioural responses here described. But further consequences can be expected, given a threefold increase in total owl numbers, presumably followed by successful breeding of most predator species. More even so, considering that ratada events usually occur sequentially over adjacent large geographic areas (Veblen 1982).

Comment [L24]: R1

For open country owls that regularly avoid forests, ratadas may allow increases in the flow of individuals east and west of the Andes. This way, while the dense forests covering the foothills of the southern Andes normally represent a barrier to the dispersion of open country birds, the sporadic corridors created by the ratadas for rodent-tracking owls may play a role in connecting disjunct populations. Consequences for forest owls are more difficult to project beyond the studied period. The unpredictability of bamboo-triggered ratadas would not favour the evolution of demographic adjustments on a cyclic basis, like those of raptors consuming voles and lemmings in the Northern Hemisphere (e.g., Korpimäki *et al.* 2002), for example. Never the less, the enhanced reproductive performance that may supervene bamboo-triggered food surplus, may lead to demographic changes in the local populations that will, eventually, impact the habitat quality through direct and indirect (via top-down) controls, for some years after the ratadas. This way, although infrequent and unpredictable, bamboo-triggered ratadas may likely cause minor demographic revolutions in the owl assemblage of the southern Andes.

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Table 1. Four replicates set for comparing owl numbers and behaviours between subsidised (outbreak rodents) and unsubsidised (no rodent outbreaks) forests in south Nahuel Huapi National Park, Argentine Patagonia. The number of survey stations within each replicate, their central coordinates (in WGS84 projection), and the dominant *Nothofagus* forest species (in parenthesis), are given. The number of pellets collected at the subsidised sites is also provided. These sites are geographically depicted in Appendix S3.

Replicate (site) **Treatment**	**Circuito chico**	**Ruta 40 sur**	**Pampa Linda**	**Los Alerces**	**Totals**
Outbreak rodents	**7** 41º03'34.96" S 71º33'56.29" W (*N. dombeyi*)	**6** 41º25'03.43" S 71º29'35.22" W (*N. dombeyi*)	**7** 41°14'57.84" S 71°44'9.24" W (*N. antarctica*)	**6** 41°21'57.75" S 71°44'1.34" W (*N. dombeyi*)	**26**
Pellets collected	22	12	17	21	
No outbreaks	**5** 41º06'45.49" S 71º28'24.53"W (*N. antactica*)	**6** 41º28'45.67" S 71º28'14.13" W (*N. antarctica*)	**7** 41°18'12.96" S 71°35'30.12" W (*N. dombeyi*)	**4** 41°20'59.45" S 71°40'2.32" W (*N. antarctica*)	**22**
Totals	**12**	**12**	**14**	**10**	**48**

FIGURE LEGENDS

Fig. 1. Responses of Rufous-legged (S.r), Barn (T.a) and Austral pygmy (G.n) owls to outbreaking rodents after a massive bamboo blooming in Argentine Patagonia. Mean numbers of recorded owls at survey stations are shown for basal (pre-blooming) surveys in 2009 (BS09), the rodent population build-up phase (autumn 2011, AS11), and the peak of the prey outbreak (spring 2011, SS11). Descriptive statistics (SD), and a measure of the precision of the sample mean (SE). are provided in the chart. Subsidised (oubreaking rodents) and unsubsidised (normal rodents) sampling sites are detailed in Table 1.

ABBREVIATED HEADINGS OF SUPPORTING INFORMATION.

S1. Free online videos showing bamboo-triggered rodent outbreaks in southern Argentina and Chile.

S2. Chart explaining the temporal course of a typical bamboo-triggered rodent outbreak.

S3. Map with the sample sites in forests of south Nahuel Huapi National Park (Argentina).

S4. Outbreak rodent populations at our Circuito Chico sampling site (translated from Spanish).

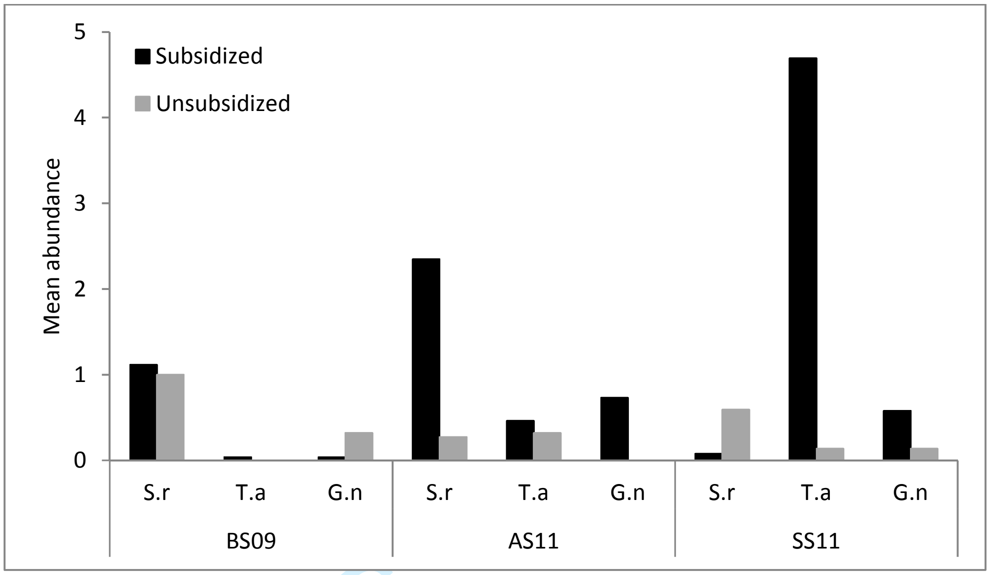
S5. Subsets of models that were compared and ranked according to the Akaike information criterion corrected for small sample sizes (AICc).

S6. Likely responses of south Andean strigiforms to bamboo-triggered rodent outbreaks.

~~S6~~S7. Barn owl (*Tyto alba tuidara*) breeding record in pristine old-growth forest of the southern Andes.

V. Ojeda, Fig. 1

Figure 1.



Owl species	Survey	Subsidized				Unsubsidized			
		N	Mean	SE	SD	N	Mean	SE	SD
S. r	BS09	4.33	1.08	0.28	0.58	4.03	1.01	0.26	0.53
	AS11	9.21	2.30	0.29	0.89	0.96	0.24	0.19	0.19
	SS11	0.29	0.07	0.15	0.08	2.29	0.57	0.14	0.22
T. a	BS09	0.14	0.04	0.19	0.07	0.00	0.00	-	0.00
	AS11	1.81	0.45	0.17	0.23	1.54	0.39	0.36	0.44
	SS11	18.52	4.63	0.24	1.02	0.65	0.16	0.24	0.20
G. n	BS09	0.14	0.04	0.19	0.07	1.32	0.33	0.34	0.39
	AS11	2.86	0.71	0.18	0.30	0.00	0.00	-	0.00
	SS11	2.31	0.58	0.05	0.07	0.64	0.16	0.29	0.24

Ojeda, V. & Chazarreta, L. (2018) Effects of episodic bamboo mast seeding on top predators in the southern Andes. *Austral Ecology* **XX**, xxxx-xxxx.

Appendix S1

Videos showing the social, health, and economic impacts in rural settlements of recent (2011) bamboo-triggered rodent outbreaks occurred in southern Chile and Argentina.

ARGENTINA

Nahuel Huapi National Park, El Manso Valley (Río Negro Province)

Coordinates: 41°35'58.91"S, 71°43'39.01"O, 450 m.a.s.l.

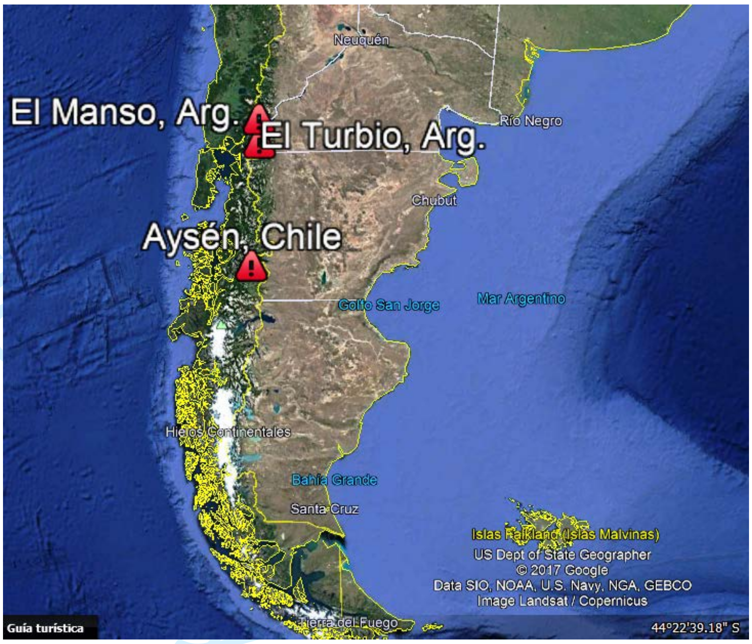
VIDEO

1) https://www.youtube.com/watch?v=wKq0-Is4NG4

El Turbio Valley (Chubut Province)

Coordinates: 42°15'8.39"S, 71°41'52.34"O, 246 m.a.s.l.

VIDEO 2) https://www.youtube.com/watch?v=_YA89kOEg8c



CHILE

Aysen Region (various sites) Central coordinates: 45°34'12.24"S, 72° 4'5.28"O, 280 m.a.s.l.

VIDEO 3) https://www.youtube.com/watch?v=ZHQ-9e4lLC4

VIDEO 4) https://www.youtube.com/watch?v=M1J17vrZVX8

VIDEO 5) https://www.youtube.com/watch?v=PUnxPaCaolE

VIDEO 6) https://www.youtube.com/watch?v=0M_V-Airmpk

Ojeda, V. & Chazarreta, L. (2018) Effects of episodic bamboo mast seeding on top predators in the southern Andes. *Austral Ecology* **XX**, xxxx-xxxx.

Appendix S1

VIDEO 7) https://www.youtube.com/watch?v=eTl_xKPE0sI

Ojeda, V. & Chazarreta, L. (2018) Effects of episodic bamboo mast seeding on top predators in the southern Andes. *Austral Ecology* **XX**, xxxx-xxxx.

Appendix S2

Temporal course of bamboo-triggered rodent outbreaks in forests of South America, based on Sage *et al*. (2001): “The chart shows major events in the phenology of the flowering bamboo and rodent populations with respect to the 5 collecting periods, the passage of the annual seasons, and the calendar dates. The graph of the intensity of reproduction in *Oligoryzomys longicaudatus* (the most abundant rodent species) shows the percentage of females that were reproductively active in a sampling period, with N indicating the number of animals autopsied”.

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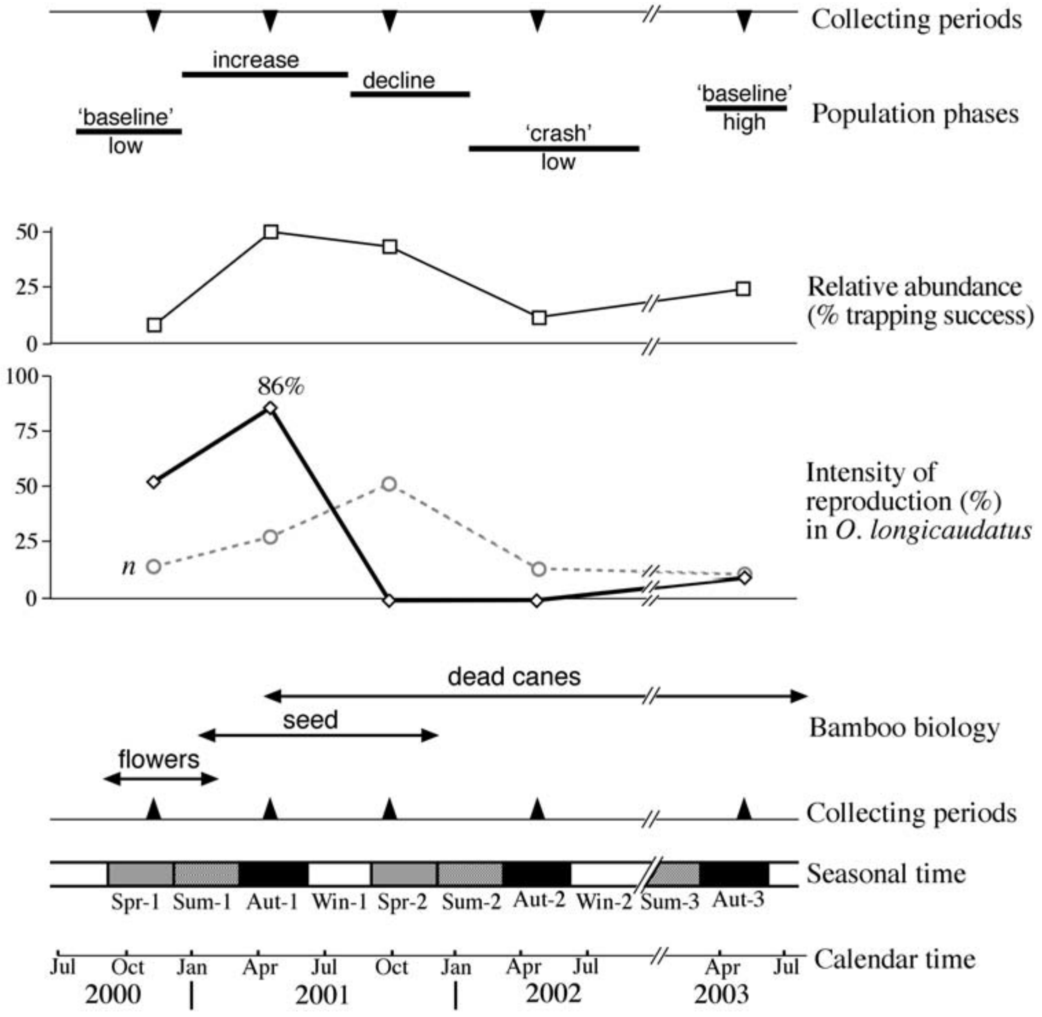

Source: Sage, R. D., Pearson, O. P., Sanguinetti, J. & Pearson, A. K. (2007) Ratada 2001: A Rodent Outbreak Following the Flowering of Bamboo (*Chusquea culeou*) in Southwestern Argentina. In: Kelt, D. A., Lessa, E. P., Salazar-Bravo, L. & Patton, J. L., eds., *The Quintessential Naturalist: Honoring the Life and Legacy of Oliver P. Pearson.* Berkeley (CA): University of California, pp. 177-224.

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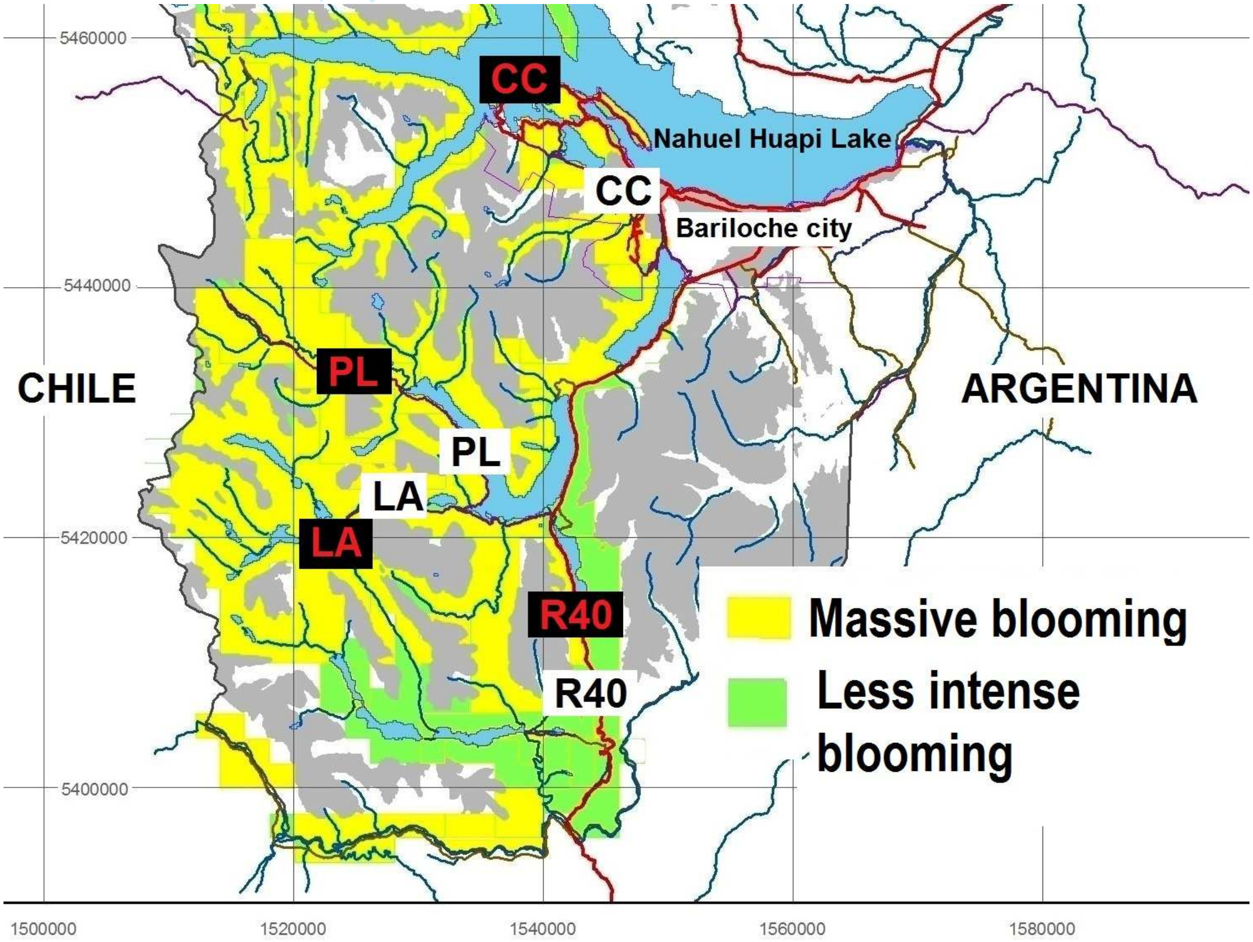
Appendix S3

Sample sites superimposed on a map showing the 2010-2011 blooming/masting of *Chusquea culeou* in forests of south Nahuel Huapi National Park (Argentina). Owl survey sites in subsidised (outbreak rodents) bamboo areas are indicated by black rectangles (red letters), and those in unsubsidised (normal rodents) bamboo areas are represented by white rectangles (black letters). Names of the sites are: Circuito Chico scenery road (CC), Pampa Linda valley (PL), Los Alerces waterfall access (LA), and Ruta 40 sur (R 40). The base map was obtained from Núñez *et al.* (2013). Geographic references are in UTM (Universal Transverse Mercator) system.



Source: Núñez, C. I., Caracotche, S. & Pérez, A. (2013) Sucesos asociados a la floración de la caña colihue 2010-2011. *Macroscopia* [online] **3**, 5-9. Available at: https://www.nahuelhuapi.gov.ar/multimedios/macroscopia_03.pdf [Accessed 5 Oct. 2017].

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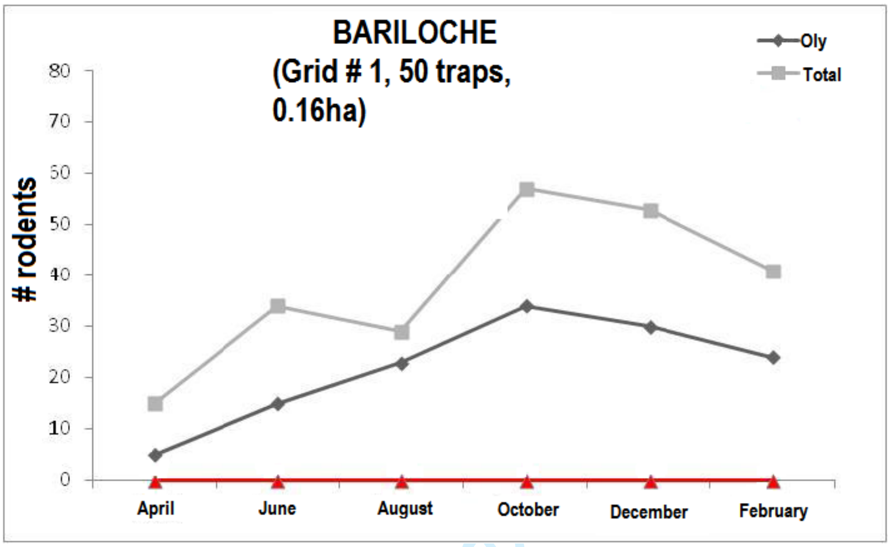
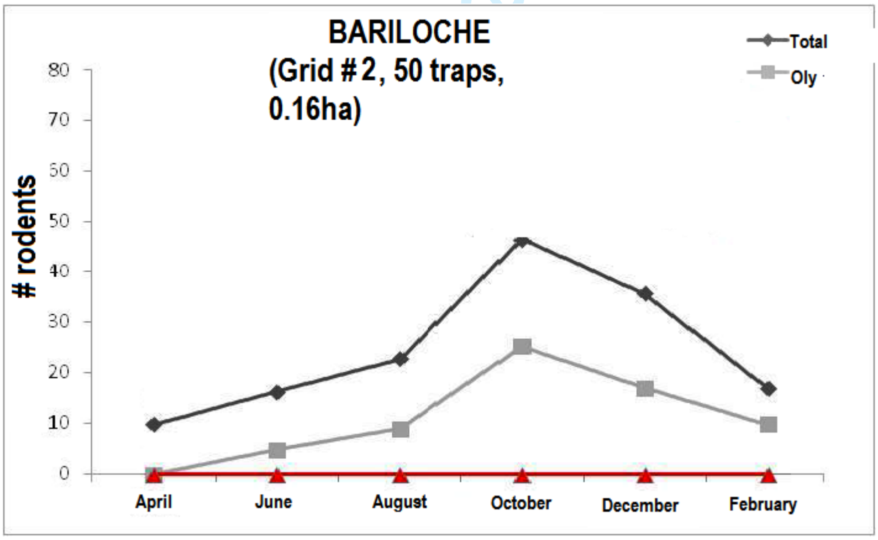
Appendix S4

Rodent increases during 2011 at two natural forest sites west of Bariloche city (coinciding with our Circuito Chico –CC—sampling site), where systematic rodent trappings were conducted by Piudo *et al.* (2012). *Oligoryzomys longicaudatus* (OLY) is shown separately, as it was especially monitored for the prevalence of the Andes hantavirus antibody.





Source: Piudo, L., Monteverde, M., Pailacura, O., *et al.* (2012) *Monitoreo de roedores con relación a la floración masiva de la caña colihue (Chusquea culeou) en la Pcia. de Río Negro. Informe Final.* [online] Junín de los Andes: CEAN-Ministerio de Salud (RN). Available at: http://www.cean.gob.ar/wp-content/uploads/2016/09/floracion-masiva-de-la-ca%C3%B1a-colihue-y-dinamica-del-sistema-Roedor-hantavirus-en-Rio-negro.pdf [Accessed 5 Oct. 2017]

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Appendix S5

Generalized linear mixed-effects models (family: Poisson) used to examine effects of changes in rodent abundance caused by episodic bamboo mast seeding on owl numbers in *Nothofagus* forests of Argentine Patagonia. Best model (lowest AICc value) for each owl species is shown in bold. Asteriscs represent interaction between variables; in parenthesis, the variable “season” (BS09/ AS11 / SS11) was considered as repeated measurements, and the variable “site”, as random effect, as detailed in the Methods section.

Species	**Candidate Model**	**AICc**
Strix rufipes	1. strix ~ effect + (season | site)	360.00
	2. strix ~ effect + season + (season | site)	353.51
	3. strix ~ effect * season + (season | site)	**315.87**
	4. strix ~ effect + season + site + (season | site)	350.76
Tyto alba	1. tyto ~ effect + season + site + (season | site)	251.16
	2. tyto ~ effect + season + (season | site)	250.27
	3. tyto ~ effect * season + (season | site)	**235.41**
	4. tyto ~ effect + (season | site)	263.72
Glaucidium nana	1. glaucidium ~ effect + (season | site)	212.95
	2. glaucidium ~ effect + season + (season | site)	214.11
	3. glaucidium ~ effect * season + (season | site)	**161.39**
	4. glaucidium ~ effect + season + site + (season | site)	219.23

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Appendix S5

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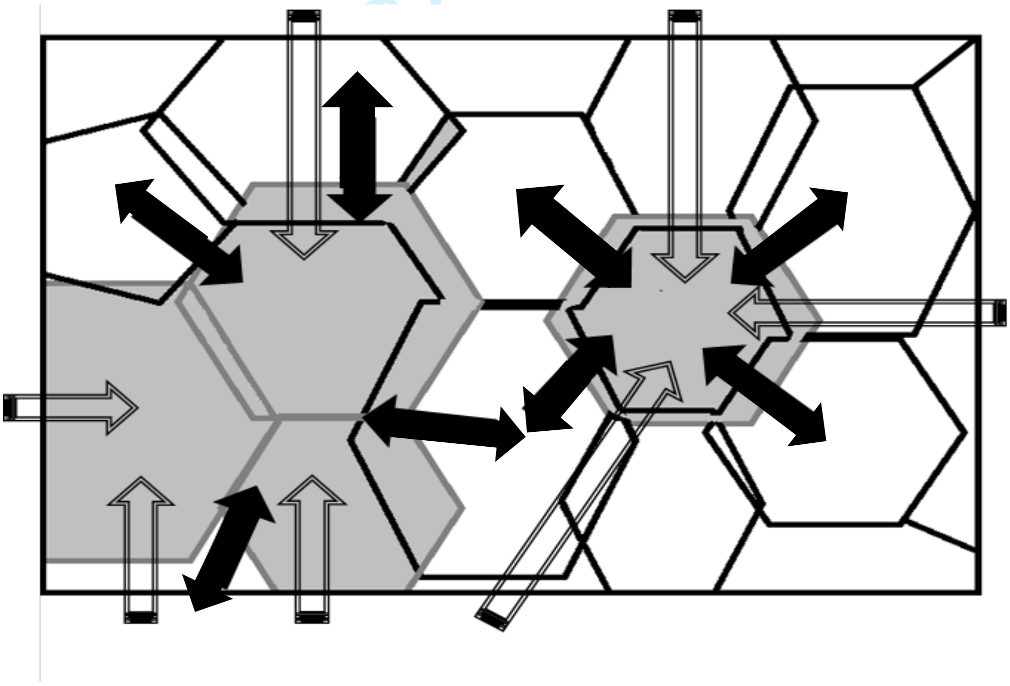
Appendix S6

Schematic representation of the likely movements of four nocturnal raptors on the course of a typical bamboo-triggered rodent outbreak in the southern Andes, based on data from Nahuel Huapi National Park, and partially from Los Alerces and Lanín National Parks, in Argentina. The rectangle represents a portion of a hypothetical area affected by a spatially heterogeneous “ratada” (rodent outbreak) event, where some owl territories (the hexagons) are subsidised, while others are not. Subsidised areas consist of hundreds of ha where bamboos underwent blooming and masting, mixed with similarly large non-flowered (unsubsidised) patches. The owl species that shown each type of response are indicated in the legends below.



⬌ ◆Short-distance (daily?), rapid response of opportunistic resident (territorial) consumers (Rufous-legged owl, Austral pygmy owl).

⇨ ◆Long-distance, retarded response of mobile (nomadic) rodent specialists (Barn owl, Short-eared owl)

⬢ ◆Subsidised (outbreak rodents) forest areas

⬡ ◆Unsubsidised (normal rodents) areas

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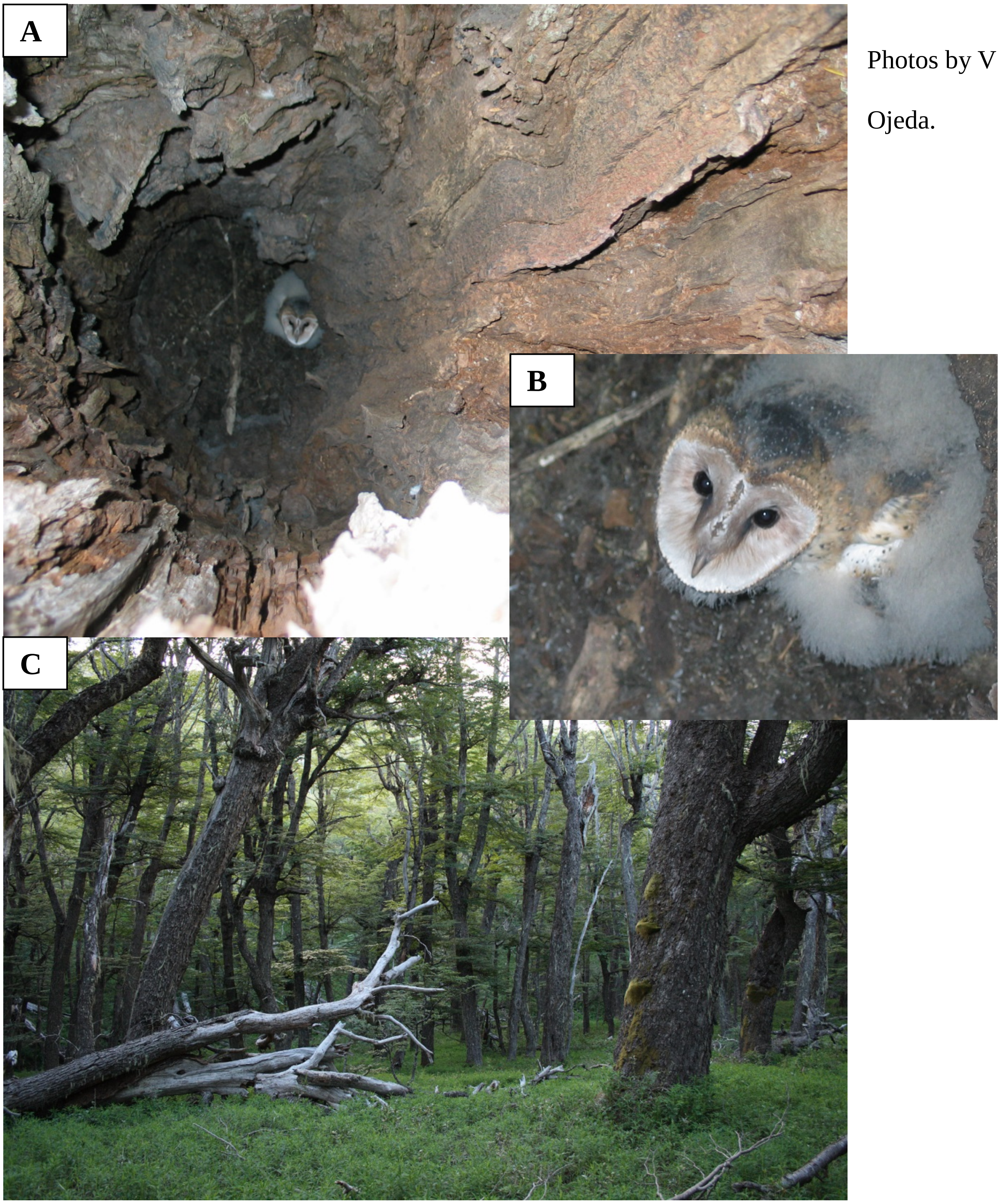
Appendix S7

Barn owl (*Tyto alba tuidara*) nest located by one of the authors in continuous old-growth monospecific *Nothofagus pumilio* forest in Nahuel Huapi National Park, Argentina. A) A hollow stump containing a single nestling. B) A closer look of the middle-aged nestling. C) Nesting site; note the old-growth tree structure and very open understory.



Photos by V. Ojeda.