Native forest replacement by exotic plantations triggers changes in prey selection of mesocarnivores

CrossMark

Darío Moreira-Arce [a,b,*], Pablo M. Vergara [b], Stan Boutin [a], Javier A. Simonetti [c], Cristóbal Briceño [d], Gerardo Acosta-Jamett [e]

[a] Department of Biological Sciences, University of Alberta, Edmonton, AB T6G 2E9, Canada
[b] Departamento de Gestión Agraria, Universidad de Santiago de Chile, Av. Lib. B. O'Higgins 3363, Santiago 7254758, Chile
[c] Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile, Casilla 653, Santiago, Chile
[d] Departamento de Medicina Preventiva Animal, Facultad de Ciencias Veterinarias y Pecuarias, Universidad de Chile, Santiago, Chile
[e] Instituto de Medicina Preventiva Veterinaria y Programa de Investigación Aplicada en Fauna Silvestre, Facultad de Ciencias Veterinarias, Universidad Austral de Chile, Casilla 567, Valdivia, Chile

ARTICLE INFO

ABSTRACT

Replacement of native forests by forest plantations may change the composition and abundance of small mammals, thus influencing the foraging behavior of mesocarnivores in these human-created habitats. We assessed how differences in prey abundance between native forests and exotic plantations in southern Chile may explain the prey selection of four mesocarnivores, as analyzed from their scats. Using a spatial zero-inflated Poisson model, we determined that the abundance of most small mammals was lower in plantations than native forests, except for three common species, which had similar or larger abundances in exotic plantations. We assessed mesocarnivores' prey selection by assessing the coefficients and log-ratios of use and availability of a Bayesian Resource Selection Function. We determined that in native forest, the preferences of kodkod (*Leopardus guigna*) for arboreal prey was stronger, whereas chilla fox (*Pseudalopex griseus*) and Darwin's fox (*Pseudalopex fulvipes*) exhibited a selective preference for ground prey. Darwin's fox also exhibited a habitat-dependent changes in their selection for Darwin's leaf-eared mouse (*Phyllotis darwini*), from a positive log ratio in native forest to a negative ratio in exotic plantations. Conversely, culpeo fox (*Pseudalopex culpaeus*) selected long-tailed colilargo (*Oligoryzomys longicaudatus*) and Chilean climbing mouse (*Irenomys tarsalis*) in plantations only, even though these prey were more abundant in native forests. Although mature commercial forest plantations may provide feeding grounds for mesocarnivores, depending on their species-specific ability to capture available prey, the decline of small mammal availability in plantations may modify the prey selection of mesocarnivores.

© 2015 Elsevier Ltd. All rights reserved.

1. Introduction

Exotic plantations are becoming increasingly widespread as natural ecosystems are replaced by productive forestry lands (FAO, 2011), thus changing the distribution and abundance of species throughout different trophic levels (Brockerhoff et al., 2008; Lindenmayer and Hobbs, 2004). Carnivores can respond positively, or negatively, to plantations depending on their ecological requirements and management prescriptions within these anthropic habitats (Acosta-Jamett and Simonetti, 2004; Di Bitetti et al., 2006; Pita et al., 2009; Mazzolli, 2010; Lantschner et al., 2012; Simonetti et al., 2013; Coelho et al., 2014). The decline in carnivore populations arising from the replacement, or loss, of natural habitats may result in cascading effects affecting the biodiversity at

lower trophic levels (Jaksic et al., 1992, Thompson and Gese, 2007, Byrom et al., 2014; Ripple et al., 2014). Assessing how exotic plantations alter prey populations and how carnivores respond to these habitat-mediated changes in prey abundance could provide a bridge between sustainable forestry management and the trophic ecology of carnivores.

Small mammal species represent a significant amount of animal biomass available for mesocarnivores in natural forest ecosystems (Carey and Johnson, 1995; Hanski et al., 2001; Korpimaki et al., 2005; Dupuy et al., 2009). Although small mammals could be abundant in productive land, such as forest plantations, due to their habitat generalism or large mammal extirpation (e.g., Muñoz-Predreros et al., 1990; Lindenmayer and Hobbs, 2004; Saavedra and Simonetti, 2005; Lantschner et al., 2011; Young et al., 2015), the overall density of small mammals tends to decrease as native habitat is disturbed. Indeed, habitat quality for small mammals decreases by the loss of habitat elements contributing to habitat complexity, such as understory cover, logs, snags and large decayed trees (Lindenmayer et al., 1994; Carey and Johnson, 1995;

* Corresponding author at: Department of Biological Sciences, University of Alberta, Edmonton, AB T6G 2E9, Canada.
E-mail address: moreira.dario@gmail.com (D. Moreira-Arce).

Lindenmayer and Hobbs, 2004; Saavedra and Simonetti, 2005; Robitaille and Linley, 2006; Fontúrbel, 2012). Small mammals living in plantations may not only be limited by food, but also by a reduced availability of natural refuges used against predators (e.g., burrows, tree holes, and cavities; Balme et al., 2007; Gorini et al., 2012; Escobar et al., 2015).

Mesocarnivores inhabiting landscapes dominated by plantations can respond to changes in small mammal composition and abundance by modifying their prey selection patterns. Predators can become more efficient at searching for, pursuing and capturing the more abundant prey species (Emlen, 1966; Murdoch, 1969; Charnov, 1976; Chesson, 1983; Jaksic et al., 1992; Joly and Patterson, 2003; Prugh, 2005; Dell'Arte et al., 2007). However, depending on their species-specific attributes, carnivores' ability to search and find prey could increase in forest plantations with poorly developed vegetation (Mills et al., 2004; Gorini et al., 2012). The sensitivity of carnivores to habitat modifications resulting from forest plantations, may depend on their species-specific habitat specialization, which influences their capacity to adjust foraging behavior in response to changing habitat conditions (Gorini et al., 2012). Therefore, depending on their ability to respond to habitat-dependent changes in prey catchability and abundance, carnivores may modify their prey selection behavior when native habitats are replaced by exotic plantations.

Mesocarnivores occurring in temperate forests of central-south Chile face considerable structural and compositional habitat change resulting from intensive forestry land use (Aguayo et al., 2009). However, recent studies have shown that exotic plantations are not "biological deserts" for these species because they can provide alternative habitats through the maintenance of native understory and landscape heterogeneity (Lindenmayer and Hobbs, 2004; Simonetti et al., 2012; Simonetti et al., 2013). Exotic plantations in this region support fewer small mammals species compared to native forests. In some cases, however, plantations might harbor a high abundance of sigmodontine species, such as long-haired field mouse (*Abrotix longipilis*), olivaceous field mouse (*Abrotrix olivaceus*) and long-tail colilargo (*Oligoryzomys longicaudatus*) (e.g., Muñoz-Pedreros, 1992; Saavedra and Simonetti, 2005; García et al., 2013). Thus, even though the structural role of exotic plantations as habitat for carnivores – and other taxa – has been documented (e.g., Simonetti et al., 2013; Cerda et al., 2015), the functional role of these human-created lands, as feeding grounds for mesocarnivores is poorly understood.

Mesocarnivores living in temperate forest have been shown to prey on a wide range of small mammals species (e.g., Jiménez et al., 1990; Roa and Correa, 2005; Sade et al., 2012). However, carnivores prey use in relation with changes in prey availability arising from the replacement of native forest by plantations is unknown. Addressing this knowledge gap is essential because exotic plantations currently cover almost 17% of forested areas in Chile (CONAF, 2011). In this study, we investigated the role of exotic plantations as feeding grounds for four sympatric native mesocarnivores inhabiting a mosaic landscape dominated by exotic plantations in central-south Chile: kodkod (*Leopardus guigna*), Darwin's fox (*Pseudalopex fulvipes*), culpeo fox (*Pseudalopex culpaeus*) and chilla fox (*Pseudalopex griseus*). The Vulnerable kodkod and the Critically Endangered Darwin's fox (Napolitano et al., 2015; Jiménez et al., 2008, respectively) have been documented to be negatively affected by exotic plantations (Acosta-Jamett and Simonetti, 2004; Moreira-Arce et al., 2015), yet mechanisms underlying their responses remain unclear. Specifically, we assessed variation in the abundance of small mammals between plantations and native forest and we asked whether this prey variation triggered changes of prey selection patterns on these carnivores. First, we predicted that in exotic plantations compared to native forest, the overall abundance of small mammals is lower as previously documented in other studies (e.g., Saavedra and Simonetti, 2005; García et al., 2013). Second, we

predicted that these mesocarnivores respond to changes in small mammal abundances by switching their prey selection patterns towards the prey species that are more abundant at each habitat type. However, we predicted that prey selection behavior of forest-specialist kodkod and Darwin's fox may also be affected by changes in habitat structure as derived from replacement of native forest into exotic plantations.

2. Methods

2.1. Study area

The study area encompassed ca. 16,000 ha and is located in Nahuelbuta Mountain Range (NMR), in Temperate Forest of southern Chile (Fig. 1). Climate is characterized by hot, dry summers (mean monthly temperature and rainfall 16.4 °C and 22.5 mm, respectively) and cool, wet winters (monthly means: 7.5 °C and 205.4 mm). The elevation of the study area ranged from 650 to 900 m. Nahuelbuta Mountain was once widely covered by continuous forest composed by mixed deciduous and evergreen species such as *Araucaria araucana*, *Eucryphia cordifolia*, *Aextoxicon punctatum* and *Laureliopsis philippiana* as well as a mixture of *Nothofagus* species (Smith-Ramírez, 2004). Currently, the landscape is a mosaic of human-created lands, composed of a combination of young and mature exotic forest plantation stands of Monterrey pine (*Pinus radiata*) and *Eucalyptus* spp., and remnants of native forest (Fig. 1). Young plantations comprise poorly developed understory, whereas mature exotic plantations are characterized by the presence of a scattered understory vegetation composed by native shrubs (e.g., *Aristotelia chilensis* and *Chusquea quila*), but also by introduced shrubs (e.g., *Rubus ulmifolius*, *Ulex europaeus* and *Teline monspesulana*, see Poch and Simonetti, 2013). Understory vegetation of the native forest includes dead trees and fallen logs, as well as a rich diversity of native shrub species, native tree saplings, mosses, ferns and climbing plants, such as *Azara* spp., *Gevuina avellana*, *Berberis* spp., *Blechnum* spp., *Luma apiculata*, *Myrceugenia exsucca* and *C. quila*.

2.2. Prey abundance

Prey abundance was assessed from relative abundance of prey estimates obtained from small mammal trapping conducted during spring 2012 and autumn of 2013. The abundance of some small mammal species tends to vary markedly from spring to autumn (Murua et al., 1986; Meserve et al., 1991; Meserve et al., 1999); hence, their abundance was assessed in these two seasons. We used a combination of wire-mesh (Tomahawk-like) and Sherman (7.6 × 8.9 × 22.8 cm) traps in 40 grids of 6 × 6 live traps each. Grids were at least 1000 m apart from each other and distributed across two habitat types, with 20 grids located in mixed forest dominated by southern beech (*Nothofagus* spp.), and 20 in monoculture exotic plantations of Monterrey pine (Fig. 1). At each grid, half traps were consistently placed on and above ground level (~2 m height) in order to improve the capture of both ground-level and arboreal small mammals (Fontúrbel et al., 2010). Trapping at each grid was conducted for five consecutive nights (totaling 7200 trap-nights), using rolled oats as bait. Captured individuals were identified to species, marked with unique patterns in their fur, and released at the capture site. Differences in small mammal abundance between native forests and plantations can be masked by the seasonal variations of some rodent species in temperate ecosystems, as explained above. Therefore, we included season as a covariate to account for seasonal fluctuations of abundance (see below).

We used the minimum number of small mammals known alive (MNKA; Lancia et al., 1994) to obtain estimates of absolute and relative small mammal abundances in different seasons and habitats.
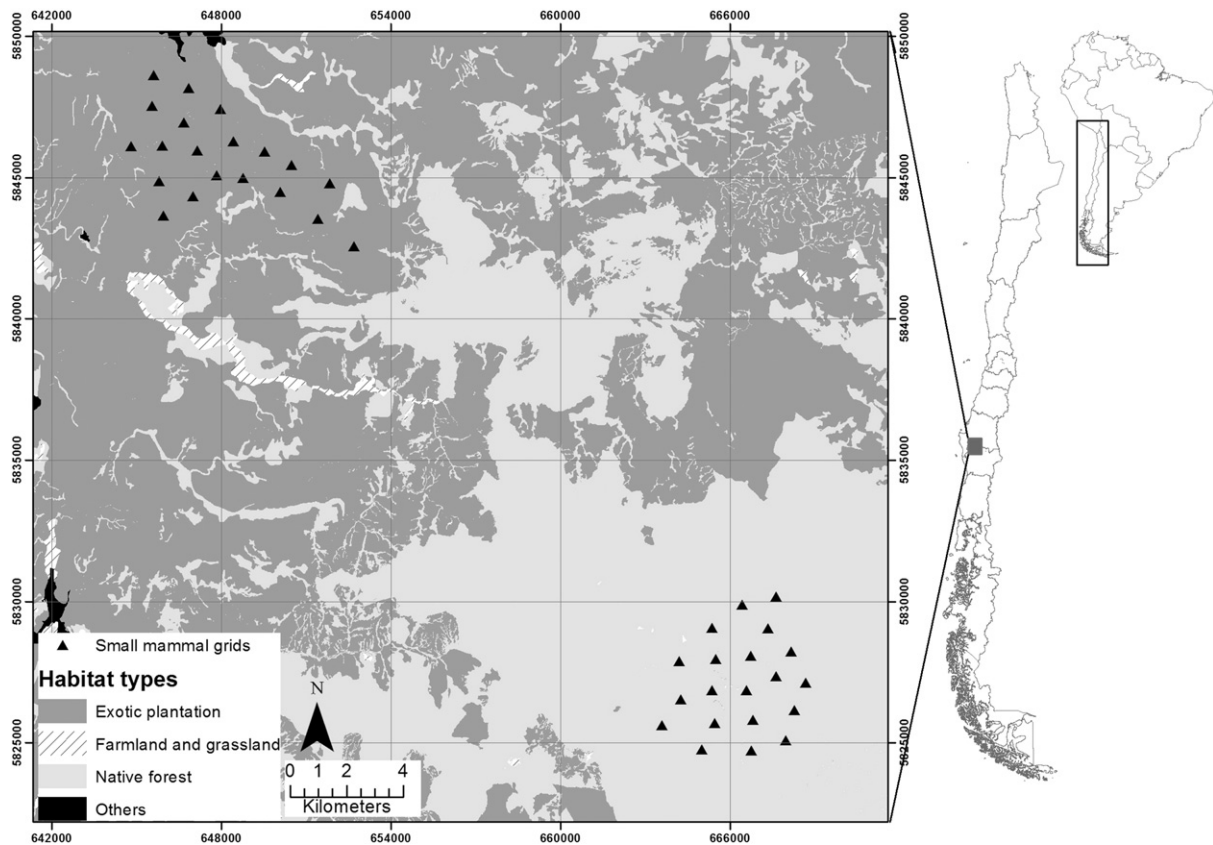
Fig. 1. Map of the study area in Nahuelbuta Mountain Range, central-south Chile, showing the dominant habitat types. Black triangles represent 6 x 6 small mammal trapping grids surveyed.

This method has been frequently used to assess population estimation of Chilean small mammals (e.g., Iriarte et al., 1989; Previtali et al., 2009; Madrigal et al., 2011). All animals were captured, marked and handled in accordance with approved governmental and institutional animal care protocols (Chilean Agriculture and Livestock Bureau; SAG resolution number 2201/2013; University of Alberta animal use protocol # AUP00000039).

2.3. Prey consumption

Prey consumption of the four studied mesocarnivores was assessed by analyzing diet composition from their scats collected around each trapping grid during spring 2012 and autumn 2013 (Fig. 1). Each grid was regularly visited every two days, totalizing 35 surveys per season. We identified carnivore scats through DNA analysis, which overcomes difficulties in identifying species on basis of the morphology and size in areas where similar body-size species co-occur. We isolated DNA from each scat using a QIAGEN Stool Mini Kit (QIAGEN, CA, USA), amplified a fragment of the mitochondrial cytochrome *b* gene, and resulting sequences compared to those of reference samples. Analyses were conducted at the Primate Immunogenetics and Molecular Ecology (PRIME) Laboratory at University of Cambridge, UK. To identify the prey items of carnivores we dried and washed scats, and examined their contents. We identified small mammals in carnivores' scat to species by using available keys for comparing teeth and hair patterns of the species occurring in the study area (Reise, 1973; Pearson, 1995). We expressed the use of each prey species by each carnivore as the proportion of that food item

in their diet, i.e. the number of occurrences of one food item divided by the total number of occurrences of all food items (Klare et al., 2011).

2.4. Prey abundance analysis

Differences in the mean abundance of small mammals between plantations and native forests across seasons were assessed using ANOVA and Bayesian Mixed Effects Zero-inflated Poisson (ZIP) models. These later models were appropriate for analyzing our abundance data at species level because they included excess zeros and overdispersion (Zuur et al., 2009). ZIP models provide a mixed likelihood function that combines: 1) a binomial logistic regression that models an excess of zeros (also known as inflation), thus, dealing with false zero counts that emerge from low detectability at the grid; and 2) a log-Poisson regression that models abundance data (Zuur et al., 2009). We specified the fixed-effects of season (spring vs. autumn), habitat type (pine plantation vs. native forest) and their interaction (season × habitat type) on the abundance of small mammals at each grid. We included grids as a random variable to account for the effects of other unobserved variables at the grid-level. The importance of each fixed effect (habitat, season and season × habitat type) was evaluated from the Bayesian Credible Intervals (BIC) of the posterior distribution of coefficients. Models with different combinations of fixed effects were assessed using Deviance Information Criteria (DIC; Spiegelhalter et al., 2003). Models were run using WinBUGSv. 1.4 (Spiegelhalter et al., 2003), which was remotely called from R v. 3.2.0 by using the R2WinBUGS package. Posterior distributions were based on three MCMC iterations, each with

20,000 iterations, discarding the first 10,000 iterations and thinning by two. We used vague non-informative prior distributions for all model parameters. We assessed convergence by visually examining trace and density plots of MCMC iterations as well as by estimating the Potential Scale Reduction factor (Gelman et al., 2003).

2.5. Prey selection analysis

We assessed prey selection of carnivore species across seasons and habitat types based on prey consumption, as obtained from diet analyses, and prey availability, measured from small mammal abundance. I considered prey availability being representative of small mammal abundances rather than true availability (a combination of prey abundance and the prey vulnerability). We used the Aebischer et al.'s (1993) Resources Selection Function model which assumes that the use of prey j, U_j, by a predator is proportional to availability of that prey, a_j, times its selection S_j, such that:

$$U_j = \frac{s_j a_j}{\sum_{j=1}^{D} s_j a_j}$$

where the denominator of Eq. (1) is the sum of the product of availability times selection over all prey ($j = 1,2 \ldots D$). We assumed that observed prey-count data, c_j, from each scat recollected in a grid, during a season, followed a Multinomial distribution with parameters U_j and N, the total count of used prey ($N = \sum_{1}^{D} c_j$). We used the relative abundance of each prey species in the grid k as an estimate of its availability (a_j). The effect of habitat type and season on selection of a particular prey species, S_j, by a carnivore species was modeled for each grid as:

$$S_{jk} = \frac{\exp(\phi_{jk})}{\sum_{j=1}^{D} \exp(\phi_{jk})},$$

with

$$\phi_{jk} = Season_j + Habitat_j + Season_j \times Habitat_j + G_k + D_k$$

where the fixed-effect coefficients $Season_j$, $Habitat_{jk}$ and $Season_j \times Habitat_{jk}$ are estimated for each prey species whereas G_k is a random factor for controlling dependence of data from each grid. The term D_k is a multivariate Gaussian term whose covariance matrix was expressed as an exponential decay function of the Euclidean distance between grid center coordinates, therefore controlling for spatial autocorrelation. Bayesian model specifications were similar to those described above for the ZIP models. To compare differences in the strength of selection of prey j between native forests and exotic plantations, we computed Bayesian estimates of log-ratios for each habitat type as $d_j = \log(U_j/a_j)$. Values of $d_j > 0$ and $d_j < 0$ imply that prey j is preferred and not preferred (i.e., avoided) for that habitat, respectively (Aebischer et al., 1993). All model coefficients and log-ratios (d_j) were assessed by examining their BCIs. The 95% BCIs that did not overlap zero were interpreted as being significant.

3. Results

3.1. Small mammal abundance

A total of 778 individuals were captured, including individuals from six rodent species as well as the marsupial monito del monte (*Dromiciops gliroides*: Microbiotheria) (Fig. 2). As predicted, total abundance of small mammals was higher in native forest compared to exotic plantations (Repeated measures ANOVA: F = 25.89, df = 1, p < 0.01).Total abundance was significantly higher during autumn (F = 9.17, df = 1, p < 0.01). However, when assessed at the species level, the mean abundance of long-haired field mouse and olivaceous field mouse was lower in native forest compared to exotic plantations (Fig. 2).

Models fitted to individual species that including habitat, season and their interactions (season × habitat) were the best-supported candidate
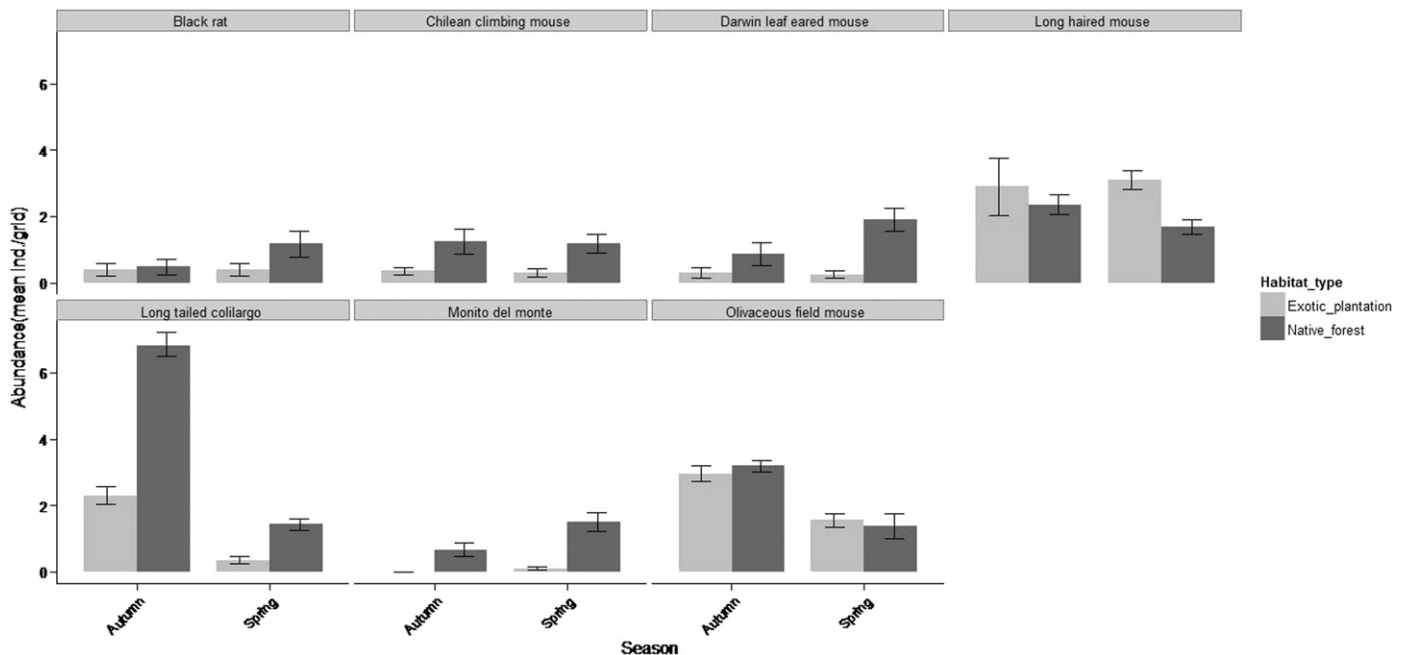

Fig. 2. Mean number of individuals of each small mammal species captured per surveyed grid (means ± standard error), out of 20 grids in native forest and 20 grids in exotic plantation during spring 2012 and autumn 2013.

Table 1
Bayesian Zero-inflated Poisson models predicting the abundance of small mammal species in the study area. The means, standard deviations (SD), and 95% lower and upper Bayesian Credible Intervals (CI) of the most parsimonious model are presented. For comparison reasons, coefficients for exotic plantation and spring levels are set at zero.

Species	Variable	Coefficient	SD	Lower BCI	Upper BCI
Long-haired field mouse (Lf)	Season	0.96	0.63	−0.28	1.68
	Habitat	−2.00	1.17	−4.43	−0.11
	Season × Habitat	−1.47	0.7	−3.02	−1.04
Monito del monte (Mm)	Season	−1.81	0.87	−3.88	−0.26
	Habitat	0.62	1.61	0.39	4.02
Olivaceous field mouse (Of)	Season	1.06	0.44	0.20	1.92
	Habitat	−0.56	0.39	−1.92	0.34
	Season × Habitat	−1.08	0.4	−1.7	0.1
Long-tailed colilargo (Lc)	Season	5.98	1.36	3.70	8.96
	Season × Habitat	−2.7	1.76	−5.14	1.0
	Habitat	1.21	0.52	0.24	1.89
Darwin's leaf-eared mouse (Dm)	Season	2.57	2.22	−1.78	6.92
	Season × Habitat	2.18	1.99	0.14	4.86
Black rat (Br)	Season	−1.37	1.02	−3.52	0.57
	Season × Habitat	2.67	1.37	−0.06	5.68
	Habitat	0.86	1.1	−1.57	4.01
Chilean climbing mouse (Cc)	Habitat	2.24	1.76	0.05	4.87
	Season × Habitat	2.88	0.78	1.35	4.40

Table 2
Significant environmental variables affecting the prey selection of small-mammals by native mesocarnivores in Nahuelbuta Mountain Range, south-central Chile, based on the Resources Selection Function combined with multinomial response distributions in a Bayesian framework. For season and habitat categories, spring and exotic plantation were set at zero and their significances are measured against autumn and native forest.

Carnivore	Prey species	Variable	Mean	Lower CI	Upper CI
	Chilean climbing mouse	Habitat	6.687	2.147	9.822
	Monito del monte	Habitat	4.889	0.086	8.864
	Black rat	Habitat	−6.909	−9.895	−2.056
	Long-haired field mouse	Season	−5.449	−9.709	−0.315
	Olivaceous field mouse	Season	−7.853	−9.861	−4.577
Kodkod	Chilean climbing mouse	Season	−8.412	−9.937	−5.315
	Chilean climbing mouse	Habitat	−7.256	−9.87	−2.682
	Long-tailed colilargo	Habitat	−6.147	−9.543	−1.818
Culpeo fox	Long-tailed colilargo	Season	5.722	1.42	9.388
	Long-tailed colilargo	Habitat	5.02	0.011	8.215
	Black rat	Habitat	−5.782	−9.803	−0.188
Chilla fox	Long-tailed colilargo	Season	6.54	2.398	9.788
Darwin's fox	Darwin's leaf-eared mouse	Habitat	7.372	2.798	9.891
	Long-tailed colilargo	Habitat	4.087	0.713	6.204

logistic and count ZIP models (ΔDIC < 2) than the null models based on DIC values (Appendix A1). The abundances of long-tailed colilargo, monito del monte and Chilean climbing mouse (*Irenomys tarsalis*) were significantly greater in native forest than plantations. Conversely, the abundance of long-haired field mouse was higher in plantations (Table 1 and Fig. 2). The interaction between season and habitat was retained in the best-supported count models of six small mammal species (Appendix A1), but this interaction was significant only for two small mammal species (Table 1). During spring, long-haired field mouse was more abundant in exotic plantations, while Darwin's leaf-eared mouse (*Phyllotis darwini*) was more abundant in native forests (Fig. 2). Season was important to only three species; the abundance of long-tailed colilargo and olivaceous field mouse increased from spring to autumn, while the abundance of monito del monte was higher in autumn than spring (Table 1 and Fig. 2).

When comparing among small mammal species, we found that the relative abundance (fraction of the total abundance) of most species varied between habitat types (Fig. 3). The abundance of Darwin's leaf-eared mouse, monito del monte and Chilean climbing mouse were 3.1, 2.4 and 2.3 times higher in native forest than in pine plantation, respectively (Fig. 3). In contrast, the relative abundance of long-haired field mouse was 2.5 times higher in pine plantation than in native forest (Fig. 3). Seasonal changes in the relative abundances of prey were detected for long-tailed colilargo (ca. 3.5 times higher in autumn compared to spring) and monito del monte (ca. 3.4 times higher in spring compared to autumn; Fig. 3).

3.2. Prey consumption and selection by mesocarnivores

We analyzed a total of 156 scat samples from chilla fox (n = 30), kodkod (n = 52), Darwin's fox (n = 18) and culpeo fox (n = 58).
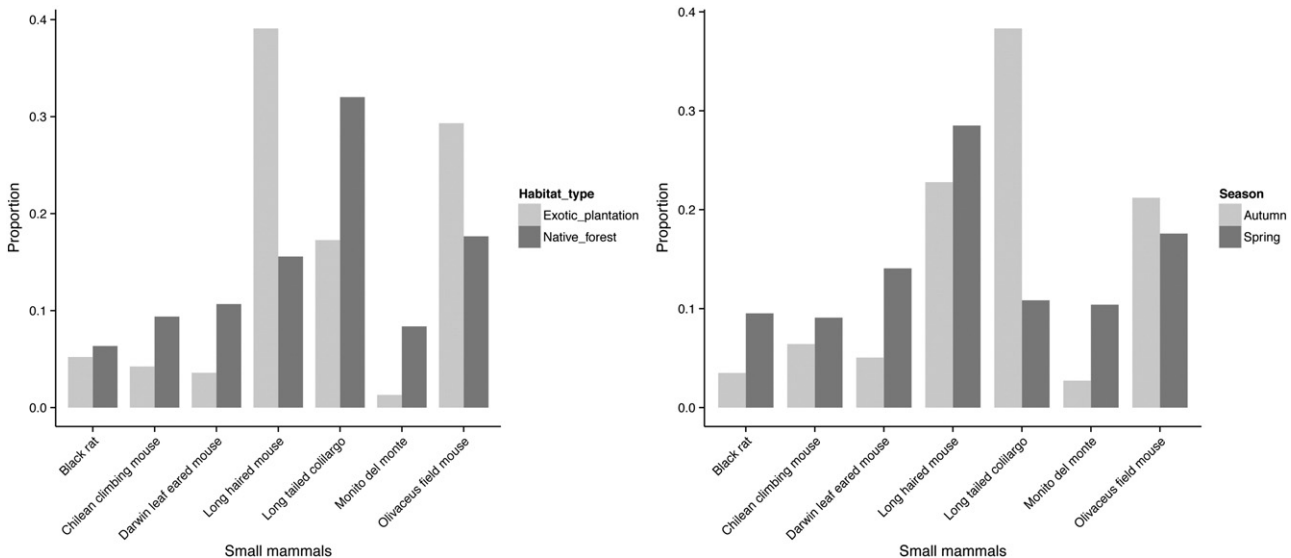

Fig. 3. Relative abundance (fraction of the total abundance) of each small mammal species in native forest and exotic plantation (left) as well as during two seasons (right), out of 20 grids in native forest and 20 grids in exotic plantations during spring 2012 and autumn 2013.
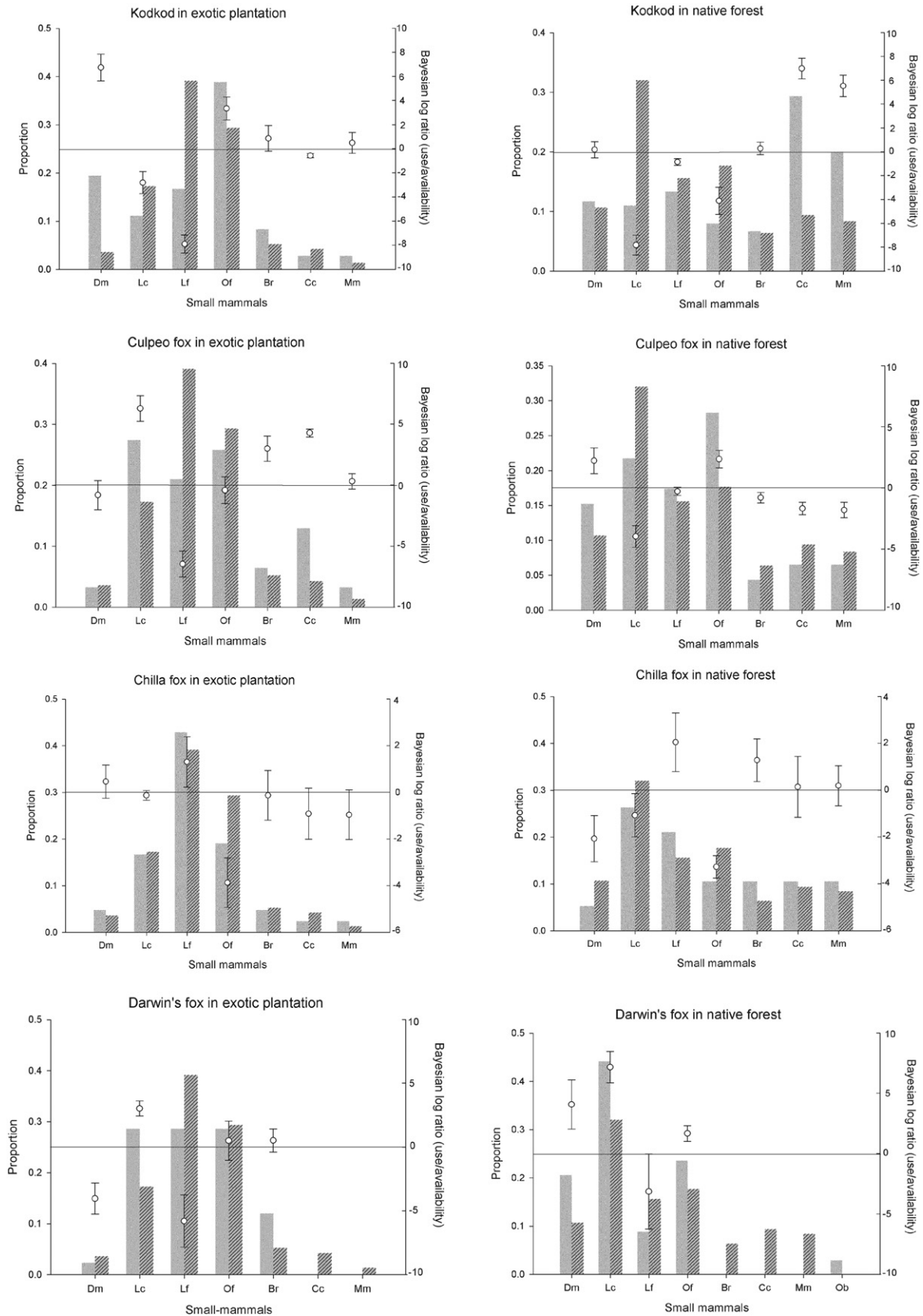
Fig. 4. The observed prey use (gray-clear bars) and prey availability (gray-shaded) as well as the Bayesian estimates of log ratios of use and availability of prey (mean: unfilled dots, bars: 95% credible intervals) of four mesocarnivore species are shown for two habitat types, native forest on the right and forest plantations on the left. Bayesian log ratios whose credible intervals overlap the zero value (isoline) indicate that the use of this prey equal its availability, whereas positive and negative ratio values represent positive prey selection and use less than available, respectively. Codes for small mammal species as follows: (Dm) Darwin's leaf-eared mouse, (Lc) Long-tailed colilargo, (Lf) Long-haired field mouse, (Of) Olivaceous field mouse, (Br) Black rat, (Cc) Chilean climbing mouse, (Mm) monito del monte and (Ob) Bridges's degus.

These scats were spatially distributed as follows: for kodkod, 37 and 15 scats were collected in native forests and plantations, respectively. For Darwin's fox, 12 and six scats were collected in native forests and plantations, respectively, whereas for chilla fox, scats were found more frequently in plantations (n = 20) than in native forest (n = 10). For culpeo fox, 21 and 37 scats were collected in native forests and plantations, respectively. Scats contained the same species captured during small mammals trapping, as well as Bridges's degu (*Octodon bridgesi*).

The most abundant small mammal species, long-tailed colilargo, long-haired field mouse and olivaceous field mouse, were also largely consumed by the four mesocarnivores, comprising over the 50% of total prey consumed by each carnivore. Less common arboreal small mammals, such as Chilean climbing mouse and monito del monte were, however, important in the diet of kodkod, accounting for ca. 50% of kodkod prey consumed in native forests. Black rat (*Rattus rattus*) and Darwin's leaf-eared mouse were mainly found in the scats of Darwin's fox and chilla fox.

Resources Selection Functions fitted to diet composition indicated that, although prey selection was influenced by habitat type and season, these effects differed among carnivores and involved different prey species (Table 2). Kodkod selection of both monito del monte and Chilean climbing mouse, was significantly and positively affected by the presence of native forests, whereas selection for black rat was positively related to the presence of exotic plantations (Table 2). Similarly, kodkod's selected olivaceous field mouse, long-haired field mouse and Chilean climbing mouse more in spring than autumn (Table 2). The selection of culpeo fox on long-tailed colilargo and Chilean climbing mouse was positively influenced by the presence of exotic plantations and by the seasonal change from spring to autumn (Table 2). The selection of long-tailed colilargo by chilla fox was significantly higher in native forest and in autumn, whereas selection for black rat was higher in exotic plantations (Table 2). Similarly, the selection of Darwin's fox on Darwin leaf-eared and long-tailed colilargo was positively related to the presence of native forest (Table 2).

Carnivores switched their prey selection between native forests and exotic plantations, as exhibited by Bayesian log-ratio changes between habitats from negative to positive values (and vice versa; see Fig. 4). Kodkod strongly selected Chilean climbing mouse and monito del monte in native forests, whereas negative log ratios indicated that kodkod consumed less Chilean climbing mouse than available in exotic plantations (Fig. 4). Conversely, kodkod cats' selection for olivaceous field mouse and Darwin's leaf-eared mouse occurred in plantations only, whereas the consumption (use) of both species in native forest was less than or equal to available in native forest (Fig. 4). Culpeo fox strongly selected long-tailed colilargo, black rat and Chilean climbing mouse in exotic plantations, but selected Darwin's leaf-eared mouse and olivaceous field mouse in native forests (Fig. 4). In spite of a high availability of long-tailed colilargo in native forests, consumption of this prey species was lower than its availability (Fig. 4). Chilla fox exhibited positive log-ratios (i.e., prey selection) for long-haired field mouse in native forests and plantations, whereas in native forest only, chillas selected black rat (Fig. 4). In exotic plantations, chilla fox also consumed long-tailed colilargo and olivaceous field mouse equally to, or less than, their availability (i.e., negative log-ratio; Fig. 4). Darwin's fox strongly selected long-tailed colilargo in both habitats (Fig. 4), but switched selection of Darwin's leaf-eared mouse; from a positive log-ratio in native forest to a negative log-ratio in exotic plantations (Fig. 4). Darwin's fox also selected olivaceous field mouse in native forests, but not in plantations. There was no evidence of consumption of arboreal small mammals (monito del monte and Chilean climbing mouse) by Darwin's fox in native forests or in exotic plantations. Similar to chilla fox and kodkod, Darwin's fox consumed black rats equally to their availability in exotic plantations. However, black

rats were not observed in the diet of this carnivore in native forests (Fig. 4).

4. Discussion

In our study area native forests and exotic plantations harbored equal compositions of small mammals. However, the abundance of some species differed between habitats, which may have promoted changes in the prey selection behavior of mesocarnivores. Both findings, suggest that plantations in our study may function as a valuable source of food for native carnivores. Variation in prey abundance was also affected by seasonality, indicating that in the absence of habitat perturbations (e.g., forestry), prey selection by mesocarnivores may be also affected by natural fluctuations in some small mammals (Murua et al., 1986; Meserve et al., 1991; Meserve et al., 1999).

Prey selection by mesocarnivores for some small mammals was also significantly influenced by the habitat in which they forage, and did not result in changes related to prey availability (measured as numerical abundance). These results provide strong support for habitat-dependent prey selection patterns of carnivores, suggesting that differences in prey selection emerge not only from different prey abundances between habitats. Despite not being quantified in this study, prey selection could also respond to the species-specific abilities of mesocarnivores to search, pursue and capture prey under different habitat conditions (Gorini et al., 2012).

4.1. Habitat-variation in small mammals abundance

While we observed no differences in small mammal composition, the absolute abundance of species was higher in native forest for most small mammal species, thus supporting our first prediction. Zero-inflated Poisson models supported the importance of native forests on the abundance of arboreal species, such as monito del monte and Chilean climbing mouse, whose abundances were larger in native forests than in plantations in both seasons. Previous studies suggest that these small mammal species are habitat specialists that use the understory and canopy vegetation in old and second-growth native forests (Fontúrbel and Jiménez, 2009; Fontúrbel et al., 2010). We found monito del monte and Chilean climbing mouse in exotic plantations, contrary to previous studies conducted in other landscapes of south-central Chile dominated by exotic plantations (Saavedra and Simonetti, 2005). The presence of mature plantations containing higher herbaceous-shrub cover across some grids could explain the presence of these forest-specialist species considering understory cover is recognized as an ecologically important habitat component for small mammals (Carey and Johnson, 1995; Kelt, 2000; Bellows et al., 2001; Lindenmayer and Franklin, 2002; Hayes et al., 2005; Amacher et al., 2008).

The native olivaceous field mouse and long-haired field mouse were frequently captured in both habitats; with abundances that were equal to, or higher, in exotic plantations than in native forests. This is consistent with previous studies conducted in Temperate Forest, which show that both species exhibit low habitat specificity (Saavedra and Simonetti, 2005; García et al., 2013), have a broad diet (Pearson, 1983; Muñoz-Predreros et al., 1990), and are associated with abundant herbaceous and shrub understory cover in exotic plantations (Muñoz-Predreros et al., 1990; Hanski et al., 2001; see also Lantschner et al., 2011). Long-tailed colilargo was more abundant in native forest than plantations, and these differences were even more important in autumn than spring. Long-tailed colilargo shows strong intra-annual cycles in response to seasonal primary productivity of temperate forests, disappearing entirely during summer (Murua et al., 1986). As documented by Meserve et al. (1999), colilargo have even been found to irrupt from a few individuals (<0.1 per ha) in Austral spring to ca. 10–20/ha in Austral winter. Given the response of native small mammals to plantations, as well

as the presence of understory vegetation in the studied exotic plantations, it is possible that small mammal assemblages in this landscape can tolerate disturbances caused by forestry land-use. This supports the idea that commercial plantations containing ground structures similar to that found in native forest, like shrubs, do fulfill at least partial habitat requirements for these species inhabiting NMR, mitigating the negative impacts on native species (Lindenmayer et al., 2006).

Black rats were similarly abundant in native forest and plantations during autumn, but during spring, their abundance was slightly higher in native forest. The habitat generalist behavior of this introduced species makes black rat an alternative prey for native mesocarnivores inhabiting landscapes dominated by plantations.

4.2. Mesocarnivore prey use and selection

Our results provide support that mesocarnivores occurring in our study area use exotic plantations as feeding grounds. Also, carnivore species did not show strict diet specialization on, and instead consumed almost all species recorded by small mammal trapping. However, we found mesocarnivores frequently preyed on the three most abundant small mammals (long-tailed colilargo, long-haired field mouse and olivaceous field mouse). Even for kodkod cat, which showed a slightly prey specialization for arboreal species in native forests, these most abundant prey became important alternative prey in plantations. These findings agree with diet patterns found in studies conducted in temperate forests and Mediterranean shrubland for these mesocarnivores (e.g., Iriarte et al., 1989; Jiménez et al., 1990; Roa and Correa, 2005; Sade et al., 2012), and imply that studied carnivores may display flexible hunting behavior when occurring in native forest and exotic plantation.

Mesocarnivores, however, differed in their prey selection behavior and modified their prey selection patterns between habitats, supporting habitat-dependent changes in prey selection. Studied carnivores intensified or weakened, their selection of some small mammal species between native forests and plantations, and these changes did not always reflect changes in prey abundance. For example, the kodkod cat consumed monito del monte and Chilean climbing mouse more than their availability in native forest, even when other ground small mammals (e.g., long-tailed colilargo) were largely more abundant in native forest. This reflected the specialization of kodkod on these small mammal species in this habitat compared with exotic plantations. Kodkod cat may be naturally good at climbing trees (Sanderson et al., 2002), which would make them more successful when hunting prey that move within overstory or large-trees (e.g. Altamirano et al., 2013). Therefore, the simplification of arboreal-vegetation structure arising from the replacement of native forests by exotic plantations could negatively impact kodkod cat by reducing the abundance of their preferred prey (e.g., arboreal small mammals) as well as reducing their effectiveness for capturing prey using arboreal strata. Thus, facilitating the development of undergrowth vegetation may turn forestry stands into secondary habitats for this carnivore as previously documented (Simonetti et al., 2013). Darwin's fox selected long-tailed colilargo independently from habitat type, whereas culpeo foxes showed strong prey selection for this small mammal species in exotic plantations only. The consistent selection of Darwin's fox on long-tailed colilargo in both habitats suggests the importance of this native rodent in the diet of this mesocarnivore, and the efficiency of Darwin's fox at capturing colilargo throughout. On the contrary, the lack of a positive association between colilargo's abundance and culpeo fox selection for this small mammal may be influenced by the ability of this carnivore to cope with anti-predatory behaviors, such as escape responses, reduced mobility or refuge use by prey (Simonetti, 1989; Norrdahl and Korpimäki, 1998).

Biological and environmental factors such as hunting behavior and spatial heterogeneity can influence prey catchability and accessibility are therefore can control the "realized availability" of prey (Balme et al., 2007; Gorini et al., 2012). Although our analyses did not account for the effect of these factors, we suggest that kodkod selection for Chilean climbing mouse and monito del monte, even when long-tailed colilargo were extremely abundant during autumn, supports the forest-specialist hunting behavior of this felid. Likewise, the flexibility of culpeo fox prey selection in different habitat conditions is consistent with the fact that culpeo foxes consume prey that are not only abundant (e.g., long-haired field mouse, olivaceus field mouse and long-tailed colilargo), but also that are easier to search and capture due to low vegetation cover frecuently found in young and medium-age plantations that increases prey vulnerability (Saavedra and Simonetti, 2005; Balme et al., 2007; Andruskiw et al., 2008; Keim et al., 2011; Gorini et al., 2012). Similarly, culpeo fox and kodkod selected black rats in exotic plantations even when black rat abundance was lower compared to native forest, indicating that the carnivores' ability to capture black rats did not decrease when exotic plantations replaced native forest. Although black rats could compete and sometimes extirpate native rodents (Stokes et al., 2009), they are up to four fold the body mass of native rodents, and hence rats could become an important source of biomass in exotic plantations for carnivores (Muñoz-Pedreros and Yañez, 2009).

A potential confounding factor emerging from this study is that the scats could have contained prey captured from outside our study boundaries. Home ranges of mesocarnivores such as kodkod and chilla fox living in disturbed landscapes of southern Chile range from 180–230 ha, with maximum movement distance varying between 2.4 and 3.7 km (Sanderson et al., 2002; Silva-Rodríguez et al., 2010). These home range sizes, as well as high carnivore activity recorded in our study sites during camera-trap surveys (Moreira-Arce et al., 2015), indicated that individuals mostly remained within the boundaries of our study area.

5. Concluding remarks

Plantations, often regarded as "biological deserts" might be feeding grounds for mesocarnivores as depicted by our results. Plantations with well developed understory vegetation sustain small mammal populations, that although in lower abundance than native habitats, are preyed upon by carnivores thriving in plantations. Therefore, if understory is enhanced in these human-created habitats, plantations might become alternative habitats for carnivores, reducing the negative impacts that plantations have had upon native biota when native forests are replaced.

In fact, the replacement of native forest by exotic plantations affects the abundance of small mammals as well as carnivores' prey selection. Reduced abundance of selected prey species resulting from habitat transformation may negatively affect carnivore populations with narrow diet and habitat requirements.

Appendix A

Table A1. Best supported Bayesian Zero-inflated Poisson models used to predict the abundance of small mammal prey species in the study area. Covariates including in the Logistic and Count model are shown separately. The number of fixed-effects in the model (K), Deviance's Information Criterion (DIC), DIC difference with the lowest DIC model (ΔDIC) and model weights (ω) are shown. Null refers to models without covariates.

Species	Logistic model	Count model	k	DIC	ΔDIC	ω
Long-haired field mouse (LH)	Season + Habitat	Season + Habitat	4	238.63	0.00	0.25
	Season + Habitat	Season × Habitat	4	238.82	0.19	0.22
	Season + Habitat	Null	2	239.19	0.56	0.19
Monito del Monte (Mm)	Season + Habitat	Season + Habitat	3	53.89	0.00	0.44
Olivaceous field mouse (OF)	Season + Habitat	Season + Habitat	4	189.28	0.00	0.37
	Season	Season + Season × Habitat	2	190.61	1.33	0.19
	Season + Habitat	Season + Habitat + Season × Habitat	5	191.01	1.73	0.15
Long-tailed colilargo (LT)	Null	Season + Season × Habitat	2	212.31	0.00	0.21
	Season	Season + Season × Habitat	3	212.49	0.18	0.19
	Null	Season + Habitat + Season × Habitat	3	212.99	0.68	0.15
	Season	Season + Habitat + Season × Habitat	3	213.45	1.14	0.12
	Season + Habitat	Season + Season × Habitat	4	213.61	1.30	0.11
Darwin's leaf-eared mouse (DL)	Null	Season + Season × Habitat	2	81.10	0.00	0.53
	Season + Habitat	Null	2	84.17	3.08	0.11
Black rat (BR)	Null	Season + Season × Habitat	2	74.85	0	0.14
	Null	Habitat + Season × Habitat	3	75.11	0.26	0.13
	Season	Season + Season × Habitat	3	75.11	0.26	0.13
	Season + Habitat	Null	2	75.23	0.38	0.12
	Season + Habitat	Season + Season × Habitat	4	75.32	0.47	0.11
	Season + Habitat	Season × Habitat	3	76.25	1.4	0.07
	Null	Null	1	76.33	1.48	0.07
Chilean climbing mouse (CC)	Season + Habitat	Habitat	3	53.89	0.00	0.37
	Season + Habitat	Season × Habitat	2	54.68	0.78	0.25
	Season + Habitat	Null	2	55.73	1.84	0.15

References

Acosta-Jamett, G., Simonetti, J.A., 2004. Habitat use by *Oncifelis guigna* and *Pseudalopex culpaeus* in a fragmented forest landscape in central Chile. Biodivers. Conserv. 13, 1135–1151.

Aebischer, N., Robertson, P., Kenward, P., 1993. Compositional analysis of habitat use from animal radio-tracking data. Ecology 74 (5), 1313–1325.

Aguayo, M., Pauchard, A., Azócar, G., Parra, O., 2009. Cambio del uso del suelo en el Centro Sur de Chile a fines del siglo XX: entendiendo la dinámica espacial y temporal del paisaje. Rev. Chil. Hist. Nat. 82 (3), 361–374. http://dx.doi.org/10.4067/S0716-078X2009000300004.

Altamirano, T.A., Hernández, F., De La Maza, M., Bonacic, C., 2013. Güiña (*Leopardus guigna*) preys on cavity-nesting nestlings. Rev. Chil. Hist. Nat. 86 (4), 501–504.

Amacher, A.J., Barrett, R.H., Moghaddas, J.J., Stephens, S.L., 2008. Preliminary effects of fire and mechanical fuel treatments on the abundance of small mammals in the mixed-conifer forest of the Sierra Nevada. For. Ecol. Manag. 255 (8), 3193–3202.

Andruskiw, M., Fryxell, J.M., Thompson, I.D., Baker, J.A., 2008. Habitat-mediated variation in predation risk by the American marten. Ecology 89, 2273–2280.

Balme, G., Hunter, L., Slotow, R., 2007. Feeding habitat selection by hunting leopards *Panthera pardus* in a woodland savanna: prey catchability versus abundance. Anim. Behav. 74 (3), 589–598. http://dx.doi.org/10.1016/j.anbehav.2006.12.014.

Bellows, A.S., Pagels, J.F., Mitchell, J.C., 2001. Macrohabitat and microhabitat affinities of small mammals in a fragmented landscape on the upper coastal plain of Virginia. Am. Midl. Nat. 146 (2), 345–360.

Brockerhoff, E., Jactel, H., Parrotta, J., Quine, C., Sayer, J., 2008. Plantation forests and biodiversity: oxymoron or opportunity? Biodivers. Conserv. 17, 925–951.

Byrom, A.E., Craft, M.E., Durant, S.M., Nkwabi, A.J.K., Metzger, K., Hampson, K., Mduma, S.A.R., Forrester, G.J., Ruscoe, W.A., Reed, D.N., Bukombe, J., Mchetto, J., Sinclair, A.R.E., 2014. Episodic outbreaks of small mammals influence predator community dynamics in an east African savanna ecosystem. Oikos 123, 1014–1024. http://dx.doi.org/10.1111/oik.00962.

Carey, A.B., Johnson, M.L., 1995. Small mammals in managed, naturally young, and old-growth forests. Ecol. Appl. 5 (2), 336–352.

Cerda, Y., Grez, A.A., Simonetti, J.A., 2015. The role of understory on the abundance, movement and survival of *Ceroglossus chilensis* in pine plantations: an experimental test. J. Insect Conserv. 19, 119–127.

Charnov, E.L., 1976. Optimal foraging, the marginal value theorem. Theor. Popul. Biol. 9 (2), 129–136.

Chesson, J., 1983. The estimation and analysis of preference and its relationship to foraging models. Ecology 64 (5), 1297–1304.

Coelho, M., Juen, L., Mendes-Oliveira, A.C., 2014. The role of remnants of Amazon savanna for the conservation of Neotropical mammal communities in eucalyptus plantations. Biodivers. Conserv. 23 (13), 3171–3184.

CONAF, 2011. Catastro de los recursos vegetacionales nativos de Chile. Monitoreo de cambios y actualizaciones Período 1997–2011. Santiago, Chile.

Dell'Arte, G.L., Laaksonen, T., Norrdahl, K., Korpimäki, E., 2007. Variation in the diet composition of a generalist predator, the red fox, in relation to season and density of main prey. Acta Oecol. 31 (3), 276–281.

Di Bitetti, M.S., Paviolo, A., De Angelo, C., 2006. Density, habitat use and activity patterns of ocelots (*Leopardus pardalis*) in the Atlantic forest of Misiones, Argentina. J. Zool. 270 (1), 153–163.

Dupuy, G., Giraudoux, P., Delattre, P., 2009. Numerical and dietary responses of a predator community in a temperate zone of Europe. Ecography 32 (2), 277–290. http://dx.doi.org/10.1111/j.1600-0587.2008.04930.x.

Emlen, J.M., 1966. The role of time and energy in food preference. Am. Nat. 611–617.

Escobar, M.A.H., Uribe, S.V., Chiappe, R., Estades, C.F., 2015. Effect of Clearcutting Operations on the Survival Rate of a Small Mammal. PLoS ONE 10 (3), e0118883. http://dx.doi.org/10.1371/journal.pone.0118883.

FAO (Food and Agriculture Organization of the United Nations), 2011. State of the world's forests. FAO, Rome.

Fontúrbel, F.E., Jiménez, J.E., 2009. Underestimation of abundances of the monito del Monte (*Dromiciops gliroides*) due to a sampling artifact. J. Mammal. 90 (6), 1357–1362.

Fontúrbel, F.E., Silva-Rodríguez, E.A., Cárdenas, N.H., Jiménez, J.E., 2010. Spatial ecology of monito del monte (Dromiciops gliroides) in a fragmented landscape of southern Chile. Mammalian Biology-Zeitschrift für Säugetierkunde 75 (1), 1–9.

Fontúrbel, F.E., 2012. Does habitat degradation cause changes in the composition of arboreal small mammals? A small-scale assessment in Patagonian temperate rainforest fragments. Lat. Am. J. Conserv. 3 (1).

García, K.P., Zapata, J.C.O., Aguayo, M., D'Elia, G., 2013. Assessing rodent community responses in disturbed environments of the Chilean Patagonia. Mammalia 77, 195–204. http://dx.doi.org/10.1515/mammalia-2011-0134.

Gelman, A., Carlin, J.B., Stern, H.S., Rubin, D.B., 2003. Bayesian Data Analysis. Second Edition. Chapman & Hall, Boca Raton, Florida, USA.

Gorini, L., Linnell, J.D.C., May, R., Panzacchi, M., Boitani, L., Odden, M., Nilsen, E.B., 2012. Habitat heterogeneity and mammalian predator–prey interactions. Mammal Rev. 42 (1), 55–77. http://dx.doi.org/10.1111/j.1365-2907.2011.00189.x.

Hanski, I., Henttonen, H., Korpimäki, E., Oksanen, L., Turchin, P., 2001. Small-rodent dynamics and predation. Ecology 82 (6), 1505–1520.

Hayes, J.P., Schoenholtz, S.H., Hartley, M.J., Murphy, G., Powers, R.F., Berg, D., Radosevich, S.R., 2005. Environmental consequences of intensively managed forest plantations in the Pacific northwest. J. For. 103 (2), 83–87.

Iriarte, J.A., Jiménez, J.E., Contreras, L.C., Jaksić, F.M., 1989. Small mammal availability and consumption by the fox, *Dusicyon culpaeus*, in central Chilean scrublands. J. Mammal. 70 (3), 641–645.

Jaksic, F.M., Jiménez, J.E., Castro, S.A., Feinsinger, P., 1992. Numerical and functional responses of predators to a long-term decline in mammalian prey at a semi-arid neotropical site. Oecologia 89, 90–101.

Jiménez, J.E., Marquet, P.A., Medel, R., Jaksić, F.M., 1990. Comparative ecology Darwin's fox in mainland and island settings of southern Chile. Rev. Chil. Hist. Nat. 63, 177–186.

Jiménez, J.E., Lucherini, M., Novaro, A.J., 2008. *Pseudalopex fulvipes*. The IUCN Red List of Threatened Species, e.T41586A10484712. http://dx.doi.org/10.2305/IUCN.UK.2008. RLTS.T41586A10484712.en.

Joly, D.O., Patterson, B.R., 2003. Use of selection indices to model the functional response of predators. Ecology 84 (6), 1635–1639.

Keim, J., DeWitt, P., Lele, S., 2011. Predators choose prey over prey habitats: evidence from a lynx–hare system. Ecol. Appl. 21 (4), 1011–1016.

Kelt, D.A., 2000. Small mammal communities in rainforest fragments in central southern Chile. Biol. Conserv. 92 (3), 345–358.

Klare, U., Kamler, J.F., Macdonald, D.W., 2011. A comparison and critique of different scat-analysis methods for determining carnivore diet. Mamm. Rev. 41, 294–312. http://dx. doi.org/10.1111/j.1365-2907.2011.00183.x.

Korpimaki, E., Oksanen, L., Oksanen, T., Klemola, T., Norrdahl, K., Banks, P.B., 2005. Vole cycles and predation in temperate and boreal zones of Europe. J. Animal Ecol. 74 (6), 1150–1159.

Lancia, R.A., Nichols, J.D., Pollock, K.H., 1994. Estimating the number of animals in wildlife populations. Research and Management Techniques for Wildlife and Habitats. The Wildlife Society, Bethesda, Maryland, USA, pp. 215–253.

Lantschner, M., Rusch, V., 2011. Influences of pine plantations on small mammal assemblages of the Patagonian forest-steppe ecotone. Mammalia 75, 249–255. http:// dx.doi.org/10.1515/MAMM.2011.031.

Lantschner, M., Rusch, V., Hayes, J., 2012. Habitat use by carnivores at different spatial scales in a plantation forest landscape in Patagonia, Argentina. For. Ecol. Manag. 269, 271–278. http://dx.doi.org/10.1016/j.foreco.2011.12.045.

Lindenmayer, D.B., Cunningham, R.B., Donnelly, C.F., Triggs, B.E., Belvedere, M., 1994. Factors influencing the occurrence of mammals in retained linear strips (wildlife corridors) and contiguous stands of montane ash forest in the central highlands of Victoria, southeastern Australia. For. Ecol. Manag. 67 (1), 113–133.

Lindenmayer, D.B., Franklin, J.F., 2002. Conserving Forest Biodiversity: A Comprehensive Multiscaled Approach. Island Press.

Lindenmayer, D.B., Hobbs, R.J., 2004. Fauna conservation in Australian plantation forests — a review. Biol. Conserv. 119 (2), 151–168. http://dx.doi.org/10.1016/j.biocon.2003.10. 028.

Lindenmayer, D.B., Franklin, J.F., Fischer, J., 2006. General management principles and a checklist of strategies to guide forest biodiversity conservation. Biol. Conserv. 131 (3), 433–445.

Madrigal, J., Kelt, D.A., Meserve, P.L., Gutierrez, J.R., Squeo, F.A., 2011. Bottom-up control of consumers leads to top-down indirect facilitation of invasive annual herbs in semiarid Chile. Ecology 92 (2), 282–288.

Mazzolli, M., 2010. Mosaics of exotic forest plantations and native forests as habitat of pumas. Environ. Manag. 46 (2), 237–253.

Meserve, P.L., Lang, B.K., Murúa, R., Muñoz-Pedreros, A., Gonzalez, L.A., 1991. Characteristics of a terrestrial small mammal assemblage in a temperate rainforest in Chile. Rev. Chil. Hist. Nat. 64, 157–169.

Meserve, P., Martínez, D., Rau, J., Murua, R., Lang, B.K., Muñoz-Pedreros, A., 1999. Comparative demography and diversity of small mammals in precordilleran temperate rainforests of southern Chile. J. Mammal. 80 (3), 880–890.

Mills, M.G.L., Broomhall, L.S., Toit, d.J.T., 2004. Cheetah *Acinonyx jubatus* feeding ecology in the Kruger National Park and a comparison across African savanna habitats: is the cheetah only a successful hunter on open grassland plains? Wildl. Biol. 10, 177–186.

Moreira-Arce, D., Vergara, P.M., Boutin, S., 2015. Diurnal human activity and introduced species affect the occurrence of carnivores in a human-dominated landscape. PLoS ONE 10 (9), e0137854. http://dx.doi.org/10.1371/journal.pone.0137854.

Muñoz-Predreros, A., Murúa, R., Gonzalez, L., 1990. Nicho ecológico de micromamíferos en un agroecosistema forestal de Chile central. Rev. Chil. Hist. Nat. 63, 267–277.

Muñoz-Pedreros, A., 1992. Ecología del ensamble de micromamíferos en un agroecosistema forestal de Chile central: una comparación latitudinal. Rev. Chil. Hist. Nat. 65 (4), 417–428.

Muñoz-Pedreros, A, Yañez, J.V. (Eds.), 2009. Mamíferos de Chile. CEA Ediciones 565p.

Murdoch, W.W., 1969. Switching in general predators: experiments on predator specificity and stability of prey populations. Ecol. Monogr. 39, 335–354.

Murua, R., González, L.A., Meserve, P.L., 1986. Population ecology of *Oryzomys longicaudatus philippii* (Rodentia: Cricetidae) in southern Chile. J. Anim. Ecol. 5 (1), 281–293.

Napolitano, C., Gálvez, N., Bennett, M., Acosta-Jamett, G., Sanderson, J., 2015. *Leopardus guigna*. The IUCN Red List of Threatened Species 2015, e.T15311A50657245. http:// dx.doi.org/10.2305/IUCN.UK.2015-2.RLTS.T15311A50657245.en.

Norrdahl, K., Korpimäki, E., 1998. Does mobility or sex of voles affect risk of predation by mammalian predators? Ecology 79 (1), 226–232.

Pearson, O., 1983. Characteristics of mammalian fauna from forests in Patagonia, Southern Argentina. J. Mammal. 64, 476–492.

Pearson, O.P., 1995. Annotated keys for identifying small mammals living in or near Nahuel Huapi National Park or Lanín National Park, southern Argentina. Mastozoología Neotropical 2 (2), 99–148.

Pita, R., Mira, A., Moreira, F., Morgado, R., Beja, P., 2009. Influence of landscape characteristics on carnivore diversity and abundance in Mediterranean farmland. Agric. Ecosyst. Environ. 132 (1), 57–65.

Poch, T., Simonetti, J.A., 2013. Insectivory in *Pinus radiata* plantations with different degree of structural complexity. For. Ecol. Manag. 304, 132–136.

Previtali, M.A., Lima, M., Meserve, P.L., Kelt, D.A., Gutiérrez, J.R., 2009. Population dynamics of two sympatric rodents in a variable environment: rainfall, resource availability and predation. Ecology 90, 1996–2006.

Prugh, L.R., 2005. Coyote prey selection and community stability during a decline in food supply. Oikos 110 (2), 253–264.

Reise, D., 1973. Clave para la determinación de los cráneos de marsupiales y roedores chilenos. Gayana Zoología 27, 1–20.

Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., et al., 2014. Status and ecological effects of the world's largest carnivores. Science 343 (6167), 1241484.

Roa, P., Correa, A., 2005. Relaciones tróficas entre *Oncifelis guigna*, *Lycalopex culpaeus*, *Lycalopex griseus* y *Tyto alba* en un ambiente fragmentado de la zona central de Chile. J. Neotrop. Mammal. 12 (1), 57–60.

Robitaille, J.F., Linley, R.D., 2006. Structure of forests used by small mammals in the industrially damaged landscape of Sudbury, Ontario, Canada. For. Ecol. Manag. 225 (1), 160–167.

Saavedra, B., Simonetti, J.A., 2005. Small mammals of Maulino forest remnants, a vanishing ecosystem of south-central Chile. Mammalia 69 (3–4), 337–348.

Sade, S., Rau, J.R., Orellana, J.I., 2012. Diet of the lesser grison (*Galictis cuja* Molina 1782) in a Valdivian fragmented forest remnant in southern Chile. Gayana 76 (2), 112–116.

Sanderson, J., Sunquist, M.E., Iriarte, J.A., 2002. Natural history and landscape-use of guignas (*Oncifelis guigna*) on Isla Grande de Chiloé, Chile. J. Mammal. 83, 608–613.

Silva-Rodríguez, E.A., Ortega-Solís, G.R., Jiménez, J.E., 2010. Conservation and ecological implications of the use of space by chilla foxes and free-ranging dogs in a human-dominated landscape in southern Chile. Austral Ecol. 35, 765–777. http://dx.doi.org/ 10.1111/j.1442-9993.2009.02083.x.

Simonetti, J.A., 1989. Microhabitat use by small mammals in central Chile. Oikos 56 (3), 309–318.

Simonetti, J.A., Grez, A.A., Estades, C.F. (Eds.), 2012. Biodiversity Conservation in Agroforestry Landscapes: Challenge and Opportunities. Editorial Universitaria, Santiago,Chile 162p.

Simonetti, J.A., Grez, A.A., Estades, C.F., 2013. Providing habitat for native mammals through understory enhancement in forestry plantations. Conserv. Biol. 27, 1117–1121. http://dx.doi.org/10.1111/cobi.12129.

Smith-Ramírez, C., 2004. The Chilean coastal range: a vanishing center of biodiversity and endemism in South American temperate rainforests. Biodivers. Conserv. 13 (2), 373–393.

Spiegelhalter, D., Thomas, A., Best, N., Lunn, D., 2003. WinBUGS user manual. Version 1.4, MRC. Biostatistics Unit. Institute of Public Health and Department of Epidemiology and Public Health. Imperial College School of medicine, UK available at http://mrc-bsu.cam.ac.uk/bugs.

Stokes, V.L., Banks, P.B., Pech, R.P., Spratt, D.M., 2009. Competition in an invaded rodent community reveals black rats as a threat to native bush rats in littoral rainforest of south-eastern Australia. J. Appl. Ecol. 46 (6), 1239–1247.

Thompson, C., Gese, E., 2007. Food webs and intraguild predation: community interactions of a native mesocarnivores. Ecology 88 (2), 334–346.

Young, H.S., McCauley, D.J., Dirzo, R., Goheen, J.R., Agwanda, B., Brook, C., et al., 2015. Context-dependent effects of large-wildlife declines on small-mammal communities in central Kenya. Ecol. Appl. 25 (2), 348–360.

Zuur A., Ieno E.N., Walker N.J., Saveliev A.A., Smith G.M., 2009. Zero-truncated and zero-inflated models for count data. Pp: 261–293 in. Mixed effects models and extensions in ecology with R (Zuur, A., E.N. Ieno, N.J. Walker, A.A. Saveliev, and G.M. Smith, eds). Statistics for Biology and Health, Springer.