



## Mesocarnivores respond to fine-grain habitat structure in a mosaic landscape comprised by commercial forest plantations in southern Chile



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### ABSTRACT

Understanding how species respond to habitat structure in landscapes transformed by human activities is crucial to design management strategies that promote the conservation of wildlife in human-created lands. The aim of this study was to test the ecological hypothesis that fine-grain habitat structure may be an important determinant of habitat use of medium-size predators across transformed landscapes when comparing with coarse habitat classification. We assess habitat use of species by using occupancy modeling framework accounting for imperfect detection, and obtained three LiDAR-derived vegetation metrics at different scale to describe the fine-grain habitat structure in a landscape comprised by native forest and exotic tree plantations in central-south Chile. Four species were detected: *Lycalopex culpaeus*, *L. griseus*, *L. fulvipes* and *Leopardus guigna*. *L. culpaeus* and *L. griseus* largely occurred throughout the study area ( $\psi = 0.54 \pm 0.08$  and  $0.18 \pm 0.04$ ). Coefficients of the better-ranked models based on AIC indicated a positive relation between understory cover at 250 m scale and the habitat use of *L. fulvipes*, *L. guigna* and *L. griseus*, while a negative relation with the habitat use of *L. culpaeus*. On the other hand, habitat use of *L. fulvipes* and *L. guigna* increased as structural diversity of forest increased while the habitat use of *L. culpaeus* and *L. griseus* decreased. Low support was found for the habitat use of *L. guigna* and *L. culpaeus* being affected by habitat type (plantation or native forest). Our results showed that habitat use of these mesocarnivores responded to fine-grain habitat structure attributes as derived from LiDAR, but only some of them responded weakly to habitat type. Both results indicate that understory structure, and not a coarse classification of habitat type, may be better determinants for explaining the habitat use of native carnivores in this landscape comprised by native habitat and forest plantations. Our results can be extended to sustainable management of forest plantations for carnivore conservation by enhancing the vegetation structure of native shrub species within these production-oriented lands.

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### 1. Introduction

Effective habitat management of threatened species living in human-modified landscapes requires accurate evaluation of species–habitat relationships at different spatial scales (Guisan and Thuiller, 2005; Margules and Pressey, 2000). Understanding species–habitat relationships is crucial in landscapes dominated by

production-oriented lands such as forest plantations and agricultural lands, where the identification of quality habitat will be critical to ensure the population viability of species (Daily et al., 2001; Fischer and Lindenmayer, 2007).

Reliable assessment of species–habitat relationships depends not only on providing unbiased estimates of presence/absence of target species (MacKenzie et al., 2002; Mackenzie and Royle, 2005), but also on how appropriately habitat is quantified (Morrison et al., 2012). For instance, some particular habitat elements such as shrub cover have been described as valuable for medium-size carnivores, because of its role in providing cover that

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facilitates predatory success, shelter and food resources (Lozano et al., 2003; Mangas et al., 2007). However, in large-scale evaluations, the description of habitat structure may be obscured by spatial constraints arising from field sampling methods and coarse-grain approaches. Field observations usually provide only a partial estimation of relevant habitat attributes (e.g., vegetation height or cover), which may limit the understanding of habitat requirement species with large home ranges such as terrestrial carnivores.

Recently, high-resolution remote sensing imagery has improved our ability to characterize habitat heterogeneity over larger spatial extents than can be accomplished in the field, allowing for detailed characterization of habitat structure (Mason et al., 2003). Remote sensing Light Detection and Ranging (LiDAR) offers a cost-effective method to obtain high-resolution environmental information on forest structure including understory vegetation density, canopy height profiles, canopy cover, and biomass (Hernández et al., 2013; Hyde et al., 2006; Vierling et al., 2008). LiDAR uses a laser that emits a light from a source and it is reflected back to a sensor as it intercepts objects in its path (Dubayah and Drake, 2000; Lefsky et al., 2002). The reflected light is detected by the sensor and is digitized, creating a record of returns that are a function of the distance between the sensor and the intercepted object. Thus, since studies linking wildlife to habitat structure at fine resolution are still scarce across in landscapes, LiDAR-derived data would become a new avenue to perform such task (Lefsky et al., 2002; Mason et al., 2003; Vierling et al., 2008) as supported by recent research (e.g., Goetz et al., 2007; Müller and Brandl, 2009; see Vierling et al., 2008 for a review).

Terrestrial carnivores living in central-south Chile have been exposed to human pressure over the last century from the accelerated replacement of native forest by exotic forest plantations (Aguayo et al., 2009; Echeverría et al., 2006). Although the perception of exotic plantations as “biological deserts” has been widely accepted among ecologists, exotic plantations harboring a complex habitat structure may act as habitat for species whose native habitats have experienced accelerated declines (Brockerhoff et al., 2008; Carnus et al., 2003). Therefore, understanding how native carnivores respond to fine-grain habitat structure, particularly within non-native land covers such as commercial exotic plantations, may help wildlife managers to elucidate whether these human-created lands act as complementary habitats for these species (Puettmann et al., 2008; Simonetti et al., 2013). Nonetheless, there is still a lack of knowledge on the habitat use of Chilean carnivores in mosaic landscapes comprising commercial plantations (e.g., Acosta-Jamett and Simonetti, 2004; Moreira-Arce et al., 2015a; Zuñiga et al., 2009), which obstructs the progress of a sustainable management of these production-oriented lands. For instance, in mosaic landscapes central Chile, the habitat use of kodkod (*Leopardus guina*) has been largely associated with vegetation cover <1.5 m height (Acosta-Jamett and Simonetti, 2004). This suggests that exotic plantations containing dense understory cover may favor the movement of this native wild cat through mosaic landscapes (Acosta-Jamett et al., 2003). More recently, Moreira-Arce et al. (2015a) documented carnivores positively responding to native forest availability and patch size at different spatial scales. Considering that exotic plantations currently cover almost 17% of forested areas in Chile (CONAF, 2011), the conservation of species with large area requirements such as carnivores in these production-oriented lands, requires the understanding of their responses to fine-grain habitat features. This valuable information can then be used by wildlife managers to identify suitable areas for carnivores across large areas from a detailed, accurate, and unbiased habitat assessment (Marques et al., 2014). In this sense, LiDAR offers detailed information about the structure of vegetation in

native forests and exotic plantations with different age and management prescriptions (Hernández et al., 2013), thus improving habitat structure description within these land types. Detailed knowledge of ecological requirements and optimal habitat features is lacking in most temperate forests for these medium-size predators, especially in landscapes dominated by commercial forest plantations (e.g., Acosta-Jamett and Simonetti, 2004; Moreira-Arce et al., 2015a; Zuñiga et al., 2009).

In this study, we analyzed the importance of some habitat characteristics in the habitat use patterns of four mesocarnivores as an attempt to test the role of fine-grain habitat attributes in the conservation of mesocarnivores within landscapes containing native forest and exotic forest plantations in southern Chile. We combined occupancy models and LiDAR-derived vegetation metrics to test the ecological hypothesis that fine-grain habitat structure may be an important determinant of habitat use of medium-size predators across the landscape when compared to coarse-grain habitat classification.

## 2. Methods

### 2.1. Study area

The study area encompassed the Caramávida basin, a privately-owned of nearly 23,800 ha located in the central Nahuelbuta Mountain Range (37° 45'S, 73° 00'W), of southern Chile. Topography within this region is rugged, with numerous ravines and ridges. The landscape of Caramávida consists of a mosaic of native forest habitats and commercial exotic plantations of Monterrey pine (*Pinus radiata*) and various eucalyptus species (*Eucalyptus* spp.), as well as open agricultural lands. Remnant native forest comprises a distinctive and relatively homogeneous association of native tree species. At the highest elevations, native forest comprises a mixed association between monkey-puzzle trees (*Araucaria araucana*), coigüe trees (*Nothofagus dombeyi*), and Antarctic beech (*Nothofagus antarctica*). At medium and high elevations a deciduous forest is dominated by roble (*Nothofagus obliqua*), whereas, at lower elevations, native forest is composed of secondary mixed broad-leaved evergreen tree species, including *Drimys winteri*, *Aextoxicon punctatum*, and *Laureliopsis philippiana* remains dominant (Wolodarsky-Franke and Herrera, 2011).

### 2.2. Carnivore surveys

We used camera-trapping to assess carnivore presence/absence across Caramávida during Austral spring and summer seasons (from October 2011 to February 2012). Previous evidence showed increased activity of species during these seasons compared to the fall and winter (Jiménez et al., unpublished data). Moreover, both spring and summer are considered critical for replenishing energetic demands and for reproduction, increasing their movement rates and therefore their probability of being recorded (Burton et al., 2015; Jakić et al., 1990; Jiménez et al., 1990; Muñoz-Pedrerós et al., 1995). We sampled carnivore presence/absence across 85 stations containing lure (fox and lynx urine) and a passive infrared-triggered camera each (Reconyx PC900 Holmen, Wisconsin and Bushnell Trophy Camera, Bushnell Corporation, Overland Park, Kansas, USA) mounted on trees ca. 50–60 cm above the ground. Cameras were set to take three photos per trigger and were revised at the end of the active period (30 days), with no lure replacement during this period. A stratified random design (considering native forest and exotic plantations) was used to place cameras throughout the study area at a minimum distance of ca 500 m and maximum distance of ca 1630 m between stations (average distance 870 m). A total of 31 and 54 stations were placed in plantations and native forest, respectively.

### 2.3. Species detection at increasing sampling effort

Prior to habitat use analyses, we used the cumulative camera-trapping days to determine if the camera survey period was sufficiently long to detect the mesocarnivores of interest. Sample effort and detection events were included in an accumulation curve and randomized 1000 times to derive 95% confidence intervals around the mean. We also calculated the latency period (LP) for each species as the average number of camera days needed to obtain the first detection using cameras with captures only. We related LPs to species' home range data (log transformed) obtained from Johnson and Franklin (1994), Jiménez (2007) and Sanderson et al. (2002). Even though cumulative camera-trapping days and LP approaches ignore imperfect detection of individual species, they become a baseline for future monitoring and provide useful information for comparison with other studies and techniques (Silveira et al., 2003).

### 2.4. Modeling habitat use with LiDAR covariates

We used occupancy modeling framework accounting for imperfect detection (*sensu* MacKenzie et al., 2002) to assess the habitat use of mesocarnivores during the study period. Given that our 'sites' were point locations of camera traps, we modeled occupancy probability ( $\psi$ ) as the probability of site use conditional on site occupancy (i.e., prob[used|occupied]) rather than true occupancy (i.e., prob[occupied]). Detection probability ( $p$ ) was modeled as the probability of detecting a species given that the site is used during each sampled occasion (i.e., prob[detected|used]). We assumed that the probability of a site being used by a carnivore varied across space as a response of vegetation structure on each site. Therefore, we included the following three vegetation attributes derived from LiDAR:

- (1) We considered *understory cover* (Und), as native dense shrub may provide refuge for carnivores from human activity and introduced species such as free-ranging dogs (*Canis familiaris*) (Acosta-Jamett and Simonetti, 2004), especially in forest plantations (Simonetti et al., 2013). Understory cover was obtained by calculating the vegetation density at a camera-trap scale (50 m radius) and within 250 m-radius buffer around each camera trap, considering the vertical stratum between 0–1.5 m as follows:

$$\text{Und} = \frac{\sum x_{\text{int veget}}}{\sum x_{\text{total}}}$$

where  $\sum x_{\text{int veget}}$  corresponds to the total pulses intercepted by vegetation and  $\sum x_{\text{total}}$  to the total amount of pulses in the determined height range (0–1.5 m).

- (2) *Complexity of habitat structure* was included as complex vegetation structure provides suitable microhabitat conditions for prey, representing better foraging conditions for mesocarnivores (e.g., Fuller et al., 2007; Lantschner et al., 2011), particularly in forest plantations (Moreira-Arce et al., 2015b). Complexity of habitat structure was expressed as a structural diversity index (SDI) that incorporated vertical and horizontal variation in vegetation (van Ewijk et al., 2011):

$$\text{SDI} = \left( -\sum_{i=1}^{HB} [(p_i * \ln(p_i))] \right) / \ln(HB)$$

where  $HB$  represents the total number of pulses for the total height classes and  $p_i$  is the proportion of pulses in the container at a given height  $i$ . The SDI index was calculated at

camera-trap station scale (within a 50 m radius of the camera site).

- (3) *Canopy height* was calculated as the max and modal canopy heights (Canopy height [MAX] and Canopy height [MOD], respectively) within a 250 m-radius of the camera site by using a moving window tool implemented in ArcGIS 10.1.

We also included the coarse classification of habitat type (native forest or exotic plantation), as well as the interaction between habitat type and understory cover. We included elevation as an additional covariate because of the possible altitudinal gradients in native prey abundance and human presence (Patterson et al., 1989). Non-categorical covariates were standardized (e.g.,  $\text{elev}_t = \text{elev}/1000$ ) and if strong collinearity was detected ( $|r| \geq 0.65$ ), they were not included in the same model. We modeled detection probability as a function of LiDAR covariates (understory cover within 250 m-radius buffer and complexity of habitat structure). We also included vegetation density measured within detection of each camera trap, which was considered as being proportional to the degree of blockage of it (Burton et al., 2015). Vegetation density was obtained by using the checkerboard-type method in front of each camera trap (modified from Nudds, 1977).

### 2.5. Species model fitting

We fitted single-season, single-species occupancy models (*sensu* MacKenzie et al., 2002) to model site use accounting by detection probabilities at camera stations for each mesocarnivore species. Records of the same species taken during a 24hr period were considered as the same detection event to avoid false counts emerging from temporal dependence. With these records, we constructed the detection history for each camera station by dividing the sampled 30 trap-days per camera into six survey periods comprised of five days each. We considered this survey period as short enough to prevent violation of site closure assumption when using occupancy models for some described species (e.g., Darwin's fox; Jiménez, 2007, but see Rota et al., 2009). We used a model selection approach and corrected Akaike Information Criterion for small sample sizes (AICc) to rank and weight candidate models. Model selection was conducted by fitting a model that best explained detection probability including LiDAR covariates and vegetation density. Then, the best detection model was used to select the model that better explained the probability of site use (as derived from occupancy probability; MacKenzie, 2006). We determined the level of support of each predictor variable by summing the Akaike weights ( $\omega$ ) across all models that contained the variable of interest ( $\omega^+$ ) (Burnham et al., 2010). We evaluated goodness of fit on the competing models by calculating a Pearson chi-square statistic and implemented a parametric bootstrapping to determine if the statistic was significantly large (MacKenzie and Bailey, 2004). Occupancy analysis was performed using the package 'unmarked' in R (Fiske and Chandler, 2011). The relative importance of the model parameters were calculated with the R package 'AICmodavg' (Mazerolle, 2012).

### 2.6. Model testing and validation

For each species, we tested the assumption of spatial independence of the residuals on the best-ranked occupancy probability model using Moran's I correlograms (Fortin and Dale, 2005) implemented in SAM4.0 (Rangel et al., 2010). In addition, we evaluated the accuracy of the final model for each carnivore species by calculating the area under the receiver operating characteristic (ROC) curve. The area under ROC curve indicates overall ability of the model to accurately predict the data used to create it (Fielding and Bell, 1997; Pearce and Ferrier, 2000). Values of this index range

from 0.5 (i.e., no better than a null model) to 1.0 (i.e., perfect accuracy). Web-based ROC analysis software (Eng, 2005) was used to generate ROC curves and to calculate area under ROC curve values for each carnivore.

### 3. Results

#### 3.1. Carnivore community

Camera traps recorded the four mesocarnivores over ca. 890 camera-days. Other larger native carnivores such as cougar (*Puma concolor*), and smaller carnivores as lesser grison (*Galictis cuja*) and Molina's Hog-Nosed Skunk (*Conepatus chinga*), as well as the domestic dog were also recorded. Latency to first detection did not differ among carnivores (ANOVA;  $F$ -value = 0.41,  $p$ -value = 0.83; Table 1), neither was positively correlated with species home range size ( $r_{\text{pearson}} = 0.65$ ;  $p = 0.11$ ). Culpeo fox and chilla fox were the most and the least recorded carnivores on 82 and 30 different surveys occasions, respectively ( $\psi_{\text{naive}} = 0.41$  and 0.15 for culpeo fox and chilla fox, respectively, Table 1).

#### 3.2. Carnivore site use probabilities and model fitting

Culpeo fox largely occurred across the study area, exhibiting the highest overall occupancy estimate ( $\psi_{\text{overall}} = 0.54 \pm 0.08$ ; Table 2), whereas chilla fox rarely occurred in the study area exhibiting the lowest overall occupancy estimate ( $\psi_{\text{overall}} = 0.18 \pm 0.04$ ; Table 2). Darwin's fox exhibited the highest overall detection probability ( $p_{\text{overall}} = 0.5 \pm 0.05$ ), while culpeo fox showed the lowest overall detection probability ( $p_{\text{overall}} = 0.24 \pm 0.03$ ; Table 2).

Models including LiDAR covariates were included in the top-ranked models ( $\Delta\text{AIC} < 3$ ) for all species, with the exception of kodkod, for which the null model was also supported (Table 2). However, the effects of LiDAR covariates (i.e., model coefficients) and model goodness-of-fit were different among species (Table 2). Likewise, there was support for the fact that carnivores were less likely to be detected as vegetation cover in front of cameras increased (Table 2).

Coefficients of the best-supported occupancy models strongly indicated: (i) understory cover at 250 m scale increased the site use probability of Darwin's fox ( $\omega^+ = 0.87$ ); (ii) elevation increased site use probability of chilla fox ( $\omega^+ = 1$ ); and (iii) kodkod site use probability increased as structural diversity of habitat increased ( $\omega^+ = 0.54$ ). On the other hand, coefficients showed moderate evidence for: (i) site use probability of culpeo fox decreased as understory cover at 250 m and elevation increased ( $\omega^+ = 0.33$  and 0.31, respectively); (ii) site use probability of Darwin's fox increased as structural diversity of habitat increased ( $\omega^+ = 0.31$ ); and (iii) site

use probability of kodkod increased ( $\omega^+ = 0.30$ ), while site use probability of chilla fox decreased ( $\omega^+ = 0.35$ ) as canopy height increased. Finally, covariate coefficients indicated low support for: (i) kodkod site use probability decreasing while culpeo fox occupancy increasing in exotic plantations ( $\omega^+ = 0.14$ ); (ii) the site use probability of chilla fox decreased as structural diversity of habitat increased ( $\omega^+ = 0.19$ ) and the site use probability of Darwin's fox increased as elevation increased ( $\omega^+ = 0.20$ ); (iii) the site use probability of culpeo fox decreased as elevation and canopy height increased ( $\omega^+ = 0.24$  and 0.16, respectively). The interaction between habitat type and understory cover was not included in the top ranked models. Details of model selection for each species are shown in Table S1. In turn, the relationships of  $\psi$  with the understory cover and complexity of habitat structure are shown in Fig. 1.

#### 3.3. Model testing and validation

For all the candidate models, there was no evidence of lack of fit (all Bootstrapping  $p$ -values were  $>0.05$ , Table S1). Moran's-I correlograms indicated that model residuals were not spatially autocorrelated ( $p < 0.05$ ). The values for area under ROC curves were 0.90 and 0.83 for Darwin's fox and kodkod models (based on the averaged 95% confidence set), respectively, whereas 0.85 for culpeo foxes, indicating considerable similarity between predicted and observed values (Fig. 2). Although less accurate than the Darwin's fox and kodkod models, the averaged chilla fox model (area under ROC curve 0.68) performed substantially better than the null model (area under ROC curve = 0.5).

### 4. Discussion

Species habitat-use models based on accurate habitat descriptions and dealing with imperfect detection of individuals are valuable tool for conservation and management, especially in human-modified landscapes. By combining non-invasive remote camera-trapping, occupancy modeling, and high-resolution LiDAR habitat data, we derived reliable habitat use estimates of mesocarnivore inhabiting a mosaic area comprising native forest and monoculture plantations with differential vegetation structure in Nahuelbuta Mountain Range. Commercial forest plantations are becoming a dominant land-use type throughout temperate forest of South America (Simberloff et al., 2010), and, if managed throughout the enhancement of understory and vertical vegetation structure, they may play an important role as habitat for wildlife (Brockerhoff et al., 2008; Simonetti et al., 2013). However, this approach also may be extended to identify habitat conditions for species living in landscapes comprising other production-oriented lands with different habitat structures (e.g., Nájera and Simonetti, 2010).

The efficiency of camera-trapping for describing the ecology of native carnivores has been widely shown by other multi-species studies in tropical ecosystems (e.g., Burton et al., 2012; Davis et al., 2011; Rovero et al., 2014; Tobler et al., 2008). In contrast, carnivore assemblages of South American temperate ecosystems, which contain several elusive species, remain poorly studied (e.g., Lantschner et al., 2012; Zuñiga et al., 2009). In Caramávida, a camera-trapping effort ca. 850 camera-days was needed to detect the four mesocarnivores in the study area. Moreover, cameras needed to be deployed in average for at least 15 days for the first detection of all the species, and no evidence of association between latency and home range size of the species was detected. In spite of this no association, factors such as how elusive the species is, animal movement behavior, and population density, have been suggested to strongly determine animal detection rates by cameras

**Table 1**

Mesocarnivores recorded in Caramávida basin, Nahuelbuta Mountain Range, central-south Chile and three main indices: Number of detected survey occasions for each species (as the number of records of each species across the detection history of all camera-traps ( $N = 85$ )), *naive* overall occupancy (number of sites that are positive to species' presence divided by the total number of sites sampled), and latency period (average number of camera-days needed to obtain the first detection for each species).

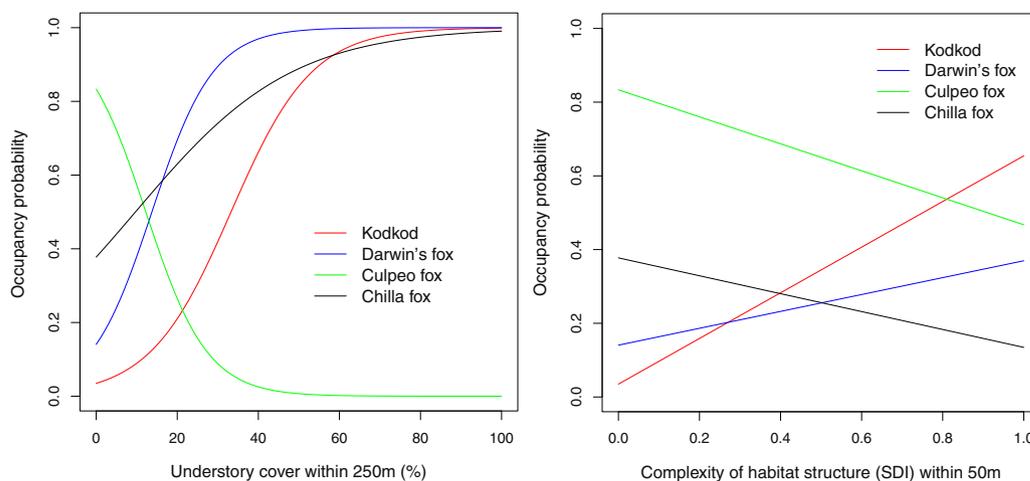
Species	Detections (n)	$\psi_{\text{overall-naive}}$	Latency period (Days $\pm$ SD)
Darwin's fox ( <i>Lycalopex fulvipes</i> )	41	0.22	15.18 $\pm$ 12.01
Kodkod ( <i>Leopardus guigna</i> )	38	0.36	16.37 $\pm$ 11.27
Chilla fox ( <i>Lycalopex griseus</i> )	30	0.15	16.00 $\pm$ 16.94
Culpeo fox ( <i>Lycalopex culpaeus</i> )	82	0.41	16.54 $\pm$ 16.01

**Table 2**

Summary of predicted overall occupancy ( $\psi_{\text{overall}} \pm \text{SE}$ ) and overall detection probability ( $p_{\text{overall}} \pm \text{SE}$ ) across the study area, estimates for four mesocarnivores in Caramávida. Outcomes of the effect of LiDAR covariates and their directionality (positive/negative) on the probability of site use ( $\psi$ ) and the probability of site detection ( $p$ ) are indicated for four mesocarnivores in central-south Chile. Parentheses denote confidence interval of  $\beta$  estimates that did not overlap zero. For  $\psi$  (habitat) variable, [ ] indicates habitat type associated with the effect.

Species	$\psi_{\text{overall}}$ (SE)	$p_{\text{overall}}$ (SE)	LiDAR covariates							
			$\psi$ (Und250)	$\psi$ (Undplot)	$\psi$ (SDI)	$\psi$ (Elev)	$\psi$ (Canopy height (MOD))	$\psi$ (Canopy height (MAX))	$\psi$ (habitat)	$p$ (Unders_camera)
Darwin's fox	0.24 (0.04)	0.5 (0.05)	(+)		(+)	+	–			(–)
Kodkod	0.47 (0.07)	0.25 (0.04)	(+)		(+)	+		+		(–)
Chilla fox	0.18 (0.04)	0.36 (0.06)	(+)		–	(+)	–	–		(–)
Culpeo fox	0.54 (0.08)	0.24 (0.03)	(–)	–	–	(–)	(–)	(–)		+ [plantation] (–)

Variable acronyms: Und250 = understory forest cover within 250 m-radius buffer; Undplot = understory forest cover within 50 m-radius buffer (camera station scale); SDI: structural diversity index measured within 50 m-radius buffer; Elev = elevation; Canopy height (MOD; MAX) = max and modal canopy height; Habitat = coarse habitat classification; Unders\_camera = understory vegetation cover within the detection range of camera-trap.

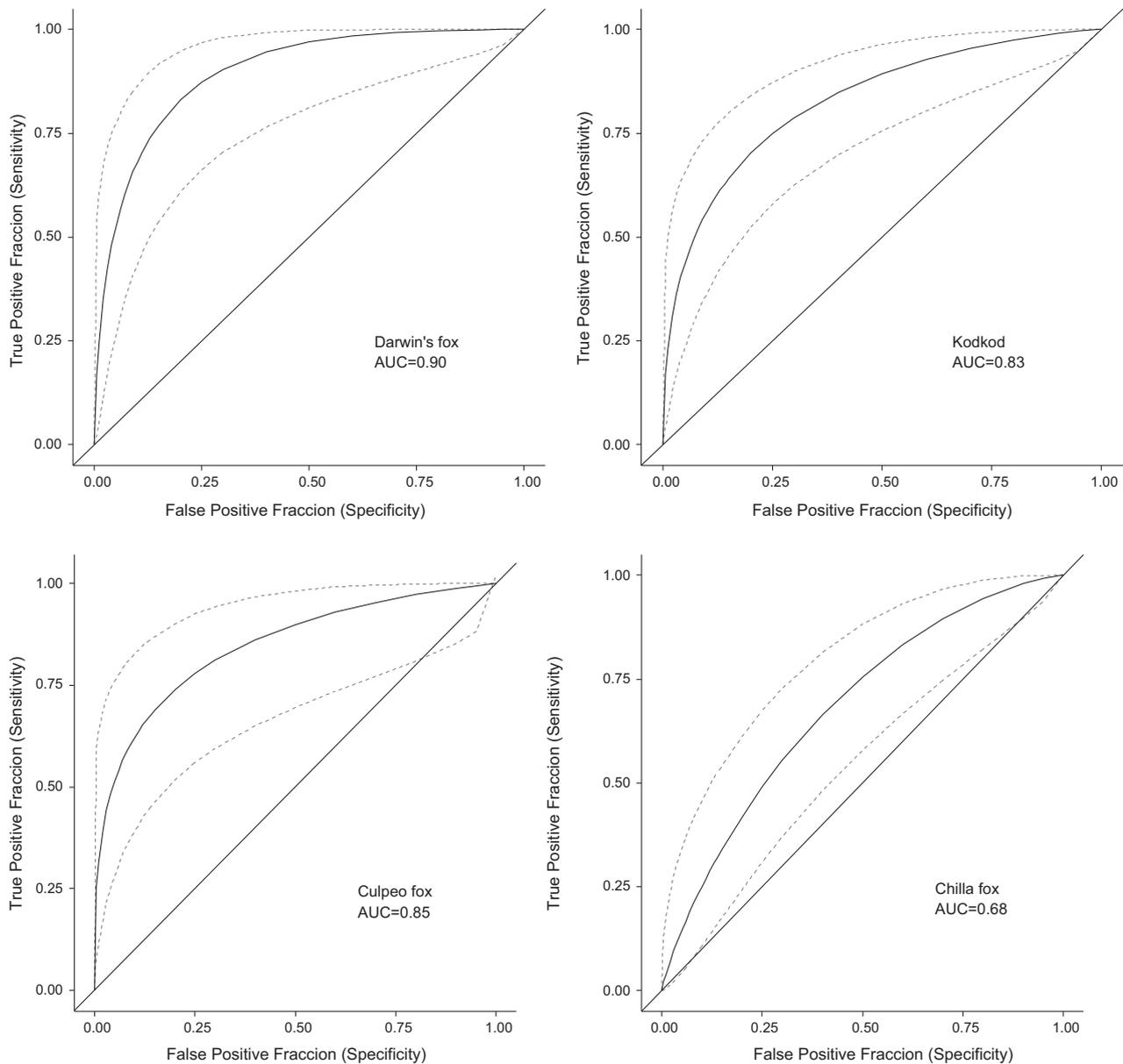


**Fig. 1.** Predicted probabilities of carnivore site use relative to variation in understory cover within 250 m-radius around each camera-trap (left), and the complexity of habitat structure within 50 m-radius around camera trap (right). Species are given in the legend.

set in a particular area (Fig. 1 in Burton et al., 2015), and therefore are important factors when designing camera-trapping surveys.

The pool of species within this mesocarnivore community included some poorly known medium-size predators, which may have low detection rates using alternative methods such as scent stations, track plates, and scat collection (Acosta-Jamett and Simonetti, 2004; Jaksić et al., 1990; Zuñiga et al., 2009). For example, the kodkod cat, considered to be a rare species in coastal fragmented temperate forests (Acosta-Jamett and Simonetti, 2004), was the second most recorded species across our camera sites ( $\psi_{\text{overall}} = 0.47$ ), agreeing with estimates from Gálvez et al. (2013) in temperate Andean forest. Another commonly recorded species in our study area, culpeo fox ( $\psi_{\text{overall}} = 0.54$ ) has been described to occur frequently in mosaic landscapes containing human-created habitats given its flexible habitat preferences (Acosta-Jamett and Simonetti, 2004; Lantschner et al., 2012). On the other hand, Darwin's fox, a low-density and elusive species in temperate forests (Farias et al., 2014), was an infrequently recorded species in Caramávida ( $\psi_{\text{overall}} = 0.24$ ). The difference between the naïve overall occupancy and estimated overall occupancy generated from models for some species, such as kodkod (0.36 and 0.47) and culpeo fox (0.41 and 0.56) highlights the need for: (1) accounting for imperfect detection (probability of animal detection <1); and (2) modeling potential spatial variation in site detection probability by using fine-grain habitat covariates (Burton et al., 2015; Rowcliffe et al., 2008).

The site use probabilities of studied mesocarnivores varied across the landscape, and were significantly affected by fine-grain habitat structure attributes as derived from LiDAR. Understory cover and the structural complexity of habitat were consistently included within the set of best-supported competing models across all carnivores, having differential effects on the site use probabilities of these species. While, as previously expected, habitat class (native forest or exotic plantation) did not improve models of site use probabilities for some mesocarnivores when compared to fine-grain habitat variables. Both results suggest that fine-scale estimates of vegetation structure may be better determinants for explaining the habitat use of some native carnivores in these mosaics containing native forest and monocultures. These results may be also extended to understand the habitat use of mesocarnivores within native forest, if these species are capable to discriminate between different forest compositions as shown in less disturbed landscapes in Chile (e.g., Jiménez, 2007) and other ecosystems (e.g., Long et al., 2010). The use of coarse categorical classification of native and non-native habitats may underestimate the relevance of selection at the habitat composition scale, with a consequent overestimation of the habitat use decisions at finer scales. Nevertheless, logistical constraints usually arise when using several habitat classes in a stratified habitat design for camera-trapping studies (affecting posterior statistical power when testing differences among several categories). Even though we focused our study in two largely contrasting habitat classes as a preliminary



**Fig. 2.** Area under Receiver–Operator–Characteristic (ROC) curves that resulted from averaging the 95% confidence sets of the best-supported models for the probability of site use for Darwin's fox, kodkod, culpeo fox, and chilla fox. Area under Receiver–Operator–Characteristic = 1.00 for a model that perfectly predicts site use at surveyed sites, and Area under Receiver–operator–characteristic = 0.5 for a model that predicts no better than a null model. Dotted lines represent upper and lower 95% confidence intervals.

approach to understand the role of understory structure in monocultures (e.g., Acosta-Jamett and Simonetti, 2004; Simonetti et al., 2013), more accurate assessments of habitat use are needed using other techniques such as satellite telemetry combined with high-resolution remote sensing imagery.

Darwin's fox, kodkod, and chilla fox were more likely to occur in areas with larger understory cover, whereas the larger culpeo fox was more likely to occur in areas with low understory cover (Fig. 1). Moreover, as habitat structure became more complex the probability of site use of kodkod and Darwin's fox increased, whereas for culpeo and chilla foxes it decreased. An increased multi-strata vegetation and shrub cover are closely correlated with the abundance of food resources for small mammals and birds in southern temperate forests (Kelt, 2000; Saavedra and Simonetti, 2005; Vergara and Armesto, 2008), and may compel these small carnivores to intensively use areas with dense understory (Gorini et al., 2012). In addition, the availability of arboreal small mam-

mals is higher in areas with a more complex habitat structure (Fontúrbel and Jiménez, 2009; Fontúrbel, 2010), favouring the arboreal hunting behavior of kodkod (Altamirano et al., 2013; Sanderson et al., 2002). On the other hand, areas containing dense vegetation might provide additional anti-predatory refuge for species such as Darwin's fox as this small carnivore has been documented to be preyed by cougar in Nahuelbuta Mountain Range (McMahon, unpublished data).

The presence of exotic plantations positively affected the presence of culpeo fox in the study area. Previous studies have documented culpeo fox responding positively (Acosta-Jamett and Simonetti, 2004) or negatively (Lantschner et al., 2012) to exotic plantations. However, this response depends on the availability of native understory present within monocultures (Simonetti et al., 2013). Similar to native forest, the development of a understory vegetation in exotic plantations would support a larger prey availability such as small mammals, making exotic plantations

with understory more suitable for this predator (Lantschner et al., 2011; Moreira-Arce et al., 2015b; Saavedra and Simonetti, 2005). Although a slightly positive effect of exotic plantations was found on this species, the negative effect of understory cover and habitat structural complexity may not support the prey availability prediction. Alternatively, we suggest that low levels of vegetation cover and simpler habitat structure could increase the hunting efficiency of *culpeo foxes* (Gorini et al., 2012), especially when hunting the introduced European rabbit (*Oryctolagus cuniculus*) and hare (*Lepus europaeus*) (Zuñiga et al., 2008), and habitat generalist small mammals, such as long-haired field mice (*Abrothrix longipilis*) (Moreira-Arce et al., 2015b).

Some mesocarnivores such as Darwin's fox and kodkod were more likely to occur in higher elevations in our study area. Previous studies conducted in native forest have shown greater abundance and diversity of prey for these carnivores at lower elevations (Patterson et al., 1989). However, in our study area, lower elevations are mainly dominated by exotic plantations, which may decrease the prey diversity and abundance when compared to native forest (Moreira-Arce et al., 2015b; Saavedra and Simonetti, 2005), but also concentrate a larger anthropic activity. Thus, we are unable to distinguish the specific mechanism behind the positive association between site use probability of these species and elevation. However, we suspect that, given that exotic plantations in our study area can be used as feeding ground for these carnivores (Moreira-Arce et al., 2015b), the positive response of Darwin's fox and kodkod to elevation might be explained by their sensitivity to human activity and exotic carnivores such as domestic dog that would occur at lower elevations and associated to human infrastructure (Moreira-Arce et al., 2015a). Contrary to our previous expectations, we found chilla fox more likely to occur in higher elevation in our study area. Chilla foxes have been documented to select open areas such grassland and farmlands (Silva-Rodríguez et al., 2010), which are more likely to be found in lower elevations in our study area. Then, we presume this pattern may be due to spatial segregation of chilla fox from the larger culpeo fox, which has been previously documented in northern Chile (Jiménez et al., 1996), rather than emerging as a positive response to suitable habitat conditions at higher elevations. In turn, the negative association between elevation and site use probability of culpeo fox would support the fact that this species may exploit habitats with intensive human activity. Alternatively, this pattern may be explained by the active use of this carnivore on exotic plantations (mainly distributed at lower elevation) where they may prey on introduced lagomorphs.

Our results should also be interpreted carefully since the estimates of habitat use obtained are conditional to the true occupancy of the species across the studied landscape. Since this occupancy value (the area a species actually occupies within its area of extent of occurrence; *sensu* Gaston, 1991) is determined by the spatial scale of the sampling unit (He and Gaston, 2000) and affected by habitat covariates, our measure of habitat use (i.e., prob[used|occupied]) can be altered by processes occurring at both scales (i.e. occupancy at the coarser scale, and habitat use at the finer scale). This is particularly important in continuous landscapes where variables can affect both true occupancy and habitat use. In this sense, the use of hierarchical models accounting simultaneously for occupancy and habitat use may become useful tools.

#### 4.1. Conclusion

The conservation of threatened carnivores occurring on human-modified landscapes dominated by exotic forest plantations requires identifying suitable habitats conditions that can be integrated within sustainable landscape management strategies. As

most carnivore species occur at low densities and occupy large home ranges, assessment methods that reduce biases arising from imperfect detection, while incorporating fine-grain environmental information, are increasingly needed to manage landscapes at larger scales. In this study, we highlight the combined use of an occupancy model framework including environmental covariates derived from LiDAR remote sensing, which describes heterogeneity in forest structure at large spatial scales as continuous rather than as categorical variables, and thus, better describe animal–habitat relationships (Vierling et al., 2008). Based on that methodological approach, our results can be extended to sustainable management of forest plantations for carnivore conservation by enhancing the vegetation structure of native shrub species within these production-oriented lands.

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#### Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2016.03.024>.

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