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## Habitat use by carnivores at different spatial scales in a plantation forest landscape in Patagonia, Argentina

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### ABSTRACT

Forest plantations are an increasingly important source of industrial wood around the world, and the design and management of plantations can greatly influence the relationship with wildlife. The aim of this study was to examine the effects of conversion of native open vegetation to conifer plantations on mammalian carnivore assemblages in NW Patagonia, Argentina. We conducted camera-trap surveys at 69 sites and assessed composition of carnivore assemblages and habitat use in conifer plantations and native vegetation. We also evaluated habitat characteristics at stand and landscape scales related to presence of carnivores. Four species of carnivores were detected: *Lycalopex culpaeus*, *Conepatus chinga*, *Puma concolor*, and *Leopardus geoffroyi*. *L. culpaeus* and *C. chinga* used continuous native vegetation most frequently, but also used dense conifer plantations and tended to be more abundant in firebreaks and sparse plantations than in dense plantations. *L. geoffroyi* was almost fully restricted to continuous native vegetation, but was also detected in firebreaks and native vegetation remnants between plantations; this species was never detected in plantations. *P. concolor* was detected in all habitat types and did not exhibit any preference. The presence of carnivores was associated with understory diversity, tree density, and prey availability at the stand scale, and with amount of area with native vegetation at the landscape scale. Our results suggest that management decisions at the stand and landscape scales can influence habitat quality for wildlife in the region.

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### 1. Introduction

Forest plantations modify the landscape and may alter habitat quality for some species, thereby shifting their distribution and abundance (Hayes et al., 2005; Brockerhoff et al., 2008). Human-modified lands can provide important habitat, offering food, shelter, or climatic conditions, and allowing dispersal and survival of some others (Lindenmayer and Franklin, 2002; Brockerhoff et al., 2008). As a result, management of human-modified lands is an important consideration in conservation, as these lands cover an increasingly large fraction of the globe. To a large extent and in many regions, the future of biodiversity depends on how productive areas are managed (Franklin and Lindenmayer, 2009).

Contemporary conservation strategies recognize that effective conservation of biodiversity must take multiple spatial scales into consideration (Franklin and Lindenmayer, 2009). In modified landscapes, for some species it is important to maintain connectivity through the establishment of corridors that link habitat patches,

but also to consider the potential of a permeable matrix to maintain connectivity across a range of scales and habitat types (Hilty and Merenlender, 2004; Fischer et al., 2005; Shepherd and Whittington, 2006).

Forest plantations provide habitat for many species of wildlife (Hartley, 2002; Carnus et al., 2006; Simonetti, 2006; Brockerhoff et al., 2008), and plantation management often has less impact on biodiversity than many other land uses (Brockerhoff et al., 2008). At the stand scale, plantations managed to develop complex structure, and particularly one similar to the region's native vegetation, tend to hold more diverse assemblages than do plantations with more simple vegetative structure (Hartley, 2002; Lindenmayer and Hobbs, 2004; Nájera and Simonetti, 2010). However, managing for increased biodiversity only at stand scale could reduce the economic productivity. Thus, managers often enhance biodiversity in plantation forests by using a landscape-scale strategy, which consists in maintaining a mosaic of diverse habitat types, such as different plantation ages and structural classes, and the retention of remnant patches of native vegetation and corridors (Lindenmayer and Franklin, 2002; Lindenmayer and Hobbs, 2004; Simonetti, 2006).

In Argentinean Patagonia, establishment of exotic conifer plantations is strongly promoted by the state. From the mid-1970's to 2010, this policy resulted in establishment of approximately

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80,000 ha of conifer plantations, and there are still around 800,000 ha of rangeland in the region that are highly suitable to be converted to forest plantations (Loguercio and Deccechis, 2006; CFI-FUNDFAE, 2009). However, there are few studies that evaluate how the replacement of native vegetation affects biodiversity in the region, including insects (Corley et al., 2006; Paritsis and Aizen, 2008), birds (Lantschner and Rusch, 2007; Lantschner et al., 2008; Paritsis and Aizen, 2008), and small mammals: (Lantschner et al., 2011); and there is almost a complete lack of information on relationships between forestry and carnivores in the region.

Carnivores may be particularly sensitive to landscape change due to their relatively low population densities and requirements for large habitat area (Carroll et al., 2001). This makes carnivores potentially valuable as focal species in regional conservation planning. As a consequence, identification of factors that influence distributions of carnivores can help define management practices at different spatial scales (Noss et al., 1996; Carroll et al., 2001). Studies of carnivores around the world have shown that influences of forest plantations as habitat vary with requirements of each species and the context in which plantations are established (Lindenmayer et al., 1999, 2000; Ferreras, 2001; Acosta-Jamett and Simonetti, 2004; Di Bitetti et al., 2006).

Plantations in Patagonia are established in a very particular landscape context, replacing the forest–steppe ecotone, a narrow zone of transition along the Andes Mountains which is dominated by a gramineous steppe with sparse shrubs and trees. Hence, habitat changes are especially marked, as open ecosystems are transformed to exotic plantations (Allan et al., 1997; Bremer and Farley, 2010). Additionally, these systems have historically been dedicated to extensive sheep and cattle production. Domestic grazing was introduced in Patagonia in the early 20th century (Soriano, 1983). Livestock are present in almost the whole region, and thus conifer plantations do not replace pristine grasslands, but systems that have already been altered (Novaro and Walker, 2005). With the introduction of livestock top carnivores were killed to avoid predation, reducing densities of these species, but apparently without effects on species' distributions (Novaro and Walker, 2005).

The aims of this study were to: (a) assess differences in habitat use by carnivore species among native open vegetation, dense conifer plantations, and alternative landscape structures like firebreaks, remnants of native vegetation between conifer plantations, and sparse conifer plantations; and (b) identify habitat variables at stand and landscape scale related to presence of carnivores in plantation landscapes.

## 2. Methods

### 2.1. Study area

We carried out our study in the Meliquina Valley (41°S, 71°W) in northwest Patagonia, Argentina. Climate is temperate to cold, with maximum and minimum annual average temperatures of  $17.1 \pm 0.5$  and  $4 \pm 2.1$  °C, respectively. Mean annual rainfall ranges between 800 and 1400 mm/year (Barros et al., 1983). Geomorphology consists of two river valleys (Meliquina, Filo-Huam, and Calefu rivers), with steep stony mountain slopes, and narrow floodplains.

The vegetation of the basin corresponds to a transition between *Austrocedrus chilensis* forest and arid steppe. It is dominated by bunchgrasses (*Festuca* spp., *Stipa* spp., and *Poa* spp.), low shrubs (*Mulinum* spp., *Berberis* spp., and *Senecio* spp.), and sparse patches of *A. chilensis* woodlands, accompanied by shrubs and other trees, including *Lomatia hirsuta*, *Aristotelia chilensis*, *Maytenus boaria*, and *Schinus patagonicus*. In wet microsites and along the borders of creeks, there are patches of shrublands dominated by *Nothofagus*

*antarctica*, a small deciduous tree. This area has been grazed since the beginning of the 20th century. Cattle are typically stocked at a low density and allowed to range freely over extensive areas (Funes et al., 2006). Vegetation structure and composition remains similar to the original ecotonal vegetation, although some areas show a reduction of herbaceous cover and replacement of some herbaceous species (Laclau, 1997; Funes et al., 2006).

Approximately 4350 ha of the basin were replaced with conifer plantations over the last 30 years, mostly of ponderosa pine (*Pinus ponderosa*), and in some cases, lodgepole pine (*Pinus contorta*) and Douglas-fir (*Pseudotsuga menziesii*). Plantations were established along the slopes and bottom of the river valleys (between 800 and 1200 m asl), distributed in stands of ca. 15–25 ha separated from each other by open strips, 30–35 m wide, designed to act as firebreaks. Initial plantation density varied between 2500 and 1111 trees/ha. Almost all plantations were pruned (at ages between 12 and 15 years), and branches were left in the stand, while approximately 60% of the planted area was thinned to densities between 1200 and 500 trees/ha (at ages between 15 and 20 years). Rotation periods are stipulated to be of 35–40 years, but no stand yet reached the harvest period.

Our sampling area was restricted to elevations ranging from 800 to 1200 m asl, corresponding to the range of elevations in the study area where conifer plantations are established. We excluded from our sampling area all human settlements, and a buffer zone of 400 m around them.

### 2.2. Sampling design

We used camera traps to estimate relative habitat use of carnivores. We determined indices of habitat use for carnivores in five types of habitats: continuous native vegetation, dense conifer plantations, sparse conifer plantations, native vegetation remnants between plantations, and firebreaks. Continuous native vegetation was selected as reference habitat of the ecosystem existing prior to planting conifers. Dense plantation was selected because it is the dominant habitat type in the plantation landscape, and we were interested in studying the main effect of replacement of native vegetation by plantations managed in the traditional way. Sparse plantations were studied to assess the effect of alternative management practices, particularly lower tree densities, which has been documented as an important variable for determining biodiversity in forest plantations. Remnants of native vegetation between pine plantations and firebreaks were selected to assess the role of these alternative landscape structures in providing complementary habitat for carnivore species in plantation landscapes.

We selected 20 sites in dense conifer plantations and 20 sites in continuous native vegetation for sampling, 10 sites in firebreaks, 10 sites in native vegetation remnants, and 9 sites in sparse conifer plantations. Sites were separated by a minimum of 1 km from one another, and we avoided selecting sites within 50 m of roads or other features used for human travel (excepting in firebreak, which are used as forestry roads in some cases).

For the purposes of this study we defined continuous native vegetation as any area >150 ha in size with vegetation composition structurally similar to that which existed prior to planting conifers and managed using traditional cattle grazing. These sites were dominated by vegetation typical of the transition between *A. chilensis* forest and arid steppe with patches of shrublands. Continuous native vegetation sites were randomly sampled from the basin and native vegetation within 500 m of conifer plantations was not sampled. Continuous native vegetation represented approximately 3200 ha in the study area (42% of the study area).

We defined dense conifer plantations as areas planted with conifers, ranging from 20 to 28 years old, with crown closure complete (canopy cover >60%), tree densities between 500 and 1200 trees/

ha, and low or absent understory cover (mean understory cover of 4%). Sampled dense conifer plantations were randomly selected from existing plantations in the study area. Sites within 70 m from the border of the plantation were not sampled. Selectable dense conifer plantations represented a total area of 3100 ha (41% of the study area), and comprised more than 90% of the planted area.

We defined firebreaks as strips 30–35 m wide and of variable length between plantation stands established for fire management, where the original vegetation was not replaced by plantations, but was partially removed. We randomly selected sites in firebreaks from the 120 ha of firebreaks available in the sampling area (2% of the study area).

We defined native vegetation remnants as patches 5–100 ha in size with native vegetation surrounded by conifer plantations. We randomly selected sites from the available patches in the sampling area. Selectable native vegetation remnants represented a total area of 1000 ha (13% of the study area).

We defined sparse conifer plantation as conifer plantations patches at least 3 ha in size with crown cover <60%, relatively low tree density (mean density of 500 trees/ha), and abundant understory vegetation (mean understory cover of 33%). These plantations were sparse because of different reasons, including lower planting density, heavy thinning, or plantation failure. We randomly selected sites from the available sparse plantations. Total area of sparse plantations in the study area was low, approximately 200 ha (3% of the study area).

### 2.3. Carnivore sampling

Each carnivore sampling station consisted of a camera trap baited with rotten eggs and valerian essence. The camera traps were Leaf River® Trail Scan Model C-1 or Cuddeback® Digital Scouting units, consisting of a camera armed with an infrared sensor programmed to shoot when a temperature change, such as presence of a homeothermic animal, is detected. The infrared beam was oriented ca. 40–50 cm above the ground and stations were set to be activated during night. We checked each camera roughly every 15 days to determine functionality and to replace batteries or film; fresh bait was added to stations as needed during these visits. Date and time of each picture were automatically recorded.

We conducted sampling from December to April in 2007–2008, 2008–2009, and 2009–2010. Each year we deployed 30 stations during each of two 60-day sampling periods. We sampled 69 sites in total; each sampling station was active for two 60-day periods along two different years. We ensured that sampling effort in the five habitat types stayed similar among each sampling period, and randomly selected a subset of stations of each habitat type for each period. Over the course of our study, we sampled 2478 trap days in continuous native vegetation, 2474 trap days in dense conifer plantations, 1270 trap days in firebreaks, 1267 trap days in native vegetation remnants, and 1144 trap days in sparse conifer plantations.

### 2.4. Habitat characterization

At the stand scale we characterized vegetation structure and composition at twenty-five 1 m<sup>2</sup> plots and ten 25 m<sup>2</sup> plots randomly located within 100-m-radius area centered on each trap station. We visually estimated total understory cover and identified all understory species (<50 cm tall) in each 1 m<sup>2</sup> plot. In each 25 m<sup>2</sup> plot we visually estimated total coverage of mid-story (50 cm to 3 m tall) and identified all mid-story species (Elzinga et al., 1998). All estimates were carried out by a single researcher, to avoid bias. We estimated canopy cover at 10 randomly selected points within the 100-m-radius of each trap station, using a convex densiometer. At each point we established four quadrants to make

one densiometer readings at each quadrant (four observations per point). We estimated tree density (trees/ha), using the nearest-neighbor method (Cottam et al., 1953), measuring the distance to four nearest neighbors of five different trees randomly selected at each site, and recorded diameter at breast height (dbh, in centimeters) of each of these trees. In sites with <50 trees/ha, we counted all trees within 100 m of the trap station, to calculate tree density. For each site, we estimated total canopy height by measuring the height of the five randomly selected trees (with a clinometer), and calculated basal area (m<sup>2</sup>/ha) based on mean DBH and tree density. We determined relative abundance of some known prey species, such as European hare (*Lepus europaeus*), wild boar (*Sus scrofa*), red deer (*Cervus elaphus*) (Novaro et al., 2000), detected with the camera-traps simultaneously to carnivore samplings (Lantschner et al., submitted for publication). We also determined the presence/absence of cattle in each site, as an indicator of existence of livestock activity.

To characterize landscapes, we used a 1:30,000 scale land-cover map based on a visual classification of two ASTER 15 m resolution georeferenced and orthorectified images (acquired on 4 May 2003 and 28 March 2007) and ground truthing for verification to characterize landscapes. We mapped eight major vegetation types: *A. chilensis* forest–steppe mosaics, *N. antarctica* shrublands, *N. pumilio* forest, conifer plantation, firebreaks, cliffs, highland vegetation, and human settlements. Landscape metrics were calculated using ArcGIS 9.2 (ESRI, Redlands, California, USA) with the Patch Analyst Extension (Rempel et al., 2008). We calculated area covered and mean patch size for each vegetation type, and total number of patches within 500, 1000, and 2000 m of the sampling station. This spatial scales were selected to include the approximate home-range size of most carnivore species (Johnson and Franklin, 1991, 1994; Donadio et al., 2001). We also calculated the distance of each sampling station to the nearest roads, rivers and streams, cliffs, and human settlements.

### 2.5. Data analysis

We estimated relative habitat use of each species by dividing the number of images of each species at each site by the sampling effort expressed in 10-day intervals. Photos of a given species separated by at least 1 h were considered to be unique events. For each habitat type, we tested for differences in habitat use of each species among different years, and among different sampling periods. Because we did not find significant differences for any of those tests (Kruskal–Wallis test,  $p < 0.05$ ), for each species we combined data of both sampling periods for each site to increase the power of the analysis. We used Kruskal–Wallis tests to compare number of detections of each species among dense conifer plantations, continuous native vegetation, sparse conifer plantations, native vegetation remnants, and firebreaks. When significant differences were found, we performed planned multiple comparisons between dense conifer plantations and each of the other habitat types, because we were not interested in all possible combination of comparisons, but only those that involved dense plantations. We used nonparametric tests because data did not meet normal distribution. We accepted statistical significance at  $p$  values <0.05.

An important assumption for a valid relative abundance index is that detectability is constant across habitat types (MacKenzie et al., 2005), however in our study, detection rates may have differed among habitats due to differences in structural characteristics. We used single-species multiple-season occupancy models implemented in program PRESENCE 4.0 (available for download from <http://www.mbr-pwrc.usgs.gov/software/presence.html>), to assess the proportion of area occupied by the species, taking detection probability into account (MacKenzie et al., 2002). These models assume that distribution is “closed” within a season, but “open” between seasons, estimating the probability of occupancy “ $\psi_t$ ”

(proportion of sites in which the species was present in season  $t$ ), the probability of colonization " $\gamma_t$ " (unoccupied sites in season  $t$  that become occupied by the species in season  $t + 1$ ), the probability of extinction " $\varepsilon_t$ " (occupied sites by the species in season  $t$  that become unoccupied in season  $t + 1$ ), and the single-visit detection probability of the species " $p$ " (MacKenzie et al., 2005). We were able to run these models only for *Lycalopex culpaeus*, because the relatively few records available for the other species did not allow us to conduct reliable occupancy estimates. Detection histories of *L. culpaeus* were constructed for each camera-trap location ( $n = 69$ ), consisting of two seasons with four sampling occasions of 15 consecutive days each season (a total of eight sampling occasions). To model occupancy ( $\psi$ ), first we assumed no habitat effect (constant), and in a second case we considered the habitat type effect as a site-specific covariate. To model detection probability ( $p$ ), we developed three models, in the first we assumed that detection probability was constant; in the second, we assumed that that detection probability was affected by habitat type; and in the third, we assumed detection probability to be affected by habitat type and season. We assumed that extinction ( $\varepsilon$ ) and colonization ( $\gamma$ ) were constant among habitat types in all models. Candidate models combining all parameters were ranked using Akaike's information criterion (AIC), to select the most parsimonious one (lowest AIC).

We performed logistic multiple regression to determine habitat characteristics most closely associated with presence of *L. culpaeus*; no other species was present in more than 1/3 of the sample sites. We used presence/absence of *L. culpaeus* in each site as the dependent variable, and included habitat variables at stand and landscape scale and the relative abundance of prey species and presence/absence of cattle, as independent variables. We included all 69 sites sampled with camera traps in this analysis. To assess autocorrelation and the potential for this creating pseudo-replication (Lennon, 1999), we calculated a coefficient  $c(r)$  that describes the autocorrelation of a variable  $x$  with lag  $r$  (Schadt et al., 2002); we found no correlation at spatial scales of 1 km or higher, the minimum distance between sampling stations. To pre-select variables to include in the model, we performed Spearman correlations with presence/absence of *L. culpaeus*, and selected those that were significantly correlated. To avoid multicollinearity, we performed Spearman correlations between pairs of predictor variables, setting a limit of  $r_p < 0.7$  for keeping two correlated variables. In case of two variables been highly correlated, we excluded the variable less correlated with presence of *L. culpaeus*. All possible combinations of selected predictor variables were modeled, using logistic regression. We calculated Akaike's Information Criterion for small sample sizes ( $AIC_c$ ), relative  $AIC_c$  ( $\Delta AIC_c$ ), Akaike weights ( $\omega_i$ ), and Nagelkerke's  $R^2$  for each model. We performed a Hosmer–Lemeshow test to assess goodness of fit of the global model ( $\chi^2 < df$ , Hosmer and Lemeshow, 2000). We created a confidence set of models by including models with Akaike weights within 10% of the highest value, which is comparable with minimum cutoff point suggested by Royall (1997). We used model-averaging to incorporate model selection uncertainty directly into parameter estimates and standard error using Akaike weights (Burnham and Anderson, 2002). We also calculated odds ratios from averaged parameter estimates ( $e^{\beta}$ ). For remaining species, we performed Spearman correlations between number of detections of each species in each site with habitat variables at stand and landscape scales.

### 3. Results

#### 3.1. Habitat use pattern

We detected four carnivore species: *L. culpaeus* (Culpeo fox, Canidae), *Conepatus chinga* (Andean hog-nosed skunk, Mustelidae),

*Puma concolor* (Puma, Felidae), and *Leopardus geoffroyi* (Geoffroy's cat, Felidae). *L. culpaeus* was the most frequently detected species (Fig. 1) and the number of records of this species differed among habitat types (Kruskal Wallis  $\chi^2 = 13.65$ ,  $p < 0.009$ ). *L. culpaeus* was detected almost five times more frequently in continuous native vegetation than in dense conifer plantations ( $p < 0.001$ ), while no differences were detected between dense conifer plantations and each of the alternative vegetation types: sparse conifer plantations ( $p = 0.311$ ), firebreaks ( $p = 0.153$ ), and native vegetation remnants ( $p = 0.725$ ). *C. chinga* and *P. concolor* were detected in all habitat types, and did not show significant differences in number of records among habitats (Kruskal Wallis  $\chi^2 = 4.904$ ,  $p = 0.297$ ;  $\chi^2 = 1.405$ ,  $p = 0.843$ , respectively). In contrast, detection rates for *L. geoffroyi* differed among habitat types (Kruskal Wallis  $\chi^2 = 10.868$ ,  $p < 0.028$ ). We recorded this species in continuous native vegetation, firebreaks and native vegetation remnants, but not in conifer plantations.

The most parsimonious occupancy model for *L. culpaeus* assumed occupancy ( $\psi$ ) to be affected by habitat type, and detection probability ( $p$ ) to be constant. This model was more likely ( $\Delta AIC > 2$ ) than the other models that considered occupancy to be constant, and/ or detection probability to vary among habitats and between seasons. Occupancy estimates ( $\pm SE$ ) of the selected model were:  $\psi = 0.742$  (0.151) for continuous native vegetation,  $\psi = 0.207$  (0.110) for dense conifer plantations,  $\psi = 0.828$  (0.204) for firebreak,  $\psi = 0.615$  (0.220) for sparse conifer plantations and  $\psi = 0.158$  (0.150) for native vegetation remnants. Detection probability ( $\pm SE$ ) for each sampling period was  $p = 0.437$  (0.050), while colonization and extinction probabilities ( $\pm SE$ ) were similar to each other,  $\gamma = 0.245$  (0.061) and  $\varepsilon = 0.232$  (0.082). Thus, differences in detectability among habitat types appear not to be significant for *L. culpaeus*, and thus relative abundance indexes for this species should be a reliable estimation of total abundance.

#### 3.2. Relationship with habitat variables

##### 3.2.1. Logistic model

We selected five of the habitat variables as candidate predictors of *L. culpaeus*, after taking into account collinearities and correlation with *L. culpaeus* presence: understory richness, tree density, mean patch size of plantations within 1 km of the sampling station, proportion of area covered by *A. chilensis* forest–steppe mosaic within 0.5 km of the sampling station, and number of detections of European hare (*L. europaeus*). All habitat and prey variables,

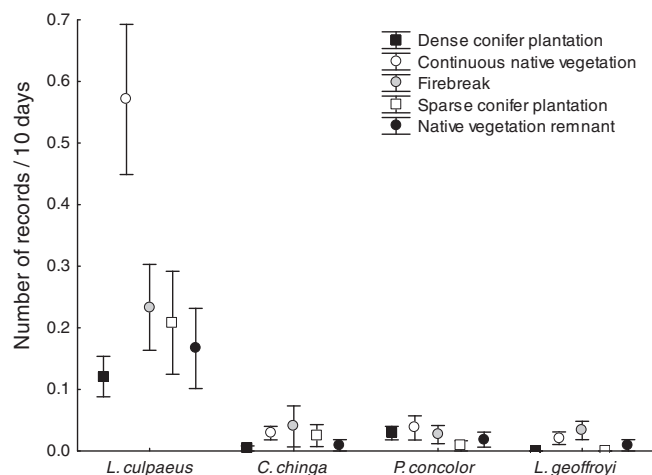


Fig. 1. Mean number of records per sampling station in dense conifer plantation, continuous native vegetation, firebreak, sparse conifer plantation, and native vegetation remnants sites for each species of carnivore (mean  $\pm$  standard error).



**Table 1**

Independent variables correlated with one or more species of carnivore. Means (standard error) for each habitat types are shown. DCP: dense conifer plantation, CNV: continuous native vegetation, FB: firebreak, SCP: sparse conifer plantation, NVR: native vegetation remnant. UndRic: understory layer richness, TreeDen: tree density, CanCov: canopy cover, BasArea: basal area, MPSPI 1 k: mean patch size of conifer plantation within 1 km of the sampling point, MPSNant 1 k: mean patch size of *N. antarctica* shrubland within 1 km of the sampling point, MPSAcSt 0.5 k: mean patch size of *A. chilensis*-steppe vegetation within 0.5 km of the sampling point, PrAcSt 0.5 k: proportion of *A. chilensis*-steppe vegetation within 0.5 km of the sampling point, Hare: number of records of European hare per site, Boar: number of records of wild boar per site. Values followed by different letters (a, b, c) are significantly different according to Dunn's test ( $\alpha = 0.05$ ).

Variables	DCP	CNV	FB	SCP	NVR	<i>p</i>
UndRic (n° spp.)	4.7 (0.7) <i>b</i>	11.2 (1.2) <i>a</i>	7.1 (0.8) <i>ab</i>	9.1 (1.3) <i>ab</i>	12.4 (1.7) <i>a</i>	**
TreeDen (indiv/ha)	815 (62) <i>a</i>	13 (6) <i>bc</i>	0 (0) <i>c</i>	555 (75) <i>a</i>	286 (100) <i>ab</i>	**
CanCov (%)	83.7 (1.8) <i>a</i>	1.5 (1.2) <i>b</i>	0.0 (0.0) <i>b</i>	35.3 (4.1) <i>a</i>	35.2 (7.9) <i>a</i>	**
BasArea (m <sup>2</sup> /ha)	52.6 (4.0) <i>c</i>	1.2 (0.7) <i>bc</i>	0.0 (0.0) <i>b</i>	22.9 (4.9) <i>a</i>	16.3 (5.5) <i>ab</i>	**
MPSPI 1 k (ha)	19.7 (2.9) <i>b</i>	4.7 (2.4) <i>a</i>	22.4 (4.0) <i>b</i>	15.4 (3.1) <i>ab</i>	16.2 (3.4) <i>b</i>	**
MPSNant 1 k (ha)	19.7 (2.9)	4.7 (2.4)	22.4 (4.0)	15.4 (3.1)	16.2 (3.4)	
MPSAcSt 0.5 k (ha)	2.9 (0.9) <i>b</i>	19.3 (3.2) <i>a</i>	2.6 (1.1) <i>b</i>	3.1 (1.1) <i>b</i>	5.1 (1.9) <i>ab</i>	**
PrAcSt 0.5 k	0.13 (0.02) <i>b</i>	0.67 (0.05) <i>a</i>	0.10 (0.03) <i>b</i>	0.20 (0.05) <i>b</i>	0.21 (0.06) <i>b</i>	**
Hare (n° rec/site)	0.09 (0.05) <i>b</i>	0.11 (0.06) <i>b</i>	0.88 (0.20) <i>a</i>	0.03 (0.03) <i>b</i>	0.40 (0.33) <i>b</i>	*
Boar (n° rec/site)	0.22 (0.07) <i>ab</i>	0.03 (0.01) <i>b</i>	0.30 (0.11) <i>a</i>	0.37 (0.11) <i>b</i>	0.00 (0.00) <i>a</i>	**

Asterisks indicate significant differences between habitat types (Kruskal–Wallis).

\*  $p < 0.01$ .

\*\*  $p < 0.001$ .

except mean patch size of *N. antarctica* shrubland, were significantly different among habitat types (Table 1).

The set of performed models revealed a considerable level of model uncertainty, with nine models with Akaike weights within 10% of the highest value (Table 2). The Hosmer and Lemeshow goodness of fit test indicated a good fit of the global model ( $\chi^2 = 7.219$ ,  $df = 8$ ). These nine models represented a sum of Akaike weights of 0.892, indicating a 89.2% chance of the best approximating models being among all models. The averaged model contained all variables (Table 3). Number of detections of European hare had the strongest positive effect on *L. culpaeus* occurrence, followed by proportion of area covered by *A. chilensis* forest–steppe mosaic, and understory richness. Tree cover had a moderately positive effect, while mean patch size of plantations was the only variable with a negative effect on *L. culpaeus* occurrence. The high unconditional standard errors of most variables suggested that considerable uncertainty existed as to the true effects of these variables on *L. culpaeus* presence/absence (Table 3).

### 3.2.2. Spearman correlations

Number of records of *C. chinga* was positively correlated with mean size of patches of *N. antarctica* within 1 km of the sampling point ( $r_\rho = 0.313$ ,  $p < 0.009$ ), proportion area covered by *A. chilensis* forest–steppe mosaic within 0.5 km of the sampling point ( $r_\rho = 0.246$ ,  $p < 0.041$ ), and mean number of *A. chilensis* forest–steppe mosaic patches within 0.5 km of the sampling point ( $r_\rho = 0.241$ ,  $p < 0.046$ ). Number of *P. concolor* detections was positively correlated with number of detections of wild boars ( $r_\rho = 0.340$ ,  $p < 0.004$ ) and mean size of plantations within 1 km

**Table 2**

Confidence set of logistic regression models we used to predict *L. culpaeus* presence–absence in our study area. Variables, number of parameters in the model (*K*), Akaike's Information Criterion adjusted for small sample size ( $AIC_c$ ), difference of  $AIC_c$  between a model and the model with the lowest  $AIC_c$  ( $\Delta AIC_c$ ), model weights ( $\omega_i$ ), and Nagelkerke's  $R^2$  values, are given for each model. Hare: number of records of European hare per site, UndRic: understory layer richness, Slope: dominant slope of the site, TreeDen: tree density, BasArea: basal area, CIDist: distance to the nearest cliff, MPSPI 1 k: mean patch size of conifer plantation within 1 km of the sampling point, PrAcSt 0.5 k: proportion of *A. chilensis*-steppe vegetation within 0.5 km of the sampling point.

Model	<i>K</i>	$AIC_c$	$\Delta AIC_c$	$\omega_i$	$R^2$
Hare + UndRic + MPSPI 1 k + PrAcSt 0.5 k	5	77.722	0.000	0.291	0.362
Hare + UndRic + TreeDen + PrAcSt 0.5 k + MPSPI 1 k	6	79.768	2.045	0.105	0.369
Hare + UndRic + TreeDen + MPSPI 1 k	5	79.774	2.052	0.104	0.331
Hare + UndRic + MPSPI 1 k	4	79.791	2.069	0.103	0.330
Hare + UndRic + TreeDen + PrAcSt 0.5 k	5	79.977	2.255	0.094	0.327
Hare + UndRic + PrAcSt 0.5 k	4	80.128	2.406	0.087	0.325
Hare + PrAcSt 0.5 k	3	80.335	2.613	0.079	0.283
Hare + TreeDen + PrAcSt 0.5 k + MPSPI 1 k	5	80.596	2.874	0.069	0.318
Hare + MPSPI 1 k + PrAcSt 0.5 k	4	80.621	2.898	0.068	0.317

**Table 3**

Model-averaged parameter estimates ( $\beta$ ), unconditional standard errors (SE), and odds ratios (OR) for habitat variables included in the confidence set of logistic regression models used to predict *L. culpaeus* presence–absence in our study area. Hare: number of records of European hare per site, UndRic: understory layer richness, MPSPI 1 k: mean patch size of conifer plantation within 1 km of the sampling point, PrAcSt 0.5 k: proportion of *A. chilensis*-steppe vegetation within 0.5 km of the sampling point.

Variable	$\beta$	SE	OR
Intercept	−0.470	0.966	0.62
Hare	3.952	3.892	52.06
UndRic	0.093	0.094	1.10
TreeDen	0.0001	0.0004	1.00
PrAcSt 0.5 k	1.941	2.024	6.97
MPSPI 1 k	−0.032	0.033	0.97

of the sampling point ( $r_\rho = 0.374$ ,  $p < 0.002$ ). Number of *L. geoffroyi* detections were negatively correlated with tree density ( $r_\rho = -0.338$ ,  $p < 0.004$ ), canopy cover ( $r_\rho = -0.319$ ,  $p < 0.007$ ), and basal area ( $r_\rho = -0.332$ ,  $p < 0.005$ ), and positively correlated with number European hare detections ( $r_\rho = 0.360$ ,  $p < 0.002$ ).

## 4. Discussion

### 4.1. General findings

We had fewer detections in conifer plantations than in native vegetation for most carnivore species of carnivore, although detection rates varied among species. Presence of each species

was associated with habitat characteristics at different spatial scales, and was a function of vegetation structure and food availability. Many of these characteristics did not clearly differ between plantations and continuous native vegetation, but gradually changed across space. As a consequence, presence of most species was not directly related to habitat type, but to the complexity or heterogeneity of vegetation structure and landscape attributes. These results are consistent with the “continuum model” (Fischer and Lindenmayer, 2006), which assumes species respond individually to their environment and suggests gradual changes in habitat quality through space. The continuum model conceptualizes landscapes as varying across gradients of food, shelter, space, and climate, which may be defined with respect to habitat variables important for each individual species. From a conservation standpoint, this model focuses on habitat heterogeneity at multiple spatial scales to enhance the number of niches available to different species (Fischer and Lindenmayer, 2006). In this way, our results suggest that conifer plantations are not inhospitable habitat for some species of carnivores, but that plantation management can significantly influence the extent of their use.

#### 4.2. Individual species changes

*Leopardus geoffroyi* was detected least often in plantation-dominated landscapes, and was detected almost exclusively in native vegetation. This differential use might be driven by prey availability, as European hare and rodents, the most preferred preys of this species (Novaro et al., 2000), are less abundant in conifer plantations (Lantschner et al., 2011). Consistent with our results, the wildcat has shown to be sensitive to prey availability, reducing their densities to the low abundance of food (Pereira et al., 2006). In central Argentina, Pereira et al. (2011) found that *L. geoffroyi*, was less abundant in areas where livestock was present potentially due to lower prey abundance in grazed areas. Alternatively, vegetation structure may have contributed to the observed response of *L. geoffroyi*. The association of this species with habitats with low tree density, and particularly with patches of *N. antarctica* forest and shrubland, is probably due to a greater availability of shelter structures such as holes in the trunks (Johnson and Franklin, 1991). In this way, dense conifer plantations may not offer the habitat structures required by *L. geoffroyi*, although presence of this species in firebreaks and native vegetation remnants evidences its use of plantation landscapes.

For *L. culpaeus*, we observed the same pattern of habitat use based on relative abundance data and on the occupancy estimation models (MacKenzie et al., 2005). Both relative abundance and occupancy of this species in dense conifer plantation were lower than in continuous native vegetation, sparse conifer plantation, and fire breaks, but similar to relative abundance and occupancy in native vegetation remnants. Detection rate for *L. culpaeus* possibly was lower in conifer plantations relative to continuous native vegetation due to reduced understory cover and vegetative diversity within dense plantations, which may result in lower availability of refuges and prey (Lantschner et al., 2011), particularly their main prey, European hare and small mammals (Novaro et al., 2000). Our results contrast with those of Acosta-Jamett and Simonetti (2004) in central Chile, who found that *L. culpaeus* was abundant in conifer plantations and scarcely used native vegetation. This difference in findings could result from differences in landscape context and vegetation structure, as well as in prey availability. Prey abundance in Chile is higher in conifer plantations than in native vegetation (Saavedra and Simonetti, 2005), whereas it was lower in conifer plantations in our study area (Lantschner et al., 2011).

For *C. chinga*, although we did not find statistically significant differences in use of habitat types, we found that the number of

records of this species was positively associated with cover and patch size of native vegetation. This finding suggests that *C. chinga* uses all habitat types as long as at landscape scale the cover of native vegetation is high, probably because of the higher availability of refuge structures and of their main preys – beetles and small mammals (Donadio et al., 2004) – in native vegetation respect to conifer plantations (Paritsis and Aizen, 2008; Lantschner et al., 2011).

*Puma concolor* was detected in conifer plantations as frequently as in continuous native vegetation. Indeed, at landscape scale it showed a positive relationship with size of plantation patches. *P. concolor* is an opportunistic predator (Novaro et al., 2000), so it may be favored by increased abundance in plantations of two introduced species, wild boar and red deer (Lantschner et al., submitted for publication), which have been described as important prey (Novaro et al., 2000). Consistent with our results, *P. concolor* was found to be more abundant in conifer plantations than in the replaced native forest in southern Chile (Zuñiga et al., 2009) and was similarly or even more frequently detected in pine and *Eucalyptus* spp. plantations in southern Brazil than in native forest (Lyra-Jorge et al., 2010; Mazzolli, 2010). There is considerable evidence that *P. concolor* is not affected, and may be benefitted, by presence of exotic forest plantations, probably due to their higher capacity to exploit a diverse array of habitats (Iriarte et al., 1990; De Angelo et al., 2011).

Because the relationships we found between species and habitat variables were not derived from an experimental study, but an observational one, inferences from these data should be made cautiously. Some of the observed patterns of relative abundance may have been the result of variables we could not account for, such as the influence of previous land uses, or interactions among species. Therefore, the pattern of habitat use by carnivore species found in this research should serve as a base for future studies that provide experimental test to the observed relations between species and habitat variables. Additionally, indexes of relative abundance for *P. concolor*, *C. chinga*, and *L. geoffroyi* should be taken with caution, since we could not assess if differences among habitat types are affecting the probability of detection.

#### 4.3. Management implications

Currently, the area of planted forest in Patagonia is relatively low and restricted in distribution, and as consequence the overall impact on carnivore species is probably low. However, in the future the amount of area of plantations will probably increase, and there will be opportunities to consider both biodiversity conservation and timber production objectives when designing and managing the new plantation landscapes.

Our results suggest that forested landscapes may be managed at different spatial scales to sustain use by some species of carnivores. Managing sites for high diversity of understory plants and low overstory cover may benefit carnivores. Understory species diversity may provide more favorable microclimates and increased abundance of prey species (Lindenmayer and Hobbs, 2004). Plantations in Patagonia are typically established at high densities (1100–1600 trees/ha); under these conditions the canopy quickly closes and the understory vegetation is shaded out. Thus, dense stands commonly support lower abundances of wildlife (Hayes et al., 1997). Reduced planting densities and early thinning would likely enhance richness and cover of plantation understory vegetation (Bailey et al., 1998). Our results suggest that sparse conifer plantations favor presence of the two species relative to traditional dense conifer plantations, *L. culpaeus* and *C. chinga*. Thus, landscapes with greater area of sparse plantations could have stronger positive effects on these species.

At the landscape scale, use by most species was associated with patch size or proportion of area covered with native vegetation. This association highlights the importance of retaining native vegetation in the landscape, and the conservation value of plantations is likely to be greater with close proximity to native vegetation (Lindenmayer and Hobbs, 2004). Therefore, from a conservation standpoint, an optimal landscape design should prevent creation of large, closed-canopy plantations located far from native vegetation. Firebreaks appear to have an important value as habitat for carnivores insides forested landscape.

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