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Occupancy patterns of two contrasting carnivores in an industrial forest mosaic

Liliana Guzmán-Aguayo[a], Franco Magni-Pérez[a], Benito A. González[b], Cristián F. Estades[b], Romina Medel[b], Héctor Jaime Hernández[a,*]

[a] Geomatics and Landscape Ecology Lab (GEP), Forestry and Nature Conservation Faculty, Universidad de Chile, Santiago, Chile
[b] Ecology and Wildlife Lab (LEVS), Forestry and Nature Conservation Faculty, Universidad de Chile, Santiago, Chile

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ABSTRACT

Normally, industrial forest landscapes are mosaics of different exotic and native vegetation patches, and, depending on their structural and functional diversity, they may be able to support potentially important biodiversity. In Central Chile, there are 3.1 million hectares of exotic forest plantations, and these environments are included as habitat, among others, of two contrasting carnivores: the generalist culpeo fox (*Lycalopex culpaeus*) and the kodkod (*Leopardus guigna*), a forest specialist cat. For this study, we sampled a large area (~350 km^2) in the coastal range of Central Chile with camera traps (n = 500) for three consecutive years to observe the summer occupancy patterns of these two carnivores. We used single season occupancy models with covariates at landscape and local scales. The main results showed that, for the culpeo fox, the proportion of harvested area had a positive influence on its occupation, whereas for the kodkod the proportion of bare soil and leaf litter had a negative and positive influence, respectively. Since both species occupy the landscape mosaic created by the forestry industry, it would be valuable to integrate the observed occupancy patterns into conservation plans at both local and landscape levels for these species.

1. Introduction

Although producing wood and biomass is the primary goal of forest plantations, over the past three decades there has been a growing interest among society and timber companies in improving the roles of these industrial forests in protecting biodiversity (Hartley, 2002; Lindenmayer and Hobbs, 2004). Forest plantation management can be compatible with biodiversity conservation as a result of the temporal and spatial patterns of vegetation it produces (Hartley, 2002). Animals that inhabit forest plantations may experience different habitat qualities depending on their use of space and general habitat requirements (Virgós et al., 2002; Lassauce et al., 2011; Cerda et al., 2015). The new environment created by silvicultural schemes has an impact on landscape and local patterns of use by creating different scenarios such as patch quality, forest vegetation composition, and the vertical/horizontal structure of stands influencing the presence and abundance of wildlife (Ramírez and Simonetti, 2011; Holbrook et al., 2019). Several investigations have shown that carnivores are among the species most affected by intensive forest management. These effects can be related to restrictions on movement (Pliscoff et al., 2020), the use of the understory forest as a secondary habitat (Simonetti et al., 2013), or the absence of negative effects of logging on the presence of carnivores (Escudero-Páez et al., 2019). Their ecological significance stems from their capacity to control prey populations and significantly alter the dynamics of the ecosystem in which they act as predators (Ripple and Beschta, 2006; Wikenros et al., 2017). Therefore, the presence of carnivores is frequently used as an indicator of healthy and sustainably managed forest ecosystems (Simberloff, 1999; Gao et al., 2015; Brockerhoff et al., 2017). Yet the interaction between carnivorous species and silvicultural management in a forest environment has scarcely been explored on various spatial scales over time (Moreira-Arce et al., 2016; Lyra et al., 2010; Rodas-Trejo et al., 2010).

The coastal range of Central Chile concentrates most of the 3.1 million hectares of the country's exotic forest plantations (Cortés et al., 2022), and at the same time is considered a world-class biodiversity hotspot (Fuentes-Castillo et al., 2020). Intensive silvicultural schemes in

* Corresponding author at: Geomatics and Landscape Ecology Lab (GEP), Forestry and Nature Conservation Faculty, Universidad de Chile, Av. Santa Rosa 11315, La Pintana, Santiago, Chile.
E-mail address: jhernand@uchile.cl (H. Jaime Hernández).

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20-year commercial cycles are the basis of the forest management in this region, which involves a harvesting-replanting cycle with a number of intermediate silvicultural treatments (i.e., thinning and pruning) (Espinosa et al., 2017). These productive cycles generate different changes at local and landscape level, influencing the presence and abundance of wildlife, especially carnivores, which must increase mobility to search and hunt their prey (Fernández et al., 2021; Iriarte and Jaksic, 2012). Two carnivores, the culpeo fox (*Lycalopex culpaeus*) and the kodkod (*Leopardus guigna)*, are common in forest plantations in south-central Chile. The culpeo fox is one of the most widely distributed carnivores in South America and the largest canid in Chile, inhabiting different vegetation formations, from mountainous terrain to deep valleys (Novaro, 1997; Iriarte and Jaksic, 2012). This canid has been considered a solitary and opportunistic hunter due to its nocturnal and crepuscular habits that allow it to feed on small mammals at night (Cadena-Ortíz et al., 2020). By contrast, the kodkod is the smallest feline in the Western Hemisphere; it inhabits forested areas such as humid and temperate forests, scrub, even pine and eucalyptus forest plantations (Iriarte and Jaksic, 2012). This small feline is active during the day and night, but where there is a human presence it has nocturnal hunting habits for small mammals (rodents and lagomorphs) (Napolitano et al., 2015; Iriarte, 2008). Due to their contrasting behaviors, becoming familiar with their responses to changes on different spatial scales over time caused by forestry practices is of great interest to inform the development of new recommendations and regulations for sustainable forest management.

Using occupancy models is one way to understand how predators use their environments where they inhabit. They estimate the probability of occurrence of a species among sampled sites while testing hypotheses on environmental factors believed to influence the occurrence of the species (MacKenzie et al., 2002). Sampling schemes designed to estimate occupancy tend to require less effort than programs aimed at estimating abundance (Manley et al., 2004). In this study, we analyzed the occupancy patterns of two carnivores with different degrees of habitat specialization at landscape and local scales over three seasons in an industrially managed forest environment. Our hypothesis was that, even in this highly modified landscape, most carnivore species would occupy environments in a way that resembles their behavior. Thus, we expected the culpeo fox, an opportunistic, generalist predator to occupy a wide range of vegetation covers, regardless of its degree of habitat modification by humans. The kodkod, a known forest-scrub specialist, was expected to occupy mainly dense forested environments (native and/or planted), concentrating in areas with low human and domestic carnivore activity.

2. Materials and methods

2.1. Study area

The study area is located on the Central coastal range of Chile, in the commune of Constitución, Maule Region, between 34° and 36° southern latitude (Fig. 1). This region is part of the *Chilean winter rainfall–Valdivian forests*, one of the world's 35 biodiversity hotspots (Zamora-Manzur et al., 2011). The climate is warm-temperate and the original native vegetation was a Maulino deciduous forest (Gajardo, 1994), an endemic forest type in central Chile dominated by *Nothofagus glauca* (Phil.) Krasser. Given the long history of timber and agriculture-livestock exploitation in the area, most native forests are secondary stands (Amigo et al., 2000; Aguayo et al., 2009; Uribe et al., 2020). In the 18th and 19th centuries, most of the original forests were clear-cut to make way for extensive agriculture, mainly dedicated to cereal production. This soil overexploitation caused serious reductions in soil fertility and degradation by erosion (Bauer, 1970), which led to the abandonment of extensive areas that were later planted with exotic forest species. In the second half of the 20th century, forest commercial plantations expanded significantly, further reducing the native forest

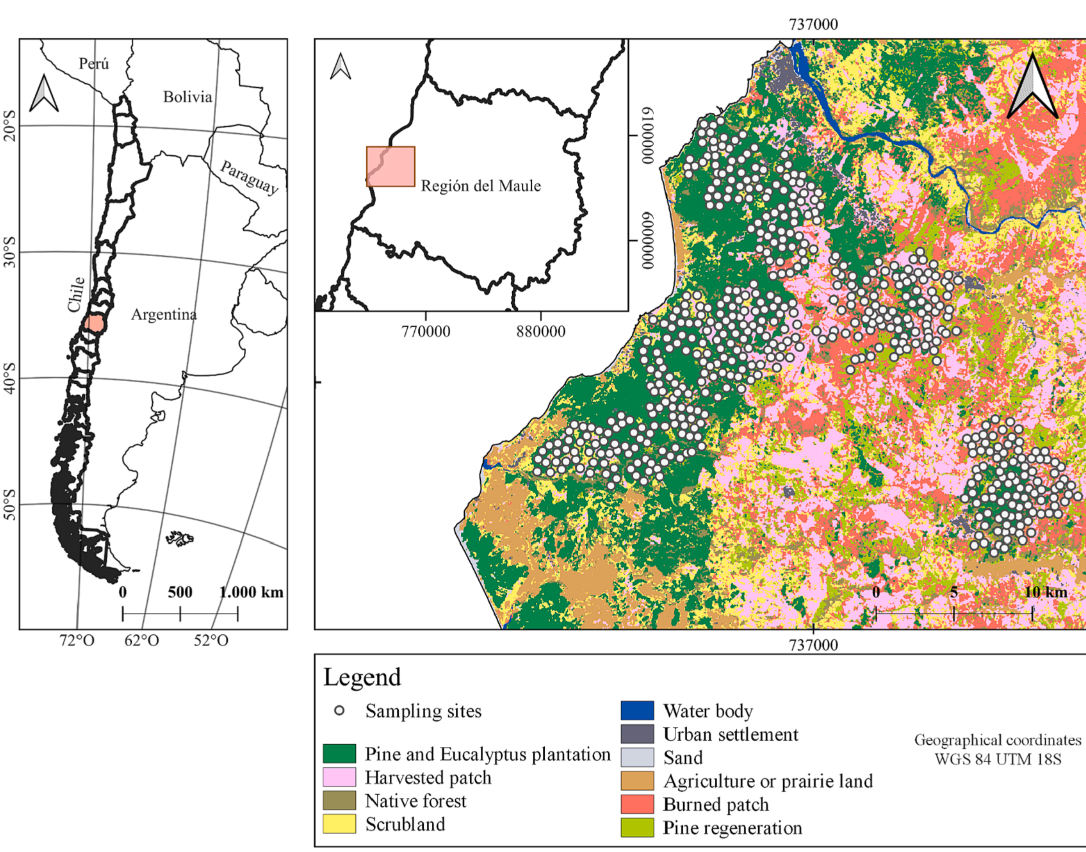

Fig. 1. Study area located on the Coastal range of Central Chile, Maule Region.

cover and increasing its fragmentation. A forest mosaic with exotic plantations of *Pinus radiata* and *Eucalyptus spp*. with some smaller remnant patches of native *Nothofagus glauca* dominates the current landscape (Uribe et al., 2020).

In the austral summer of 2017, Central Chile suffered one of its largest wildfires ever recorded. This megafire affected mainly the O'Higgins, Maule and Biobio Regions. In the Maule region, this forest fire, called "Las Máquinas", consumed over 279,000 ha, with 185,000 of these belonging to plantations of *Pinus radiata*, *Eucalyptus globulus* or *Eucalyptus nitens* (CONAF, 2017). The "Las Máquinas" megafire started in the commune of Cauquenes and spread through the communes of Empedrado and Constitución, leaving a large fire scar on the landscape. The main mammalian carnivores include the culpeo fox (*L. culpaeus*), chilla fox (*Lycalopex griseus*), kodkod cat (*L. guigna*), Andes skunk (*Conepatus chinga*), lesser grison (*Galictis cuja*), and puma (*Puma concolor*) (Iriarte and Jaksic, 2012).

2.2. Study design

Using Strike Force ProXD camera traps, we set 500 sampling units to study the target species during the austral summers of 2020, 2021, and 2022. We used five sampling zones (L1 to L5), each encompassing between 60 and 80 km^2 and containing 100 sampling units (Fig. 1). These sampling zones were selected for having different proportions of the main land covers present in the study area. The camera traps were set up for at least 14 days and were attached to trees or stumps at approximately 50–100 cm above ground level. To ensure replicability the same installation protocol, was followed during the whole study. Each camera trap unit was placed between 500 and 1000 m to the nearest camera trap unit. They were programmed to take three photos every 10 s each time an animal or object crossed the infrared beam. The home ranges were 1.3–22.4 km^2 for kodkod in fragmented environments (Napolitano et al., 2015) and 4.9–8.1 km^2 for the culpeo fox in different types of environments (Castellanos et al., 2022). To increase the likelihood of photo capture of individuals passing through the camera area, we used a punctured can of tuna fish as a short-range olfactory attractant (Escudero-Páez et al., 2019; Moreira-Arce et al., 2016). This can was nailed to the ground and removed when the period was over. Total sampling effort per season was 7,112 trap days. Renaming photographs, organizing data and classifying images were performed following the Small Wild Cat Conservation Foundation guidelines (https://smallcats.org/resources/). To avoid over-estimations in the analysis, species presence in photographs were considered independent events only if they were recorded 24 h between one detection and another of the same species (García et al., 2021; Osorio et al., 2020). Then, each photographic record was used to estimate the relative abundance index of each species by dividing the number of independent photographic events by the trap days at each station (Maffei et al., 2002; Cuellar et al., 2006).

2.3. Covariates

A group of variables representing different aspects of habitat and human influence were obtained for use as covariates in the occupancy models. They were selected because they have proven to be relevant for carnivores at local scale (Simonetti et al., 2013; Gálvez et al., 2021; Pliscoff et al., 2020), landscape scale (Beltrami et al., 2021; Ordiz et al., 2021; Ramírez and Simonetti, 2011; Gálvez et al., 2013) or both (Fernández et al., 2021; Guntiñas et al., 2021) in other similar areas. Centered at each camera location, using a sample site of 40 $\times$ 40 m^2, local covariates were the dominant tree height, tree density, pruning height and percentage of space covered by the various components on the floor. Landscape covariates were the proportions of land cover classes derived from Landsat 8 scenes of summers of the three sampling seasons. Land cover maps were obtained by supervised classification with the Random Forest approach in the Google Earth Engine. Using a 500 m area of influence at each camera site, the percentage of native forest, *Pinus radiata*, *Eucalyptus* sp., scrub, harvested areas and burned patches were recorded and assigned to each sampling point. Additionally, at the landscape scale, Euclidean distance to the nearest stream, urban areas, paved and unpaved roads (Escudero-Páez et al., 2019; Rodríguez et al., 2021) was recorded. These covariates (Table S1 in Supplementary material) were normalized using the Z-score method. Prior to modeling, multicollinearity was tested among the environmental variables using a Pearson correlation coefficient (r) for pairwise comparisons. Covariates with r $>$ 0.5 were not included in the same models (Graham, 2003; Wilson and Schmidt, 2015).

2.4. Occupancy model

To ensure the temporal independence of the records, the sampling events can be divided into a given number of hours or a day (Boitani, 2016). However, it is not always appropriate to have too many temporary detection units, since there may be convergence problems or biases in the accuracy of the models in cases where the species is not detected in most of the repetitions (i.e., many zeros in the detection history) (Guillera-Arroita et al., 2015; Steenweg et al., 2016; MacKenzie et al., 2017; Sollmann, 2018). Therefore, it is possible to "collapse" or divide the detection histories into a greater number of days or even weeks without affecting the occupancy estimate. A valid strategy to define the sampling event is to analyze the change in the accuracy of the occupancy probability or the model fit under different collapse intervals (MacKenzie and Bailey, 2004). A detection history matrix was built using the "camtrapR" package (Niedballa et al., 2016) to later estimate occupancy. To reduce nondections and facilitate modeling (Wevers et al., 2021; Wong et al., 2019) we decided to collapse all detection histories in 72 h (3-days). Sampling occasions were defined at 3-day intervals (five sampling occasions per year).

The occupancy modeling approach (MacKenzie and Bailey, 2004) was used to obtain the probabilities of occupancy ψ and probability of detection p for each species. Taking the effect of the other carnivores present in the area into account, each of their occupancy models were built to obtain the respective probability of occupancy and detection to then input them as covariates in the culpeo fox and kodkod models. We assumed that species migration or dispersion was unlikely to occur for three years, so the occupancy status remained constant under the time closure assumption (Linkie et al., 2007; Shannon et al., 2014; Guharajan et al., 2021). The influence of predictor covariates on ψ and p was evaluated using a maximum likelihood estimation with single-species, single-season models with the 'unmarked' package in R-project (Fiske and Chandler, 2011).

The modeling process had two steps and a final integration. First, while holding ψ constant we modeled p as a function of one covariate, two covariates and three covariates for all possible covariates and covariate combinations (MacKenzie et al., 2017; Schuette et al., 2013). The models were then ranked to select the most appropriate for detection using the Akaike Information Criterion (AIC) and best-supported models considered with a Δ AIC $\leq$ 2 (Burnham and Anderson, 1998). The selected models were then used in the next set of models to explore variation in occupancy. With the detection probability models already selected, a model set was created in which ψ was constant, a function of one covariate, then two and three in all possible combinations. Finally, the best models for p and ψ were combined and we were able to determine the best overall model that explained both parameters simultaneously.

The AIC weight is a value between 0 and 1, with the sum of AIC weights of all models in the candidate set being 1, which can be considered analogous to the probability that a given model is the best approximating model (Symonds and Moussalli, 2011). When more than one model was selected, we calculated the weighted average for ψ and p and their respective standard errors (SE) using AIC weights. As we considered only models having Δ AIC $\leq$ 2, these weights were corrected for the sum to be 1.

3. Results

Over the three years, the two carnivores in the study were recorded many times. For the culpeo fox, the number of presences detected by camera traps increased over the years ($n_{2020} = 220$; $n_{2021} = 252$; $n_{2022} = 268$). For the kodkod, after the first year there was a drop and then the number of detected presences stabilized ($n_{2020} = 83$; $n_{2021} = 49$; $n_{2022} = 51$). Other native carnivores that were also recorded in descending order of number of records were: the chilla fox, the Andes skunk, the lesser grison, the puma, as well as exotic species such as the domestic dog (*Canis familiaris*) and cat (*Felis silvestris catus*). Lesser grisons and pumas had only few records, so their occupation models were not considered in the analyses.

In the multicollinearity analysis, bare soil correlated negatively with leaf litter, and positively with harvested areas and rocks for the three years. In the case of harvested areas, it was negatively correlated with tree height, and positively with rocks.

The predicted occupancy probability for the culpeo fox was $\psi_{2020} = 0.39$ (SE: 0.06); $\psi_{2021} = 0.34$ (SE: 0.05); $\psi_{2022} = 0.38$ (SE: 0.06), and for the kodkod was $\psi_{2020} = 0.55$ (SE: 0.25); $\psi_{2021} = 0.52$ (SE: 0.22); $\psi_{2022} = 0.24$ (SE: 0.11). Fig. 2 shows the trend over time.

The best occupancy models (Table 1) presented similarities in the significant covariates from one year to another. For the culpeo fox, the proportion of harvested areas in the neighborhood significantly increased the occupancy of the species, whereas its detection probability increased with less cover from pine plantations (2021), and further away from urban settlements or more bare soil (2022). For the kodkod, the proportion of bare soil at the local scale significantly reduced the occupancy of the species every year and the proportion of litter increased the occupancy for 2020, while its detection probability increased with greater coverage of pine plantations. (2020) and with a lower proportion of harvested areas (2021). The coefficients of the covariates in the best models are presented in Table S2 in Supplementary material.

4. Discussion

Our study stands out for incorporating a simultaneous evaluation of the effect of the variables of local scale and surrounding landscape on two contrasting carnivores based on a large sampling effort, complementing the findings of previous biodiversity studies in forest plantations in Chile (Ramírez and Simonetti, 2011; Moreira-Arce et al., 2016; Fernández et al., 2021; Uribe et al., 2020). The data show that the industrial forest mosaic present in the coastal range of Central Chile, even after a long history of heavy human modifications, contains a considerable number of carnivores, including native and exotic species. Specifically, our results confirm the hypothesis that carnivores are occupying environments in a way that resembles their behavior, since the presence of the six carnivores that should be found in the area were recorded.

The results concerning the occupancy patterns of *L. culpaeus* reject the proposed hypothesis that this carnivore occupies a wide range of vegetation covers, as only the harvested areas and, to a lesser extent, the burnt patches were found to be occupied by *L. culpaeus*. On the other hand, the results for *L. guigna*, indirectly confirm the hypothesis that this forest specialist carnivore uses extensive forest environments. Among the identified occupation patterns, bare soil—a variable associated with open spaces lacking vegetation due to harvesting or urbanization—had a negative impact on this species.

However, the responses of carnivores to the different scales of landscape composition varied between species (Rodríguez et al., 2021). *L. culpaeus,* a generalist fox with wide distribution areas, takes advantage of harvested areas in the landscape, being less affected by productive forestry activity (Guntiñas et al., 2021; Moreira-Arce et al., 2016). The harvested areas, which present great human intervention, were a positive attribute for the abundance of this species and is the reason for the open areas often that potential prey, such as rodents and lagomorphs, of *L. culpaeus* often inhabit (Zúñiga and Fuenzalida, 2016).

On the other hand, the results suggest that for *L. guigna* the presence of bare soil is negatively affecting its occupation on the landscape, and leaf litter has a positive influence. The multicollinearity analysis determined the relationship of some variables at different scales, such as the bare soil at local level to the harvested area at landscape level, which is devoid of vegetation and thus contains a higher proportion of bare soil. This shows that one of the occupation patterns of *L. guigna* is the vegetation cover of its habitat, characterized by forest cover and without major human intervention (Moreira-Arce et al., 2016; Gálvez et al., 2013). The absence of native forest cover as a predictor of kodkod occupancy reflects a lack of the supposed strong dependence of this species on these forest types (Napolitano et al., 2015). Instead, research suggests that forest fragmentation and the condition of the forest understory significantly influence the activity of this specialist carnivore (Moreira-Arce et al., 2016; Gálvez et al., 2013). Empirical evidence is consistent with the possibility that this species is likely selecting areas with tree cover, regardless of their origin.

The proximity to human settlements or urban areas with anthropogenic influence could be restricting the use of the landscape by some native carnivores (Pereira and Novaro, 2014; Smith et al., 2018; Rodríguez et al., 2021). The results of the occupation patterns of this study show that human intervention is not favorable for *L. culpaeus*, since the greater the distance to an urban area, the greater its detection. In the case of *L. guigna*, close distances had no influence. Moreover, the literature indicates that native vegetation in industrial forest landscapes contributes to their complexity and structural diversity, favoring biological connectivity and the existence of complementary areas for food and shelter, contributing to the conservation of native carnivores (Cerda et al., 2015; Holbrook et al., 2019; Castro et al., 2022). Based on these results, it is reasonable to consider transitioning to spatially heterogeneous landscapes that locally reduce large tracts of bare soil and increase

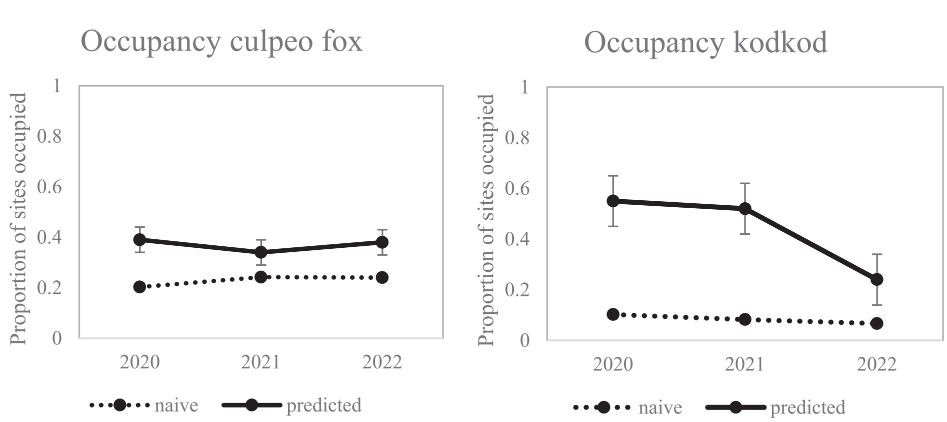

Fig. 2. Summary of the probability of sites occupied, naive and predicted, with the best model by species: a) culpeo fox, b) kodkod.

Table 1
Occupancy models for the culpeo fox and kodkod. * indicates statistically significant covariates; covariates with positive effects are in bold; capital or lower-case letters indicate landscape or local scale covariates, respectively.

Specie	Year	ψ Model covariates	p Model covariates	K	AICc	ΔAICc	AICwt
culpeo fox	2020	HARVESTED AREA* + BURNED PATCH	DISTANCE URBAN AREA + ψ domestic dog	6	1023.24	0.00	0.54
	2021	- HARVESTED AREA + ψ chilla fox	- PINE PLANTATION*	5	1237.41	0.00	0.42
	2022	HARVESTED AREA* + bare soil	DISTANCE URBAN AREA* + bare soil	6	1202.16	0.00	0.41
		HARVESTED AREA* + bare soil	DISTANCE URBAN AREA + bare soil* + ψ domestic dog	7	1204.07	1.16	0.80
kodkod	2020	- bare soil	leaf litter - HARVESTED AREA	5	526.68	0.00	0.32
		leaf litter* - bare soil*	- HARVESTED AREA - bare soil	6	526.72	0.045	0.64
		-HARVESTED AREA	PINE PLANTATION* - bare soil	5	527.74	1.06	0.83
	2021	- bare soil*	- HARVESTED AREA*	4	437.12	0.00	0.38
		- bare soil	- HARVESTED AREA* - bare soil*	5	437.86	0.74	0.64
	2022	- bare soil* + shrubs	(.)	4	376.55	0.00	0.45
		- bare soil* + shrubs	- HARVESTED AREA	5	378.51	1.74	0.64

the proportion of area covered by leaf litter and shrubs.

5. Conclusions

Forest mosaics in Central Chile, consisting of patches of plantations and native forests, provide habitats for wild carnivores. Given that forest plantations dominate land cover in central-southern Chile, the findings from this study have implications for designing sustainable landscape management strategies in other regions characterized by similar forest mosaics and carnivorous species. Furthermore, integrating the revealed occupancy patterns of these two contrasting carnivores into conservation plans at local and landscape levels would be valuable. Management strategies could explore the implementation of measures targeting both levels. This study demonstrates that the two carnivore species exhibit different occupancy patterns within the forest landscape. Therefore, the maintenance of forest mosaic landscapes, comprising a blend of native forests and plantations, is crucial as it provides a range of occupation options for these species.

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CRediT authorship contribution statement

Liliana Guzmán-Aguayo: Methodology, Writing – review & editing. **Franco Magni-Pérez:** Methodology. **Benito A. González:** Conceptualization, Methodology. **Cristián F. Estades:** Conceptualization, Methodology. **Romina Medel:** Data curation, Formal analysis, Writing. **Héctor Jaime Hernández:** Conceptualization, Methodology, Supervision, Funding acquisition, Project administration, Data curation, Formal analysis, Investigation, Resources, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2023.121170.

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