

Universidad de Concepción Facultad de Ciencias Naturales y Oceanográficas Magíster en Ciencias con Mención en Zoología

NICHE ASPECTS THAT ALLOW THE COEXISTENCE OF A CARNIVORE COMMUNITY IN DIFFERENT HABITATS OF ANDEAN MOUNTAIN RANGE IN CENTRAL CHILE

Tesis presentada a la Facultad de Ciencias Naturales y Oceanográficas de la Universidad de Concepción para optar al grado académico de Magister en Ciencias con mención en Zoología

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Marzo, 2024 Concepción, Chile

STATEMENTS

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ACKNOWLEDGMENTS

We thank the FONDECYT 1201506, 1220998, and VRID 220.113.100-INV projects for the funding and opportunity to carry out this work. Thanks are due to the members of the Mammal Laboratory and the members of the Evolutionary Ecology and Phyloinformatics Laboratory, as well as to Boris Castillo, Cristóbal Araneda, Pablo Fuentes, Raíza Sánchez, and all my friends who helped me in this academic process, in the field and laboratory work. I also thank my partner and family who gave me all the love I needed to have enough emotional stability to complete this program. All these people made the completion of this degree possible.

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FIGURE INDEX

1. RESUMEN

La competencia es producida por el solapamiento de nicho, especialmente en especies morfológica, ecológica, filogenéticamente similares y simpátricas. Sin embargo, si los recursos son suficientes las especies realizaran una partición del nicho en 3 ejes fundamentales: comida, tiempo y espacio. Entender las interacciones de los depredadores nos permite entender las relaciones ecológicas dentro de una comunidad. En Chile central hay especies de carnívoros viviendo en simpatría. A su vez, esta área concentra una mayor antropización del hábitat, llevando a las especies a coexistir en un ambiente con menor disponibilidad de recursos. Es por esto que el objetivo principal de este trabajo fue comprender como los tres ejes principales permiten la coexistencia de estos depredadores en un ambiente con recursos limitados. Proponemos que las especies de carnívoros relacionados ecológica y morfológicamente exhibirán una mayor segregación espaciotemporal para evitar el riesgo de agresión y la competencia de recursos. Mas aun, esperamos que, en el hábitat nativo, los carnívoros segregaran sus dietas debido a la alta diversidad de alimento. En el hábitat antropizado, más ítems de alimento exóticos será consumida dada la disminución de ítems nativos, cambiando la dinámica trófica entre los carnívoros. Para esto, comparamos un hábitat antropizado con un hábitat nativo en el parque nacional Radal Siete Tazas. Evaluamos el eje espaciotemporal con cámaras trampa, y para el eje trófico se colecto y analizo fecas de los carnívoros y se capturaron pequeños mamíferos en el área de estudio. Obtuvimos datos de 6 de 8 carnívoros. Casi todas las especies prefirieron las horas de oscuridad con excepción del quique, y presentaron distintas preferencias de hábitats. La dieta de los carnívoros estuvo compuesta en su mayoría de pequeños roedores, la mayoría especies exóticas. En el hábitat nativo, se observó un mayor número de interacciones entre los carnívoros con valores de solapamiento moderados y altos, mientras que en el hábitat antropizado hubo un menor número de especies depredadoras y menor disponibilidad de recursos, es por esto que se encontró

un menor número de interacciones, pero todas con un alto solapamiento de nicho. De los tres ejes principales, la segregación del nicho espacial y las distintas preferencias de hábitat parecen ser la llave para la coexistencia de esta comunidad de carnívoros a través de los diferentes tipos de hábitat; el nicho trófico y temporal por hábitat y especies también juegan un rol fundamental para evitar la competencia de recursos cuando el eje espacial esta solapado.

2. ABSTRACT

Competition is produced by niche overlap, especially in morphologically, ecologically, phylogenetically similar species, and sympatric. However, if resources are enough, species would do a niche partitioning in 3 fundamental axes: food, time, and space. Understanding predator interaction allows us to understand the ecological relationship inside a community. In central Chile, there are carnivore species living in sympathy. In turn, this area concentrates a greater anthropization of the habitat, leading species to coexist in an environment with less resource availability. Therefore, the main objective of this work was to comprehend how the three principal axes allow the coexistence of these predators in an environment with limited resources. We proposed that carnivore species with closely related ecology and morphology exhibit greater spatialtemporal segregation to avoid aggression risk and resource competition. Furthermore, we expect that in the native habitat, carnivores segregate their diets due to the high diversity of food. In the anthropized habitat, more exotic food items will be consumed due to the decrease of native items, changing trophic dynamics among competitive carnivores. To do that, we compared an anthropized habitat with a native one in Radal Siete Tazas National Park. We evaluated the spatialtemporal axis with camera traps, and for the trophic niche, we collected and analyzed carnivore scats and captured small mammals in the study area. We obtain data from 6 of 8 carnivores. Most species preferred dark hours, except quique, and had different habitat preferences. Carnivores' diet was mainly composed of small rodents, mostly exotic species. In the native habitat, we observe a greater number of niche interactions among carnivores with moderate and high overlap values, while in the anthropized habitat, there were fewer predator species and less resource availability; therefore, there was less niche interaction, but those were all high niche overlap. From the three principal axes, spatial niche segregation and different habitat preferences seem to be the keys to the coexistence of this carnivore community through these different habitats;

trophic and temporal niches per habitat and species also play a key role in avoiding resource competition when the spatial axis is overlapped.

3. INTRODUCTION

Concepts of niche and competition by resources are fundamentals for our comprehension of how sympatric species coexist. While the niche concept refers to all relevant resources for the existence of a species and its role within the ecosystem, the competition theory postulates that \geq two species cannot coexist if they depend on the same resources since these have a limited supply (Gause 1934; Hutchinson 1957; Tokeshi 1999). Competition can be induced by coexistence, and like a product of ecological niche overlap, this interaction is especially apparent within the mammalian carnivore guilds (Mammalia: Carnivora) because are the top or superior predators in most terrestrial communities and have evolved specialized morphology, physiology, behaviors and ecological requirements which drives to competitive interactions when they are in sympatry (Gittleman 1989; Hutchinson 1957; Hardin 1960; Schoener 1974; Alley 1982; Jaksic 2007). Nevertheless, if resources are enough, species will partition existing resources to coexist, reducing niche overlap by dividing into three main axes: food, space, and time (Hutchinson 1957; Pianka 1973; Chesson 2000; Macarthur & Levins 1967). Niche partitioning promotes biodiversity and is critical to ecosystem functioning and stability (Chesson 2000).

Also, anthropogenic disturbance is restructuring terrestrial ecosystems with global consequences for niche dynamics and biotic interactions (Foley et al. 2005, 2011). Currently, carnivores face significant anthropogenic threats in agricultural areas from habitat loss and fragmentation, disturbance by domestic free-roaming dogs and cats, and direct hunting by humans (Gálvez et al. 2021). Some effects of expanding human footprints on carnivores are restricting animal movements in space, increased wildlife nocturnality, and transforming resource niches and prey partitioning with widespread consequences for population, community, and ecosystem dynamics (Tucker et al. 2018; Gaynor et al. 2018; Thompson et al. 2012; Smith et al. 2018; Moss et al. 2016; Magioli et al. 2019).

These alterations can also affect interspecific competition. For example, decreasing prey density can increase resource competition, intensifying the negative interaction between carnivores (Powers & Jetz, 2019). For carnivores, all principal niche axes have rarely been explored concurrently to explain carnivore community structure and interactions (but see Thornton et al. 2004; Dröge et al. 2017; Miller et al. 2018). Ultimately, niche partitioning among carnivores is structured by body size (Polis et al. 1989; Donadio & Buskirk 2006): apex carnivores limit mesocarnivores, which limit small carnivores (Newsome & Ripple 2014). Thus, apex carnivores often create ecological opportunities for small carnivores, although the particular axis that is made available varies by the system (Prugh & Sivy 2020; Sévêque et al. 2020). Accordingly, understanding the mechanism structuring carnivore communities requires that all critical niche axes be quantified simultaneously (Rodriguez et al. 2022).

Chile has suffered significative spatial transformation due to fragmentation and the replacement of native habitats due to different human activities (Romero et al. 2003; Montenegro et al. 2004; Vogiatzakis et al. 2006; Lara et al. 1996; Acosta 2001; Echeverría et al 2006; Zuñiga 2009). The central zone of Chile mainly represents an ecologically important ecosystem due to the high concentration of endemic species, which characterizes it as a biodiversity hotspot, which is distinguished for having a marked seasonality (cold-wet winters and hotdry summers), its vegetation composed of the Chilean shrubland, and its high anthropization, where live more than 80% of the Chilean population (Arroyo et al., 2008; Mooney & Dunn 1970; Myers et. al 2000; Blondel & Fernández 2012). This has historically generated high anthropic pressure, forcing different native species to coexist in a highly modified habitat and constant contact with humans (Montenegro 2004; Vogiatzakis et al. 2006; Napolitano et al. 2020). In Chilean fragmented forests, it has been possible to identify a greater co-occurrence of terrestrial carnivore species in plantation areas than in native forests. Also, these species show diet homogenization, and it has been proposed that they are in a

strong competitive condition (Zuñiga et al. 2005; Zuñiga et al. 2009). Whereas, in undisturbed environments, the greater environmental availability of prey resources coupled with small differences in diet associated with temporal partitioning could contribute to the coexistence of carnivorous species (Walker et al. 2007; Napolitano et al. 2008; Nagy-Reis et al. 2019). In Central Chile, it is possible to find seven native species of terrestrial carnivores inhabiting the same ecosystems: Conepatus chinga, Galictis cuja, Leopardus guigna, L. colocola, Lycalopex griseus, L. culpaeus, and Puma concolor, which use similar environmental resources. According to niche theory, species using the same resource may partition their niches or segregate in another niche dimension, allowing their coexistence in the same habitat. However, what happens when these dynamics are disturbed by human activities? This question becomes more relevant when considering that predator resources in fragmented systems tend to homogenize because of the decrease of native prey in anthropized forests. Therefore, a competitive scenario can be promoted by facilitating the development of a new niche, at least in the trophic axis (Pasitschniak-Arts and Messier, 1998).

Following this niche partitioning conceptual framework, we hypothesize that carnivore species with closely related ecology and morphology (*i.e.*, between felids or mustelids and foxes) would exhibit greater spatial-temporal segregation to avoid aggression risk and resource competition. This dynamic would repeat in anthropized and native habitats. Furthermore, we expect that in the native habitat, carnivores segregate their diets due to the high diversity of native "food"/prey availability. In the anthropized habitat, carnivore species would consume more of human resources subsidies and exotic species due to availability and decreased native "food". This change in trophic dynamic would increase niche overlap among competing carnivores, particularly between specialist predators and hypercarnivores (*i.e.*, felids). To explore this mechanism of niche partitioning for these carnivores in an anthropized habitat, our objectives were:

- 1. Characterize the three main niche dimensions of a predator community in the Andes Mountains in central Chile: trophic, spatial, and temporal.
- 2. Evaluate how these niche axes change for the carnivore species between two different habitats (anthropized and native).
- Generate base material for developing evidence-based conservation policies for this group of terrestrial mammals, which is widely threatened in Chile.

4. MATERIALS AND METHODS

4.1 Study area. - The study was carried out in the Radal Siete Tazas National Park (-71.026 W, -35.458 S) located in Region del Maule, Chile, 50 km southeast of Molina, between 650 and 2156 m.a.s.l. The park is a privileged site due to its great biodiversity and endemism, playing a fundamental role in the conservation of the original ecosystems of the area (Molina Communal Ecological Council, 2015). The park is highly visited each summer, with more than 2000 people per day, and during 2023 winter was strongly affected by the rainy season enhanced by El Niño Southern Oscillation. We identified two contrasting areas for the study inside the park: an anthropized and a native landscape. The anthropized area corresponds to an abandoned pine plantation close to the "El Toro" sector, which has houses and campsites and a high summer population flux. In the pine plantation, most of the soil is bare and covered only with pine needles. The area also has isolated presence of Lithraea caustica, Gevuina avellana, Podanthus mitiqui, and Rubus sp. The native area corresponds to two different adjacent landscapes: 1) A Nothofagus semi-dense forest with abundant presence of Aristotelia chilensis and Lomatia dentata, and 2) a shrubland area with sandy soil and isolated trees of Nothofagus, Lomatia hirsuta, and Austrocedrus chilensis.

4.2 Trophic niche

4.2a Diet data. - Feces were collected by walking around the native and anthropized study areas following Muñoz (2008) protocol. Only whole feces were

considered, identified by morphology according to Muñoz-Pedreros (2010). Once in the lab, to preserve the samples, they were dried at 60°C for 24 hrs (Phillip et al. 2007). The samples were individually placed in a nylon mesh bag and washed in an automatic washing machine, with water only retaining the remains. These were dissected to identify digested prey items in each sample (fur, teeth, bones, seeds, feathers). Then, the items were classified into four food categories: arthropods, birds, mammals, and plant matter, and further identified to the lowest possible taxonomic level according to specialized literature (i.e., Chehébar & Martín 1989; Reise 1973; Pearson 1995), plus a database obtained with samples from the Zoology Museum of the Universidad de Concepción and small mammals captured in the study area during the fieldwork.

4.2b Diet analyses. - To estimate the trophic niche for each carnivore species, we calculated the relative frequency of occurrence of food items in predator feces (%FO). The reliability of the scat sample size was assessed for each species by plotting accumulation curves for prey species (Ray and Sunquist 2001). Next, we estimate trophic preferences, diet breadth, and similarity between carnivores with a correspondence analysis (CA) using %FO of each prey item for each predator and employing the "FactoMineR" package (Lê et al., 2008). We used bootstrap confidence ellipses to graphically represent the variability of the diet of each carnivore in the CA dimensions. Complementarly, we use the Levins standardized index ranging from 0 to 1 (i.e., specialist to generalist food habits, respectively; Levins 1968). To evaluate trophic niche overlap, we use Pianka's index, varying from 0 (exclusive food niches) to 1 (complete dietary overlap) (Krebs 1989). Finally, we evaluated significant changes in carnivore diets between habitats using bootstrapped empirical distribution and Mann-Whitney's U-test (Wilcoxon 1992). We use the Bonferroni correction for each p-value obtained to correct for the effect of multiple comparisons.

4.2c Prey availability. - To characterize prey availability per habitat, we estimate small mammals' abundance, richness, and diversity by live trapping with Sherman traps (5 m to 10 m spacing). With 160 traps, we set 2 capture lines by habitat spaced between 100 m with a layout that maximizes the distance to the edges of the designated habitat (Fernández et al. 2013). Traps were operated for periods of 3 to 5 nights. These were checked at dawn to reduce the capture time and were baited with crushed oats, vanilla, and peanut butter.

Richness was calculated as the total number of captured species. Abundance was estimated by directly listing small mammals (Hilborn et al. 1976) since the assumption of homogeneity of recapture probabilities is not required (Simonetti 1986). Also, we considered the independent records of small mammals obtained by the camera traps as potential prey. Diversity was calculated with the Shannon-Wiener diversity index (H; Cardenas et al. 2003). The H index considers the number of species and their representation (how many individuals per species) and measures diversity as $H = -\sum_{i=1}^{s} p_i \ln(p_i)$ with $p_i = \frac{n_i}{N}$. Where n_i is the number of individuals of *i* species, N is the pooled abundance of the species, and s is the observed richness. H value is bounded between 0 and ln(s) and tends to zero in communities that are not very diverse (Soler et al. 2012). In addition, we made a habitat grouping analysis based on species composition (presence/absence), using Jaccard's similarity index (Cardenas et al. 2003). Jaccard index, modified by Ellenber (1956), is only qualitative and it doesn't consider the degree of participation of each species in the ecological dominance, where a value closer to 1 indicates greater similarity (Magurran 1988). This index is defined as $J_{ij} = \frac{C}{S_1 + S_2 - C}$. Were S₁ = the number of species observed in zone 1, S_2 = the number of species observed in zone 2 and C = the number of shared species for S₁ and S₂ (Soler et al. 2012). Food item's availability and use were compared using the Pearson's correlation coefficient (r). These analyses were made in R software.

4.3 Temporal and Spatial niche

4.3a Camera trap data collection. - We placed 15 camera traps (Campark Upgrade Trail Camera T70 16 MP 1080P Game & Hunting Camera) in the native area and 15 in the anthropized area. We use a minimum camera spacing of 200 m to cover the largest possible area and maximize the probability of detecting the presence of the focal species (Silver et al., 2004). We considered sites with markings or traces of the species of interest, such as latrines or animal trails (Balme et al. 2009). To avoid affecting the behavior of target species, we did not use any bait or lure on the camera stations (Soyumert 2020). We set the cameras to take three photos per trigger without delay between pictures, in a continuous operation of 24 hours from November 2022 to January 2024. Cameras were checked at the end of every season to compile the information and to replace the batteries or SD cards. We divided the independent records of each species into 1-hour intervals over the 24-hour circadian cycle.

4.3b Daily activity patterns and temporal and spatial distribution overlap. - First, we calculated the relative frequency of records (Relative Abundance Index, RAI) in each camera trap as the number of detections per 100 days/trap for each habitat (Ferreiro et al. 2021). Then, to describe the activity patterns, we classified the records as diurnal if 90% of the independent records were found in daylight hours, nocturnal to those that 90% of the records were found in darkness, and cathemeral to those that presented activities during the day and at night (Gómez et al. 2005). We consider diurnal the records between 8:00 and 20:00 and nocturnal from 20:00 to 8:00, like an average of daylight hours since in Chile, seasons are marked with longer daylight hours in summer and shorter ones in winter. Also, we evaluated temporal segregation between the activity patterns of carnivore species pairs and tested for shifts in daily activity patterns between anthropized and native habitat using the nonparametric Mardia-Watson-Wheeler test (MWW, Batschelet 1981) with the "circular" package

(Agostinelli & Lund, 2017). Finally, we used the nonparametric Kernel density function to estimate the activity overlap coefficient (Δ) between carnivore species and habitat type (Ridout & Linkie 2009; Linkie & Ridout 2011). This coefficient, defined as the area under the curves formed by the two density functions at each time unit, varies from 0 (no overlap) to 1 (total temporal overlap of the activity; Ridout & Linkie 2009). We obtained 95% confidence intervals for the estimated overlap coefficients from 1000 bootstrap samples (Linkie & Ridout 2011; Meredith & Ridout 2018). We use the $\Delta 1$ coefficient for small samples (<75 records for at least one of the compared pairs) and the $\Delta 4$ coefficient for large samples (>75) records; Ridout & Linkie 2009). These analyses were performed with the "Overlap" package of R (Meredith & Ridout 2018; R Development Core Team 2020). Activity overlap between each comparison was classified as follows: low overlap ($\Delta \le 0.5$), moderate overlap ($0.5 < \Delta \le 0.75$), and high overlap ($\Delta > 0.75$) (Monterroso et al. 2014). We performed pairwise comparisons of the activity patterns of predators in each study site only in those cases where we had more than ten independent records (Fisher, 1995).

Habitat use was estimated as the relative frequency of each photographic record of each species in each habitat type (Zuñiga & Jiménez 2018). Furthermore, we calculated the pairwise species overlap between the activity centers of carnivores based on the RAI data of each habitat for each camera (Ferreiro-Arias et al. 2021). The activity centers were spatially represented for each carnivore species and site using the packages "*ggmap*" and "*ggplot2*" (Kahle & Wickham, 2013; Wickham, 2016). We calculated the spatial overlap between predators using Pianka's index (PI; Pianka 1973). We calculated bootstrapped confidence intervals around PI using the "*spaa*" package (Zhang et al. 2013). All analyses were conducted using R Software (R Core Team, 2020).

5. RESULTS

5.1 TROPHIC NICHE

During the study period, we identified and stored 167 scats. We collected scats of güiña, culpeo fox, and puma in both habitats. Scats of colocolo cats were only found in the shrubland area of the native habitat, and we did not find scats of Quique or Chingue (Table 1). Given the results of the species accumulation curve, all diets in this study were representative except for the puma in the anthropized habitat, which was excluded from further analysis (Table 1, Fig. 2). We can recognize a decrease in the number of scats collected during the winter season due to the heavy rains experienced in the 2023 summer.

5.1a Diet composition and correspondence analysis. – With the U-test (Table 2), we found significant differences in niche breadth and diet composition between all the carnivore species evaluated. Also, we found that güiña and culpeo fox had significant differences in their diet composition between the anthropized and the native habitats (p>0.05; Table 2). According to Levins index, culpeo fox had the broader trophic niche in both habitats ($B_{est} = 1$), followed by the puma at the native habitat ($B_{est} = 0.61$), güiña at the anthropized habitat ($B_{est} = 0.54$), colocolo cat in the native ($B_{est} = 0.3$) and güiña at the native habitat (0.18) (Table 1).

Güiña showed a specialist diet in both habitats but with a wider niche amplitude in the anthropized habitat. It also showed significant differences in diet composition (Native $B_{est} = 0.18$; Anthropized $B_{est} = 0.54$, Table 1; p >0.05 Table 2). In the native habitat its diet was composed strictly by small mammals (%FO = 96.3%) mainly exotic species such as rats (%FO = 40.7%) and native rodents like *O. bridgesi (%FO = 22.22%)*. This species, in the anthropized habitat, had a broader diet composed of small mammals ((%FO= 55.8%) mostly exotic species, arthropods (%FO= 26.47%) and plant matter (%FO= 14.7%) like *Prunus* sp seeds.

Colocolo cat showed a specialist diet ($B_{est} = 0.3$, Table 1) in the native habitat, composed of small mammals (%FO= 85.7%) and arthropods (%FO= 14.3). The Colocolo cat preys mostly on rats (%FO= 28.57%), rabbits (%FO= 23.81%) and native rodents like *Octodon bridgesi* (%FO= 14.29) and *P. xanthopygus* (%FO= 9.52).

Puma showed a more generalist diet in the native habitat ($B_{est} = 0.61$; Table 1) than the other felids, feeding mainly on small mammals (%FO = 56.76%), arthropods (%FO = 29.73%) and plant matter (%FO = 8.11%). Puma's main prey were *Oryctolagus cuniculus* (%FO= 21.6%), *Rattus* sp (%FO = 8.11%) and *Phyllotis xanthopygus* (%FO = 8.11%). Also, puma consumed coleoptera species like *Bolborhynum* sp, *Heliofugus* sp and *A. cummingii,* and *Prunus* sp fruits.

In both habitats, the culpeo fox had the broadest diet of all carnivore species and showed significant differences in diet composition between the anthropized and native habitats ($B_{est} = 1$; p>0.05; Table 1,2). Its primary food item was arthropods (%FO native-anthropized = 36 - 37%) with species like *Acanthinodera cummingii, Heliofugus* sp or *Brachystermus* sp, followed by plant matter (%FO native-anthropized = 32-33%) with species as *Malus domestica* in the native habitat and *Cryptocacrya alba* in the anthropized as the most important, and small mammals (%FO native-anthropized = 20-24%). While in the anthropized habitat, it consumed more exotic species, mainly *Rattus* sp (%FO = 8.08%), in the native habitat, it preyed upon native and exotic species equally (%FO = 9.09%).

The first two dimensions of the correspondence analysis (CA) explained 70.37% of the variability of carnivore diets (Fig. 3). Axis 1, which explained 40.39% of the variation, points out trophic preferences of güiña, colocolo cat, puma, and culpeo fox in the native habitat. Güiña and colocolo cats showed close values due to their specialist behavior and preferences for exotic and native small

mammals. Puma showed greater variety of trophic items, having an intermediate position between the specialist small felids and the generalist, culpeo fox. Axis 2 explained 29.98% of the variance generated by güiña and culpeo fox trophic preferences in the anthropized habitat. Güiña showed a wider variety of items in the anthropized habitat, including arthropods and vegetal matter. Meanwhile, the culpeo fox remains a generalist species that consumes the same groups in the anthropized habitat, and specific items of those groups change between habitats.

5.1b Trophic niche overlap. - We found the highest overlap values and more cases of niche overlap between carnivore species in the native habitat than in the anthropized one (Table 2). Here the highest value of Pianka's index was for the overlap of the güiña and colocolo cat PI =0.86(0.54-0.95), followed by colocolo cat with puma PI=0.77 (0.57-0.92), culpeo fox and puma PI=0.58(0.45-0.75), and the lowest overlap was found between güiña with puma 0.56(0.34-0.71). At the anthropized habitat, we only found one trophic niche overlap between güiña and culpeo fox with a moderate overlap value PI = 0.7(0.47-0.89).

5.1c Prey availability. - 38 individuals were captured, and we obtained 1004 independent records of small mammals in the park. The native area was the richest site for small mammal species and abundance, with 37 captures and 620 independent records (Table 3). The following species were recognized in the native area: *Abrothrix olivacea, A. longipilis, Oligoryzomys longicaudatus, Octodon bridgesi, Phillotys xanthopygus, Dromiciops bozinovici, Rattus* sp and *Orictolagus cuniculus*. The anthropized area was the poorer in terms of species and individuals. We find *O. longicaudatus, O. cuniculus* and *Rattus* sp. As measured by the Shannon-Wiener index, species diversity showed that the native area was more diverse than the anthropized (H native = 0.74, H anthropized = 0.5). The Jaccard index showed that the prey availability of the native habitat was not similar to that of the anthropized habitat (J = 0). Pearson correlation indicates that Colocolo cat (r=0.52), culpeo fox (r=0.69), and puma (r=0.86) in the native

habitat had an opportunistic behavior with a high correspondence between small mammals available and small mammals consumed while güiña showed as more specialist (r=0.26). In the anthropized habitat, the culpeo fox had a lower correspondence prey available/consumed (r=0.17) and güiña showed more opportunistic (r=0.73) (Table 3).

5.2 SPATIAL-TEMPORAL NICHE

We recorded six of seven carnivores expected for the study area (Table 4). The number of records ranged from 245 for the culpeo fox to just two records for the puma. Due to the low number of records, the latter species was excluded from all posterior analyses. The total sampling effort was 424 days/trap. We obtained 1135 photographs, from which 344 were independent records. The most abundant species considering both habitats (anthropized and native) were culpeo fox (RAI=2.31, N = 245) and güiña (RAI = 0.34, N = 36), followed by chingue (RAI = 0.25, N = 26), quique (RAI = 0.18, N = 19), colocolo cat (RAI = 0.15, N = 16) and puma (RAI = 0.02, N = 2). RAI values for most predators were highest in the native habitats except for güiña (RAIanthropized = 2.42) and puma (RAIanthropized = 0.44) (Table 4).

Most species preferred dark hours, but only chingue and colocolo cat were strictly nocturnal (96.2% and 93.8% of records in dark hours, respectively; Table 4). Güiña and culpeo fox were categorized as cathemeral, mostly nocturnal (25/75% and 24.9/75.1% of records light/dark hours respectively; Table 4), and quique was the only carnivore strictly diurnal (100% of records in light hours; Table 4) with its highest activity at midday. Chingue and güiña showed their activity peak between 00:00 and 6:00. While colocolo cat and culpeo fox went from 18:00 to 00:00 (Fig. 4). Most of the carnivores except quique decreased their activity patterns between 12:00 and 18:00, starting at dusk and finishing at dawn (Table 4). Only the culpeo fox had enough records per habitat to compare its daily

activities between anthropized and native habitats, and its time distribution patterns were very similar between habitats (Δ =0.82[0.73-0.91]; W = 0.77, *p*-value = 0.67; Table 4; FigS. 1).

5.2a Temporal overlap. - Temporal overlap values between carnivores varied widely from 0.14 to 0.82 (Fig. 4; Table 5). The activity distribution test indicated significant differences in the activity patterns for 5 of 10 carnivore contrasts (Table 5). We found that quique is the only carnivore that does not overlap its temporal activity with the other species and has the lower overlapping value with chingue ($\Delta = 0.14$; W = 34.4, *p*-value <0.001). On the contrary, colocolo cat and culpeo fox showed the highest temporal overlap ($\Delta = 0.82$; W = 0.46, *p*-value = 0.79), followed by chingue and güiña ($\Delta = 0.81$; W = 2.4, *p*-value = 0.3), and güiña and culpeo ($\Delta = 0.79$; W = 6.53, *p*-value = 0.03). While güiña and colocolo cat ($\Delta = 0.71$; W = 2.35, *p*-value = 0.3), chingue and colocolo ($\Delta = 0.66$; W = 39.07, *p*-value = 0.14), and chingue and culpeo fox ($\Delta = 0.66$; W = 11.32, *p*-value <0.01) showed moderate overlapping values. For more information, see supplementary material.

5.2b Habitat preferences and Spatial overlap. - For habitat preferences, only chingue (92.3% records) and colocolo cat (100% records) were limited to the native habitat, while güiña mainly appeared in the anthropized area (94.4% records). Quique was found almost equally in both habitats (52.6% records in anthropized and 47.4% native) and culpeo fox was also in both habitats but mostly in the native area (36.6% records in anthropized and 63.7% native) (Table 4).

Carnivores showed similar activity centers (peak RAI values) (Fig. 5) along one year of sampling, but moderate and variable spatial overlap values across the two study sites. In the native habitat, PI values go from 0 to 0.69. We found three pairs of carnivores with moderate spatial overlap values: quique with chingue PI = 0.69 (0.05-0.94), güiña with culpeo fox PI = 0.66 (0.34-0.9), and Quique with culpeo fox PI = 0.63 (0.29-0.83). While in the anthropized habitat, there was only one pair of species with high spatial overlap value quique and güiña PI = 0.79 (0.17-0.98) and one with moderate overlap value culpeo fox with güiña PI = 0.5 (0.3-0.8) (Table 6).

6. DISCUSSION

Our work reveals two major results. The first one is that the coexistence of this carnivore community among anthropized and native habitats in Radal Siete Tazas NP is driven mainly by habitat preferences and spatial niche segregation. In addition, we find resource partitioning in the other two axes evaluated (temporal and trophic) on a finer scale to avoid resource competition when the spatial axis overlaps, becoming evident in different activity peaks between species or a slight diet composition variability through habitats. Spatial segregation or differential space use among sympatric carnivores is likely context and species-dependent, changing with community membership and landscape characteristics (Heim et al. 2019). This reinforces the idea that the coexistence mechanisms underlying community structure are multidimensional and must be analyzed integratively (Ferreiro-Arias et al. 2021). Our second significant result is the poorer prey diversity in the anthropized than in the native habitat. Consequently, the anthropized habitat hosts fewer carnivore species and few overlapping interactions but with higher overlap values. Carnivores' habitat use is strictly related with prey availability (Mortelliti & Boitani 2008). Also, carnivores often change their abundance following prey density (Angerbjorn et al. 1999; Gilg et al. 2006; Pereira et al. 2006). Resource availability is a strong predictor of carnivore spatial distribution (Rich et al., 2017; Ver Schueren et al., 2021), and spatial overlap between is usually higher when prey densities are lower to maximize resource acquisition (Karanth et al., 2017). Thus, the spatial niche interactions found here suggest that prey densities in the anthropized area are insufficient to support the predator community increasing competition between species.

The effective conservation of carnivores in their natural environment requires an understanding of how these carnivores coexist without competitively excluding one another (Muller et al. 2022). Our results show a high temporal overlap of the species activity in dark hours, starting at sunsets and decreasing through the morning, except for quique which shows mainly diurnal activity. However, variation was noticed in their activity peaks. Muller et al. (2022) found similar variation between caracal and leopard temporal activity; caracal activity peaked around midnight, while leopard activity peaked around dawn and dusk. It has been suggested that temporal segregation is uncommon between potential competitors possibly due to constraints in the biological clock of the species and the costs of shifting from one circadian cycle to another (Palomares & Caro 1999; Schoener 1974; Kronfeld-Schor & Dayan 2003). Although it is clear that carnivore temporal overlap is high, given that temporal activity patterns have evolved to satisfy a variety of selection forces that differ amongst species to minimize interactions with competitors, while increasing chances of hunting success (Hayward & Slotow, 2009; Karanth et al., 2017), it is plausible that smaller species like quique, chingue, and güiña could alter their peak activity to optimize this trade-off and also avoid potential bigger predators of the area such as culpeo fox or colocolo cat. The latter alter their peak activity to avoid puma, facilitating the coexistence of these species, especially if they are spatially overlapping. Subordinate carnivores can They are potential prey for larger body-size carnivores. Therefore, they can display prey strategies such as modifying their behavior by balancing their need to forage and avoid large predators ("Ecology of Fear", Brown et al. 1999). Therefore, food-rich habitat patches with significantly high predation risk could remain spatially or temporally unoccupied (Linkie and Ridout 2011).

Moreover, there is a trophic niche overlap in the two habitats, which was detected for the three feline species and the culpeo fox. We could not find any scat from chingue or quique. However, we presume possible the trophic niche overlap between these species and the other carnivores since they feed mainly on arthropods and small mammals depending on their availability in the environment (Donadio et al. 2004; Zapata et al. 2001; Zuñiga et al. 2005; Sade et al. 2012), and trophic overlap has already reported between quique and culpeo fox in central Chile (Elberspenger 1991) and between quique and chilla fox in Argentina (Palacios et al. 2012). On the other hand, güiña, colocolo cat, and puma showed high overlap in their trophic niche, at least in the native habitat, mainly consuming small exotic mammals. This agrees with previous studies for neotropical small felids, whose also present temporal overlap and diets based mainly on rodents, lagomorphs and marsupials (Bisceglia et al. 2008; Silva-Pereira et al. 2011; Iriarte & Jaksic 2012; Pérez-Irineo et al. 2017; Foster et al. 2013; Gutiérrez-González & López-González 2017; Harmsen et al. 2009; Porfirio et al. 2017; Scognamillo et al. 2003; Hernandez-Sanchez & Santos-Moreno 2020).

Interestingly, the güiña, a species with a narrower diet compared to the colocolo cat and puma, could use the pine plantation from 2022 to 2024 consistently. This shows that the güiña has more ecological flexibility than the colocolo cat, which was limited to the native scrubland habitat. In our study area, güiña was as abundant in the anthropized habitat as the colocolo cat was in the native habitat. Although morphological and niche similarities between these species, güiña seems to be more resilient than the colocolo cat to habitat anthropization by exploiting other types of resources, indicating that the almost exclusive presence of the colocolo cat in the native habitat could be a good indicator of the ecosystemic health. The literature postulates that generalist species are better adapted to changes in their habitat, while specialists are less likely to adapt, being relegated to less disturbed areas (Oehler, 1995; Morán-López et al., 2006; McDougall et al., 2006; Sánchez-Hernandéz et al., 2001; Tabeni and Ojeda, 2005; Heim et al. 2019). However, our results suggest that the güiña could be more ecologically plastic than other feline species recognized as

a specialist predator in the native habitat and as a generalist predator in the anthropized habitat, expanding their niche breadth, consuming small mammals present in the habitat, arthropods and even plant matter. Similarly, Balme et al. (2020) found that leopard populations may consist of a heterogeneous mix of specialist and generalist individuals, with ecological opportunity as the primary driver of dietary specialization, influenced by phenotypic constraints (e.g., the sex of individuals or experience), and environmental conditions (e.g., prey diversity), as predicted by the optimal foraging theory (Stephens & Krebs, 1986).

Species with ecological plasticity can respond to changes in food, competition, and the presence of novel resources through spatial segregation as an avoiding mechanism, which could be a recurrent strategy to avoid competition or intraguild aggression events (Greenberg, 1990a). In relatively homogeneous landscapes, where a general habitat type dominates, similar species may use different patches that support a set of resources sufficient to fulfill their requirements (Soto 2015). Spatial segregation is discernible even at a fine scale for species with high temporal and trophic overlap, with mesocarnivores actively avoiding each other, putatively to not engage in intraguild killing (Ferreiro-Arias et al. 2021). Particularly, güiña and culpeo fox are "extreme opposite predators" in the native habitat. While güiña had a specialist diet and selective behavior, the culpeo fox was the most generalist predator with opportunistic behavior. However, in the anthropized habitat, decreased small mammal diversity implied that these predators 1. changed their diet composition and foraging behavior, the güiña became more generalist and opportunistic while the culpeo fox became more specialist in consuming other food items; and 2. These changes in their trophic axis meant a high dietary overlap between them, interaction absent in the native habitat. The flexible hunting behavior of güiña and culpeo fox supports them as predators that feeds habitat-dependent (Moreira-Arce et al. 2015). Güiñas preferences for exotic mammals in exotic plantations have already been recorded (e.g., Correa & Roa 2005; Sade et al., 2012, Moreira-Arce et al., 2015). However,

in our study, güiña preyed on rats, available or not, in each habitat type. Also, the rest of the carnivores did it, suggesting a replacement for the role of native small mammals in the trophic network of the park. Since rats are up to fourfold the body mass of native rodents, they could become an essential source of biomass for carnivores (Muñoz-Pedreros & Yañez, 2009). This phenomenon appears to be widespread in southern South America. (Novaro et al. 2000) (i.e. Moreira-Arce et al. 2015; Lambertucci et al. 2009; Zanon et al. 2012; Rau & Jimenez 2002). Given the preference and high consumption of the "rat" resource by this carnivore community, the population fluctuations of this rodent could promote the variation of the niche axes for these predators. We speculate that this variation could be seen enhanced after the strong rainy season associated with the "El Niño Southern Oscillation" phenomenon that occurred in winter 2023 (Cordero et al. 2024) due that under conditions where moist soil persists for several months, rats can breed over an extended period having a massive impact on their populational density (Madsen and Shine 1999).

Although we were not able to cover all axes of all species, this work supports the idea that coexistence may be much more complicated and even dynamic than has mostly been evaluated (Linnell 2000). Resource partitioning is not always distributed along straightforward food, space, or time axes but could also be 'hidden' in finer-scale behavioral interactions between carnivores (Karanth et al., 2017; Lahkar et al., 2020). Promoting habitat diversity and segregation opportunities can help reduce the intensity of interspecific competition and benefit the conservation of threatened species (Thakur, 2023). Understanding the impacts of habitat alterations on interspecies interactions is crucial for conservation practices. This is the first study in Chile that evaluates the three central axes of a carnivore community and their fluctuation between anthropized and native habitats. Also, it is the first study of the ecological aspects of Leopardus colocola since it was raised to the species category, now a feline endemic of central Chile (D'Elia et al. 2020). Here, we recorded its specialist diet and preferences for small mammals, strictly nocturnal behavior, and niche axis interactions with other sympatric carnivore species. Also, we recorded and corroborated the ecological plasticity of guiña and culpeo fox previously reported (Correa & Roa, 2005; Sade et al., 2012; Moreira-Arce et al., 2015; Castillo-Ravanal et al., 2018), and how these species can adjust their niche through habitat types. We hope this knowledge can help the management of conservation plans for carnivores and their ecosystems by providing new insights into the natural history of the species studied and their community dynamics.

7. CONCLUSION

The coexistence of predators is driven by multidimensional resource partitioning, where the three principal axes fluctuate depending on community members and environmental aspects such as prey availability. In our case, the coexistence of the carnivore community between habitat types in Radal Siete Tazas National Park can be facilitated by spatial segregation with different habitat preferences among species, but trophic and temporal resource partitioning at fine-scale behavior, like different peak activity or a slight diet composition variability through habitats, also plays a key role in decreasing competition. Our results showed a significant abundance, but only some prey species available in a homogeneous habitat cannot host the total number of predators due to increased competition. Therefore, conservation strategies not only would have to consider carnivores by themself but must begin to consider the critical elements such as the small mammals that support the predator assemblage and the interactions that this resource entails between carnivores, especially in species without enough ecological plasticity to use new resources.

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9. TABLES

Table 1.- Habitat and scat numbers. The Levins index (in the parentheses is the standardized value) for each carnivore per habitat in the National Park Radal Siete Tazas from Andean Central Chile. Sampling was made during the years 2022-2023. %FO indicates the relative frequency of occurrence of each item in the total of occurrences of all items. Values next to the column of habitat type signify the number of samples collected per habitat for each carnivore species.

	Guiña		Colocolo cat		Culpeo fox		Puma	
Habitat	Native (20)	Antrophized (13)	Native (13)	Native (16)	Antrophized (28)	Native (12)	Antrophized (4)	
Levins index(<i>Best</i>)	3.66(0.18)	10.7(0.54)	5.58(0.3)	16.18(1)	18.4(1)	10.29(0.61)	4(0.18)	
Trophic item	%FO	%FO	%FO	%FO	%FO	%FO	%FO	
Mammals	96.30	55.88	85.71	20.00	24.24	56.76	100.00	
Leopardus guigna	0.00	0.00	0.00	1.82	0.00	0.00	0	
Chelemys macronyx	0.00	0.00	0.00	0.00	0.00	0.00	0	
Abrothrix olivacea	0.00	0.00	4.76	1.82	0.00	8.11	0	
Octodon bridgesi	22.22	8.82	14.29	0.00	5.05	2.70	0	
Oligorizom ys longicaudatus	0.00	2.94	4.76	3.64	1.01	5.41	0	
Phyllotis xanthopygus	0.00	0.00	9.52	1.82	2.02	8.11	25	
Rattus sp	40.74	17.65	28.57	3.64	8.08	8.11	25	
Orictolagus cuniculus	18.52	17.65	23.81	5.45	2.02	21.62	25	
Capra hircus	0.00	2.94	0.00	0.00	2.02	0.00	0	
Undetermined	14.81	5.88	0.00	1.82	4.04	2.70	25	
Birds	0.00	2.94	0.00	5.45	5.05	5.41	0	
Arthropods	3.71	26.47	14.29	36.36	37.37	29.73	0.00	
Acanthinodera cummingii	0.00	5.88	4.76	3.64	10.10	5.41	0	
Diptera sp	0.00	0.00	0.00	0.00	1.01	0.00	0	
Heliofugus sp	0.00	2.94	0.00	5.45	1.01	5.41	0	
Carabidae sp	0.00	0.00	0.00	0.00	0.00	0.00	0	
Rhyephenes sp	0.00	0.00	0.00	0.00	2.02	0.00	0	
Pepsis sp	0.00	0.00	0.00	0.00	0.00	0.00	0	
Hymenoptera sp	0.00	5.88	0.00	3.64	4.04	0.00	0	
Tenebrionidae sp	0.00	0.00	0.00	0.00	1.01	0.00	0	
Coleoptera sp	0.00	0.00	0.00	0.00	1.01	0.00	0	
Bothriuridae sp	0.00	0.00	0.00	1.82	0.00	0.00	0	
Cratom elus armatus	0.00	0.00	0.00	3.64	0.00	2.70	0	
Brachysternus sp	0.00	0.00	4.76	5.45	5.05	0.00	0	
Bolborhinum tricorde	0.00	0.00	0.00	0.00	0.00	0.00	0	
Bolborhinum sp	0.00	2.94	0.00	3.64	2.02	8.11	0	
Ceroglossus chilensis	0.00	0.00	0.00	0.00	3.03	0.00	0	
Undetermined	3.71	8.82	4.76	9.09	7.07	8.11	0	
Plants	0.00	14.71	0.00	32.73	33.33	8.11	0.00	
Cryptocarya alba	0.00	2.94	0.00	0.00	10.10	0.00	0	
Poaceae	0.00	0.00	0.00	0.00	1.01	0.00	0	
Gevuina avellana	0.00	0.00	0.00	0.00	2.02	0.00	0	
Lithraea caustica	0.00	0.00	0.00	0.00	1.01	0.00	0	
Rubus ulmifolius	0.00	2.94	0.00	0.00	0.00	0.00	0	
Smilax aspera	0.00	0.00	0.00	0.00	1.01	0.00	0	
Prunus sp	0.00	5.88	0.00	5.45	9.09	5.41	0	
Prunus armeniaca	0.00	2.94	0.00	3.64	2.02	2.70	0	
Aristotelia chilensis	0.00	0.00	0.00	1.82	0.00	0.00	0	
Vachellia caven	0.00	0.00	0.00	0.00	5.05	0.00	0	
Berberis sp	0.00	0.00	0.00	1.82	0.00	0.00	0	
Malus domestica	0.00	0.00	0.00	10.91	2.02	0.00	0	
Undetermined	0.00	0.00	0.00	9.09	0.00	0.00	0	

Table 2.- Trophic overlap among the carnivore species in the National Park Siete Tazas. Pianka values (PI) with its 95% CI in parentheses. Above the diagonal is the indicated PI value for the pair species compared in the native habitat, while under the diagonal it is indicated PI value for the pair species compared in the anthropized habitat. PI values with an * mean that niche amplitude between the paired species was significantly different. The diagonal, colored with grey, indicates the significance value from the Shannon index (H') corrected by Bonferroni for the trophic diversity of each carnivore between the two types of habitats, anthropized and native. Species without representative diet or absent per habitat were represented with x.

Carnivore	Guiña	Colocolo cat	Culpeo fox	Puma
Guiña	<0.05	0.86(0.54-0.95)*	0.27(0.14-0.44)*	0.56(0.34-0.71)*
Colocolo cat	-	х	0.37(0.23-0.54)*	0.77(0.57-0.92)*
Culpeo fox	0.7(0.47-0.89)*	-	<0.05	0.58(0.45-0.75)*
Puma	x	-	х	х

Table 3.- Prey availability per habitat type. Total abundance of small mammals captured and registered since 2022-2024 of the study area in the National Park Radal Siete Tazas (N). The following indexes are shown: Shannon index (H) for small mammals diversity per habitat, Jaccard's similarity index (J) between habitats, and Pearson's correlation coefficient (r) for every carnivore per habitat.

Habitat		Native	Anthropized
Small mammals		Ν	Ν
Abrothrix olivacea		22	0
Abrothrix longipilis		4	0
Abrothrix sp		1	0
Phyllotis xanthopygus		13	0
Oligorizomys longicaudatus		28	7
Octodon bridgessi		21	0
Dromiciops bocinovichi		1	0
Thylamys elegans		4	0
Rattus sp		6	64
Orictolagus cuniculus		514	357
	Н		
		0.74	0.50
	J		
			0
	r		
Guiña		0.26	0.73
Colocolo cat		0.52	-
Culpeo fox		0.69	0.17
Puma		0.86	-

Table 4.- Daily activity patterns of carnivores in Siete Tazas National Park. Relative Abundance Index (RAI). Species were classified into activity categories based on the percentage of records falling in light or dark hours of the day (light: 8:00 am to 20:00 pm; dark: 20:00 pm to 8:00 am). N is the number of records in total and each habitat. Δ measures the species overlap in their temporal niche between the anthropized and native habitats (with the respective 95% confidence intervals). Habitat use was calculated as the relative frequency of records for every carnivore per hábitat.

Carnivores	N(Total)	RAI	Activity (% day/night)	N (anthropized/ native habitats)	RAI(anthropized/ native habitats)	Habitat use (% anthropized/native)	∆anthropized/native habitats (95% CI)	MWWanthropized/ native
Chingue	26	0.25	Nocturne (3.8/96.2)	2/24	0.3/3.16	Native (7.7/92.3)	-	-
Quique	19	0.18	Diurnal (100/0)	9/10	1.01/2.14	Both (52.6/47.4)	-	-
Güiña	36	0.34	Catemeral mostly nocturnal (25/75)	34/2	2.42/0.24	Anthropized (94.4/5.6)	-	-
Colocolo cat	16	0.15	Nocturne (6.3/93.8)	0/16	0/2.61	Native (0/100)	-	-
Culpeo fox	245	2.31	Catemeral mostly nocturnal (24.9/75.1)	89/156	4.81/9.23	Mostly native (36.6/63.7)	0.82(0.73-0.91)	0.778(0.67)
Puma	2	0.02	Unclassified (0/100)	2/0	0.44/0	Unclassified (100/0)	-	-

Table 5.- Temporal niche overlap values of carnivores in the different habitats of National Park Radal Siete Tazas. Overlapping coefficient values (Δ) with their respective 95% confidence intervals are between parentheses and are represented above the diagonal. Mardia-Watson-Wheller test values (W), with their respective statistical significance (*p*, between parentheses) are represented below the diagonal. Statistically significant values are shown in italics. Carnivores with <10 records per habitat or absent are represented with an x.

Carnivores	Chingue	Quique	Güiña	Colocolo cat	Culpeo fox
Chingue	-	0.14(0.02-0.28)	0.81(0.66-0.94)	0.66(0.43-0.86)	0.66(0.51-0.8)
Quique	34.446(<0.001)	-	0.31(0.16-0.46)	0.17(0.02-0.35)	0.31(0.18-0.44)
Güiña	2.393(0.3)	26.778(<0.01)	-	0.71(0.5-0.89)	0.79(0.68-0.91)
Colocolo cat	39.072(0.14)	21.837(<0.01)	2.35(0.3)	-	0.82(0.66-0.96)
Culpeo fox	11.329(<0.01)	33.044(<0.001)	6.53(0.03)	0.46(0.79)	-

Table 6.- Spatial overlap among the carnivore species in the National Park Siete Tazas. Pianka values (PI) with its 95% CI in parentheses. Above the diagonal is indicated PI value for the pair species compared in the native habitat, while under the diagonal it is indicated PI value for the pair species compared in the native habitat. Species without records in one habitat type were represented with x.

Carnivore	Chingue	Quique	Güiña	Colocolo cat	Culpeo fox
Chingue	-	0.69(0.05-0.94)	0.31(0.12-0.79)	0.13(0-0.84)	0.63(0.29-0.83)
Quique	0	-	0	0.2(0-0.99)	0.48(0.18-079)
Güiña	0.36(0.07-0.88)	0.79(0.17-0.98)	-	0	0.66(0.34-0.9)
Colocolo cat	x	х	x	-	0.35(0.22-0.7)
Culpeo fox	0.29(0.16-0.65)	0.4(0.24-0.85)	0.5(0.3-0.86)	х	-

10. FIGURES



Figure 1.- Map of the study area in Radal Siete Tazas National Park. The park is marked with light green in the upper box, and with white lines in the lower boxes. Anthropized habitat is colored in pink and the native habitat is colored in light blue. Camara traps are symbolized like black dots.

Native habitat



Figure 2.- Accumulation curves for prey species in every carnivore's diet per habitat.



Figure 3.- Niche segregation along the trophic axis among carnivores in National Park Radal Siete Tazas. Individual dots indicate every food item consumed by the species in the park. The first two CA axes (Dim 1, Dim 2) explain 70% of the variability in diet composition between species and habitats. The first dimension represents a gradient of diet variability between güiña and culpeo fox in the native habitat, while the second dimension separates the diet of carnivores in the anthropized and native habitats.



Figure 4.- Density estimates of daily activity patterns and extensions of their overlap among pairs of carnivores in National Park Radal 7 Tazas, central Chile. Temporal activity for every carnivore species is represented with one line color. Overlap is represented by the shaded yellow area. Significant differences in the MWW test are indicated by an asterisk after overlap coefficient values (Δ). Habitat preferences and activity patterns are represented with symbols for every carnivore species on the corresponding figure.



Species pairs

Native habitat

Anthropized habitat







Figure 6.- Carnivore species recorded in Radal Siete Tazas National Park from 2022-2024.