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Activity Patterns of Native Carnivores in Central Chile: Are They Influenced by Landscape Type?

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Abstract: Landscapes can be selectively used by different carnivore species, leading to habitat specialization, which acts as a limiting resource for maintaining healthy populations. Between 1 March 2021 and 31 March 2022, we set up 30 camera traps in three different landscapes of central Chile: (a) Mediterranean coastal sclerophyllous forest (SF), (b) Mediterranean coastal thorn forest (TF), and (c) exotic monoculture tree plantations (MP), with a total capture effort of 10,046 camera-days (3098 TF, 3446 MP, and 3502 SF). We described the daily activity patterns for each native carnivore species recorded in each landscape, based on the density of independent records per hour of the day. We assessed the overlap between the activity patterns of each carnivore species in the different macrohabitats based on their coefficient of overlapping (Δ). We identified 9120 carnivore records, corresponding to 3888 independent events: 3140 for *Lycalopex* fox species, 276 for guiña *Leopardus guigna*, 434 for skunk *Conepatus chinga*, and 38 for the lesser grison *Galictis cuja*. Our study revealed differences of activity patterns with high to medium overlap, among landscape types for *C. chinga* and *Lycalopex* spp.—for skunk, between native forests and exotic monoculture tree plantations, and for foxes, among all landscape types. The carnivore community of the highly anthropized central Chile is mostly composed of habitat generalists and habitat specialists with high adaptability to landscape fragmentation, which has been crucial for their long-term survival.

Keywords: activity rhythms; Mediterranean landscapes; carnivore community; land use change

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1. Introduction

Carnivores play a key ecological role from their position at the apex of trophic systems [1]. Given their large habitat requirements to maintain viable populations, they also act as umbrella species whose protection may benefit others further down the trophic cascade [2]. However, ensuring the habitat requirements for one species may still fall short and does not necessarily assure the persistence of sympatric species, which led to the idea of picking multiple "umbrellas" that cover broader ranges of habitat gradients and thus protect a larger fraction of the ecosystem [3].

Landscape characteristics and available habitats model the composition of the carnivore guild according to the availability of these limited resources. Coexistence is likely

facilitated by dietary, spatial, and/or temporal niche partitioning, as they reduce interspecific competition within the guild [4]. Seven carnivore species have been described in the Central Chilean Coast Range: chilla fox *Lycalopex griseus* and culpeo fox *Lycalopex culpaeus* (Canidae), pampas cat *Leopardus colocola colocola,* guiña *Leopardus guigna*, and puma *Puma concolor* (Felidae), as well as hog-nosed skunk *Conepatus chinga* (Mephitidae) and lesser grison *Galictis cuja* (Mustelidae) [5].

Understanding the community of carnivores within landscapes, as well as the interactions and ecological dynamics of their functional assembly, is essential for proposing effective conservation strategies [6,7]. When carnivores coexist in sympatry, their ecological niches can overlap; however, coexistence is maintained through segregation strategies, where differential use of space and temporal animal rhythms are the most common mechanisms [8,9]. Landscape characteristics and available habitats shape carnivore composition according to resource availability, influencing community attributes or ecological parameters [10], even in human-dominated or exotic tree plantation landscapes [11,12].

In the present study, we aimed to assess the activity patterns and their overlap in native carnivores from the coast range of central Chile and explore whether they are influenced by landscape type. Our general hypothesis was that the activity patterns of carnivores and their overlap varied in relation to the different vegetation macrohabitats, especially between native forests and exotic tree plantations. We aimed to determine activity patterns of native carnivores in both native and exotic vegetation covers to inform conservation and management decisions for the long-term persistence of their populations in the highly human-impacted Coast Range of central Chile.

2. Materials and Methods

2.1. Study Area

The Chilean Coast Range extends over 3000 km from north to south along the Pacific coast of South America. Geologically older than the Andes Mountain Range, it is a descending formation whose highest summit reaches 3114 m above sea level [13]. But while the Andes Mountains more than double its height, the geophysically heterogeneous Coast Range is home to an extraordinary biodiversity with a high degree of endemism, especially in remnants of native forest [14].

In the Central Chilean Coast Range, there are three different landscapes or vegetation macrohabitats: (a) Mediterranean coastal sclerophyllous forest (composed mainly of *Lithrea caustica*, *Quillaja saponaria*, *Cryptocarya alba*, *Peumus boldus*, and *Azara integrifolia*), (b) Mediterranean coastal thorn forest (dominated by *Acacia caven*, *Maytenus boaria*, *Trevoa trinervis*, and *Talguenea quinquinervia*), and (c) exotic monoculture tree plantations (*Pinus radiata* and *Eucalyptus globulus*) [15]. Sclerophyllous forest and thorn forest have gradually been converted to exotic monoculture tree plantations since the 1970s, leading to habitat alteration and an overall reduction in the surface area covered by these native forests, with its corresponding impact on the associated native biodiversity [16].

In terms of food resources, these ecotypes have been shown to harbor, with relative abundance, prey available for carnivores, including introduced exotic species: lagomorphs (*Lepus europeus*, *Oryctolagus cuniculus*) and rodents (*Rattus norvergicus*, *Rattus Rattus*); as well as small marsupials and native rodents: (i.e., *Tylamys elegans*, *Octodon lunatus*, *Abrocoma bennetti*, *Phyllotis* sp. *Abrothrix* sp. *Olygorizomis longicaudatus*) [5,17].

To compare activity patterns between different macrohabitats, we selected three sites within the Coastal Range of the O'Higgins Region in central Chile with the following dominant vegetation cover: (A) La Estrella representing the Mediterranean coastal thorn forest (TF), (B) Alto Colorado for exotic monoculture tree plantations (MP), and (C) Callihue for Mediterranean coastal sclerophyllous forest (SF) (Figure 1, upper and middle row). At

each of these locations, we selected an area of 1000 ha with a homogeneous and continuous composition of its respective vegetation cover. Taking into account the accessibility of these areas and according to Trolliet et al. [18], we distributed 10 camera traps in each site in a uniform monitoring grid with 1000 m of separation between individual monitoring points (Figure 1, bottom row).

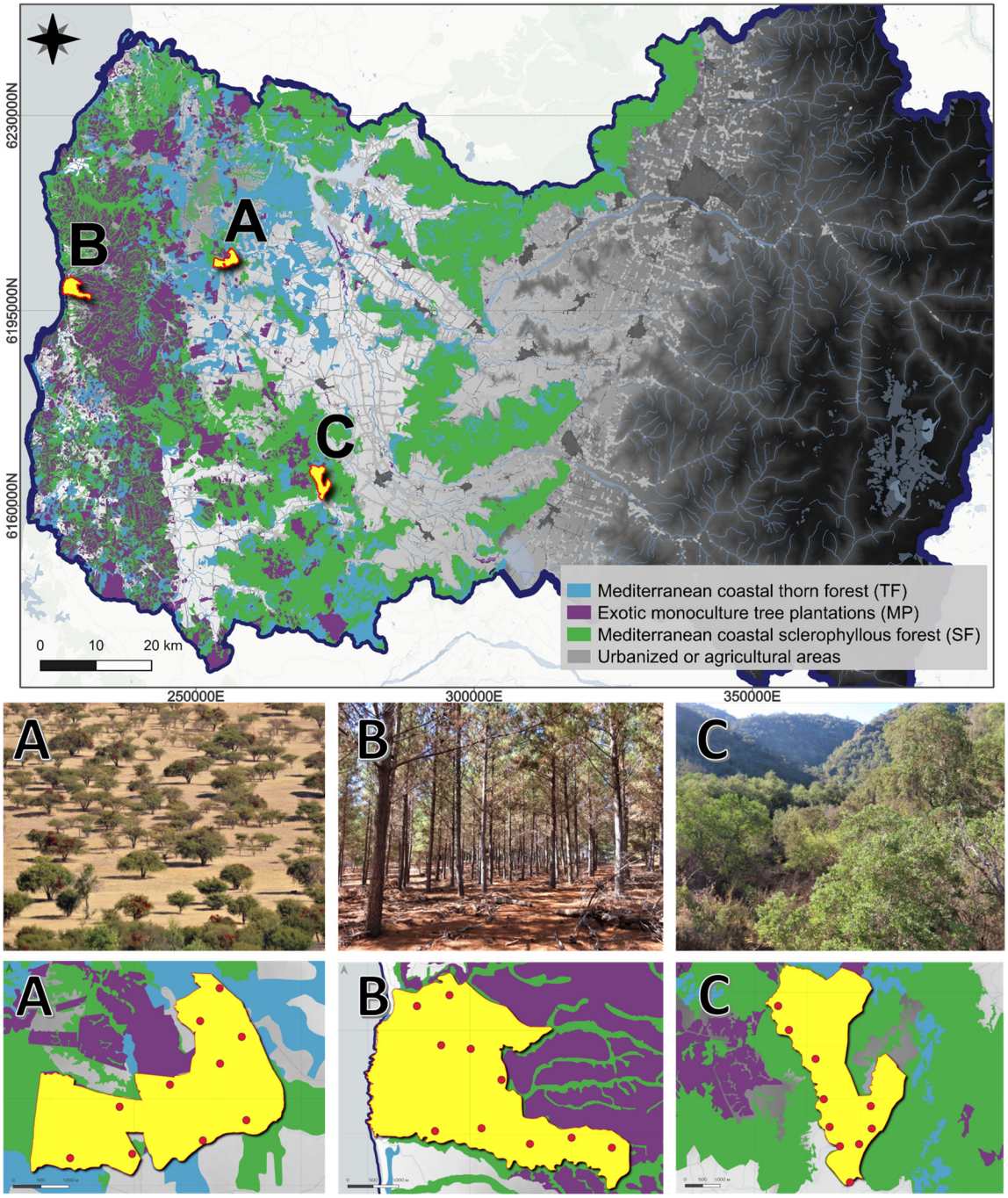

Figure 1. Different landscapes in the Coast Range of the O'Higgins Region in central Chile. (**Upper** row): Light blue areas represent Mediterranean coastal thorn forest; purple areas correspond to exotic monoculture tree plantations; green areas are Mediterranean coastal sclerophyllous forest; grey background stands for urbanized or agricultural areas. (**Middle** row): Representative pictures of the landscapes (A) Mediterranean coastal thorn forest, (B) exotic monoculture tree plantations, (C) Mediterranean coastal sclerophyllous forest. (**Bottom** row): Red dots show the distribution of camera traps at each site, (A) La Estrella, (B) Alto Colorado, (C) Callihue.

2.2. Data Collection

All cameras were oriented towards trails, passageways, or other areas with attributes indicating a potential passage of fauna. We did not use attractors. Bushnell 24MP Trophy Cams (Bushnell Corporation, Overland Park, KS, USA) model 119719CW were set to camera mode taking two pictures at each event with a minimum delay of three seconds between events. Sensor sensitivity was adjusted in auto mode, and cameras were working 24 h a day. Cameras were active between 1 March 2021, and 31 March 2022, and were checked in the field every two months and batteries were replaced. After a visual inspection of the pictures obtained, only those showing native carnivores were selected for further analysis.

We used the freely available CameraSweet version 4.5 program [19] to classify, organize, and analyze camera trap data. We ran the SpecialRenamer, DataOrganize, and DataAnalyze protocols following the methodology described by Vázquez-Ibarra et al. [20]. For the analysis, we classified records among the following identified species: *L. guigna*, *C. chinga*, *G. cuja*, and the *Lycalopex* genus. While the two native fox species present in our study area differ in morphological features [5], the use of camera traps to distinguish *Lycalopex* species is prone to errors, particularly in nighttime photos or when the animals are not completely or clearly shown in the images [21–23]. In addition, the existence of hybridization, introgression, or incomplete lineage sorting within the *Lycalopex* genus has been discussed in recent years and may be another potential source of error when attempting to identify species in low-resolution photos [24,25]. Thus, in order to avoid mistakes in the identification and classification of *L. culpaeus* and *L. griseus*, we grouped the two species as *Lycalopex* spp. canids. For the temporal activity analysis, two records were considered as independent events if separated by >60 min.

2.3. Activity Patterns, Overlap, and Landscape Dependency

Independent events of activity were counted in hourly intervals for all carnivore species recorded and also for the *Lycalopex* spp. group. We calculated the relative frequency of observations per hour as a proportion of the activities registered for each species. We used the program Oriana 4 (Kovach Computing Services, Anglesey, Wales, UK) to represent those counts in pie charts.

To compare the daily activity patterns of species as a function of landscape, we relied on the density of independent registers per hour of the day. Information on hour, date, species, and location was extracted from camera records using the camtrapR package in RStudio 4.0.3 [26]. We then followed the method described by Ridout and Linkie [27] to assess the overlap between activity patterns of carnivores in different macrohabitats: We determined the coefficient of overlapping (Δ), which ranges from nil $\Delta = 0$ (no overlap between patterns) to $\Delta = 1$ (total overlap between patterns compared), and the respective confidence intervals at 95% for each comparison. We used Δ_4 to compare datasets exceeding 50 samples, and Δ_1 for comparisons where one or both datasets contained fewer than 50 samples. Comparisons based on series comprising less than 10 records were not considered due to low statistical support. Comparisons were assessed with the Overlap package in RStudio 4.0.3 [28]. For each activity pattern comparison, the existence of significant differences was evaluated using a significance of 0.05. For this purpose, a randomization test was used to create a null distribution from 10,000 bootstrap iterations of random densities of activity per hour, which was compared with the observed activity patterns to define whether they belong to the same distributions. For this, we used the function compareCkern of the Activity package for Rstudio 4.0.3. [29]. In terms of overlap categorization, we considered $\Delta \geq 0.8$ to indicate a high overlap, $0.8 > \Delta > 0.5$ to be medium overlap, and $\Delta \leq 0.5$ to designate low overlap or patterns with high differentiation [30].

3. Results

3.1. Activity Patterns

With a total photo-trapping effort of 10,046 camera-days (3098 in TF, 3446 in MP, and 3502 in SF), we obtained a total of 13,112 camera trap pictures from which 9120 (70%) were records of carnivore species. These records corresponded to 3888 independent events from the following species: 3140 for *Lycalopex* spp., 276 *L. guigna*, 434 *C. chinga*, and 38 *G. cuja*. We did not obtain records for *L. c. colocola* or *P. concolor*.

The overall activity pattern of the skunk *C. chinga* (n = 434), is concentrated between nighttime and early morning (between 07:00 pm and 07:00 am). In Alto Colorado (MP), the location with the least number of events of this species (n = 60), it has a specific peak of activity around 03:00 am, decreasing gradually until 06:00 am. In La Estrella (TF) (n = 144), it presents a relatively constant activity pattern from 07:00 pm to 06:00 am. In Callihue (SF) (n = 230), two peaks of activity can be observed, at around 11:00 pm and at around 07:00 am, with constant activity throughout the total activity schedule (Figure 2a).

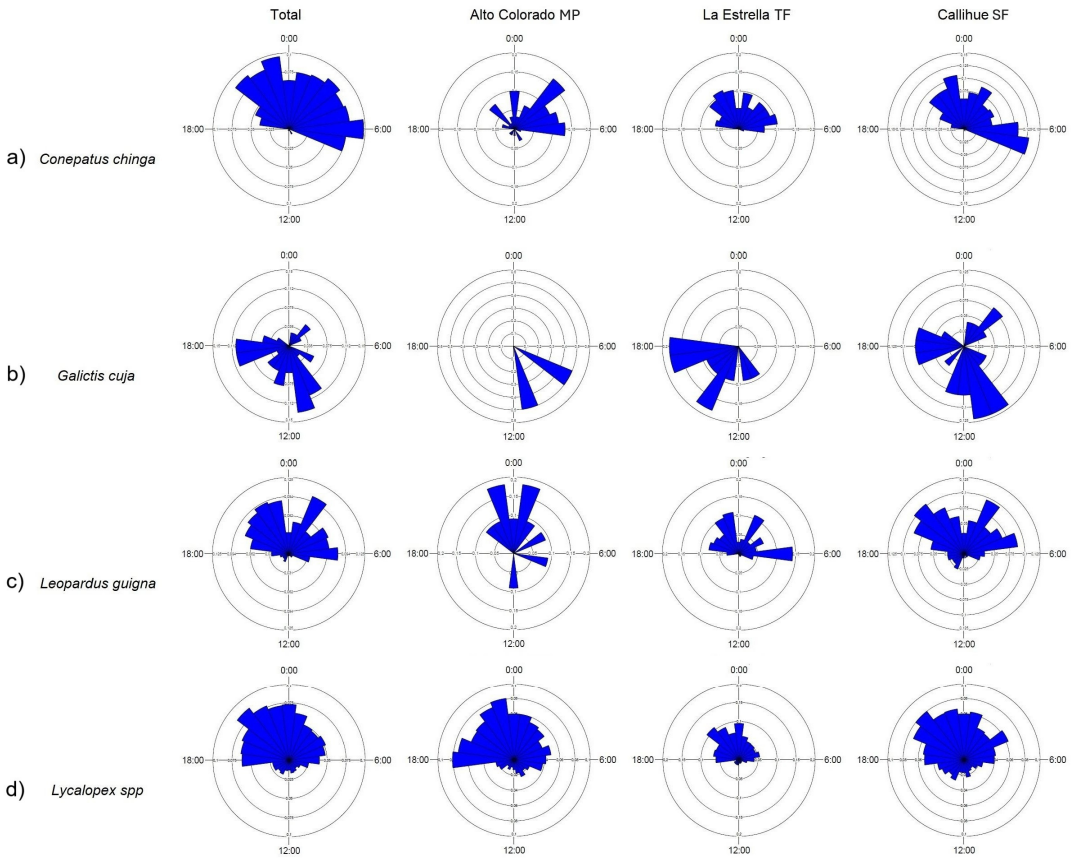

Figure 2. Circular daily activity patterns of native carnivores from central Chile. The overall activity pattern (Total) calculated with all the data from independent observations is shown followed by the activity patterns for each of the landscape types separately. Alto Colorado: exotic monoculture tree plantations; La Estrella: Mediterranean coastal thorn forest; Callihue: Mediterranean coastal sclerophyllous forest. The length of each blue column represents the frequency with which the species was detected at that time.

For the lesser grison *G. cuja* (n = 38), the overall activity pattern is mainly diurnal and crepuscular, with its highest level of activity between 10:00 am and 06:00 pm, and specifically two peaks of activity at 11:00 am and 05:00 pm. In Alto Colorado (MP), only two independent observations were obtained for this species; therefore, no analysis on activity patterns could be conducted. In La Estrella (TF) (n = 11), although few data were

obtained, a tendency towards a diurnal pattern of activity was observed, with a peak of activity around 05:00 pm. In Callihue (SF) (n = 25), activity was detected throughout the 24 h, but most of it was concentrated during the day, especially around 10:00 am (Figure 2b).

The overall activity pattern of the small wild cat *L. guigna* (n = 276) is mainly crepuscular and nocturnal (between 07:00 pm and 07:00 am), with a high activity peak before sunset, and another around 02:00 am. In Alto Colorado (MP) (n = 11), the guiña has a nocturnal activity pattern with a peak around 11:00 pm and 01:00 am, and sporadic activity in the morning. In La Estrella (TF) (n = 125), it also presents crepuscular and nocturnal activity but with a peak of activity at 06:00 am. In Callihue (SF) (n = 140), it also presents crepuscular and nocturnal activity, but more evenly distributed compared to the other locations, with a peak of activity around 09:00 pm (Figure 2c).

For *Lycalopex* spp. (n = 3140), the activity pattern is mainly crepuscular and nocturnal, with less activity during the morning, and with an activity peak around 09:00 pm. In general, it has the same activity pattern in all locations, with slight variations in the activity peak for each of them. In Alto Colorado (MP) (n = 718), it presents a relatively continuous activity pattern, with two activity peaks, the first around 06:00 pm and the second around 11:00 pm. In La Estrella (TF) (n = 1191), it has the lowest activity levels among the three locations, with two activity peaks between 09:00 pm and midnight. In Callihue (SF) (n = 1231), a continuous activity pattern is observed along the night, with a peak of activity around 09:00 pm (Figure 2d).

3.2. Comparisons and Overlap of Activity Patterns Among Landscape Types

For *C. chinga*, we found significant differences between the exotic plantations in Alto Colorado (MP) and the other two native vegetation locations (Alto Colorado (MP) vs. Callihue (SF): $\Delta = 0.76$, p-value < 0.05; Alto Colorado (MP) vs. La Estrella (TF): $\Delta = 0.76$, p-value < 0.05). In the comparison between Alto Colorado (MP) and Callihue (SF), the main difference was around 06:00 am, where in Alto Colorado (MP) the species concentrates the highest activity of the day, compared with Callihue (SF), where it decreases its activity. When comparing Alto Colorado (MP) and La Estrella (TF), these locations have different peaks of activity, being in La Estrella (TF) concentrated around midnight while in Alto Colorado (MP) around 06:00 am. The activity patterns in Callihue (SF) and La Estrella (TF) showed no significant differences (Callihue (SF) vs. La Estrella (TF): $\Delta = 0.87$, p-value = 0.09) (Figure 3a).

For *G. cuja*, the comparison between the two native vegetation locations, Callihue (SF) and La Estrella (TF), showed no significant differences in activity patterns (Callihue (SF) vs. La Estrella (TF): $\Delta = 0.55$, p-value = 0.17). This could be explained due to the low number of photos obtained for this species (Figure 3b). Alto Colorado (MP) could not be compared due to limited data.

For *L. guigna*, we found no significant differences among landscape types (Alto Colorado (MP) vs. Callihue (SF): $\Delta = 0.73$, p-value= 0.19; Alto Colorado (MP) vs. La Estrella (TF): $\Delta = 0.76$, p-value= 0.17; Callihue (SF) vs. La Estrella (TF): $\Delta = 0.85$, p-value= 0.12). A slight difference in activity patterns could be observed in Alto Colorado (MP), with a different activity peak at around 12:00 (Figure 3c).

For the *Lycalopex* spp. group, significant differences were recorded across all landscape types. For the comparison between Alto Colorado (MP) and Callihue (SF), although no major differentiation is observable in the distribution of activity throughout the day, significant differences are identified based on differences in the density of activity records for each locality. In comparison with the activity pattern of La Estrella (TF), a peak of activity is observed around 22:00 h, distinguishing it from the other analyzed localities (Figure 3d).

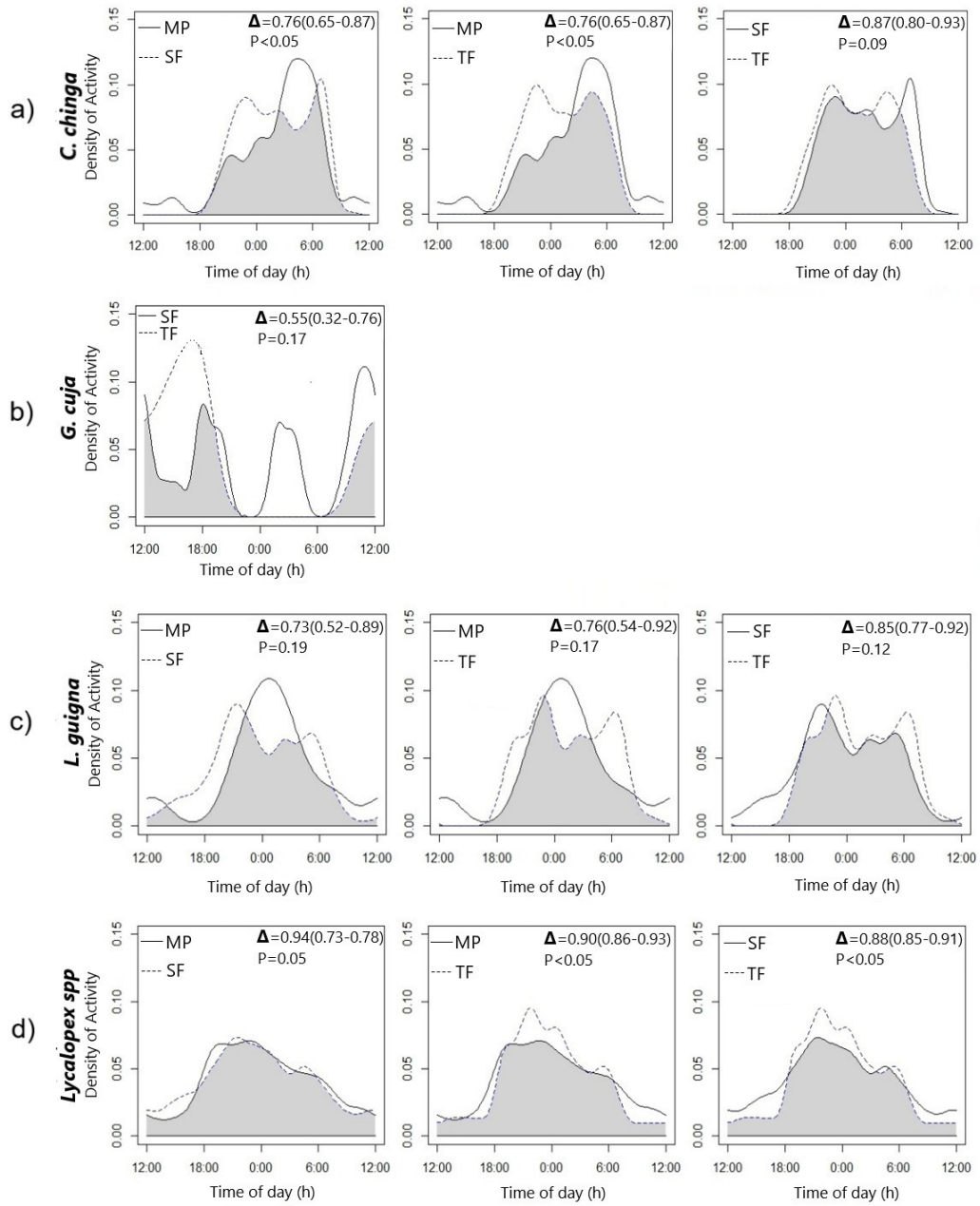

Figure 3. Comparisons of activity patterns of *C. chinga*, *G. cuja*, *L. guigna*, and *Lycalopex* spp. among the different landscape types in central Chile. For each comparison, the respective coefficient Δ (with a respective confident interval at 95%) and *p*-value are presented. MP = exotic monoculture tree plantations (Alto Colorado); TF = Mediterranean coastal thorn forest (La Estrella); SF = Mediterranean coastal sclerophyllous forest (Callihue).

4. Discussion

In this study, we found differences of activity patterns with high to medium overlap, among landscape types for *C. chinga* and *Lycalopex* spp.—for skunk, between native forests and anthropogenic landscapes (exotic monoculture tree plantations), and for foxes, among all landscape types.

Landscapes can be used selectively by certain species of carnivores, both spatially and temporally, producing specialization in the use of the habitat, which therefore could constitute a limiting resource for maintaining healthy populations [31,32]. This becomes even more evident when looking at landscape mosaics such as those occurring in central Chile. Specifically for the O'Higgins region, landscape homogeneity and continuity are

lost, especially towards the west, where monoculture tree plantations such as in the Alto Colorado location might act as impermeable landscape barriers for native forest-associated habitat specialists (Figure 1). Home range sizes and mobility are species-specific attributes and have an impact on whether such human-altered landscapes remain permeable for wildlife or not, allowing animals to leave the patch and disperse into and beyond the surrounding fragments connecting populations [33].

By contrast, habitat generalist species are adaptable in the use of the territory and its various landscapes, with no limiting factors for their settlement [6]. In this context, some carnivore species detected in the present study have been described as habitat generalists: *C. chinga* occurs in areas of grassland, steppe, shrubland, and open xerophytic forest in the Coastal and Andean Mountain ranges, Andean valleys, and the altiplano throughout central and southern Chile [34]. For this habitat generalist species, we found differences in activity patterns between native forests (SF, TF) and anthropogenic landscapes (exotic monoculture tree plantations; MP). Patterns observed in SF and TF are highly similar, with activity uniformly distributed between dusk and dawn. In MP, however, although it shows intermediate levels of overlap with SF and TF indicating that the hours in which this species is active are similar, the intensity with which they are used is different. Skunks are significantly less active before midnight, and their activity concentrates between midnight and early morning. A previous study suggested that the landscape-dependent change in felid behavior may respond to human and/or domestic animal interference [35]. Similar factors may play a role in this case, although for MP we did select a study area where no logging or other forestry work was scheduled or conducted during the study period.

Chilla and culpeo foxes, *L. griseus* and *L. culpaeus*, respectively, are closely related species known to occupy similar and highly varied landscapes ranging from shrublands to forests and steppe [17,36]. In this study, we detected landscape-dependent differences between activity patterns of the habitat generalists *Lycalopex* spp. across landscape types. However, the general observable distribution of these activity patterns is relatively similar, especially between MP and SF, with a high degree of overlapping, and thus significant differences are mostly due to the intensity of activity for each hour throughout the day for each locality. The peak activity of foxes across landscape types was observed between sunset and midnight, with fewer records obtained during night and early morning hours. Activity in TF has a peak around 22:00 h, distinguishing it from the other two analyzed landscape types.

Another carnivore species described as a habitat generalist and detected in the present study is *G. cuja*, the only diurnal species assessed in this work, recorded to inhabit highly diverse landscape types [37]. No significant differences in activity patterns were found in this study between the two native vegetation locations; however, we could not assess comparisons with the exotic tree plantation landscape type due to limited data. The overall detection rate for *G. cuja* was very low in MP, while a sufficient number of records were only obtained for SF and TF.

In contrast, *L. guigna* has been described as a habitat specialist, due to its close association with vegetation cover, especially with the native Mediterranean forests and scrubland in central Chile and the Valdivian temperate rainforest in southern Chile. However, this species has also been shown to have a high level of adaptability in landscapes characterized by intense agriculture, where it uses vegetation corridors to move across human-dominated landscapes [38]. For *L. guigna*, around half of the events we registered occurred before midnight, resulting in a similar activity pattern to that described for spotted coat individuals in the southern subspecies *L. g. guigna*, in Valdivian temperate rain forests and in deciduous *Nothofagus* forests in the foothills of the Andes in La Araucanía Region [38,39]. By contrast, in the northern subspecies *L. g. tigrillo* (this study; [40,41]) melanistic individuals, which are

common in *L. g. guigna* but very rare in *L. g. tigrillo* [42], were reported to be mostly active after midnight [39]. Thus, our results are consistent with previous reports on the activity of this species in other landscapes including behavioral variations for different coat colors.

Conservation measures for carnivore populations require a high-level approach and must consider the permeability of distinct landscapes at different points in time [43]. Our results suggest that monoculture tree plantations do not currently pose an insurmountable barrier to landscape connectivity in central Chile, which is very helpful for the preparation of habitat connectivity maps including the identification of obstacles to wildlife movement [44]. Transport and mobility infrastructure commonly interferes with carnivore mobility [45], but forestry works and the eventual logging of monoculture tree plantations also imply changes in the permeability of these landscapes. With regard to the former, it may be useful to educate about and eventually adapt human activity in the matrix between high-quality patches of habitat, in such a way that the permeability of these landscapes increases at times of wildlife species' main activity [46,47]. Of course, this does not preclude the adoption of permanent measures to improve connectivity across those barriers and in between. To name just one example, the design of common priority areas for natural habitat restauration may help to mitigate the impact of repeated intervention in monoculture tree plantations.

For this study site, species richness did not differ between the three assessed landscape types [42]. Trail camera records confirmed the presence of *C. chinga*, *G. cuja*, *L. guigna*, and *Lycalopex* spp. in both types of native forests, sclerophyllous and thorn forests, as well as in monoculture tree plantations. This result argues against landscape-dependent spatial segregation between carnivore species in this study site, while spatial segregation at a finer scale cannot be ruled out. Such segregation has been described for chilla and culpeo foxes in a study conducted in Torres del Paine National Park, where their respective home ranges were interspersed in a mosaic-like arrangement but spatially segregated without interspecific overlap [48].

Two species that were potentially distributed in our study area were not detected: *P. concolor* and *L. c. colocola*. The pampas cat *L. c. colocola* is endemic to central Chile according to the latest taxonomic assessment, has low abundance and scarce populations, and is therefore considered to have a higher conservation threat [49]. The puma *P. concolor* has been previously recorded in the Coast Range of central Chile [50]. However, it has cryptic movements and low detection rates, even with a high sampling effort (e.g., [51]). Therefore, the lack of detection of both species is not unusual given their ecological traits, and they may act as indicators of human landscape disturbance, reflecting a certain level of anthropogenic impact they can no longer tolerate.

There may be limitations and biases in our study. The sample size for some of the species and habitat types studied could limit and/or bias the inferences from our findings, limiting the possibility of addressing possible statistically significant patterns in the relationship between variables. However, this study was designed to target different landscape types in order to test our hypotheses. This study is the first descriptive stage of a larger, long-term research, in which we plan to address more variables, associations between variables and habitat selection, to help us better understand the relationship between landscape types and the presence and abundance of carnivores in a changing environment.

According to our findings, the carnivore community in central Chile is composed mostly of habitat generalists (except for *L. guigna*) whose overall ability to adapt to land use change and landscape fragmentation has likely been crucial for their long-term survival in this area [52]. So, these mammals could be used as focal species in connectivity conservation and ecological network planning [53,54].

The highly anthropized central Chile area has faced intensive past and current land use change rates [55,56]. Therefore, in order to gain a comprehensive understanding of the implications of landscape human-alteration for biodiversity, we need to look under the umbrella: different processes are likely taking place already in this area that may have an impact on the future of Central Chile's carnivore populations in the form of extinction debts (i.e., delayed species extinctions as a consequence of ecosystem perturbation [57]). Functional or ecological extinctions (i.e., when a species' abundance is so reduced that it cannot perform its ecological functions [58]) and the extinction of ecological interactions (i.e., ecosystem services) often precede local and global species extinctions, being key aspects to consider when studying biodiversity in the current changing world [59,60].

Beyond describing only species presence, future efforts should focus on studying ecological functions and interactions among species in this community (e.g., seed dispersal by foxes, rodent control by felids), long-term monitoring, and more studies on different taxa and landscapes [61] to detect the potential disappearance in the future of functions, interactions, and/or species in habitat patches that remain occupied today. These insights could inform future conservation and management decisions and efforts at the landscape level to better protect biodiversity in the highly human-impacted Coast Range of central Chile, for example, suggesting the better sites and time to detect species following their activity patterns, carrying out a threat analysis for these species, and providing suggestions to select indicators for monitoring of these mammals [62].

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Data Availability Statement: The original contributions presented in this study are included in the article. Further inquiries can be directed to the corresponding authors.

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