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NESTEDNESS IN A CARNIVOROUS MAMMAL ASSEMBLAGE IN FOREST FRAGMENTS OF THE ARAUCANÍA REGION, SOUTHERN CHILE

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Nestedness in a Carnivorous Mammal Assemblage in Forest Fragments of the Araucanía Region, Southern Chile. Sanhueza, R., Moya, W., Rau, J. R. — Habitat fragmentation is one of the main factors threatening biodiversity, especially in regions where natural ecosystems are under anthropogenic pressure, such as the Araucanía region in southern Chile. This study explores the presence of nestedness patterns in the composition of carnivorous mammal species in six fragments along the southern part of the Coastal Range in the Araucanía region. Using scent stations and actively searched five species were recorder over a nine-month period: hog-nosed skunk, kodkod, cougar, gray fox, and culpeo fox. The analysis revealed that the nested pattern, with a temperature of 13.661 °C, suggests a risk of local extinction in smaller fragments (less than 14 ha). The hog-nosed skunk was detected in four fragments, including one of the smaller ones (3.1 ha), while the cougar and kodkod were more restricted, being recorded in three and two fragments, respectively. The culpeo fox and gray fox were present in only one or two fragments. These results support the island biogeography theory, highlighting that larger fragments sustain greater species diversity. This study highlights the importance of conserving larger forest fragments to maintain carnivore diversity, as specialized species rely on denser and more connected habitats. It is recommended to prioritize the preservation of continuous forest areas and restore connectivity between fragments to mitigate the negative effects of fragmentation.
Key words: habitat fragmentation, carnivore density, nestedness, Araucanía Forest, species composition.

Introduction

Habitat loss and fragmentation are among the most critical threats to biodiversity (Teckentrup et al., 2019; Ntshanga et al., 2021), significantly impacting ecosystem functions through alterations in species richness and abundance (Saura, 2021; Palmeirim et al., 2020; Liu et al., 2018). Fragmentation often leads to local extinctions and distinctive patterns in species richness and composition (Rybicki et al., 2020).

Over the past 30 years, central-southern Chile has experienced ongoing and increasing fragmentation of forested areas, with some effects also observed in the surrounding mountainous regions (Rau et al., 2001; Echeverría et al., 2006). In less than a century, the landscape of the La Araucanía region has transformed from a dense, impenetrable forest (Verniory, 2017) to one marked by novel landscapes and clear signs of environmental degradation. The severity of forest fragmentation primarily impacts mammal populations, depending on their habitat requirements (Zúñiga et al., 2014; Palmeirim et al., 2019), diet (Zúñiga et al., 2016), and behavioral adaptations, such as hunting and territoriality (Bista et al., 2022).

Since species exhibit varying levels of sensitivity to habitat fragmentation, species loss within the remaining habitat fragments does not occur randomly. Instead, it frequently follows a nested pattern, where species composition becomes progressively simplified as more sensitive species are lost (Patterson and Atmar, 1986; Atmar and Patterson, 1993, 1995; Deane & He, 2018; Hovestadt et al., 2024). This pattern is driven by factors promoting compositional disaggregation (García-Quintas and Parada-Isada, 2017; Flores et al., 2018). Nestedness is especially prevalent in fragmented systems shaped by local extinctions (Patterson and Atmar, 1986; Luther et al., 2020), playing a key role in landscape ecology. It provides a metric for assessing non-random species presence-absence across different assemblages and communities, enabling the quantification of species vulnerability to habitat changes (Luther et al., 2020).

Nestedness patterns have been studied in various taxa, including raptors (Rau et al., 2015), bird assemblages (Dardanelli and Bellis, 2021), ants (Flores et al., 2018), and amphibians (Rodríguez et al., 2023). However, little is known about the nestedness patterns of carnivorous mammals in fragmented landscapes. Carnivorous mammals are a valuable focus for this study as they represent the second most researched group in relation to the role of the matrix in fragmented landscapes (Ferreira et al., 2018). This study aims to investigate the nestedness patterns of five carnivorous mammal species across six forest habitat fragments to determine the likelihood of their local extinction. Given the ongoing and increasing habitat fragmentation in the study area, we expect to observe nestedness at the species composition level, considering the specific habitat requirements of each species.

Material and methods

Study area

The study area is located in the southern part of the Coastal Range in the Araucanía Region, southern Chile (fig. 1), extending from the southern side of the Toltén River to the border with the Los Ríos Region, covering a total area of 209,430 hectares. This region is characterized by Valdivian laurel forest vegetation, including species such as *Laurelia sempervirens*, *Persea lingue*, and *Lophozonia obliqua*. Historically, the area has been heavily modified by human activity and is now primarily composed of remnants of mixed vegetation and secondary growth forests (Gutiérrez and Becerra, 2018).

Sampling method

We selected 20 native forest fragments larger than 1 hectare based on land-use and land cover mapping derived from the 2003 Landsat ETM+ satellite image (Regional Plan for Urban Development and Territory — PRDUyT, LPT-UCT 2003). Each fragment was visited to verify its land-use category, level of intervention, and the feasibility of conducting fieldwork (e. g., accessibility and permission). Following this verification, the sample was reduced to six fragments, with one sample collected from each, except for the "Boroa Norte 1" and "Nueva Etruria" fragments, which were sampled twice.

Table 1 presents the characteristics of the six sampling sites within the fragmented forest landscape of the Coastal Mountains in the Araucanía Region. The fragment sizes ranged from 3.1 to 239.1 hectares and were in the communes of Pitrufquén, Toltén, Gorbea, and Loncoche. These fragments consisted of old-growth native forest, secondary native forest, and mixed forest (native species interspersed with exotics). In each of the six fragments, we identified the presence of carnivorous mammals using indirect detection techniques (Valente

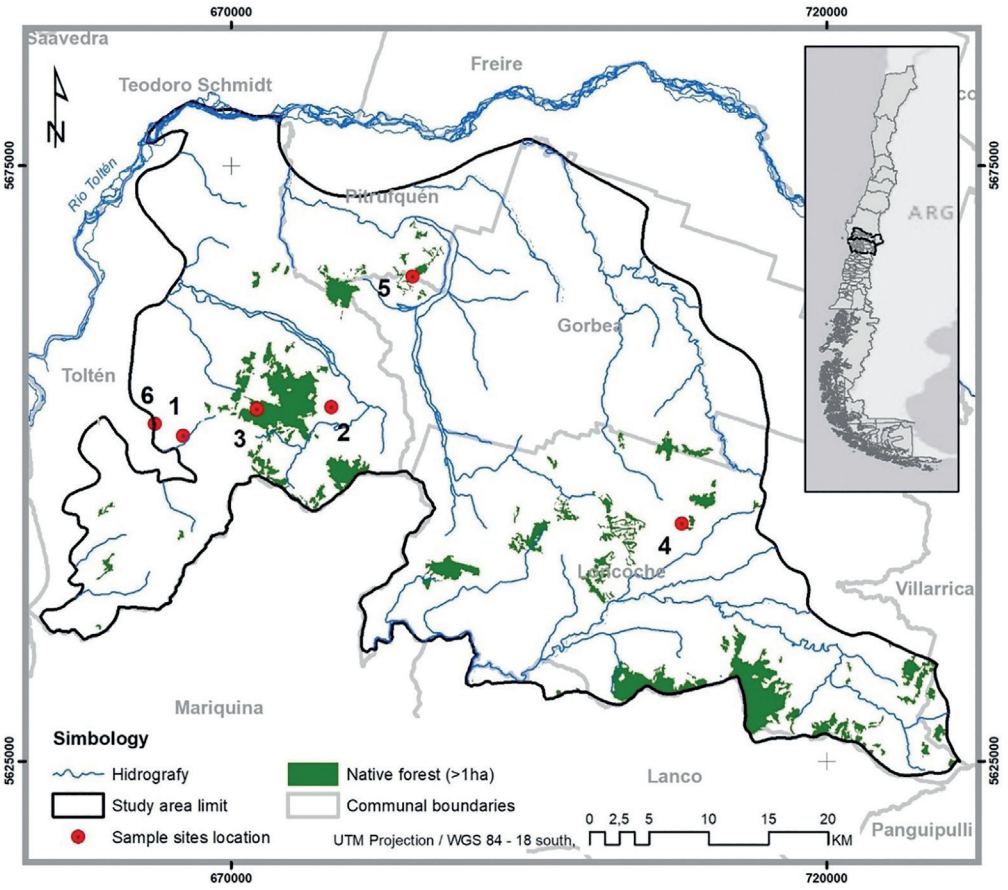

Fig. 1. Location map of the seven sampling sites in the Coastal Mountains of the Araucanía Region, southern Chile: 1 — Boroa Norte 1; 2— Licancullín; 3 — El Socorro; 4 — Afquintué; 5 — Nueva Etruria; and 6 — Boroa Norte 3.

Table 1. Characterization of the seven sampling sites within a fragmented forest landscape in the Coastal Mountains of the Araucanía Region, southern Chile

ID Fragment	Site	Sector	Commune	Coord. Ref (UTM)	Area (ha)	Category of use	Matrix
1	Boroa Norte 1	Boroa Norte	Toltén	665984N/5652334 E	14.0	BNA	AF
2	Licancullín	Colonia San Jorge	Toltén	678416N/5654733 E	46.8	RN	AF
3	El Socorro	Colonia San Jorge	Toltén	672161N/5654558 E	239.1	BNA	F
4	Afquintué	Afquintué	Loncoche	707838N/5644950 E	6.8	BNA	AF
5	Nueva Etruria	Comuy y Nueva Etruria/Mantahue	Pitrufquén/ Gorbea	685227N/5665714 E	146.5	RN	F
6	Boroa Norte 3	Boroa Norte	Toltén	663638N/5653327 E	3.1	RN	AF

Note: BNA — Adult native forest (old-growth forest); RN — Native secondary forest; BM — Mixed forest; AF — Agroforestry; F — Forestry.4

et al., 2018), such as scent stations (Webster & Beasley, 2019) and active searches for signs (feces and tracks) (da Silva Chaves et al., 2019) along roads and paths.

Mammal survey

We placed scent stations approximately every 200 meters along existing roads and trails within the native forest fragments and surrounding areas, such as forestry or agroforestry matrices, to avoid repeated visits to the same stations (Muñoz-Pedreros et al., 1995). To attract carnivores, we used American wildcat (*Lynx rufus*) urine as bait (Muñoz-Pedreros et al., 1995). Additionally, we actively searched for tracks and feces along roads

and paths throughout the entire sampling period in each fragment. Track identification was based on both field experience and Acosta and Simonetti's guide (1999).

Data collection took place over a period of nine months, from July 2006 to May 2007, with four effective sampling weeks per fragment. Scent stations were active for two consecutive nights in each of the six fragments. The "Licancullín" and "El Socorro" fragments were sampled in February 2007, "Afquintué" in March 2007, and "Boroa Norte 3" in May 2007. The "Boroa Norte 1" and "Nueva Etruria" fragments were sampled twice, in July 2006 and January 2007, and in September 2006 and March 2007, respectively. These fragments were sampled twice due to suboptimal climatic conditions during the initial sampling, which hindered carnivore detection. Therefore, sampling was repeated at a different time to ensure the validity of the data.

Data analysis

To identify the presence of nestedness patterns in the composition of carnivorous mammal species, we utilized the Binary Matrix Nestedness Temperature Calculator (BINMATNEST), which has gained prominence for detecting and quantifying nestedness in recent years (Rodríguez-Gironés and Santamaría, 2006; Zungu et al., 2019; Ferrarini et al., 2023). This program also incorporates the earlier Nestedness Temperature Calculator (NTC) developed by Atmar and Patterson (1993, 1995), as well as a second model developed by Fischer and Lindenmayer (2002) in which has been used in ecological networks studies (Lin et al., 2018).

BINMATNEST offers several advantages: (1) it implements a perfectly ordered line that is uniquely defined; (2) it uses genetic algorithms to reorder rows and columns in a way that minimizes matrix temperature; and (3) it provides three alternative null models; model 1 (Atmar and Patterson, 1993, 1995), model 2 (Fischer and Lindenmayer, 2002) and model 3 (Rodríguez-Gironés and Santamaría, 2006), to calculate the statistical significance of matrix temperature. The program also compares the observed adjacency matrix with a "perfectly ordered" matrix.

The results generated by this program indicate that higher temperatures (approximately 100 °C) **reflect a lower degree of** nestedness, suggesting a reduced probability of local extinctions. Conversely, lower temperatures (around 0 °C) **indicate a higher degree of** nestedness, with an increased likelihood of local extinctions.

Results

Among the carnivore species potentially present in our study area, we recorded the following five: the hog-nosed skunk (*Conepatus chinga* Molina, 1782), kodkod (*Leopardus guigna* Molina, 1782), cougar (*Puma concolor* Linnaeus, 1771), gray fox (*Lycalopex griseus* Gray, 1837), and culpeo fox (*Lycalopex culpaeus* Molina, 1837). The hog-nosed skunk was recorded at four sites: the two largest fragments, El Socorro and Nueva Etruria, as well as two smaller fragments, Boroa Norte 1 and Boroa Norte 3. The cougar was observed in three fragments, including the two largest (El Socorro and Nueva Etruria) and one smaller fragment (Boroa Norte 3). The kodkod was detected in two fragments: one large (Nueva Etru-

Table 2. Number of records of five species of carnivorous mammals in six fragments in the Coastal Mountains of the Araucanía Region, southern Chile

Fragments/Species	Culpeo fox	Gray fox	Hog-nosed skunk	Kodkod	Cougar	Total per fragment
Nueva Estruria	1	2	1	1	2	7
El Socorro	0	0	1	0	3	4
Boroa Norte 3	0	0	1	0	1	2
Boroa Norte 1	0	0	1	0	0	1
Licancullín	0	0	0	1	0	1
Afquintúe	0	2	0	0	0	2
Total per species	1	4	4	2	6	17

Table 3. Presence and absences of five species of carnivorous mammals in six fragments in the Coastal Mountains of the Araucanía Region, southern Chile

Fragments/Species	Culpeo fox	Gray fox	Hog-nosed skunk	Kodkod	Cougar
Nueva Estruria	1	1	1	1	1
El Socorro	0	0	1	0	1
Boroa Norte 3	0	0	1	0	1
Boroa Norte 1	0	0	1	0	0
Licancullín	0	0	0	1	0
Afquintúe	0	1	0	0	0

ria) and one small (Licancullín). The gray fox was specifically recorded in Nueva Etruria and Afquintúe, while the culpeo fox was found only in Nueva Etruria (table 2).

The nesting temperature calculated by the BINMATNEST software was 13.661°C, indicating a nested pattern and the potential for local extinctions. The mean and variance (mean ± var.) for the three models were as follows: 27.516 ± 92.051 ($p = 0.04$) for model 1, 23.981 ± 107.290 ($p = 0.14$) for model 2, and 21.624 ± 102.047 ($p = 0.24$) for model 3. Model 1, developed by Atmar and Patterson (1993, 1995), demonstrated greater robustness, as indicated by a significant p-value and the lowest variance.

By other hand, table 3 presents the presence and absence of the five identified carnivore species across six forest fragments in the Coastal Mountains of the Araucanía Region.

Discussion

The studies of species composition emphasize life history traits and interactions among species (i. e., a biological approach), allowing for the identification of those most sensitive to habitat fragmentation. Our research focused on species composition to better explain potential nested patterns, as opposed to solely studying species richness, which tends to adopt a more statistical or mathematical approach (see Rau, 2020).

Our results revealed a nested pattern in the species composition of the carnivorous mammal assemblage within forest fragments in the Coastal Mountains of the Araucanía Region. This pattern persisted despite the high mobility of carnivorous mammals, which is associated with their large home ranges and territorial behavior, as well as their generalist habitat use. It is important to clarify that this study focused exclusively on forest fragments, meaning that other biotopes, such as open fields, agricultural lands, or wetlands, were not included in the analysis. This limitation is significant because many carnivorous mammals are known to use a variety of habitats beyond forests, particularly for foraging or movement between fragmented areas. For example, the hog-nosed skunk, with an estimated average home range of 1.9 km² (Iriarte and Jaksic, 2017), occupies a variety of environments across its distribution, including shrublands, savannas, forests, mountains, high plateaus, parks, and steppes (Donadio et al., 2001; Riojas-López et al., 2019)

Another carnivore, the kodkod, with an estimated home range of 2.4 to 2.9 km² (Iriarte and Jaksic, 2017), is typically a forest specialist (Correa and Roa, 2005; Marín et al., 2022; Marín, et al., 2022). In contrast, the cougar, with home ranges estimated between 65 and 90 km² for males and 40 to 80 km² for females (Franklin et al., 1999; Iriarte and Jaksic, 2017), prefers more open habitats or exotic plantations, such as *Pinus radiata*, in areas with

open canopies that facilitate hunting (Lira and Naranjo, 2003; Charre-Medellín et al., 2012; Dumont et al., 2022). The culpeo fox and gray fox, with home ranges ranging from 4.5 to 1,140 km² and 3 to 4 km², respectively, occasionally inhabit forested areas but generally favor more open habitats or shrublands, where small mammals are more abundant and accessible (Quintana et al., 2009; Medel et al., 2022).

In the fragments of Boroa Norte 1, Licancullín, El Socorro, and Afquintúe, the canopy is denser, accompanied by a thicker and more extensive layer of leaf litter. In contrast, the fragments of Nueva Etruria and Boroa Norte 3 have a more open canopy, with a greater prevalence of herbaceous plants and shrubs. Our findings align with previous studies on the culpeo fox conducted in central Chile (Acosta-Jamett and Simonetti, 2004), central Argentina (Pia et al., 2013), Colombia (Noguera-Urbano et al., 2016), and the high-Andean ecosystems of Ecuador (Guntiñas et al., 2019), which found that this species is more abundant in high-altitude areas characterized by high humidity, extreme temperatures, and homogeneous vegetation typical of open, treeless habitats.

In a separate studies, Lantschner (2012) and Haley-Marie (2023) have found that the culpeo fox and gray fox primarily use continuous native vegetation but also inhabit dense conifer plantations. These species tend to be more abundant in fire-affected zones and sparse plantations than in dense ones. In contrast, the cougar is present across all habitat types, showing no preference (Winkel et al., 2023). The kodkod, on the other hand, is closely associated with native Mediterranean forests and temperate rainforests, favoring areas with significant vegetation cover (Schüttler et al., 2017). This species has been sparsely studied, and its ecology and habitat use remain poorly understood.

However, studies such as Schüttler et al. (2017) have found that the kodkod is forest-dependent and makes intensive use of forest edges, particularly near water sources in Chilean temperate rainforests. The kodkod compensates for the lack of continuous forest by maintaining a larger habitat range and efficiently utilizing forest edges, likely due to higher prey availability in these areas. Additionally, this species is adaptable to fragmented landscapes dominated by human activity, using small forest fragments and vegetation corridors within agricultural matrices to navigate the landscape (Gálvez, 2013). There are also reports of kodkods inhabiting dense pine plantations (Acosta-Jamett and Simonetti, 2004).

This species (kodkod) has a restricted distribution, primarily found in central and southern Chile (30°–48° S), including the large island of Chiloé off the southern coast, and marginally in adjacent areas of southwestern Argentina (39°–46° S, west of 70° W) (Napolitano et al., 2015). However, more recently, Napolitano et al. (2020) reported new records from the southern Coquimbo and northern Valparaíso regions, marking the northernmost confirmed occurrences of this species to date. In contrast, little is known about the habitat use of the gray fox. A recent study by Osorio (2021) found that this species is tolerant to landscape changes, showing no significant response to burns, and is often found near human settlements and rivers.

Although our study attributed the presence of highly mobile carnivores to the forest fragments, it is likely that these fragments serve primarily as corridors or stepping stones within their larger home ranges. For instance, the presence of cougars, which have large home ranges, is likely more attributable to the overall landscape rather than the specific fragments. Carnivores, in general, are highly vulnerable to local extinction due to habitat fragmentation, primarily because of their low population densities and large territorial requirements (Rocha et al., 2018). However, not all carnivores are equally sensitive to landscape and local-level variables; their vulnerability is largely de-

termined by body size. Larger, more generalist carnivores, such as the culpeo fox, have larger home ranges and are therefore more sensitive to habitat fragmentation (Crooks, 2002). In contrast, specialist carnivores, such as the kodkod, are likely the most affected (Swihart et al., 2003).

In Chile, the effects of native forest fragmentation on the kodkod and culpeo fox have been studied in Los Queules National Reserve and the surrounding pine fragments and plantations (Acosta and Simonetti, 2004). For the kodkod, it has been suggested that fragmentation and habitat loss may severely impact the species, particularly females, which are more sedentary and have smaller home ranges (Sanderson et al., 2002). In contrast, the culpeo fox, a habitat generalist (Medel and Jaksic, 1988), may be less affected by forest fragmentation. This species appears to prefer large areas of native forest over fragments and plantations, likely due to the protection they offer. It is generally expected that smaller fragments will support a less diverse set of species compared to larger areas (Rau et al., 2015).

On the other hand, the nesting temperature of 13.661 °C obtained in our study indicates a high degree of order in the carnivorous mammal assemblage in the forest fragments studied. In terms of nestedness theory, a low temperature suggests that communities are hierarchically organized, with some species being more frequent and widely distributed, while others are restricted to specific habitats or fragments (Mittelbach and McGill, 2019). This level of order may reflect local extinction processes or the preferential selection of habitats by certain species.

Previous studies using BINMATNEST, such as those by Atmar and Patterson (1993, 1995), Lin et al. (2018), Mariani et al. (2024) consider that the rank of each species invariably depends on the interactions stipulated with other species through the adjacency matrix of the network. A common ranking method in economic and ecological networks is to sort the nodes such that the layout of the reordered adjacency matrix looks maximally nested with all nonzero entries packed in the upper left corner, called Nestedness Maximization Problem (NMP) have shown that lower temperatures are typically associated with highly structured systems and significant levels of nestedness, often linked to habitat fragmentation and the differential ability of species to persist in fragmented environments. In contrast, higher temperatures imply greater randomness in species distribution, indicating less hierarchical structuring. In our case, the relatively low temperature supports the hypothesis that forest fragments are undergoing local extinction processes, leading to a nested pattern in the species present.

The presence/absence and the number of species records in each fragment could indeed be influenced by the specifics of our data collection. Although we conducted fieldwork over a period of nine months, using scent stations for two consecutive nights per fragment, it is possible that the number of days dedicated to data collection was insufficient to capture the full diversity of carnivore species in each fragment. For example, two nights might not be enough time to detect species with large home ranges, like the cougar, which may not pass through the fragments during such short timeframes.

Moreover, climatic conditions and the season during which the sampling took place could have impacted the detection of carnivores. Some species may exhibit seasonal behavior changes, such as reduced activity during unfavorable weather conditions or breeding seasons, which could have reduced the likelihood of detection (Caravaggi et al., 2018; Levy et al., 2019; Guiden and Orrock, 2020; Abrahms et al., 2022). This is particularly relevant for fragments like “Nueva Etruria” and “Boroa Norte 1,”

which were sampled twice due to suboptimal weather conditions during the initial sampling. Therefore, the variation in the number of species recorded across fragments may reflect not only habitat characteristics but also temporal limitations in the data collection process. To address these potential biases in future studies, extending the sampling period, increasing the number of active days per fragment, and considering seasonal variations in carnivore activity could provide a more comprehensive understanding of species presence and distribution within the forest fragments.

We pointed out that to planning an effective biodiversity conservation measure for fragmented environments, it is essential to safeguard the probability of recolonization of carnivorous mammals (e. g., to plan the management of the fragmented landscape so that it is a suitable (permeable) substrate for the dispersal of individuals). This probability of recolonization depends on the spatial relationships between landscape elements used by populations, including habitat patches and matrix elements, dispersal characteristics of the organisms, and the temporal changes in the structure of the landscape (Fahrig and Merriam, 1994). Therefore, to minimize the effects of fragmentation and to protect the associate carnivore mammals its essential to have good knowledge of species biology and its habitat use.

Conclusion

This study provides important insights into the composition and distribution of carnivorous mammals across fragmented forest habitats in the Coastal Mountains of the Araucanía Region, Chile. Five carnivore species were recorded in the study area: the hog-nosed skunk, kodkod, cougar, gray fox, and culpeo fox. These species exhibited varying degrees of sensitivity to habitat fragmentation, which may reflect their different ecological requirements and life history traits. Also, the study reveals a nested pattern in the species composition of carnivores, as indicated by the low nesting temperature. This suggests that local extinctions are likely, particularly in smaller fragments where species such as the hog-nosed skunk and kodkod, which have smaller home ranges, may be more vulnerable.

The findings suggest that species with larger home ranges and generalist habits, such as the cougar and culpeo fox, are less sensitive to fragmentation and may use fragmented habitats as corridors or stepping stones. In contrast, species more closely associated with dense forest cover, such as the kodkod, are likely more affected by fragmentation, as they depend on specific habitat features for survival. However, the species distribution and nested pattern observed in this study may not fully represent the wider landscape use of these predators, as it was restricted to the forest fragments and not other biotypes.

Finally, the study highlights the importance of larger forest fragments in maintaining carnivorous mammal diversity. Smaller fragments are likely to support a less diverse assemblage of species, as predicted by the theory of island biogeography. For conservation efforts, it is essential to prioritize the preservation of larger continuous forest areas and the restoration of connectivity between fragments to mitigate the negative effects of fragmentation on sensitive species, particularly the kodkod and hog-nosed skunk. Further research is needed to monitor the long-term impacts of fragmentation and to explore how different species adapt to changing landscapes, particularly in regions like the Araucanía, where human-driven land-use changes are accelerating.

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