Vallejos-Garrido *et al.*
Revista Chilena de Historia Natural (2024) 97:8
https://doi.org/10.1186/s40693-024-00131-x

Revista Chilena de Historia Natural

REVIEW

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Where is dinner? The spatiality of the trophic niche of terrestrial mammalian carnivores in Chile, a systematization for their conservation

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Abstract

Knowing what the highest-level mammalian carnivores and intermediate levels eat throughout the geography and how human activities may affect their community dynamics is relevant information to focusing and deciding on conservation efforts within a territory. In this review, we characterize geographically the accumulated knowledge about the trophic niche of terrestrial mammalian carnivore species and evaluate the spatial relationship between the species richness distribution and the geographical distribution of their trophic knowledge in Chile. We found 88 peer-reviewed papers that include trophic studies per se, theses, and short notes carried out in Chile, where at least one trophic element was reported for terrestrial mammalian carnivore species. We found a positive relationship between the species richness distribution pattern and the spatial distribution of accumulated trophic knowledge, i.e., most of the papers have been conducted in Central-southern Chile (Central Chile and Temperate Forest ecoregions) responding to the highest co-occurrence of carnivore species within the limits of the biodiversity hotspot, the most threatened area in the country. Despite this general relationship, we recognize gaps in knowledge regarding regions of the country that require more research effort, such as O'Higgins, Maule, and Ñuble regions, as well as focus efforts on certain species with no or almost no knowledge of their trophic ecology, such as *Leopardus colocola*, *Lyncodon patagonicus* and *Conepatus chinga*. Except for the northern Chilean ecosystems, there is a generalized report of high consumption of exotic mammals in the diet of carnivores in the center and south of the country. However, of the 98 localities recognized in the 88 papers, 20.4% correspond to an anthropized environment, while most (79.6%) correspond to a "non-anthropized" environment or protected area. We hope this review allows researchers and decision-makers to consider the knowledge and lack thereof of carnivore trophic interactions as an opportunity to conserve entire natural communities throughout the Chilean territory.

Keywords Carnivora, Chilean mammals, Diet, Anthropization, Trophic niche

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Introduction

Biological communities comprise all sympatric species of different taxa and life histories that can interact at a given locality. However, the difficulty of thoroughly analyzing all their interactions to understand intrinsic relationships inside the system has led researchers to focus the inter-specific questions on restricted groups of species as "assemblage-guilds" [68, 71, 129, 134, 149] or "indicator species" [16, 42]. Here, mammalian carnivores of the order Carnivora play an essential role as they are the highest-level predators in most terrestrial communities. By occupying the top or superior positions of the energy pyramid, the descent or removal of these predators of an environment can generate a trophic cascade that can alter the ecological structure of a community modifying the interactions that regulate predator and prey populations [27, 50, 128, 150] and act as secondary seed dispersers [56]. This environmental sensitivity has earned them the label of "biological indicators", giving them great ecological value because their predation interactions create impacts that can ripple downward through the trophic levels of an ecosystem, having a fundamental role in the preservation of the biodiversity of terrestrial communities [44, 55, 64, 101, 111]. Carnivora includes several primary conservation icon species, many others are considered flagship, umbrella, keystone, and indicator species. However, Gittleman et al. [50] highlighted that carnivore conservation would be more effective if conservation strategies were focused on prioritizing geographical areas or entire ecological communities rather than addressing individual species separately. Feeding, and consequently the prey availability, is a fundamental factor in the life of carnivores and, in many cases, one of the most limiting n-dimensions of their ecological niche [57]. For example, it has been demonstrated that the greatest threat to tiger (*Panthera tigris*) conservation is the population reduction of tiger prey [81, 82]. In this sense, knowing what the highest-level mammalian carnivores (hypercanivores) and intermediate levels (mesocarnivores to omnivores) eat throughout the geography and how human activities may be affecting their community dynamics is very relevant information to focus and decide on conservation efforts within a territory. Then, studying the trophic relationships of Carnivora predators is an effective approach for detecting the composition of communities. However, studying carnivores is challenging due to their elusive nature, low abundance, and nocturnal habits [64]. As a result, the ecology of many carnivore species and their communities, such as the Andean small cats in Chile, is poorly understood [28].

The study of carnivores' feeding strategies and diet often utilizes non-invasive methods, such as fecal analysis and observation of food availability. This helps determine the species role in the ecosystem, potential interspecific competition, and impact on prey populations [83]. In this sense, the results of diet analyses might have a far-reaching effect on the development of carnivore management plans, especially if economically important or endangered species are involved [48, 83, 84]. This is essential to understand the geographical context of knowledge and identify gaps and fragmented information. This type of study and knowledge becomes even more relevant in an ecosystem of high international priority for biodiversity conservation, such as the *Chilean Winter Rainfall-Valdivian Forests* (henceforth, Chilean hotspot), characterized as one of the 34 biodiversity hotspots worldwide [2, 103, 106, 143].

Currently, 15 terrestrial native carnivore species of four different families are found in Chile [29], one Mephitidae: *Conepatus chinga*; three Canidae: *Lycalopex culpaeus, Lycalopex griseus*, and *Lycalopex fulvipes*; four Mustelidae: *Galictis cuja, Lontra felina, Lontra provocax*, and *Lyncodon patagonicus*; seven Felidae: *Leopardus colocola, Leopardus garleppi, Leopardus pajeros, Leopardus jacobita, Leopardus geoffroyi, Leopardus guigna*, and *Puma concolor*. Moreover, in southern Chile, the American mink (*Neovison vison*) is an exotic and invasive mustelid that has strongly affected and continues to threaten the Patagonian ecosystems [73, 132]. Chile has the highest carnivore species richness and endemism levels in the Chilean hotspot. Therefore, it is crucial to understand their ecological aspects to develop effective conservation strategies. The main goals of this review are: 1) geographically characterize the accumulated knowledge about the trophic niche of terrestrial mammalian carnivore species present in Chile, 2) evaluate the relationship between the geographical distribution of the mammalian carnivore species richness and the geographical distribution of published information on trophic aspects of these species throughout Chile. We hope to find more studies in central-south Chile due to the high number of sympatric species in the global conservation priority area. This also translates into a significant knowledge gap in extreme regions of the country, 3) recognize the gaps in knowledge about species' diets and areas throughout their respective geographic distributions in Chile allows future and urgent conservation efforts to be geographically focused.

Methods

Search of studies/ bibliographic compilation

We reviewed the scientific literature on the diets of 16 terrestrial mammalian carnivore species (15 native + American mink) by searching for keywords and titles in both English and Spanish through Google Scholar, Web of

Science, and SCOPUS. We used the following keywords for each search: "scientific binomial name" AND "diet" OR "feeding habits" OR "trophic niche". We consider the variants and changes of taxonomic names as 1) "*Lycalopex*, "*Pseudalopex*" and "*Dusicyon*" for the South American foxes and 2) Recent taxonomic arrangement as proposed for *Leopardus colocola* [29, 108]. Original/research articles, short notes, and theses (hereinafter "papers") that provide detailed information or the report of a particular trophic item were included. The bibliographic review was carried out between July 2023 and April 2024. To provide detailed diet descriptions by species (Supplementary Information), papers from nearby localities in adjacent countries that cover the same ecoregion as the Chilean distribution of the species were considered for species with less than three papers conducted in Chile.

Gathering information / geographic information

To characterize the geographical locality of each paper, we recorded the geographic coordinates of the study locality reported and identified the administrative province and region to which the locality corresponds. In addition, the ecoregion associated with the study locality was identified. For this, six ecoregions within the country were distinguished, following the classification proposed by the Biodiversity Support Program [8] and Dinerstein et al. [30] and updating the limits of these ecoregions according to the zonal vegetation unit presented in "Bioclimatic and Vegetational Synopsis of Chile" [89]. Ecoregions are the Coastal Atacama Desert, Puna, Central Chile (Mediterranean sclerophyllous forest + Andean Steppe), Temperate Forest (Deciduous + Evergreen), Patagonian Steppe, and Subpolar Forest. Then, we quantified the number of papers and study localities per species conducted by political region, province, and ecoregion. In addition, we categorized each study locality as a "non-anthropized" or "anthropized" environment, according to the paper. We recorded the percentage of exotic prey items in the species' diet reported in each study as another factor that accounts for anthropization.

Spatial relationship and statistical analysis

We describe the spatial pattern of species richness in Chile and statistically determine the areas of the country that present a greater (hotspot) and lower (coldspot) number of species than expected by chance through Gi* statistic [49]. Briefly, Gi* identifies spatial concentrations of high or low values of an entity (in this case, species richness per $0.25 \times 0.25°$ cells). To establish statistically significant areas, a feature must have high or low values and be surrounded by other cells with similar values. Consequently, the local sum of an entity and its neighbors is compared proportionally to the sum of all entities. A significant Z score is assigned if the local sum differs from the random expectation. Significant values of $Z > 0$ provide evidence of significant hotspots, while those of $Z < 0$ provide evidence of groups of entities with values lower than those expected by chance. The statistical determination of hotspots and coldspots was performed in ArcGIS 10.4.1 software [40]. To evaluate the relationship between species richness and the number of localities by administrative region and ecoregion, spatial (Simultaneous autoregressive, SAR and conditional autoregressive, CAR) and non-spatial (Ordinary Least Squares regression, OLS) regression methods were performed. Both CAR and SAR incorporate spatial autocorrelation using neighborhood matrices, which specify the relationship between the residuals at each location (i) and those at neighboring locations (j) [86]. The model selection approach was applied to search for the model with the best fit [77]. The selection was carried out using the delta AIC (Δi, using the formula Δ AIC = AICi – min AIC, where AICi is the AIC of model i, and min AIC is the AIC value of the "best" model. As a rule, $\Delta i < 2$ suggests substantial evidence for the model, values between 3 and 7 indicate that the model has less support, while $\Delta i > 10$ indicates that the model is unlikely [13]. Analyzes were performed through the "MuMin" package [7]. Since the models did not reveal significant spatial autocorrelation (Supplementary Information, Table S1), we chose OLS models to study the relationship of species richness versus localities by administrative regions and ecoregions of Chile. Regression analyses were performed with the ncf [9], spdep, and spatialreg [117] packages in R software [122].

Results

We found 88 papers that included original/research articles, theses, and short notes conducted in Chile, where at least one trophic element was reported for terrestrial mammalian carnivore species (Supplementary Information, Table S2). Papers were collected from 1978 [155] to 2024 [158]. The number of papers per year in Chile shows a slight increase over time, with two peaks in 1991 and 2014 (Fig. 1a). The distribution of the number of papers by species shows that the greatest number have been conducted for *L. culpaeus* and *L. griseus* and highlights that three species do not present trophic studies in Chile: *C. chinga*, *L. patagonicus* and *L. pajeros* (Table 1 and Fig. 1b). A summary of the diet in Chile for each of the 16 species is available in Supplementary Information. Of the 88 papers, we quantify 98 study localities. The distribution of the number of study localities by ecoregion shows that the greatest number is found in the central-south ecoregions (Central Chile, Temperate Forest, and

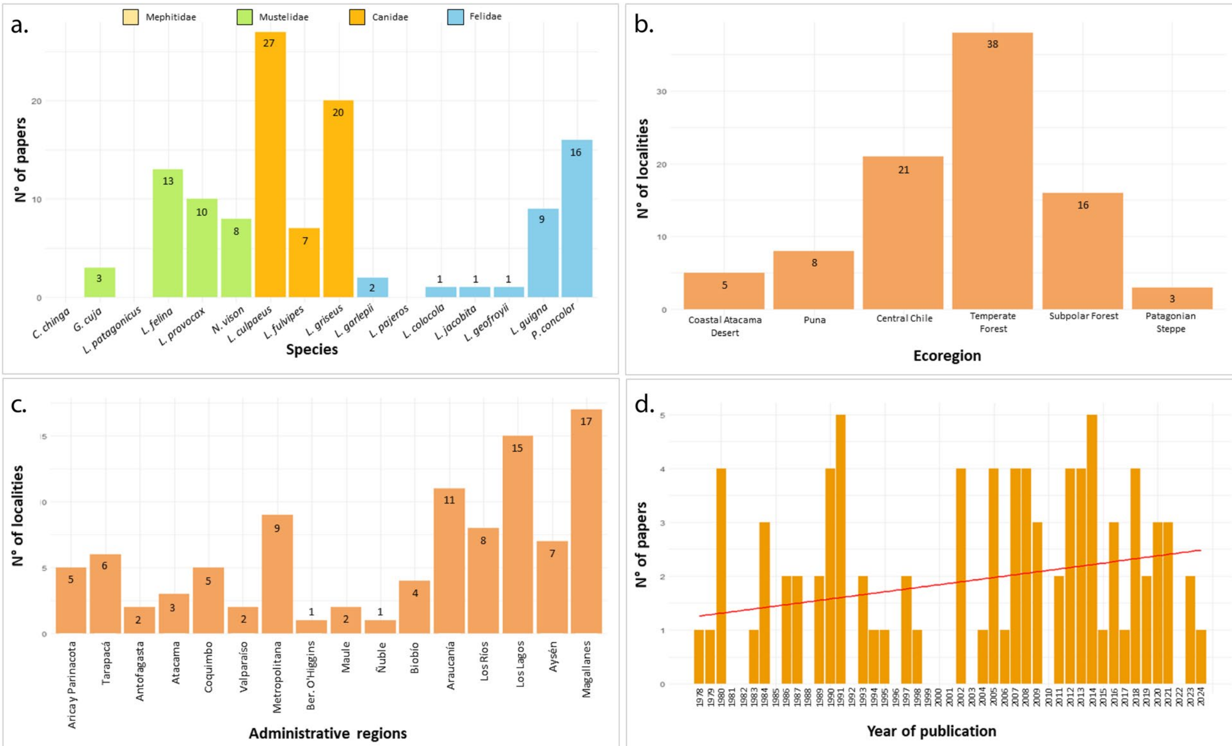

Fig. 1 **a** Distribution of the number of papers per species; **b** Distribution of the number of study localities per ecoregion; **c** Distribution of the number of study localities per administrative regions; and **d**) Distribution of the number of papers over time ($R^2 = 0.045$)

Subpolar Forest), with a decrease towards the ecoregions of both the northern (Atacama Coastal Desert) and the southern (Patagonian Steppe) extremes (Table 1 and Fig. 1c). When considering the spatial distribution of study localities in the context of the political-administrative division of the country, the 98 localities are grouped in 37 provinces belonging to the 17 administrative regions of the country (Supplementary information, Table S3). The distribution of research per administrative region showed that the majority are in Araucanía, Los Lagos, and Magallanes. In contrast, Antofagasta, O'Higgins, Maule, and Ñuble regions show only one study (Table 2 and Fig. 1d).

Geography of anthropization

Of the 98 study localities, 20 (20.4%) report being an anthropized environment or with some degree of anthropization, mainly in central-southern Chile. One locality in Puna (Antofagasta region), six localities in Central Chile (four in the Metropolitan region, one in Valparaíso, and one in Maule region), 12 localities in Temperate Forest (four in the Araucanía region, three in Biobío, two in Los Lagos, two in Los Ríos and one in Maule region) and, one in Subpolar Forest (Magallanes region; Fig. 2). By contrast, most study localities (79.6%) correspond to "non-anthropized" environments or protected areas concentrated mainly in the northern and southern extremes of the country (Fig. 2). Furthermore, the 77.3% of the papers reports a study locality in an "anthropized" environment corresponding to research from 2005 to the present. The study locality by species and anthropized environments revealed that *L. culpaeus* (11 sites) and *L. griseus* (7 sites) have the greatest number of papers in these environments, while *L. garleppi*, *L. jacobita*, and *L. geofroyii* do not have papers in anthropized environments (Supplementary Information, Table S3). Concerning the exotic prey items reported in the different papers, despite not describing anthropized environments for the Atacama Coastal Desert ecoregion, the presence of exotic rodents *Mus musculus* and *Rattus rattus* has been reported in the diet of *L. griseus* and *L. culpaeus* in the Tarapacá region [15, 91]. For the Puna ecoregion, there are no reports of exotic prey items in the diet of terrestrial mammalian carnivore species. For Central Chile, several localities, mainly in the Metropolitana region but also in Atacama, Coquimbo, O'Higgins, and Valparaíso regions, report a greater breadth of exotic prey items, highlighting the presence of *Oryctolagus cuniculus*, *Lepus europaeus*, and *R. rattus* in the diet of *L.*

Table 1 Trophic papers conducted in Chile by ecoregion

Species/ Ecoregion	Atacama Coastal Desert	Puna	Central Chile	Temperate Forest	Subpolar Forest	Patagonian Steppe	N° papers per species
Conepatus chinga	–	–	–	–	–	–	**0**
Galictis cuja	–	–	[34]	[131, 164]	-	–	**3**
Lyncodon patagonicus	–	–	–	–	–	–	**0**
Lontra felina	–	–	[18, 20, 35, 90, 113, 153]	[20, 21, 35, 90, 97, 110, 113, 119, 133]	[20, 138, 139]	–	**13**
Lontra provocax	–	–	–	[43, 94, 95, 98, 99, 133, 137]	[35, 138, 151]	–	**10**
Neovison vison	–	–	–	[17, 94, 99]	[26, 60, 76, 135, 151]	–	**8**
Lycalopex culpaeus	[53, 91]	[15, 85, 91]	[19, 33, 34, 61, 67, 87, 92, 100, 112, 130, 140, 142, 155, 158]	[22, 66, 104, 159, 165]	[59, 70, 79, 156]	[70]	**27**
Lycalopex fulvipes	–	–	–	[38, 72, 74, 75, 93, 104, 127]	–	–	**7**
Lycalopex griseus	[91]	-	[33, 67, 92, 105, 145, 155, 166]	[22, 93, 104, 125, 141, 160, 161, 163, 164]	[79]	[3, 70]	**20**
Leopardus garleppi	–	[47, 107]	–	–	–	–	**2**
Leopardus pajeros	–	–	–	–	–	–	**0**
Leopardus colocola	–	–	[158]	–	–	–	**1**
Leopardus jacobita	–	[107]	–	–	–	–	**1**
Leopardus geofroyii	–	–	–	–	[78]	–	**1**
Leopardus guigna	–	–	[158]	[1, 22, 39, 41, 46, 104, 164]	[32]	–	**9**
Puma concolor	–	–	[112, 158]	[25, 62, 124, 127, 146, 162, 164, 165]	[4, 11, 62, 63, 154, 157]	[37]	**16**
N° papers per ecoregion	**3**	**5**	**21**	**46**	**22**	**3**	

griseus, *L. culpaeus*, *P. concolor* and *G. cuja* [34, 67, 87, 105, 112, 130, 142, 145, 155, 158]. Eight of the nine species of mammalian carnivores distributed in the Temperate Forest ecoregion show exotic items in their diet. In this ecoregion, exotic prey items are reported in 24 different localities through Maule, Ñuble, Biobío, Araucanía, Los Lagos, and Los Ríos regions. The presence of the exotic fish *Salmo trutta* in the diet of the semi-aquatic *L. provocax* and the invasive *N. vison* in the Los Ríos Region stands out [43, 94], and the presence of exotic rodents and lagomorphs in the diet of all species of terrestrial predators (e.g., [104, 124, 126, 164, 165], Supplementary Information, Table S3). For the Subpolar Forest ecoregion, most of the study localities are in the Torres del Paine National Park and adjacent sites (Magallanes region), where feeding of *Ovis aries* cattle by *P. concolor, L. griseus,* and *L. culpaeus* was reported in several papers [63, 79, 157]. The only research for *L. geoffroyi* in Chile stands out here. The study shows that this species feeds on the exotic lagomorph *Lepus capensis*, which has a local high abundance [78]. In addition, in the southern part of Patagonia, at Tierra del Fuego National Park, the invasive *N. vison* also preys on exotic rodents and lagomorphs [151]. In the Patagonian Steppe ecoregion, the presence of exotic prey items such as cattle and lagomorphs are reported in all study localities (Aysén and Magallanes regions) for the diet of *P. concolor*, *L. griseus* and *L. culpaeus* [3, 37, 70] (Supplementary Information, Table S3).

Table 2 Number of papers and study locations by administrative region

Administrative region	N° of papers	N° of localities
Arica y Parinacota	2	5
Tarapacá	4	6
Antofagasta	2	2
Atacama	5	3
Coquimbo	7	5
Valparaíso	2	2
Metropolitana	7	9
Libertador Bernardo O'Higgins	1	1
Maule	2	2
Ñuble	1	1
Biobío	6	4
Araucanía	13	11
Los Ríos	10	8
Los Lagos	17	15
Aysén	4	7
Magallanes y la Antártica Chilena	21	17

Spatial analyses

The spatial distribution of mammalian carnivore species richness in Chile shows the highest diversity in the Central Chile ecoregion, with a peak of six species occurring in an area of ~27 km^2 (0.25° cell). This area corresponds to Valparaíso, Metropolitana, O'Higgins, and Maule regions, while the areas with the lowest species number are in Coastal Atacama Desert and some areas of Patagonia with a minimum of one species (Fig. 3a). Areas with the highest species richness than expected by chance correspond to two areas in the Puna, a great extension in Central Chile + Temperate Forest, and an area in southern Chile that encompasses the Subpolar Forest and Patagonian Steppe ecoregions (Fig. 3b). The OLS model had a better fit than an autoregressive one, showing a positive and significant relationship (with transformed and untransformed data) between the spatial distribution of species richness and the number of localities by ecoregion ($R^2 = 0.71$; $p = 0.02$), in the same way, the species richness also shows a positive and significant relationship with the number of localities by administrative region ($R^2 = 0.45$; $p = 0.002$; Table 3, Fig. 4).

Discussion

Knowledge—species and knowledge—area relationship

The positive relationship between the species richness distribution pattern of mammalian carnivores and the spatial distribution of accumulated knowledge (measured as the number of papers) about the trophic relationships allows us a first general and encouraging interpretation that most of the studies have been conducted in Central-southern Chile (Central Chile and Temperate Forest ecoregions) which corresponds in turn to the highest co-occurrence of carnivore species area, being this within the limits of the biodiversity hotspot, the most threatened area in the country [103, 106, 143]. However, despite this general relationship, we can recognize gaps in knowledge regarding areas of the country that require greater research effort and focus efforts on certain species with no knowledge of their trophic ecology. A clear spatial bias that is necessary to consider to address new research projects or conservation efforts is the non-uniform distribution of papers by administrative regions within the Chilean hotspot, with one paper for the regions of O'Higgins [112], Ñuble [19], two for Valparaíso [18, 105] and two for the Maule region [22, 158], being these regions part of most affected by the intense change in land use towards productive activities [58]. Indeed, in these regions, it is necessary to evaluate the effects of this landscape transformation on mammalian community interactions. Conversely, most papers are concentrated in the northern portion of the biodiversity hotspot (Coquimbo and Metropolitana regions) and the southern portion (Biobío, Araucanía, Los Ríos, and Los Lagos regions). In the Chilean hotspot, mammalian carnivore species have been exposed to strong human pressure over the last century due to the accelerated replacement of native forests with productive plantations and human settlements (e.g., [104, 112, 114, 160]). However, the largest number of papers have been conducted in public and private protected areas, where the explicit effect of human pressures and landscape transformation on natural communities is difficult to evaluate. In these areas, sometimes far from human productive activities, the trophic papers reflect in the same way a high presence and abundance of exotic species in the diet, such as lagomorphs and rats, accounting for their wide spatial expansion of these species. Concerning South America, in Chilean territory, wild exotic mammals exhibit their most invasive ranges and where they are present at the highest densities [10, 12, 39, 116, 147, 165]. Therefore, carnivores have shown flexible trophic behavior due to this new food supply in protected and transformed areas. Research in anthropized landscapes supports the idea that species such as *L. guigna*, *P. concolor*, *G. cuja*, and the foxes of the genus *Lycalopex* may use productive plantations as feeding areas [22, 61, 74, 104, 112, 131, 158]. Another example of the consumption of exotic rodents in anthropized areas is reported for *L. provocax* [43]. Nevertheless, research is key and urgent for species without trophic information in the pristine and anthropized habitats of the Chilean hotspot. This includes species such as *C. chinga*, *L. patagonicus*. Although there are trophic

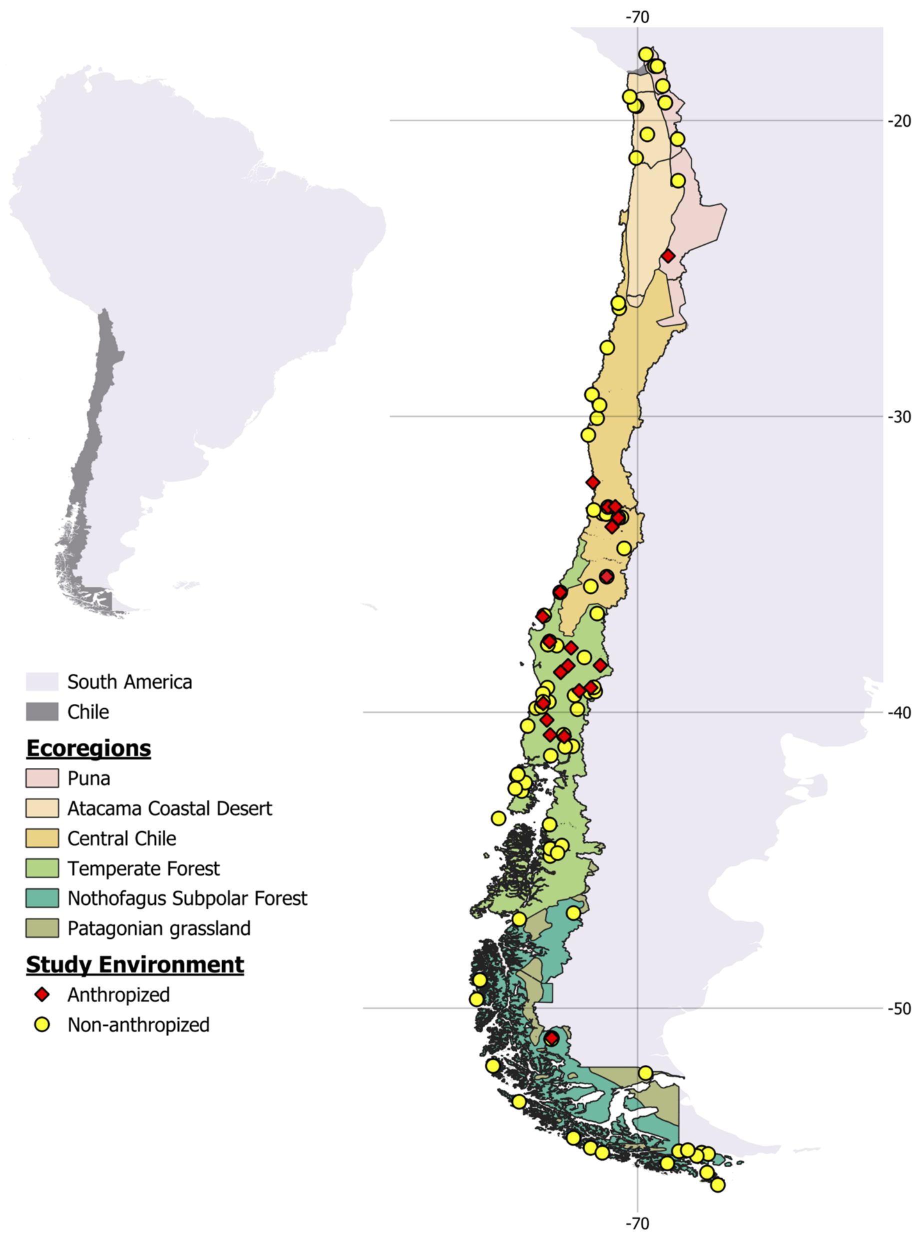

Fig. 2 Spatial distribution of the study localities reported in the 88-papers found. Colored polygons correspond to each ecoregion. Yellow circles correspond to non-anthropized study localities, and red diamonds correspond to anthropized study localities

studies for *C. chinga* in other countries and ecoregions (e.g., [31, 96, 115]) that could give light on its community role in northern and southern Chilean territory, it is relevant to know the role of this insectivorous predator on insect assemblages considering that the diversity of Coleoptera in Central Chile is highly endemic [148, 152]. An example of extreme information deficit is the case of *L. patagonicus*. It is a species with an unknown natural history in Chile and one of the least known carnivores from southern South America [36, 120, 121]. Thus, research priority is required to confirm its current ecological requirements and understand its role in native and anthropized landscapes. Another species with an almost unknown natural history is *Leopardus colocola,* endemic of Central Chile. The subspecies *L. colocolo colocola* has recently been elevated to the category of species [29, 108]. However, until the thesis of Zamora-Cornejo [158] in an Andean foothill range protected area of the Maule Region, there was no explicit knowledge about the colocolo's diet in its distribution range of Central Chile. Here,

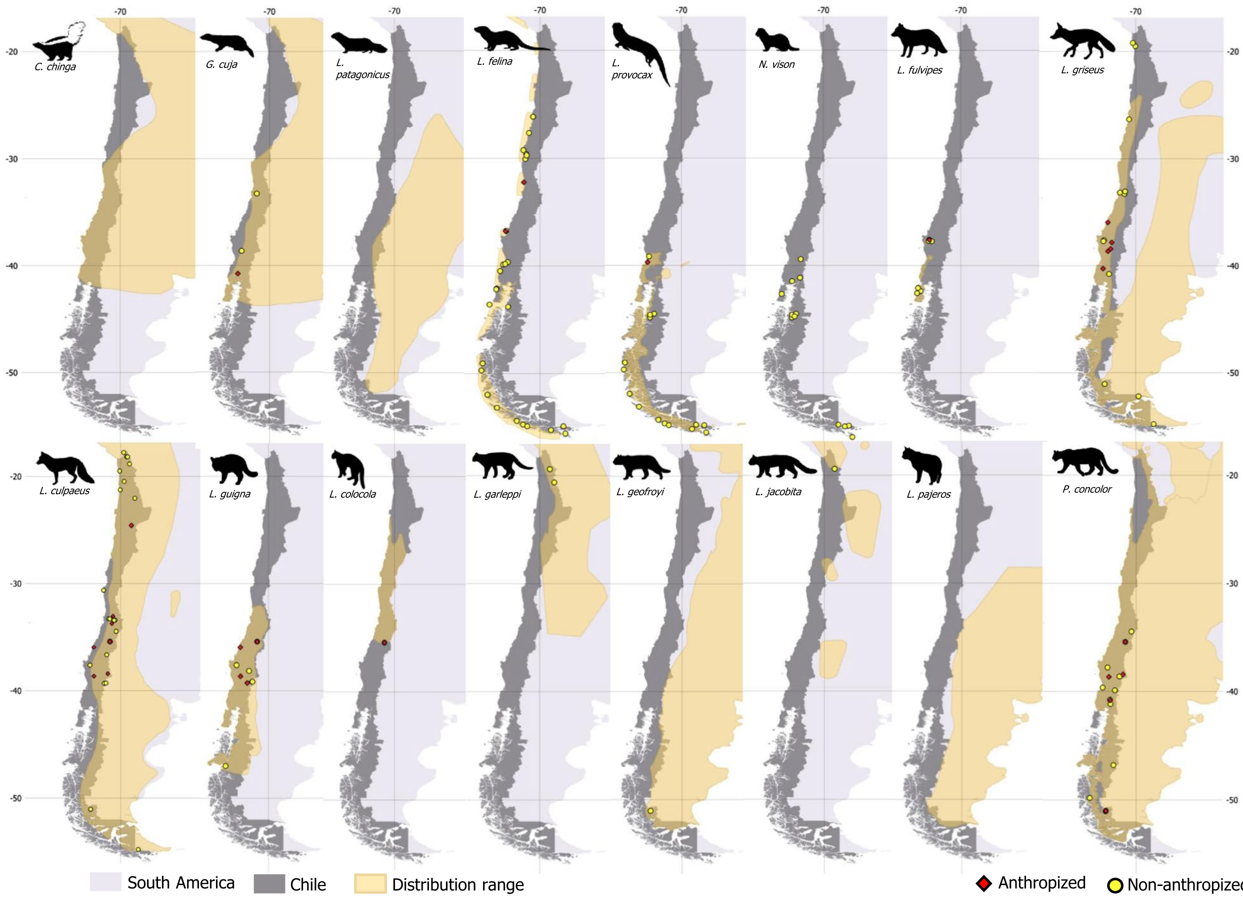

Fig. 3 Study localities for each species of terrestrial mammalian carnivores. The pale-yellow polygon represents the species' distribution range (Digital Distribution Maps on The IUCN Red List of Threatened Species, UICN [65] and Francisca Zamora-Cornejo). Yellow circles are "non-anthropized" localities and red diamonds are "anthropized" localities

Table 3 Statistical models for the evaluation of the spatial relationship between the distribution of species richness of terrestrial mammalian carnivores in Chile and the number of study localities

	Species richness ~ N° of localities per ecoregion					Species richness ~ N° of localities per administrative region				
	df	logLik	AICc	ΔAIC	AIC weight	df	logLik	AICc	ΔAIC	AIC weight
OLS	**3**	**-3.241**	**14.481**	**0**	**0.715**	**3**	**0.434**	**17.133**	**0**	**1**
SAR	4	-2.935	17.507	3.026	0.157	4	2.476	43.048	25.915	0
CAR	4	-3.146	17.928	3.447	0.128	4	0.558	46.884	29.751	0

the diet shows a high proportion of exotic mammals and a small proportion of native mammals.

Concerning the north of the country, all papers in the Puna ecoregion have been conducted in non-anthropized areas (except [85]) and without exotic prey items in the diets of carnivores. Here, the lack of knowledge of the diet of the well-studied (in other latitudes) puma stands out. For this region, Perovic et al. [118] and Napolitano et al. [107] point out a high overlap in the trophic niche of *L. garleppi* and *L. jacobita*, highlighting the lack of information for the southern part of their distribution. Knowledge about the trophic ecology of these vulnerable species and their ecological interactions can increase significantly by considering the growing information collected and not published in the context of environmental consulting services for environmental impact studies of the highland mining industry, one of the main threats to the habitat of these cats [45, 80, 88]. For *L. jacobita*, it has been proposed their presence is not continuous throughout its distribution range [23], with isolated

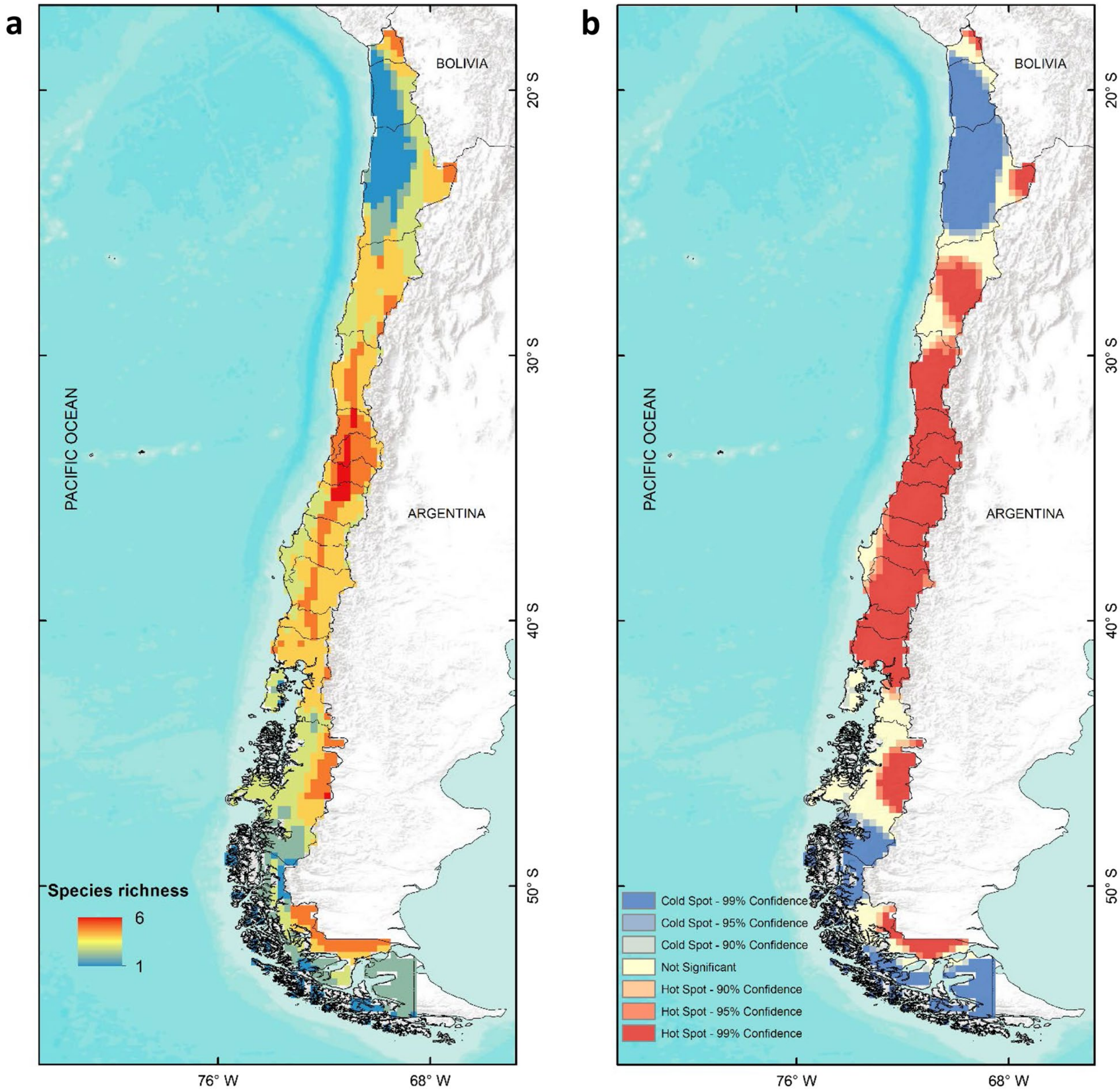

Fig. 4 **a** Spatial variability of the mammalian carnivore richness pattern in Chile, **b** Getis-Ord Gi* Hot Spot Analysis of mammalian carnivore richness across Chile

records found up to the Maule region (see Fig. 5) where no paper about its trophic ecology has been published. Regarding southern Chile, more papers are available on different species in the Subpolar Forest than the Patagonian Steppe, despite both areas having the same maximum species richness. Most of papers have been conducted in Torres del Paine and Tierra del Fuego National Park, both in the Magallanes region, highlighting the prevalence of exotic species and livestock in the diet of all carnivores except for the two aquatic species belonging to the genus *Lontra*. In Patagonia, replacing native prey with introduced species is a widespread phenomenon [109]. The natural diet composition of Patagonian carnivores has been dramatically altered in the last 150 years due to hunting and the widespread overgrazing by livestock. In the northern Patagonian cattle farms, native herbivores are ecologically extinct in their role as prey, and carnivores mainly consume exotic species [115]. Thus, as in the protected and anthropized landscapes of the Chilean hotspot, the change from native to exotic prey seems

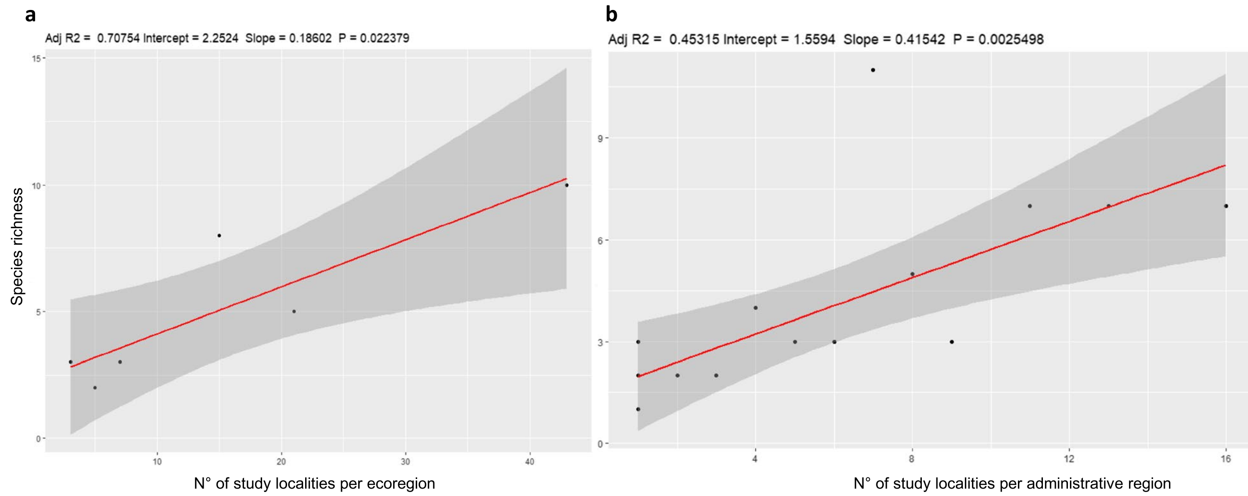

Fig. 5 The spatial relationship between the distribution of species richness of terrestrial mammalian carnivores in Chile and the number of study localities. **a** Localities by ecoregion and **b** Localities by administrative region

favorable for mammalian carnivores because exotic prey items are more profitable than most native prey due to their number, body size, and vulnerability. In areas of high livestock density, carrion also provides a widespread and profitable food source [12, 52, 63]. The extensive use of exotic resources by carnivores in Central and South Chile implies a clear conservation opportunity for these species. On the other hand, restoring native ecosystems may involve eradicating profitable prey such as lagomorphs, which are categorized as plague due to their native impact on vegetation [69, 73, 144], and native prey populations [24]. Thus, the primary importance of exotic animals as lagomorphs in the food webs lies in their positive or negative impact on the species with fewer interactions in the community, which could be more vulnerable if these exotic animals were controlled or extirpated [6, 52]. Predators with a narrow dietary range or hypercarnivores, such as *Leopardus* species, could depend on lagomorph abundance compared to native rodents. The lagomorph elimination plan will likely negatively affect the survival of puma in central Chile because it has become a great alternative in the absence of its native prey, such as *Lama guanicoe* [112]. Given this background, it is necessary to evaluate throughout the territory whether carnivores, both specialist and generalist, can increase their fitness (survival and reproduction) and become more abundant or less vulnerable in the areas where they can exploit these abundant introduced resources compared to carnivores in regions with a less altered native prey base. For instance, an open question is if *Lycalopex* foxes in Central Chile and Temperate Forest will show a higher fitness due to the exotic items in their diet compared to the *Lycalopex* foxes of the Puna and Atacama coastal desert. Several unresolved research questions at individual, populational, and communitarian levels may motivate new research to evaluate the apparent benefits and direct or indirect consequences for predators and their variation across the territory. Finally, studying the spatial patterns of the trophic ecology of the invasive *N. vison* in areas of the Temperate Forest and Subpolar Forest can aid in developing effective management strategies. Such studies can help identify priority areas for resource allocation and control efforts and help understand predation's impact [26]. There are already successful examples in the Lanín National Park in Argentina, where local birdlife has increased in abundance and richness after mink control [51]. The areas with the highest number of birds, located in regions with a high density of emergent vegetation, should be the primary focus for control efforts. It is important to consider that minks could seriously impact the nesting of solitary species found on the ground or shorelines with rocky outcrops [5, 123, 136].

Cryptic community interactions

Knowledge of the trophic ecology of terrestrial mammalian carnivores is a helpful approach to understanding indirect and difficult-to-detect local relationships, such as cascading effects within a community. It is, therefore, a crucial tool to focus research interest on ecological interactions (e.g., predation, competition, mutualism) rather than individual species, being a more integrative approach to the biological conservation of entire communities. Example 1: *L. griseus* may influence the vegetation structure of the landscape by restricting the low-scale spatial distribution of *Octodon degus*, its main native prey in Central Chile, through predation and seed dispersal [14, 155]. Example 2: Given that the larvae of the cantaria (*Chiasognathus grantii*), a native lucanid beetle protected by the Chilean hunting law, are consumed in a high proportion by the invasive European wild boar (*Sus scrofa*) in southern Chile, an indirect effect of the predation by pumas on European wild boars would also have beneficial effects on the recovery of populations of these insects [146]. Example 3: In Chiloé, the occasional feeding of Bromeliaceae inflorescences could represent an adaptive and opportunistic behavior for *L. fulvipes* because thorny leaves surround the fruits in a rosette and are accessible to Darwin's fox only after the coipos (*Myocastor coypus*) feeding on the roots [38]. Example 4: The dietary study of semiaquatic carnivores can contribute to knowledge of the population status of endangered species or species of commercial interest. *L. provocax* has shown an important preference for *Diplomystes camposensis*, an endangered and endemic catfish species with little ecological information [43, 54]. Furthermore, knowing the feeding rate of prey that are also a fishing resource (e.g., *Concholepas concholepas*, *Trachurus murphyi*) can help manage the extraction quota responsibly, considering the availability of food for *Lontra* species [21, 90].

Challenges and opportunities

Although the most knowledge about the trophic ecology of mammalian carnivores in Chile is in the areas with the highest co-occurrence of these species, this review identifies two knowledge gaps. The first type is the null or low number of trophic papers for some species, such as *C. chinga*, *G. cuja*, *L. patagonicus*, *L. pajeros*, and *L. colocola* in Chile. This demonstrates a tangible difficulty in developing conservation strategies for their populations. A higher number of trophic studies in the different areas of the Chilean territory would allow us to correctly characterize the breadth of this niche axis to each species and thus have a most evident approach to the potential vulnerability to the change in available prey, to the anthropic effect, and to the particular predatory role of each species in different localities of their distribution. The second gap is the lack of information in specific areas of the country's strongly transformed and highly vulnerable landscapes, such as the Maule, O'Higgins, Valparaíso, and Ñuble regions. In Chile, the Ministerio del Medio Ambiente (MMA) is the organism that entrusts its Natural Resources and Biodiversity Division with the implementation and monitoring of biodiversity and allocates the necessary budget for the different administrative regions of the country. In this sense, we hope that this review contributes to the National Biodiversity Strategy 2017–2030 [102] and allows public entities and researchers to pay attention to knowledge about community dynamics that can be addressed by studying interactions between carnivores in different biogeographic and administrative regions of the territory. Indeed, this information can be vital to research and conservation efforts by focusing on specific administrative regions and indicator species such as mammalian carnivores.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s40693-024-00131-x.

Supplementary Material 1

Supplementary Material 2

Supplementary Material 3

Acknowledgements

We acknowledge the enjoyable discussions with various colleagues that have inspired a better approach to the problems for the conservation of the fauna of southern South America. We are deeply grateful for the important insights, comments and discussions made by the reviewers.

Authors' contributions

P. V-G devised the research, conducted the literature search, organized and systematized the spatial data, prepared the results tables, coordinated the collaborations, and wrote the manuscript; F. Z–C cooperated in the literature search, organized and systematized the spatial data, and made Figs. 2 and 3; R.R. performed the statistical and spatial analyzes presented in Figs. 4 and 5; F. C-R helped in updating the literature search and systematizing the information; E. R-S cooperated in the draft of the manuscript and final revision of the document. All authors reviewed the final version of the document.

Funding

This work was founded by ANID FONDECYT Grants 1201506 and 1220998, and VRID-UdeC Grant VRID220.113.100-INV.

Availability of data and materials

All data generated or analyzed during this study are included in this published article [and its supplementary information files].

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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Received: 29 May 2024 Accepted: 27 July 2024
Published online: 15 August 2024

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