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Different coexistence patterns between apex carnivores and mesocarnivores based on temporal, spatial, and dietary niche partitioning analysis in Qilian Mountain National Park, China

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Abstract

Carnivores play key roles in maintaining ecosystem structure and function as well as ecological processes, understanding how sympatric species coexistence mechanism in natural ecosystems is a central research topic in community ecology and biodiversity conservation. In this study, we explored intra- and interspecific niche partitioning along spatial, temporal, and dietary niche partitioning between apex carnivores (wolf *Canis lupus*, snow leopard *Panthera uncia*, Eurasian lynx *Lynx lynx*) and mesocarnivores (Pallas's cat *Otocolobus manul*, red fox *Vulpes vulpes*, Tibetan fox *Vulpes ferrilata*) in the Qilian Mountain national park of China using camera trapping data and DNA metabarcoding sequencing data. Our study showed that apex carnivore species had more overlap temporally (the value of time overlap from 0.661 to 0.900) or trophically (the value of diet overlap from 0.458 to 0.892), mesocarnivore species had high dietary overlap with each other (the value of diet overlap from 0.945 to 0.997), and apex carnivore and mesocarnivore species had high temporal overlap (the value of time overlap from 0.497 to 0.855). Large dietary overlap was observed between wolf and snow leopard (Pianka's index=0.892) and Pallas's cat and Tibetan fox (Pianka's index=0.997) and suggesting increased resource competition for these pair species were existed. We conclude that spatial niche partitioning playing a key role in facilitating the coexistence of apex carnivore species, spatial and temporal niche partitioning facilitate the coexistence of mesocarnivore species, and spatial and dietary niche partitioning facilitate the coexistence between apex and mesocarnivore species. Our findings address, for the first time, niche partitioning was considered across temporal, spatial and dietary dimensions and diverse coexistence patterns of carnivore species were presented in the Qilian Mountain national park of China. These finding will contribute substantially to current understanding of carnivore guilds and effective conservation management in fragile alpine ecosystems.

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Introduction

Carnivores play key roles in maintaining ecosystem structure and function, as well as ecological processes (Ripple et al., 2014). They are classically specialized hunters occupying top trophic positions that work to suppress the number of herbivores and other carnivores through predation, competition and trophic cascades (Ripple et al., 2014; Newsome et al., 2017; Ritchie and Johnson, 2009). Understanding how sympatric species coexist in natural ecosystems is a central research topic in community ecology and biodiversity conservation (Chu et al., 2017). Previous studies on carnivore niche partitioning, interspecies interactions, and food web structure covering all the three dimensions are scarce due to limitations in research methodology and scale (Cusack et al., 2017; Dröge et al., 2017). This has severely limited the theoretical and practical understanding of carnivore competition and coexistence. Overgrazing, human disturbance and climate change have resulted in habitat degradation and the decline of carnivore populations (Li et al., 2021; Manlick and Pauli, 2020; Ripple et al., 2014), which could affect interspecific interactions. The strategies adopted by carnivores to alleviate increasingly fierce interspecific competition and coexistence has become a hot topic in animal ecology.

The competitive exclusion principle dictates that species with similar ecological requirements are unable to successfully coexist (Hardin, 1960; Gause, 1934). Instead, competitors must adapt to avoid or reduce resource overlap, a process called niche partitioning. Niche partitioning can occur along spatial, temporal, and trophic dimensions (Schoener, 1974). Spatial niche partitioning reflects the habitat preference of animals. Habitats with high spatial heterogeneity provide various habitat types, which could meet the varying needs of carnivore species to promote coexistence (Garrote and Pérez de Ayala, 2019). Carnivores may deposit scat, urine, or other chemosensory or visual signals to inform competitors of their presence in an effort to alter their use of the same space, and may even take action in the form of intimidation and death (Haswell et al., 2018). The spatial relationships of carnivores are altered in response to topography, habitat quality, prey availability, and human activity (Liu et al., 2021; Monterroso et al., 2020; Sévêque et al., 2020; Marneweck et al., 2019). For example, grazing activity compresses the living space of carnivores and intensifies use of suboptimal habitats. In addition, the presence of livestock in suboptimal habitat provides a choice between predation benefit and risk, breaking the original spatial dimension being used by species within the carnivore guild and possibly increasing competition (Filazzola et al., 2020). Temporal niche partitioning refers to the temporal differences in animal activity rhythms that relieve competitive pressure, and is characterized by high levels of elasticity and flexibility (Qi et al., 2021; Vilella et al., 2020). However, studies on the temporal rhythms of carnivores have been hampered by limitations in technology and their generally cryptic behavior. Trophic, or dietary, niche partitioning refers to the varied use of food resources by species. Trophic niche partitioning can effectively alleviate competition among carnivores, but is easily influenced by prey richness (Steinmetz et al., 2021), interspecific competition (Donadio and Buskirk, 2006), and body mass (Lanszki et al., 2019). For example, carnivores may specialize on a narrow breadth of energetically profitable prey in prey rich areas, resulting in reduced competition(Steinmetz et al., 2021). In contrast, carnivores in prey poor areas may consume more numerous but low-reward smaller prey, thus becoming more generalist and potentially leading to more competition (Steinmetz et al., 2021; Pokheral and Wegge, 2018). At present, many studies have focused on the interspecific relationships of sympatric carnivores within a single dimension (Hacker et al., 2022; Alexander et al., 2016; Anwar et al., 2011), which prohibits comprehensive understanding of the mechanisms that allow carnivore

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coexistence.

In more recent years, new research methods making it possible to study apex carnivores and mesocarnivores have been developed. Camera trapping has become a helpful tool for accumulating large amounts of time-recorded data, and is widely used to investigate species coexistence (Frey et al., 2017). For example, Li et al.(Li et al., 2019) used camera trap data to conclude that temporal segregation is a key mechanism for promoting the coexistence of tigers (*Panthera tigris*) and leopards (*P. pardus*). DNA metabarcoding provides a noninvasive molecular tool of greater ease and accuracy than traditional dietary discernment methods and has overcome many of the limitations surrounding inaccurate and low taxonomic resolution (Deiner et al., 2017; Newmaster et al., 2013). This technology has been applied across numerous taxa, including invertebrates, herbivores and carnivores, and has offered profound insight into the ecology, conservation and biological monitoring of at-risk species (Deagle et al., 2019; Kartzinel et al., 2015). For example, Shao et al.(Shao et al., 2021) found that dietary niche partitioning promoted the coexistence of species in the mountains of southwestern China based on DNA metabarcoding.

Qilian Mountain is a biodiversity hotspot with one of the richest carnivore assemblages in China. China's pilot program aimed at creating nature reserves and a national park system has amplified species protection, ultimately improving species diversity and the ecosystems they inhabit. However, this restoration has increased competition between carnivores. In conjunction, climate change, human activities and overgrazing continue to alter habitat and add a layer of complexity to conservation decision making and bring great challenges to the coexistence of species (Li et al., 2021; Sévêque et al., 2020; Filazzola et al., 2020). However, few studies have documented the temporal, spatial and dietary dimensions of partitioning for intra- and interspecific niches between apex carnivores and mesocarnivores in the Qilian Mountains.

Here, we explored the habitat preference, activity rhythm, and prey item composition of a sympatric carnivore guild in an attempt to reveal interspecific relationships and mechanisms of niche partitioning along the axes of space, time and diet across the Qilian Mountain nation park using camera trap data and DNA metabarcoding data. The main objectives of this study were: 1) to explain the spatial distribution patterns among sympatric carnivore species; 2) to elucidate daily activity patterns among sympatric carnivore species; 3) to examine dietary composition, diversity and similarity among sympatric carnivore species; and 4) to analyze species coexistence patterns based on temporal, spatial and dietary dimensions among sympatric carnivore species.

Results

Sympatric carnivore identification

Of the 480 scat samples sequenced, those which had no sequencing data, were inconclusive, consisted of non-target species, or host species with low sample sizes (1 Asian badger (*Meles leucurus*) and 4 upland buzzard (*Buteo hemilasius*)) were removed (Figure S1). The remaining 404 scat samples were composed of three apex carnivores (49 wolf, 147 snow leopard, 19 Eurasian lynx) and three mesocarnivores (63 Pallas's cat, 87 red fox, 39 Tibetan fox).

Spatial distribution difference and overlap

A total of 322 camera trap sites were surveyed, of which 3 cameras were failed due to loss. We analyzed data from 319 camera sites and obtained 14,316 independent detections. We recorded wolf in 26 sites, snow leopard in 109 sites, Eurasian lynx in 36 sites, red fox in 92 sites, and Tibetan fox in 34 sites.

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To analysis the spatial distribution and overlap, we performed occupancy models to estimate carnivores' occupancy and detection probability by 43 models of each species. Snow leopard had a higher occupancy probability than other carnivore species with the occupancy probability estimated as 0.423 (Table 1). Eurasian lynx had a lower occupancy probability with the estimated as 0.155. Spatial projection showed that occupancy probability of wolf and Eurasian lynx were higher in western of the study area, red fox and Tibetan fox were higher in north-western and southern portion of the study area, and snow leopard was higher throughout the study area (Figure 2). However, the camera detection rates of Pallas's cat were too low to analyze the occupancy model and daily activity patterns.

Wolf and Eurasian lynx occupancy probability declined with increasing NDVI and roughness index (Table 2, Figure 3). Wolf exhibited the strongest relationship between occupancy probability and roughness index. Tibetan fox occupancy probability increased with increasing elevation and distance to road. Snow leopard and red fox exhibited no strong relationships between occupancy probability and variables. Detection probability was highest for snow leopard (*Pr* = 0.428, Table 1) and lowest for wolf (*Pr* = 0.117). Elevation had a positive relationship with detection probability of wolf, snow leopard, red fox and Tibetan fox. Prey had a positive relationship with the detection probability of Eurasian lynx and Tibetan fox (Table 2).

The Sørensen similarity index (S) ranged from 0.1 to 0.5 (Table 3). Compared with other combinations of apex-mesocarnivore pairs, snow leopard and red fox (S=0.477) had relatively high spatial overlap, while Eurasian lynx and Tibetan fox (S=0.198) had the lowest spatial overlap. Moreover, spatial overlap of apex versus apex carnivores and mesocarnivores versus mesocarnivores was relatively low.

Daily activity patterns and differences

A total of 1444 independent records were obtained for five carnivore species, consisting of 79 records of wolf, 458 records of snow leopard, 126 records of Eurasian lynx, 421 records of red fox, and 359 records of Tibetan fox. Among apex carnivores (Table 3, Figure S2), the daily activity was similar between snow leopard and Eurasian lynx and their diel activity overlap was close to 1 (Δ_4=0.900, *P*=0.285), their daily activity peak was at 21:00 hr and dawn. However, the wolf had a significantly different daily activity pattern with snow leopard (Δ_4=0.676, *P*<0.001) and Eurasian lynx (Δ_4=0.661, *P*<0.001), and its daily activity peaked happened around 9:00 and 18:00 hr. Tibetan fox and red fox had different activity patterns and peaks (*P*<0.001). The activity peak for red fox activity peaked at 3:00 and 21:00 hr, while the Tibetan fox had a prolonged active bout between noon and dusk. Temporal activity patterns between apex carnivores and mesocarnivores were significantly different, except for wolf and Tibetan fox (Δ_4=855, *P*=0.118).

Dietary composition, diversity and similarity

A total of 26 unique prey species were identified from 9 taxonomic orders (Figure 4, Table S1). Artiodactyla and lagomorpha were the most frequently detected in the diets of apex carnivores and mesocarnivores, accounting for 32.81% and 70.18% of prey counts, respectively. Blue sheep made up 26.50% of prey counts in apex carnivore diet, while plateau pika made up 67.11% of prey counts in mesocarnivore diet. Livestock were present in 17.98% of apex carnivore diet counts and were present in

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4.82% mesocarnivore diet counts.

The dietary niche overlap among all carnivore species can be found in Table 3. Wolf and snow leopard had the highest dietary niche overlap value among apex carnivores (O_{jk}=0.892). The value of Pianka's index was generally low between apex carnivores and mesocarnivores, except wolf and red fox (O_{jk}=0.811). In contrast, observed dietary overlap was greatest among the mesocarnivores, especially Pallas's cat and Tibetan fox, with a value of 0.997.

Red fox had the greatest richness of prey with a value of 16, while Pallas's cat and Tibetan fox had the lowest diversity of prey with richness value of 6 (Table S2). Dietary similarity was assessed using inversed Jaccard's Coefficients (Jaccard's Distances, Table S3). Diets were most similar between wolf and snow leopard with a value of 0.588 and least similar between Pallas's cat and Tibetan fox with a value of 0.200. All other pairs fell between the values of 0.2 and 0.5.

Discussion

Our study addresses, for the first time, the coexistence patterns of carnivore species present on Qilian Mountain national park across multiple niche partitioning. This work substantially contributes to current understanding of carnivore guilds and offers helpful information for biodiversity conservation at the regional scale. Moreover, our study provides important insights into the protentional mechanisms of niche partitioning among sympatric carnivores, particularly intra- and interspecific relations between apex carnivores and mesocarnivores. Specifically, we found that the overall trend of spatial overlap across carnivores is relatively low, that apex carnivores overlap in time and diet, that mesocarnivores showed a high degree of dietary overlap, and that there was substantial similarity in diel activity patterns between apex carnivores and mesocarnivores. These results suggest that carnivores with similar ecological traits foster co-occurrence by adjusting their daily activity patterns and using differing food resources to minimize competitive interactions.

We found dietary and temporal overlap among apex carnivores, suggesting that spatial partitioning is responsible for their successful coexistence in this area. Wolf and snow leopard had the highest dietary overlap and prey similarity between apex carnivore pairs in our case, showing that the avoidance of space and time plays an important role in their coexistence. Recent evidence suggests that habitat preference facilitates the coexistence of wolf and snow leopard (Shrotriya et al., 2022). Their hunting strategies may be impacted their habitat selection. Solitary snow leopards are more suitable for hiding in habitats features as ambush predators, while wolves hunt in packs (Shrotriya et al., 2022). It is clear that wild ungulates (e.g., blue sheep) constituted the primary proportion of wolf and snow leopard diet, followed by small mammals such as plateau pika, Himalayan marmot (*Marmota himalayana*), and woolly hare (*Lepus oiostolus*). In addition, livestock consumption also contributed to the high degree of overlap in their diets (Wang et al., 2014). This supports the optimal foraging theory, in which large predators preferentially select food resources that provide maximum benefit (Brown et al., 1999), but also showed that greater competition for resources is likely to occur between wolf and snow leopard due to their use of the same prey species in this area. This may be especially true in times of habitat stress when resources are poor. Snow leopard and Eurasian lynx had the highest temporal overlap between apex carnivore pairs in our case, suggest that spatial and dietary partitioning may facilitate the coexistence. The Eurasian lynx is considered an opportunistic predator, and its prey varies among different regions with its primary dietary resource being ungulates and small mammals. For example, Eurasian lynx showed a strong preference for brown hare *L. europaeus* in Turkey, edible dormice *Glis glis* in Slovenia and Croatia, and

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chamois *Rupicapra rupicapra* or roe deer *Capreolus capreolus* in Switzerland (Mengüllüoğlu et al., 2018; Krofel et al., 2011; Molinari-Jobin et al., 2007). Varied prey selection may be related to sex, age, population density and season (Mengüllüoğlu et al., 2018; Odden et al., 2006). Our results show that woolly hare make up the majority of the Eurasian lynx diet, followed by blue sheep. Woolly hare is mainly distributed in shrubland, meadow, desert and wetland, while blue sheep tend to choose highly sheltered areas, close to bare rocks and cliffs as habitat. Prey preferences between snow leopard and Eurasian lynx also contributes to spatial avoidance.

Mesocarnivores showed substantial overlap in diet, indicating that food resources may be a major competitive factor, making spatial and temporal partitioning the key mechanisms driving successful coexistence. This is in alignment with previous studies showing that mesocarnivores use temporal and spatial segregation to reduce competition and the probability of antagonistic interspecific encounters(Ferreiro-Arias et al., 2021; Li et al., 2022a). The differences in habitat preference may lead to spatial niche partitioning among mesocarnivores (Wang et al., 2022). In addition, species can adjust temporal periods of behavior to respond to environmental change, competition, and predation risk (Gallo et al., 2022; Finnegan et al., 2021; van der Vinne et al., 2019). Pallas's cat is a diurnal hunter and inhabits montane grassland, shrub steppe and cold montane deserts (Ross et al., 2019). Red fox is mainly nocturnal and is widely distributed across various habitats (Reshamwala et al., 2022; Pandolfi et al., 1997), with the habitat type dependent on the abundance of prey (Gołdyn et al., 2003). Tibetan fox is a diurnal hunter of the Tibetan plateau and inhabits shrub meadow, meadow steppe and alpine meadow steppe (Gong and Hu, 2003). It is worth noting the substantial overlap in diet between Pallas's cat and Tibetan fox. The dietary overlap between the two was extremely high, with a Pianka's value close to 1. Dietary analyses showed that pika contributed to more than 85% of their collective diets, with 90% of Pallas's cat diet being pika. Pika may be an optimal prey item in the area because of size and year-round activity (Ross, 2009). Previous studies have shown that the Pallas's cat and Tibetan fox are specialist predators of pikas (Harris et al., 2014; Ross, 2009). However, specialization on pika is facultative in that Pallas's cat and Tibetan fox can select other prey items when pika availability is low (Harris et al., 2014; Ross, 2009). This was observed in our study, even though dietary diversity was low.

Apex carnivores and mesocarnivores showed substantial overlap in time overall, indicating that spatial and dietary partitioning may play a large role in facilitating their coexistence. As confirmed by previous research, kit foxes (*V. macrotis*) successfully coexisted with dominant carnivores by a combination of spatial avoidance and alternative resources(Lonsinger et al., 2017). The differences of body mass may play a crucial role in minimizing dietary overlap, effectively reducing interspecific competition between apex and mesocarnivores. Of exception in our study, however, was wolf and red fox, who exhibited more dietary overlap, indicating that temporal and spatial avoidance may promote their coexistence. As canid generalist-opportunist species, the wolf and red fox consumed similar prey, albeit the red fox may have obtained livestock and ungulate species via scavenging or by preying on very young individuals (Hacker et al., 2022). Recent research has found that the red fox may coexist with the wolf by exploiting a broader niche (Shrotriya et al., 2022). This was confirmed by occupancy model in our study, where significant differences in the relationship with NDVI between wolf and red fox were observed.

Several restrictions remain for this research. The first limitation involves differences in samples sizes. Although the scat samples of Tibetan fox were relatively low, the accuracy of DNA metabarcoding

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in informing species presence in diet ensures that data are informative and thus still important for species conservation management decisions(Hacker et al., 2022). Second, the methodology of foraging (e.g., predation or scavenging) and the condition of prey item (e.g., age or size) cannot be identified in dietary studies (Hacker et al., 2022). Pika is a prime component of diet among mesocarnivores, especially in the diet of the Pallas's cat and the Tibetan fox. We surmise that the simultaneous dependence on pika led to partial overlap in spatial and activity patterns, resulting in increased potential competitive interactions. Due to the lack of spatial and temporal analysis of Pallas's cat in our study, further monitoring is needed to develop a comprehensive conservation plan. Despite these limitations, our study provides a foundation from which future studies interested in niche partitioning among carnivores along spatial, temporal, and dietary dimensions, can be modeled.

In summary, our study has shown that the coexistence of carnivore species in the landscapes of the Qilian Mountain national park can be facilitated along three niche axes, with spatial segregation being relatively pronounced. Apex carnivore species tended to overlap temporally or trophically, mesocarnivore species had high dietary overlap with each other, and apex carnivore and mesocarnivore species displayed similarity in time. Pika, blue sheep and livestock were found to make up a large proportion of carnivore diet. The resource competition between wolf and snow leopard and the interspecific competition between Pallas's cat and Tibetan fox were strong in this area. Based on the results presented above, we propose that further protection and management work should be undertaken in the following areas. First, greater efforts are needed to protect habitat. For example, the development of habitat corridors and optimization of grassland fence layouts could be prioritized to protect migration passage routes. Second, resource competition should be carefully monitored between snow leopards and wolves, and between Pallas's cat and Tibetan foxes. More attention is needed for pika at our study site considering the role they play in the conservation of Pallas's cat and Tibetan fox populations. Campaign of pika poisoning was previously implemented because of concerns that pika could cause grassland degradation (Smith and Foggin, 1999). Recent research shows that the health of pika population and their habitat are the most important factor for Pallas's cat's distribution (Greenspan and Giordano, 2021). Further, it is necessary to be alert to the preponderance of smaller prey in predator diets, as this may indicate severe loss of larger prey, which will increase the risk of interference competition(Steinmetz et al., 2021). Third, focusing on the recovery of wild prey, strengthening the management of grazing areas, and ensuring herder livelihoods will be crucial to reduce livestock predation events that may trigger human-carnivore conflicts. It is necessary that daily patrols of protected areas and primary habitat spaces occur and that educational presentations are given to conservation staff and herders. This could include education surrounding environmental policy and laws, nature ecology, how to set up camera trapping and methods of field investigation, so that herdsmen can play a more important role in the protection of carnivores. Our study corroborates and complements the findings of prior studies on these species and their coexistence mechanisms, and also has implications for wildlife conservation in the area.

Material and methods

Study sites

The Qilian Mountains laterally span Gansu and Qinghai Provinces in China, located in the northeastern edge of the Qinghai-Tibetan Plateau (Figure 1). The Qilian Mountains National Park covers an area of approximately 52,000 km^2, with an average elevation of over 3000 m. The area is an alpine

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ecosystem with a typical plateau continental climate. The average annual temperature is below -4℃ and the average annual rainfall is about 400 mm, with habitats mainly consisting of deserts, grassland, meadows, and wetland (Zheng, 2011). Wildlife present include the wolf (*Canis lupus*), snow leopard (*P. uncia*), Eurasian lynx (*Lynx lynx*), red fox (*Vulpes vulpes*), Tibetan fox (*V. ferrilata*), Tibetan brown bear (*Ursus arctos*), Chinese mountain cat (*Felis bieti*), wild yak (*Bos mutus*), blue sheep (*Pseudois nayaur*), alpine musk-deer (*Moschus chrysogaster*), Tibetan antelope (*Pantholops hodgsonii*), Himalayan marmot (*Marmota himalayana*), woolly hare *(Lepus oiostolus*), and plateau pika (*Ochotona curzoniae*), among others (Ma et al., 2021; Xue et al., 2019).

Camera-trap monitoring and non-invasive sampling

The study area was subdivided into sample squares of 25 km^2 (5×5 km) as a geographical reference for placing camera survey sites and collecting scat samples (Xue et al., 2019). Species occurrence was recorded using camera-trap monitoring (Ltl-6210; Shenzhen Ltl Acorn Electronics Co. Ltd). Two camera traps were placed in each square with a distance of at least 1 km between them. However, due to limitations of terrain, landform, road accessibility and other factors, the number of camera sites in some squares was adjusted in accordance to field conditions. Camera traps were set in areas believed to be important to and heavily used by wildlife, such as the bottoms of cliffs, sides of boulders, valleys and ridges along movement corridors. We placed a total of 280 cameras and each camera worked for 4 to 6 months and considered whether to relocate to another position based on the detections of animals. The camera trap was set to record the time and date on a 24 hr clock when triggered, and to record a 15s video and 1 photo with an interval of 2 minutes between any two consecutive triggers. Carnivores were monitored from December 2016 to February 2022 (Figure 1).

Non-invasive sampling of scats believed to be of carnivore origin were collected within camera trapping areas. A small portion of scat (approximately 1/3) was broken off and stored in a 15 ml centrifuge tubes with silica desiccant covered by clean filter paper to separate the desiccant from the scat (Janecka et al., 2008). Gloves were replaced between sampling to avoid cross-contamination. Sampling place, date, and sample number were labeled on the tube; GPS coordinates, elevation, and nearby landscape features were recorded on the sample collection sheet (Hacker et al., 2021). A total 480 scat samples were collected from April 2019 to June 2021 (Figure 1).

Data Analysis

Spatial analysis

All pictures captured by the camera traps without animals or people were removed. Only photos or videos of the same species taken at intervals of 30 min were considered as an effective shot to ensure capture independence (Li et al., 2020). To investigate the spatial distribution of carnivores, as well as the influence of environmental factors on the site occupancy of species in the study area, we performed occupancy models to estimate carnivores' occupancy (ψ) and detection (*Pr*) probability (Li et al., 2022b; Moreno-Sosa et al., 2022). We created the matrix that each carnivore species was detected (1) or not (0) during each 30-days (that is 0-30, 31-60, 61-90, 91-120, 121-150, >150 days) for each camera location. Based on the previous studies of habitat selection of carnivores (Greenspan and Giordano, 2021; Alexander et al., 2016), we assessed elevation (ele), normalized difference vegetation index (ndvi), distance to roads (disrd) and roughness index (rix) as variables in the occupancy models. In addition, we used elevation and prey (the number of independent photos of their preferred prey based on dietary

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analysis in this study; wolf and snow leopard: artiodactyla including livestock, Eurasian lynx and Pallas's cat: lagomorpha, red fox and Tibetan fox: lagomorpha and rodentia) as covariates that affects the detection rate. Here, we used 43 models to estimate species distribution. Road data was obtained from Open Street Map (OSM, https://www.openstreetmap.org). Others environment data were obtained from the Resource and Environment Science and Data Center (https://www.resdc.cn). We fitted all possible combinations of covariates by logit link function. We used Akaike's information criterion (AIC) to rank candidate models, and selected $\Delta AIC \leq 2$ model as the optimal model. If there are more than one optimal model, the covariate estimates are obtained by using the equal-weight average.

Carnivore co-occurrence was evaluated using the Sørensen similarity index (value = 0, indicating maximum segregation and value = 1, indicating maximum co-occurrence) based on binary presence absence data within the 5 km × 5 km camera trap grid (Torretta et al., 2021; Sorensen, 1948). Spatial analyses were performed using ArcGIS 10.8 (ESRI Inc.) and the "vegan" packages (Oksanen et al., 2019) and "unmarked" package (Fiske and Chandler, 2011) for R studio (version 1.1.463).

Temporal analysis

Estimates of the coefficient of overlap (Δ) for activity patterns were estimated using the non-parametric kernel density method and applying the time data obtained by the camera traps. Because the smallest sample had more than 50 records, we used the Δ_4 estimator for pairwise comparisons between carnivore activity patterns, and used a smooth bootstrap scheme to generate 1000 resamples with 95% confidence intervals to test the reliability of the overlap value (Ridout and Linkie, 2009). Activity pattern analyses were performed using the "overlap" R packages. Values of the Δ_4 estimates were calculated relative to 1000 simulated null models of randomized overlap data using the 'compareCkern' function in the "activity" R package to test for differences in daily activity patterns (Ridout and Linkie, 2009; Rowcliffe et al., 2014).

Species identification and dietary analysis

Host species and diet were identified using metabarcoding. DNA was extracted using the QIAamp Fast DNA Stool Mini Kit (QIAGEN, Germany) following standard protocols and the MT-RNR1 (12S) and COX1 (cytochrome c oxidase subunit I) gene segments amplified using 12SV5-F/R primer and COX1 primers, respectively (Hacker et al., 2021; Riaz et al., 2011). PCR reaction conditions followed the methods described in Hacker et al. (Hacker et al., 2021). The resulting library was sequenced on an Illumina NovaSeq platform and 250 bp paired-end reads were generated (Guangdong Magigene Biotechnology Co., Ltd. Guangzhou, China).

We used CLC Genomics Workbench v12.0 (QIAGEN, Denmark) to determine the host species as well as the prey consumed by each carnivore by mapping sequence reads to reference sequences of possible prey downloaded from GenBank and BOLD (Barcode of Life Data Systems) with representative haplotypes compiled into one .fasta file. Raw reads were required to have at least 98% similarity across at least 90% of the reference sequence for mapping (Hacker et al., 2021). Species and prey identification were made based on the reference taxa with the highest number of reads mapped and the fewest mismatches. Samples in which species could not be identified were analyzed to ensure the reference file was not incomplete by using the *de nova* assembly tool in CLC, then blasting the resulting contig sequence with the nucleotide databases in NCBI (https://blast.ncbi.nlm.nih.gov/Blast.cgi). As an

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additional precaution, the geographic range of the determined host and prey species was researched using the IUCN Red List (https://www.iucnredlist.org/) to ensure that it overlapped with the study site. For complete methods on data parameters and methods used, see Hacker et al. (Hacker et al., 2021). Dietary data were summarized by the frequency of occurrence of prey species in scats observed. The "bipartite" R package was used to construct food web networks (Dormann, 2011). Dietary diversity for each carnivore host species was assessed by calculating richness and Shannon's Index (Shannon and Weaver, 1949). Interspecific dietary niche overlap was evaluated using Pianka's Index (O_{jk}) (value = 0, no dietary overlap and value = 1, complete dietary overlap) and 95% confidence intervals were obtained by bootstrapping with 1000 resamples via the "spaa" R package (Zhang, 2016). Dietary similarity between any two given carnivore species was assessed by calculating the inversed value of Jaccard's Index based on binary presence absence data of prey.

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Author contributions

Wei Cong, Conceptualization, Formal analysis, Investigation, Methodology, Software, Validation, Visualization, Writing-original draft, Writing-review and editing; Jia Li, Conceptualization, Funding acquisition, Investigation, Methodology, Resources, Software, Writing-review and editing; Charlotte Hacker, Investigation, Methodology, Writing-review and editing; Ye Li, Investigation; Yu Zhang, Investigation, Funding acquisition; Lixiao Jin, Investigation; Yi Zhang, Investigation; Diqiang Li, Funding acquisition, Methodology, Resources, Supervision, Writing-review & editing; Yadong Xue, Investigation, Resources, Writing-review and editing; Yuguang Zhang, Conceptualization, Funding acquisition, Investigation, Methodology, Resources, Supervision, Writing-review and editing.

Declaration of interests

The authors declare no competing interests.

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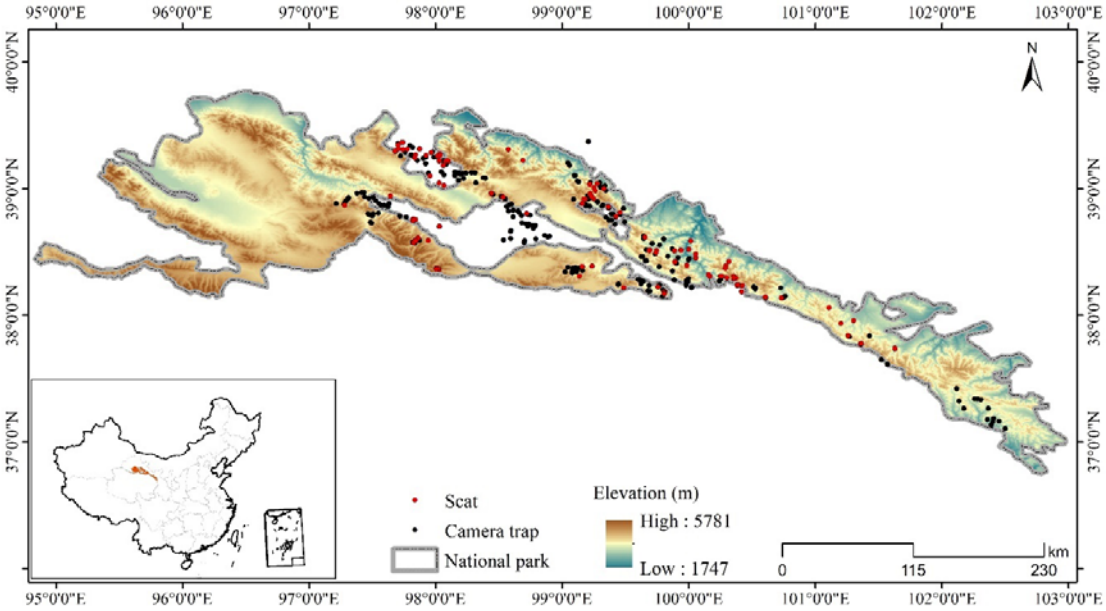

Figure 1 Locations of camera trap stations and scat collection sites in this study.

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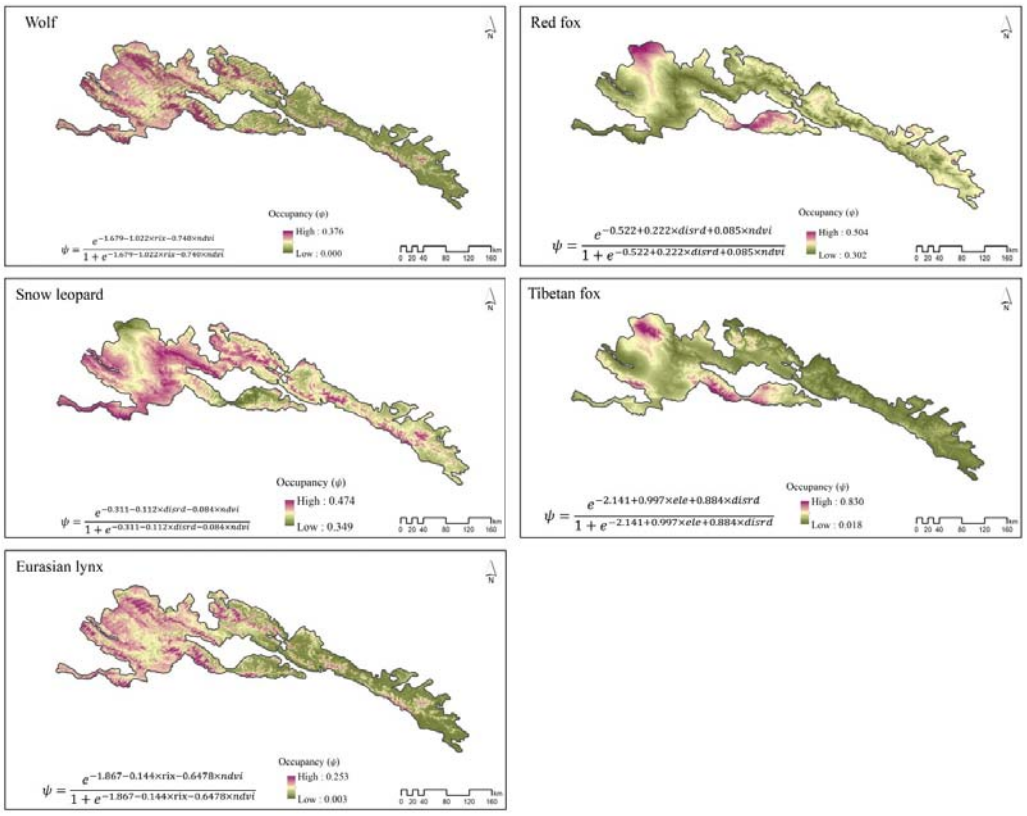

Figure 2 Spatial projection of carnivore species occupancy probability (ψ) based on the average optimal models (ΔAIC≤2).

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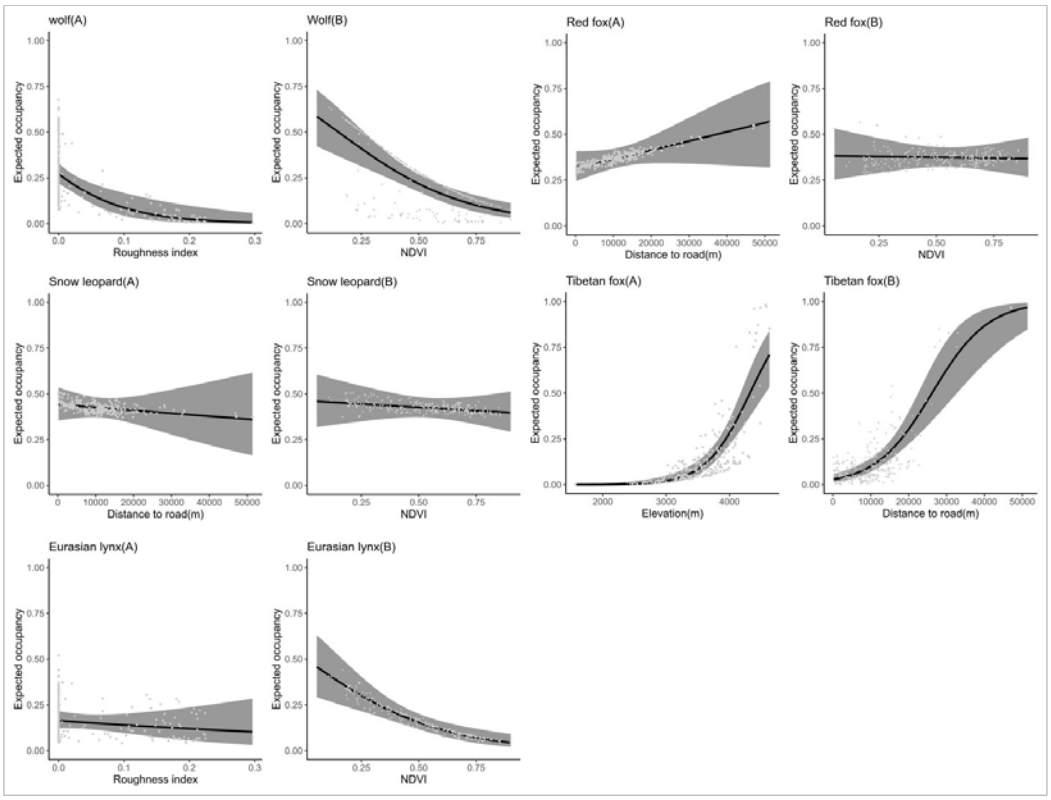

Figure 3 The relationship between carnivore species occupancy probability and covariates by the optimal models (ΔAIC≤2). Solid line represents the fitted with polynomial regression, gray area represents 95% confidence intervals.

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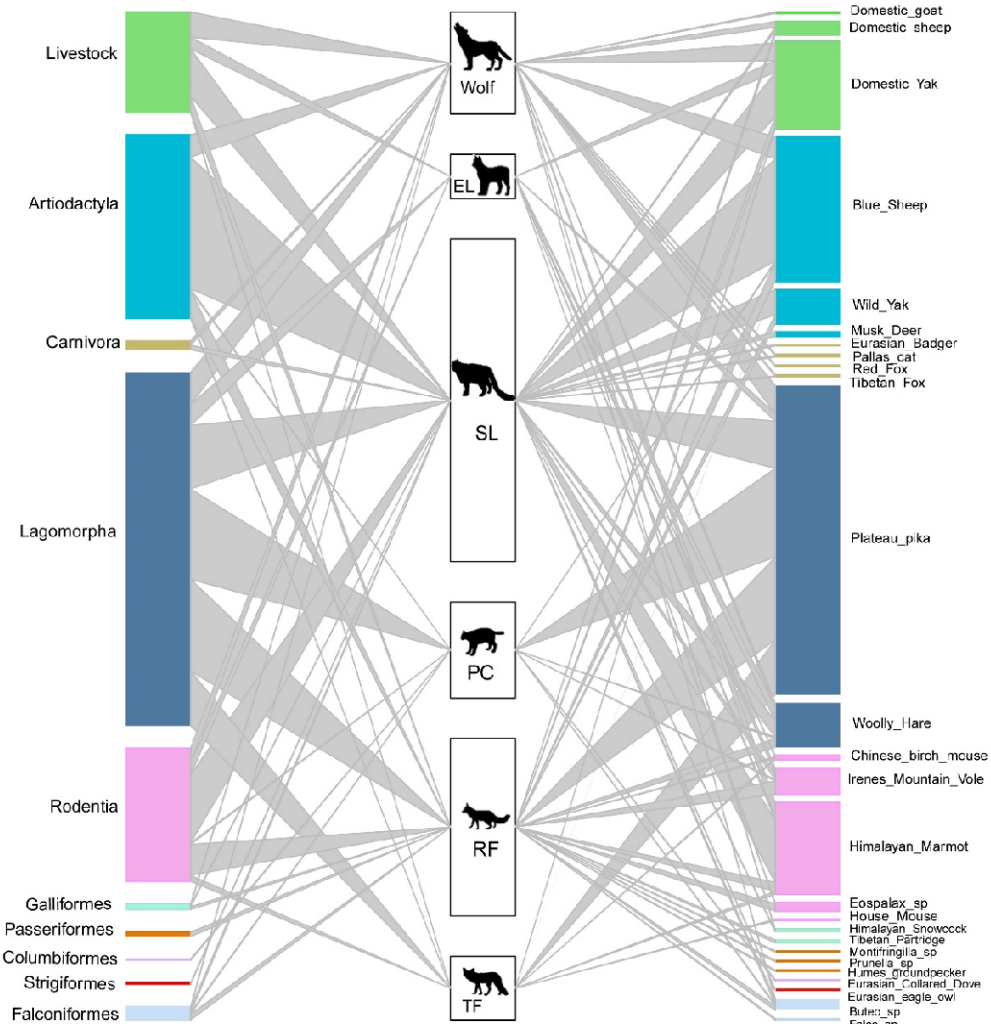

Figure 4 The food web of carnivore species (SL-snow leopard, EL-Eurasian lynx, PC-Pallas's cat, RF-red Fox, TF-Tibetan Fox). The widths of the upper bars represent the frequency of occurrence of prey species in scats, the widths of the middle bars represent the number of samples for each carnivore, and the widths of the lower bars represent the taxonomic order of prey species. The colors of prey match the taxonomic orders. The connecting line widths represent the prey frequency of occurrence in the diet of each carnivore species.

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Table 1 Summary of occupancy rate and detection probability of different species for the optimal models (ΔAIC≤2).

Species	Models	Number of parameters	AIC	ΔAIC	AIC $_{wt}$	R^2	ψ	*Pr*
Wolf	*Psi* (rix+ndvi); *P* (ele)	5	284.75	0.000	0.490	0.150	0.211	0.120
	Psi (rix+ndvi); *P* (ele+prey)	6	286.58	1.830	0.190	0.151	0.219	0.115
	Model average						**0.215**	**0.117**
Snow leopard	*Psi* (disrd+ndvi); *P* (ele)	5	982.41	0.000	0.080	0.027	0.425	0.423
	Psi (.); *P* (ele)	3	982.68	0.270	0.070	0.013	0.428	0.422
	Psi (disrd); *P* (ele)	4	983.14	0.730	0.056	0.018	0.428	0.420
	Psi (ndvi); *P* (ele)	4	983.35	0.940	0.050	0.017	0.425	0.424
	Psi (ele+disrd); *P* (ele)	5	983.67	1.260	0.043	0.023	0.419	0.427
	Psi (disrd+ndvi); *P* (.)	4	983.69	1.280	0.042	0.016	0.418	0.437
	Psi (ele+disrd); *P* (.)	4	983.84	1.430	0.039	0.016	0.414	0.438
	Psi (ele); *P* (ele)	4	984.06	1.640	0.035	0.015	0.422	0.427
	Psi (ele); *P* (.)	3	984.11	1.700	0.034	0.008	0.417	0.437
	Psi (disrd+ndvi); *P* (ele+prey)	6	984.12	1.710	0.034	0.028	0.428	0.420
	Psi (ndvi); *P* (.)	3	984.13	1.720	0.034	0.008	0.420	0.436
	Psi (rix); *P* (ele)	4	984.22	1.810	0.033	0.014	0.428	0.421
	Psi (.); *P* (.)	2	984.33	1.920	0.031	0.000	0.418	0.437
	Psi (disrd); *P* (ele+prey)	5	984.35	1.940	0.030	0.021	0.433	0.417
	Model average						**0.423**	**0.428**
Eurasian lynx	*Psi* (rix+ndvi); *P* (prey)	5	374.11	0.000	0.122	0.081	0.157	0.321
	Psi (rix+ndvi); *P* (.)	4	374.31	0.200	0.110	0.071	0.151	0.348
	Psi (ndvi); *P* (prey)	4	374.33	0.220	0.109	0.071	0.159	0.318
	Psi (ndvi); *P* (.)	3	374.68	0.570	0.092	0.060	0.152	0.348
	Psi (disrd+ndvi); *P* (.)	4	374.95	0.840	0.080	0.068	0.153	0.347
	Psi (disrd_ndvi); *P* (prey)	5	374.96	0.860	0.079	0.077	0.158	0.322
	Psi (rix+ndvi); *P* (ele)	5	375.88	1.770	0.050	0.073	0.151	0.359
	Psi (rix+ndvi); *P* (ele+prey)	6	375.88	1.780	0.050	0.082	0.156	0.329
	Psi (disrd+ndvi); *P* (ele)	5	376.04	1.930	0.046	0.072	0.155	0.359
	Psi (ndvi); *P* (ele+prey)	5	376.07	1.970	0.046	0.072	0.158	0.327
	Model average						**0.155**	**0.338**
Red fox	*Psi* (disrd+ndvi); *P* (ele)	5	910.36	0.000	0.066	0.028	0.373	0.395
	Psi (disrd+ndvi); *P* (.)	4	910.94	0.580	0.049	0.019	0.369	0.403
	Psi (disrd); *P* (ele)	4	910.94	0.580	0.049	0.019	0.373	0.396
	Psi (disrd+ndvi); *P* (prey)	5	911.02	0.660	0.047	0.025	0.377	0.387
	Psi (disrd+ndvi); *P* (ele+prey)	6	911.20	0.840	0.043	0.032	0.379	0.384
	Psi (disrd); *P* (.)	3	911.26	0.900	0.042	0.011	0.370	0.402

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	Psi (disrd); *P* (prey)	4	911.32	0.950	0.041	0.017	0.377	0.386
	Psi (.); *P* (ele)	3	911.56	1.200	0.036	0.010	0.373	0.395
	Psi (disrd); *P* (ele+prey)	5	911.74	1.380	0.033	0.023	0.379	0.384
	Psi (disrd+rix); *P* (ele)	5	911.75	1.390	0.033	0.023	0.374	0.395
	Psi (disrd+rix); *P* (.)	4	912.05	1.690	0.028	0.015	0.371	0.402
	Psi (disrd+rix); *P* (prey)	5	912.08	1.720	0.028	0.022	0.379	0.386
	Psi (.); *P* (prey)	3	912.22	1.860	0.026	0.007	0.376	0.386
	Psi (.); *P* (.)	2	912.27	1.910	0.025	0.000	0.368	0.402
	Model average						**0.374**	**0.393**
Tibetan fox	*Psi* (ele+disrd); *P* (ele+prey)	6	328.13	0.000	0.560	0.361	0.159	0.219
	Model average						**0.159**	**0.219**

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Table 2 Covariates influencing carnivores occupancy rate and detection probability based on the optimal models (ΔAIC≤2). Abbreviations: Ele-elevation, Disrd-distance to roads, NDVI-normalized difference vegetation index, Tpop-people population density.

Species	Model component	Covariates	Estimate (β)	SE	*Z*	*P*
Wolf	Occupancy	Intercept	-1.679	0.459	3.656	<0.001***
		Rix	-1.022	0.500	2.043	0.041*
		Ndvi	-0.740	0.294	2.516	0.012*
	Detection	Intercept	-2.183	0.430	5.082	<0.001***
		Ele	0.700	0.252	2.783	0.005**
Snow leopard	Occupancy	Intercept	-0.311	0.141	2.203	0.028*
		Disrd	-0.112	0.150	0.746	0.456
		Ndvi	-0.084	0.139	0.604	0.546
	Detection	Intercept	-0.299	0.119	2.518	0.012*
		Ele	0.177	0.167	1.058	0.290
Eurasian lynx	Occupancy	Intercept	-1.867	0.232	8.029	<0.001***
		Rix	-0.144	0.233	0.619	0.536
		Ndvi	-0.647	0.199	3.246	0.001**
	Detection	Intercept	-0.685	0.256	2.681	0.007**
		Prey	0.122	0.165	0.740	0.459
Red fox	Occupancy	Intercept	-0.522	0.148	3.522	<0.001***
		Disrd	0.222	0.169	1.315	0.189
		Ndvi	0.085	0.144	0.590	0.555
	Detection	Intercept	-0.435	0.124	3.495	<0.001***
		Ele	0.069	0.100	0.689	0.491
Tibetan fox	Occupancy	Intercept	-2.141	0.461	-4.650	<0.001***
		Ele	0.997	0.403	2.480	0.013*
		Disrd	0.884	0.272	3.250	0.001**
	Detection	Intercept	-1.462	0.492	-2.970	0.003**
		Ele	0.742	0.305	2.440	0.015*
		Prey	0.436	0.155	2.820	0.005**

The different superscript letters represent the significant, *** $p< 0.001$, **$0.001<p<0.01$, * $0.01 < p< 0.05$.

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Table 3 Spatial overlap (Sørensen's index), diel activity overlap (Δ) and dietary overlap (Pianka's index), as well as confidence intervals for carnivore species.

	Sørensen's index	Δ	Pianka's index
Wolf – Snow leopard	0.277	0.676 (0.562-0.756)	0.892 (0.804-0.982)
Wolf – Eurasian lynx	0.272	0.661 (0.541-0.759)	0.585 (0.141-0.881)
Snow leopard – Eurasian lynx	0.305	0.900 (0.854-0.992)	0.458 (0.160-0.886)
Wolf – Pallas's cat	—	—	0.658 (0.053-0.950)
Wolf – Red fox	0.365	0.497 (0.359-0.563)	0.811 (0.497-0.962)
Wolf – Tibetan fox	0.350	0.855 (0.777-0.937)	0.689 (0.456-0.967)
Snow leopard – Pallas's cat	—	—	0.354 (0.092-0.827)
Snow leopard – Red fox	0.477	0.814 (0.756-0.863)	0.586 (0.568-0.941)
Snow leopard – Tibetan fox	0.292	0.711 (0.629-0.744)	0.390 (0.299-0.905)
Eurasian lynx – Pallas's cat	—	—	0.376 (0-0.921)
Eurasian lynx – Red fox	0.205	0.800 (0.728-0.878)	0.536 (0.442-0.910)
Eurasian lynx – Tibetan fox	0.198	0.695 (0.601-0.756)	0.385 (0.078-0.919)
Pallas's cat – Red fox	—	—	0.945 (0.369-0.988)
Pallas's cat – Tibetan fox	—	—	0.997 (0-1)
Red fox – Tibetan fox	0.349	0.576 (0.467-0.580)	0.949 (0.279-0.988)