Contents lists available at ScienceDirect

# Global Ecology and Conservation

journal homepage: www.elsevier.com/locate/gecco

Original Research Article

# Impacts of free-roaming dogs on spatiotemporal niches of native carnivores in Taiwan

Hsin-Cheng Ho<sup>a</sup>, Tzung-Su Ding<sup>a</sup>, Hsiao-Wei Yuan<sup>a</sup>, Jo-Szu Tsai<sup>b</sup>, Guo-Jing Weng<sup>c</sup>, Yu-Hsiu Lin<sup>d</sup>, Hsiang Ling Chen<sup>e</sup>, Yu-Bo Huang<sup>f</sup>, Shih-Ching Yen<sup>g,\*</sup>

<sup>a</sup> School of Forestry and Resource Conservation, National Taiwan University, No 1, Section 4, Roosevelt Road, Taipei City 106319, Taiwan

<sup>c</sup> Institute of Wildlife Conservation, College of Veterinary Medicine, National Pingtung University of Science and Technology, No. 1, Shuefu Rd., Neipu Township, Pingtung County 912301, Taiwan

<sup>d</sup> Taiwan Biodiversity Research Institute, No. 1, Minsheng E. Rd., Jiji Township, Nantou County 552005, Taiwan

e Department of Forestry, National Chung Hsing University, 145 Xingda Rd., South Dist., Taichung City 402202, Taiwan

<sup>f</sup> Observer Ecological Consultant Company, 4F., No. 9, Ln. 293, Nanjing W. Rd., Datong Dist., Taipei City 103002, Taiwan

g Center for General Education, National Tsing Hua University, No. 101, Section 2, Kuangfu Rd., East Dist., Hsinchu City 30013, Taiwan

ARTICLE INFO

Keywords: Interspecific competition Niche partitioning Camera trap Kernel density estimation Occupancy model

# ABSTRACT

Among animals of the same trophic level, niche partitioning often occurs to facilitate coexistence. However, when a new common predator appears, they may adjust their activity temporally and spatially to avoid the predator. Such changes may increase their niche overlap with each other. Dogs (Canis familiaris) are invasive carnivores that are distributed widely, and they pose serious threats to native mammals in Taiwan. We hypothesize that free-roaming dogs dominate spatial and temporal resources, which forces native mesocarnivores to adjust their realized niches to avoid dogs. We predict that threats from free-roaming dogs result in (1) the activity levels of native carnivores being correlated negatively with those of dogs, (2) native carnivores undergoing spatial or temporal avoidance in response to the presence of dogs, and (3) increased spatial or temporal niche overlap among native carnivores. This study covers four mesocarnivores in Taiwan: the masked palm civet (Paguma larvata), ferret badger (Melogale moschata), small Indian civet (Viverricula indica), and crab-eating mongoose (Herpestes urva). With data from 1270 camera traps, we used relative activity index (RAI), occupancy models, and kernel density estimation to analyze changes in abundance and spatiotemporal niche overlaps. A significant negative correlation was found between dog RAI and those of ferret badgers (p < 0.001) and crab-eating mongooses (p < 0.05). The ferret badgers also avoided dogs spatially (Species Interaction Factor, SIF < 1). However, crab-eating mongooses co-occurred with dogs spatially (SIF > 1), possibly due to their strong dependence on specific environments (i.e., forests around freshwater environments). We did not detect changes in spatiotemporal niche overlap among native carnivores. Variations in niche overlap may need to be observed at finer scales or across other dimensions. This study demonstrates the impact of free-roaming dogs on ferret badgers and crab-eating mongoose, which highlights the importance of conserving riparian environments from the threat of dogs. Future research that integrates other niche dimensions is necessary to better understand the impact of dogs.

\* Corresponding author.

E-mail address: yensc@mx.nthu.edu.tw (S.-C. Yen).

https://doi.org/10.1016/j.gecco.2025.e03411

Received 28 August 2024; Received in revised form 10 December 2024; Accepted 6 January 2025

Available online 7 January 2025





<sup>&</sup>lt;sup>b</sup> Department of Biological Resources, National Chiayi University, No. 300, Xuefu Rd., East Dist., Chiayi City 600355, Taiwan

<sup>2351-9894/© 2025</sup> The Author(s). Published by Elsevier B.V. This is an open access article under the CC BY-NC license (http://creativecommons.org/licenses/by-nc/4.0/).

#### 1. Introduction

When two species of similar trophic levels coexist, their niches should be partitioned in at least one dimension to reduce interspecific competition, thereby increasing species fitness (Hardin, 1960; Creel, 2001; Barros et al., 2024). This concept is known as the limiting similarity theory (MacArthur and Levins, 1967). Niche partitioning occurs primarily across spatial, temporal, and dietary dimensions, with spatial partitioning being predominant among taxa, especially in terrestrial mammals (Schoener, 1974; Cong et al., 2024). Specifically, in Schoener's research (1974), which reviewed niche partitioning methods across various taxa, 90 % of the species pairs separated their niches by habitat. However, temporal partitioning also facilitates the coexistence of sympatric species, notably within carnivore guilds, where competition risks are higher due to intraguild predation (Schoener, 1974; Palomares and Caro, 1999; Hayward and Slotow, 2009; Marshall et al., 2023). For instance, among the six coexisting feline species in Sumatra, those with similar body sizes or prey preferences had lower temporal overlap, which indicated a pattern of temporal separation (Sunarto et al., 2015).

Roughgarden and Feldman (1975) further explored the effect of predation pressure on niche partitioning. In the presence of a common predator, species may partition their niches with the predator to avoid fatal threats, thereby increasing their niche overlap within the guild (Azlan and Sharma, 2006; Brook et al., 2012). For example, Shores et al. (2019) discovered that the overlap in activity patterns between bobcats (*Lynx rufus*) and coyotes (*Canis latrans*) increased in areas occupied by gray wolves (*Canis lupus*). The influence of top predators on native mesocarnivore guilds not only shapes species coexistence but also leads to broader community and ecological impacts through top-down effects (Ritchie and Johnson, 2009; Monterroso et al., 2016; Sévêque et al., 2020).

In recent years, large carnivores worldwide have faced population declines, shrinking distributions, and extinctions, which has led to a decline or loss of their ecological functions (Ripple et al., 2014). Consequently, dogs (*Canis familiaris*), which are the most widespread and abundant carnivore in the world (Hughes and Macdonald, 2013), may become the dominant predator in areas where large carnivores are scarce (Estes et al., 2011; Ritchie et al., 2014). For example, in areas where large carnivores are absent (Victoria, Australia; van Bommel and Johnson, 2016) or sparse (Maharashtra, India; Vanak and Gompper, 2009a), dogs became the dominant predator that influenced the distribution and behavior of large herbivores and mesopredators. However, dogs can reach alarmingly high densities with human food subsidies (Vanak and Gompper, 2009b). Combined with their surplus killing behavior, this exacerbates their impact on wildlife populations (Shepherd, 1981; Taborsky, 1988; Ritchie et al., 2014). This situation prevents dogs from replacing the functional roles of native large predators and, instead, poses a significant threat to biodiversity (Gompper, 2014; Hughes and Macdonald, 2013; Doherty et al., 2017). For example, studies in India and Iran report that free-roaming dogs attack and consume a wide range of species, emphasizing the urgent need for proper management policies (Nayeri et al., 2022; Mahar et al., 2024). Similarly, in southeastern Brazil, where dogs are the most abundant carnivore, their presence has been documented to disrupt ecosystems by killing or competing with at least 26 native species, highlighting their significant and detrimental impact on local biodiversity (Guedes et al., 2021).

At present, an estimated 160,000 free-roaming dogs exist in Taiwan (Animal Protection Information Network, 2022). In the absence of large native carnivores in mid to low-altitude areas, free-roaming dogs have become the top, albeit invasive, predators (Yen et al., 2019). Lim et al. (2023) revealed that dog attacks were the primary lethal cause of death for adult masked palm civets (*Paguma larvata*) in urban areas. Lethal attacks have also occurred for Reeve's muntjac (*Muntiacus reevesi*) (Ho et al., 2024), Chinese pangolins (*Manis pentadactyla*) (Sun, 2023), and small Indian civets (*Viverricula indica*) (Yen et al., 2015). Yen et al. (2019) found that the species richness and probability of occurrence of native mammalis were impacted negatively by free-roaming dogs in Yangmingshan National Park. They also discovered that several native mammalian species reduced their overlap in temporal activity with dogs during their breeding season. Such spatial and temporal avoidance of dog threats may influence niche partitioning within the mammalian community in Taiwan.

Most studies focus primarily on the direct impacts of dogs on native species (Gompper, 2014). In this study, we aim not only to investigate the direct impact of free-roaming dogs on individual native carnivores but also to discover how dogs affect interspecific interactions within the native carnivore guild. We hypothesize that free-roaming dogs dominate spatial and temporal resources, posing risks to native mesocarnivores and forcing them to adjust their realized niches to avoid dogs. Therefore, niche overlap between native carnivores may increase.

To test this hypothesis, we used occupancy models and kernel density estimation to analyze camera trap data to assess the spatiotemporal niche dynamics of dogs and native carnivores. We predict that (1) the activity levels of native carnivores were correlated negatively with those of free-roaming dogs, (2) native carnivores practiced spatial or temporal avoidance in response to the presence of free-roaming dogs, and (3) free-roaming dogs contributed to increased spatial or temporal niche overlap among native carnivores.

# 2. Material and methods

#### 2.1. Study area

Taiwan (21°55′–25°20′N, 119°30′–122°00′E) is a mountainous island located between the tropical and subtropical regions (Li et al., 2013). It covers approximately 36,000 km<sup>2</sup>, with elevations that range from 0 to 3950 m. The island experiences a tropical marine climate characterized by warm and humid conditions, with a mean annual temperature of 23 °C in the lowlands and annual precipitation that exceeds 2500 mm (Central Weather Administration of Taiwan, 2024). Taiwan's diverse landscape and abundant rainfall have fostered various vegetation types. Forested mountains cover two-thirds of the island, and broad-leaved evergreen forests are the

predominant vegetation type below 1500 m (Li et al., 2013).

Taiwan is home to nine native carnivore species. Except for the Asian black bear (*Ursus thibetanus*), these species are all medium to small-sized carnivores that weigh < 15 kg (Cheng and Chang Chien, 2015). This study focused on four mesocarnivores that dwell primarily in mid to low-elevation areas: the ferret badger (*Melogale moschata*), the masked palm civet, the small Indian civet, and the crab-eating mongoose (*Herpestes urva*). The ferret badger and masked palm civet are distributed widely in Taiwan, but the crab-eating mongoose and small Indian civet are currently under the protection of the Wildlife Conservation Act due to their smaller population sizes and fragmented distribution (Cheng et al., 2017).

Among these four species, the ferret badger, masked palm civet, and small Indian civet are nocturnal, and the crab-eating mongoose is diurnal. These four native mesocarnivores are all generalists that are capable of consuming a wide range of invertebrates, amphibians, reptiles, birds, small mammals, and plants, although they also adjust their food habits based on different environmental conditions (Chuang and Lee, 1997; Chiang et al., 2012; Chang, 2018; Lim et al., 2023). These four species dwell mainly in broad-leaved forests, while the crab-eating mongoose relies heavily on freshwater habitats surrounded by forests (Chiang et al., 2012).

Free-roaming dogs are opportunistic predators found throughout Taiwan, primarily in areas close to human activity. They are active both day and night, with activity peaks at dawn and dusk (Yen et al., 2015; 2019). Therefore, they may threaten the four native carnivores both spatially and temporally.

# 2.2. Data collection and processing

We analyzed camera trap data to observe the niche relationships among dogs and the four native mesocarnivores. To test whether the activity levels of native carnivores correlated negatively with those of free-roaming dogs (prediction 1), we built generalized linear models on the relative activity index (RAI) of these species. To test whether native carnivores partitioned their spatial or temporal niche with dogs (prediction 2) and whether dogs contributed to increased spatial or temporal niche overlap among native carnivores (prediction 3), we applied occupancy models and kernel density estimation to explore the spatial interactions and activity patterns, respectively (Table 1).

# 2.2.1. Data collection

Camera trapping is an optimal tool for surveying medium-sized mammals and lends itself to analysis using various analytic methods (Caravaggi et al., 2017). In this study, we collected multiple camera trap datasets from various sources, which included governmental agencies, private companies, and academic institutions (Appendix A: Table A1). Sampling methods for these datasets included systematic sampling, stratified random sampling, and convenience sampling. A total of 1270 camera traps deployed across Taiwan were collected, which ranged in elevation from 1 to 2540 m during 2010–2021. We then filtered these data according to the requirements of different models.

#### 2.2.2. Data processing

First, we excluded all camera trap data from elevations > 1500 m because the primary distributions and overlapping elevational ranges of four target species were below this elevation (Chung and Shao, 2022). We then divided the data into the breeding season (May to August) and the non-breeding season (September to April) (Liu et al., 2007; Lin et al., 2008; Ju, 2013; Yu, 2019).

For spatial analyses, we used only data from the breeding season because using data that were collected over a long period of time can lead to high naïve occupancy and fail to identify significant factors that affect species occurrence (MacKenzie et al., 2017). Each camera trap was treated as a unit of statistical analysis to understand species dynamics. We filtered out camera traps that were in operation for < 35 d to ensure a sufficient survey effort. If a camera operated for more than one breeding season, we only used data from the one with the most extensive survey effort. Following these criteria, we included 478 camera traps (Fig. 1) with a total of 11, 472 independent trap events of native carnivores (i.e., 4855 for ferret badger, 4489 for masked palm civet, 1772 for crab-eating mongoose, and 356 for small Indian civet) and 2175 independent trap events of free-roaming dogs.

For temporal analysis, the kernel density estimation requires sufficient data from each species in a pair, but data from a single

Table 1

Predictions and corresponding models of the relationships between free-roaming dogs and native carnivores in Taiwan.

Prediction	Content	Spatial / Temporal	Model	Indicator
P1	Activity levels of native carnivores correlated negatively with those of free-roaming dogs.	Spatial	Generalized linear model	Relative activity index
P2	Native carnivores partition their spatial or temporal niche	Spatial	Single-species occupancy model	Occupancy
	with dogs.	Spatial	Two-species occupancy model	Species interaction
				factor
		Temporal	Kernel density estimation and generalized linear model	Coefficient of temporal overlap
Р3	Dogs contribute to increased spatial or temporal niche overlap among native carnivores.	Spatial	Two-species occupancy model	Species interaction factor
		Temporal	Kernel density estimation and generalized linear model	Coefficient of temporal overlap



Fig. 1. (Left) The distribution of 478 Camera traps for the relative activity index and occupancy models. (Right) The distribution of 54 camera trapping plots (discriminated by different colors) for the kernel density estimation.

camera trap was not enough for a meaningful analysis. Therefore, we divided camera traps into plots (Ridout and Linkie, 2009) and estimated temporal overlap based on these plots. The division of plots followed three criteria: (1) a maximum elevation difference of 1000 m, (2) no obvious geographic barriers (e.g., major roads, rivers, or mountain ridges > 3000 m in elevation), and (3) similar land cover types. After data filtering, we analyzed a total of 875 camera traps across 54 sampling plots (Fig. 1) with 73,292 independent trap events of native carnivores (i.e., 33,433 for ferret badger, 25,760 for masked palm civet, 10,712 for crab-eating mongoose, and 3387 for small Indian civet) and 12,750 independent trap events of free-roaming dogs. The data were divided into breeding and non-breeding seasons and analyzed separately with kernel density estimation.

Due to the fragmented distribution range of the crab-eating mongoose and the small Indian civet, we excluded data from areas where these species were confirmed not to exist in models that included them. Additionally, if a species had < 10 independent detections in a plot, we excluded the plot's data from models that included the species to avoid bias.

#### 2.3. Environmental factors

We derived various environmental factors using ArcGIS Pro (version 3.0.3), which included road density, elevation, slope, monthly average rainfall, annual average temperature, and forest coverage (Appendix B). Also, given the dependence of crab-eating mongooses on riparian environments, we included the distance to the nearest water body as a factor in the RAI model and the single-species occupancy model of crab-eating mongooses (Appendix B).

Before model construction, we assessed the correlations between environmental factors using Pearson correlation analysis. If the absolute values of the correlation coefficient between the two factors exceeded 0.7 ( $|\mathbf{r}| > 0.7$ ), we only retained one (Dobrowski et al., 2006; Gálvez et al., 2021). The results showed a high correlation between elevation and annual average temperature (p < 0.001, r = -0.72), and we kept the elevation factor because it influenced the annual average temperature primarily (Li et al., 2013). Furthermore, after examining the distribution of these factors and the relationships between environmental factors and the dependent variables, we performed a logarithmic transformation on road density to mitigate the skewness of the data (Keene, 1995) and included the squared term of elevation and monthly average rainfall in the models.

#### 2.4. RAI

RAI is often used as an indicator of species activity or relative abundance in camera trapping surveys (Sollmann et al., 2013; Lijun et al., 2019). It is calculated as the number of independent trap events per 100 d. Trap events of the same species at identical locations were considered independent if there was at least a 30-min gap between detections (Kelly and Holub, 2008). Next, we built a generalized linear model with a log-normal distribution to observe the factors that influenced the RAI of native carnivores, and we selected the best model through the forward selection method (Witten and James, 2013). The order in which variables were chosen indicated the extent to which they explained the model residuals, which reflected their relative importance to the dependent variable. The RAI was transformed logarithmically to reduce the influence of RAI variability on the model.

# 2.5. Spatial niche partitioning

#### 2.5.1. Single-species occupancy model

We applied single-season, single-species occupancy models (MacKenzie et al., 2017) to identify the significant factors that influenced species occupancy ( $\Psi$ ). Occupancy is the probability of a species being present in an area, regardless of the number of individuals detected. Unlike RAI, which represents species activity levels, occupancy is often used as an indicator of species distribution. This allowed us to estimate changes in spatial use of species and their realized spatial niches based on variations in their occupancy. It was especially suitable for monitoring the distribution of species with smaller population sizes, such as carnivores (MacKenzie et al., 2017). The occupancy model assumed that the populations were closed during a single season (MacKenzie et al., 2017). With multiple survey periods in a season, we obtained a series of detection/non-detection data and estimated the detection probability based on it. The detection probability was used to reduce model bias and to adjust naïve occupancy to realized occupancy (Mackenzie, 2006; Long, 2008). In this study, we set the survey period as 7 d. We ran models in the unmarked package (Fiske and Chandler, 2011; Kellner et al., 2023) in R (version 4.3.1, R Core Team, 2021), and we used forward selection to select the model (Witten and James, 2013).

#### 2.5.2. Conditional two-species occupancy model

Two-species occupancy models are often used to estimate the spatial interactions between pairs of species. We used the conditional two-species occupancy model developed by Richmond et al. (2010) to estimate the occupancy of the dominant species and the subordinate species in the presence or absence of the dominant species. A related indicator, the Species Interaction Factor (SIF), was then calculated by the estimated occupancies (Richmond et al., 2010). It was calculated as:

$$SIF = - \frac{\psi^A \psi^{BA}}{\psi^A \; (\psi^A \psi^{BA} + (1-\psi^A) \psi^{Ba})}$$

where  $\Psi^{A}$  is the occupancy of the dominant species, and  $\Psi^{BA}$  and  $\Psi^{Ba}$  are the occupancies of the subordinate species with and without the presence of the dominant species, respectively. If SIF = 1 (or  $\Psi^{BA} = \Psi^{Ba}$ ), the distribution of the two species was considered independent. SIF > 1 (or  $\Psi^{BA} > \Psi^{Ba}$ ) indicated a co-occurrence pattern between the two species, and SIF < 1 (or  $\Psi^{BA} < \Psi^{Ba}$ ) indicated a tendency of avoidance (Richmond et al., 2010; MacKenzie et al., 2017; Gálvez et al., 2021).

In this study, SIF was used to assess the co-occurrence patterns among free-roaming dogs and native carnivores. The dominant and subordinate species were determined by their body sizes (Donadio and Buskirk, 2006; Ritchie et al., 2014). In the models between dogs and native mesocarnivores, dogs were considered dominant (around 17 kg, Vanak and Gompper, 2010), but in the models between native carnivores, dominance was ordered in the following way: the masked palm civet (3.5–5 kg), the crab-eating mongoose (1.8–3.2 kg), the small Indian civet (2–4 kg), and the ferret badger (1–1.75 kg) (Chung and Shao, 2022). The body weights of the crab-eating mongoose and the small Indian civet were similar. However, because crab-eating mongooses were more likely to form groups (Weng, 2010), we placed them higher in the dominance order than the small Indian civets.

Models were run in the R package "RPresence" (MacKenzie and Hines, 2018). We followed the two-step method (Richmond et al., 2010; Gálvez et al., 2021) to construct candidate models. First, we evaluated whether the detection probability of subordinate species was affected by the occurrence or detection probability of the dominant species. Second, we included combinations of occupancy covariates in these models. We selected the best-performing ( $\Delta$ AIC < 2) models and built average models based on them (Burnham et al., 1998). Through this approach, for each combination of dog-native carnivore pairs, we built 4372 candidate models for each detection probability model. For each combination of native carnivore pairs, we built 15307 candidate occupancy models.

#### 2.6. Temporal niche partitioning

Kernel density estimation (KDE) transforms point count data into probability density functions that display species activity patterns (Wand and Jones, 1994). In addition to understanding the activity patterns of individual species, Ridout and Linkie (2009) proposed the coefficient of temporal overlap ( $\Delta$ ) to quantify the overlap in activity patterns of paired species.  $\Delta$  ranged from 0 to 1, where larger values indicated higher overlap between the activity patterns of the two species.

Ridout and Linkie (2009) evaluated five methods for calculating  $\Delta$ , and they found that  $\Delta 1$  was suitable for small sample calculations (samples < 50), and  $\Delta_4$  was suitable for larger samples (samples > 75). In this study, we first calculated  $\Delta_4$  values of all species pairs and estimated the confidence intervals through 10,000 bootstraps to understand the overall overlap of activity patterns between species. Subsequently, we divided cameras into plots to examine whether dog RAI or other environmental factors influenced the

#### H.-C. Ho et al.

overlaps of activity patterns (Ridout and Linkie, 2009). Because most plots had small sample sizes, we calculated  $\Delta_1$  for the following analysis.

For dog RAI and environmental factors, we calculated the mean of each factor across all camera traps in the plot and computed  $\Delta$  values for the breeding season (May to August) and non-breeding season (September to April) separately. We built generalized linear models with a negative binomial distribution to observe the factors that influenced the activity overlaps and applied the forward selection method to the candidate models. The calculation of  $\Delta$  values was conducted using the R package "overlap" (Ridout and Linkie, 2009).

# 3. Results

# 3.1. RAI models

In the model for ferret badgers, the RAI of ferret badgers was correlated negatively with the dog RAI (p < 0.001) and the quadratic term of elevation (p < 0.05). Dog RAI was the first selected variable during forward selection. The RAI of masked palm civets was correlated negatively with elevation (p < 0.001) and monthly average rainfall (p < 0.001) and correlated positively with road density (p < 0.01). The RAI of crab-eating mongooses was correlated negatively with dog RAI (p < 0.05) and distance to the nearest water body (p < 0.01) and correlated positively with forest coverage (p < 0.001). The RAI of small Indian civets was correlated negatively with elevation (p < 0.001) and correlated positively with monthly average rainfall (p < 0.001) and forest coverage (p < 0.001). The RAI of small Indian civets was correlated negatively with elevation (p < 0.001) and correlated positively with monthly average rainfall (p < 0.001) and forest coverage (p < 0.001) (Table 2).

# 3.2. Spatial niche partitioning

# 3.2.1. Single-species occupancy models

In the best occupancy model for ferret badgers, the effect of dog RAI was negative and significant (p < 0.01); however, unlike the RAI model, dog RAI was no longer included in the best occupancy model for crab-eating mongooses (Table 3). Other significant factors included the following: occupancy of ferret badgers was correlated positively with forest coverage (p < 0.01), occupancy of masked palm civets was correlated negatively with elevation (p < 0.001), and occupancy of crab-eating mongooses was correlated positively with forest coverage (p < 0.001). Finally, occupancy of small Indian civets was correlated positively with monthly average rainfall (p < 0.001) and forest coverage (p < 0.001) and correlated negatively with slope (p < 0.05) and elevation (p < 0.05) (Table 3).

# 3.2.2. Conditional two-species occupancy models

In pairs between dogs and native carnivores, the ferret badger exhibited significant spatial avoidance (SIF = 0.883, CI: 0.807-0.958), but the crab-eating mongoose showed a co-occurrence pattern with dogs (SIF=1.323, CI: 1.192-1.454) (Fig. 2, Appendix A: Table A2). In pairs between native carnivores, none of them exhibited significant spatial avoidance or coexistence (i.e., the confidence intervals for SIF spanned 1).

In three of the six native species pairs, the best-performing models included dog RAI, which suggested that dogs influenced their cooccurrence patterns (i.e., affected  $\Psi^{BA}$  or  $\Psi^{Ba}$ ) (Fig. 3). These three pairs included masked palm civet – small Indian civet, crab-eating mongoose – small Indian civet, and small Indian civet – ferret badger.

# 3.3. Temporal niche partitioning

Among pairs between dogs and native carnivores, the dog – crab-eating mongoose pair had the highest activity overlap;  $\Delta_4$  reached

#### Table 2

The relative activity index (RAI) model that performed best for each species	s. The order of the variables (from top to bottom) represents the sequence
in which the variables were selected in forward selection.	

Species	Variable	<b>Regression Coefficient</b>	<i>p</i> -value
Ferret badger	Intercept	1.700	
	RAI <sub>dog</sub>	-0.274	< 0.001
	Elevation <sup>2</sup>	-0.00000329	< 0.05
Masked palm civet	Intercept	2.218	
	Elevation	-0.00128	< 0.001
	Road density	91.540	< 0.01
	Monthly average rainfall	-0.000134	< 0.05
Crab-eating mongoose	Intercept	0.474	
	Forest coverage	0.888	< 0.001
	Distance to the nearest water body	-0.000561	< 0.01
	RAI <sub>dog</sub>	-0.115	< 0.05
Small Indian civet	Intercept	-0.476	
	Monthly average rainfall	0.000244	< 0.001
	Forest coverage	0.413	< 0.001
	Elevation	-0.000287	< 0.001

#### Table 3

The single-species occupancy model that performed best for each species. The order of the variables (from top to bottom) represents the sequence in which the variables were selected in forward selection.

Species	Variable	Regression Coefficient	<i>p</i> -value
Ferret badger	Intercept	0.0298	
	Forest Coverage	1.271	< 0.01
	RAIdog	-0.264	< 0.01
	Elevation	-0.000564	0.108
Masked palm civet	Intercept	1.957	
	Elevation	-0.505	< 0.001
Crab-eating mongoose	Intercept	-1.990	
	Forest coverage	2.960	< 0.001
Small Indian civet	Intercept	-5.298	
	Monthly average rainfall	0.0106	< 0.001
	Forest Coverage	3.643	< 0.001
	Slope	-0.0206	< 0.05
	Elevation	-0.00171	< 0.05



Fig. 2. Species interaction factors (SIF) and the 95 % confidence intervals for each pair of species calculated from the best-performing models.

0.811 (95 % CI: 0.803–0.819). The activity overlaps of dogs and the three nocturnal species were relatively low ( $\Delta_4$  around 0.3) (Fig. 4). In comparisons among native species, the activity overlaps of the three nocturnal species were high ( $\Delta_4 > 0.8$ ), but  $\Delta_4$  between the crab-eating mongoose and other species was low ( $\Delta_4 < 0.2$ ) (Fig. 4). The generalized linear model indicated that  $\Delta_1$  of all species pairs were not significantly correlated with any factors (Appendix A: Table A3).

# 4. Discussion

In this study, we observed a significant negative correlation between the RAIs of dogs and ferret badgers and between dogs and crab-eating mongooses (Prediction 1). We also observed avoidance of dogs by ferret badgers in habitat use through single-species and two-species occupancy models (Prediction 2). However, we did not find a significant correlation between the activity level of dogs and the niche overlap among native carnivores (Prediction 3).



Fig. 3. The correlation between the co-occurrence pattern of native carnivore pairs and the RAI of free-roaming dogs (log-transformed). The red line is the occupancy of species A ( $\Psi^{A}$ ), the blue line represents the occupancy of species B given the presence of species A ( $\Psi^{BA}$ ), and the green line represents the occupancy of species B given the absence of species A ( $\Psi^{Ba}$ ). The dotted lines and gray shaded areas indicate the 95 % confidence intervals.



Fig. 4. The activity overlaps for each pair of species. The solid lines represent the activities of the dominant species, and the dotted lines represent the activities of the subordinate species. The gray areas show the overlapping of activities. The coefficient of temporal overlap ( $\Delta$ ) and their 95 % confidence intervals are marked on the graphs.

#### 4.1. Impact of free-roaming dogs on native carnivores

Of the four native carnivores in this study, ferret badgers were the most affected species by free-roaming dogs. Our study provides evidence that the abundance and distribution of ferret badgers were affected by dogs. Also, ferret badgers showed significant spatial avoidance of dogs (SIF < 1). Because ferret badgers were the smallest carnivores in this study, they were likely the most vulnerable species to dog threats. The negative impacts of dogs on ferret badgers in Taiwan have been documented in recent years. Previous

studies showed that ferret badgers reduced their activity overlap with dogs during their breeding season to avoid threats (Yen et al., 2019). Also, ferret badgers in south Taiwan were recorded to be infected by canine distemper that was transmitted by free-roaming dogs (Chen et al., 2008).

The RAI of crab-eating mongoose was correlated negatively with that of free-roaming dogs, which implied that dogs reduced the abundance of crab-eating mongooses. However, crab-eating mongooses showed significant spatial co-occurrence with dogs and exhibited the highest overlap in activity patterns. We infer that, although dogs may have a negative impact on mongooses, the mongooses may be unable to avoid encounters with them effectively. Crab-eating mongooses depended strongly on specific landscapes (i.e., forests near freshwater environments) (Huang, 1995; Chiang et al., 2012), which may have restricted their flexibility to adjust their habitats and to avoid dogs spatially. Therefore, there is a critical need for conservation efforts, particularly for riparian environments. Also, another endangered carnivore threatened by dogs, the leopard cat (*Prionailurus bengalensis*), prefers habitat near freshwater sources as well (Shanida et al., 2023). Protecting the riparian environments from dogs could be highly beneficial for conserving these carnivores.

The current study found a significant positive correlation between the RAI of masked palm civets and road density. This was likely due to their increasing adaptation to urban environments in Taiwan in recent years (Lim et al., 2023). The adaptation of masked palm civets to urban areas may be related to their ability to utilize vertical spaces because they can nest on steel beams of buildings and forage on fruits from street trees (Lim et al., 2023). As urban areas expand, species better adapted to anthropogenic environments, like the masked palm civet, may extend or switch their habitat to human-dominated areas to reduce intra-guild competition (Frey et al., 2020). However, the adaptability of the masked palm civet to anthropogenic environments may obscure the negative effects of dogs. Due to the close relationship between dogs and humans, dogs are also common in suburban areas (Hsu et al., 2003; Gompper, 2014). Therefore, large-scale spatial models may be unable to distinguish the two opposite effects. The absence of the dog RAI variable in the occupancy models should not be interpreted as dogs having no impact on masked palm civets. In fact, Lim et al. (2023) found that dog attacks were the primary cause of death for urban masked palm civets in Taichung, the largest city in central Taiwan. A recent study in Shoushan National Nature Park in Taiwan also revealed that the RAI and occupancy of masked palm civets declined strongly under threat from free-roaming dogs (Ho et al., 2024). The impact of dogs on masked palm civets may be more obvious by observations on a smaller scale.

The small Indian civet is the most endangered species among the four target species. It has long exhibited a fragmented distribution due to overexploitation and other unknown environmental changes (Pei, 2004; Yen et al., 2015). The data sampling issues may make it difficult to detect the spatial and temporal impacts of dogs on small Indian civets at a large scale. For instance, many trap events for the small Indian civet came from Yangmingshan National Park, where annual rainfall is up to 4000 mm, which may have led to significant positive correlations between monthly average rainfall and the RAI and occupancy of small Indian civets. However, Yen et al. (2015) recorded a high overlap in distribution between free-roaming dogs and small Indian civets in Yangmingshan National Park and documented that dogs killed small Indian civets. Additionally, Dahmer (2001) observed that dog killing was the major cause of mortality for small Indian civets in Kau Sai Chau, Hong Kong. Moreover, Yen et al. (2019) observed that the overlap in activity patterns between small Indian civets and dogs decreased during the breeding season. These studies indicate that dogs still pose severe threats to small Indian civets.

#### 4.2. Niche partitioning among native carnivores

This study did not detect the influence of dogs on the spatial or temporal niche overlaps of native carnivores. In the findings from the two-species occupancy models, dog RAI was incorporated into the top-performing models for the pairs that consisted of small Indian civets. However, the confidence intervals of  $\Psi^{BA}$  and  $\Psi^{Ba}$  overlapped greatly, which indicated that the effects of dog RAI were insignificant. Additionally, we did not discover any factor that influenced species' temporal overlap.

There are three possible reasons for this observation: First, only the ferret badger exhibited significant spatial avoidance of dogs. This led to the shift in niche being insufficiently large to be detected. Second, the spatiotemporal niches of native carnivores may partition on a finer scale than models could detect. For example, the masked palm civet may have increased vertical space use to avoid dogs and to mitigate competition with sympatric carnivores, which could not be addressed in this study. Finally, there may be more influential factors that shape the spatial and temporal niches of native carnivores. For instance, even though the abundance of crabeating mongooses was affected negatively by dogs, their specific habitat requirements made it difficult to adjust their spatial niche in response to these threats (Gálvez et al., 2021).

This study found no significant factors correlated with the temporal overlaps among species. The extent of temporal overlap among species was related solely to their activity patterns: the three nocturnal species exhibited greater temporal overlap with each other, but there was less overlap between the nocturnal species and diurnal crab-eating mongooses. Correspondingly, previous studies have shown that species typically relied less on temporal strategies to avoid threats (Schoener, 1983). This is likely because their activity patterns were determined predominantly by their internal biological clocks (Kronfeld-Schor and Dayan, 2003; Ferreiro-Arias et al., 2021). Additionally, changes in activity patterns may be finer-scale improvised responses that are not easily detectable when analyzing data at large scales (Sévêque et al., 2022). This could explain why this macroscale study in Taiwan found different results compared with Yen et al. (2019), who observed that six mammal species altered their activity patterns to avoid dogs within a single national park.

#### 4.3. Research limitations

Due to carnivores' relatively low abundance and the resulting insufficient data, a trade-off between sample size and spatial

#### H.-C. Ho et al.

resolution was necessary. For example, calculating  $\Delta$  values at a finer scale (e.g., individual camera sites) in kernel density estimation could have resulted in instability and potential distortion due to insufficient data. As a result, we chose to conduct analyses at a larger scale to ensure more stable and reliable results, although it came at the cost of overlooking finer-scale dynamics.

Finally, the data used in this study were not collected systematically on a unified nationwide scale; instead, they were gathered from multiple sources and then processed. Although the data sources were not uniform, the estimated occupancies in this study, where species with higher endangerment levels had lower occupancies and vice versa, reflected the current situation for native carnivores in a reasonable way.

In conclusion, this study demonstrates the negative impact of free-roaming dogs on ferret badgers and crab-eating mongooses, which underscores the urgent need for conservation efforts. Given the severe ecological consequences, the government must implement an effective population-control policy for free-roaming dogs to mitigate their ecological impacts. First, feeding dogs must be prohibited to reduce the environmental carrying capacity for unowned dogs. Second, the government should strictly enforce the Animal Protection Act regarding owner responsibilities, particularly prohibiting pets from roaming freely. Third, we propose that the removal of free-roaming dogs should replace the current trap-neuter-return method as the primary management strategy, especially in areas with public safety and conservation concerns (Read et al., 2020; Contreras-Abarca et al., 2022). While the TNR method has become the predominant measure for managing unowned dogs in Taiwan due to the no-kill policy, its effectiveness and efficiency are highly questionable (Ho et al., 2024; Lambertucci et al., 2024). It is impractical to rely solely on TNR to manage free-roaming dog populations across the island. Furthermore, to gain a complete understanding of the impacts of dogs on native carnivores, we suggest that future studies incorporate other niche dimensions, such as the trophic dimension, to understand the interspecific interactions comprehensively.

# Funding

This research was supported by Project No. 112-2621-B-007-001-MY2 of the National Science and Technology Council, Taiwan, R. O.C.

# Ethical statement

All procedures of this study were performed in compliance with relevant laws and institutional guidelines. This study did not involve any activities that required formal ethical approval or permits from institutional or governmental committees.

# CRediT authorship contribution statement

Hsin-Cheng Ho: Data curation, Formal analysis, Methodology, Visualization, Writing – original draft. Tzung-Su Ding: Methodology, Writing – review & editing. Jo-Szu Tsai: Methodology, Writing – review & editing. Guo-Jing Weng: Data collection, Writing – review & editing. Yu-Hsiu Lin: Data collection, Writing – review & editing. Hsiang Ling Chen: Data collection, Writing – review & editing. Yu-Bo Huang: Data collection, Writing – review & editing. Shih-Ching Yen: Conceptualization, Funding acquisition, Data collection, Methodology, Project administration, Supervision, Writing – original draft.

#### **Declaration of Competing Interest**

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Shih-Ching Yen reports financial support was provided by National Science and Technology Council, Taiwan. Hsin-Cheng Ho reports financial support was provided by National Science and Technology Council, Taiwan. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

# Acknowledgments

We are grateful to all the researchers who generously provided camera trap data that facilitated the completion of this study. We thank James E. Hines for his technical support with occupancy modeling and Thomas A. Gavin for his help with language editing.

# Table A1

Sources of the camera trap datasets that were used for evaluating spatiotemporal niche overlaps among native carnivores and free-roaming dogs in Taiwan

Data source	Location	Year	Camera count	Sampling method
Lin et al., (2020)	Nantou County, Changhua County, and Miaoli County	2012-2019	112	Systematic sampling and convenience sampling
Yen et al., (2019)	Taipei City and New Taipei City	2012-2017	140	Systematic sampling with $1 \times 1$ km grids
Yen, (2017)	Hualien County	2016-2017	38	Stratified random sampling
Ho et al., (2024)	Kaohsiung City	2021-2022	58	Systematic sampling with 500 $\times$ 500 m grids
Cheng et al., (2021)	Taichung City	2021-2022	10	Convenience sampling
Chen et al., (2020)	Nantou County	2018-2022	32	Convenience sampling
Weng, (2021)	Entire Taiwan	2018-2021	183	Systematic sampling
Liu et al., (2023)	Entire Taiwan	2010-2021	692	Convenience sampling
Hsiang Ling Chen unpublished data	Yilan County	2022	5	Convenience sampling

# Table A2

The best-performing models in two-species occupancy modeling of all species pairs. Two occupancy equations were used for comparison: (1)  $\Psi^A \Psi^B$  $\Psi^{BA}$ , the occupancy of species B was affected by species A, and (2)  $\Psi^A \Psi^B$ , the occupancy of species A and species B were estimated separately. In addition, the interaction between variables and species (SP) may take two forms: conditional (C) or unconditional (U). The former means that the extent of species B's occupancy affected by a variable was affected by species A's occupancy, but the latter was the opposite. That is, if a variable interacted with species conditionally, this variable influenced the difference between  $\Psi^{BA}$  and  $\Psi^{Ba}$ . Following our prediction that RAI<sub>dog</sub> influenced species co-occurrence patterns, we allowed only RAI<sub>dog</sub> to interact conditionally with species in our candidate models. Three detection formulas were included in our candidate models: (1)  $p^A p^B$ , meaning that the detection of species A; and (3)  $p^A p^B r^{BA} r^{Ba}$ , the detection of species B was affected by the presence of species A, but not by the detection of species A; and (3)  $p^A p^B r^{BA} r^{Ba}$ , the detection of species B was affected by the presence of species A (Richmond et al., 2010)

Occupancy Model	Occupancy Covariates <sup>a</sup>	Detection Model	K	-2 Log- Likelihood	ΔAIC	AIC wt
Masked palm cive	et-Ferret badger					
$\Psi^A \ \Psi^B \ \Psi^{BA}$	Forest, Rainfall <sup>2</sup> , RAI <sub>dos</sub> , RD, Elevation <sup>2</sup> ×SP(U), Slope×SP(U)	$p^{A} p^{B} r^{BA} r^{Ba}$	16	11835.84	0	0.5
$\Psi^A \ \Psi^B \ \Psi^{BA}$	Rainfall <sup>2</sup> , RAI <sub>dog</sub> , RD, Slope, Forest $\times$ SP(U), Elevation <sup>2</sup> $\times$ SP(U)	p <sup>A</sup> p <sup>B</sup> r <sup>BA</sup> r <sup>Ba</sup>	16	11835.84	0	0.5
Masked palm cive	et-Crab-eating mongoose					
$\Psi^A \Psi^B \Psi^{BA}$	$RAI_{dog}$ , Forest×SP(U), Elevation <sup>2</sup> ×SP(U), Rainfall <sup>2</sup> ×SP(U), RD×SP(U),	p <sup>A</sup> p <sup>B</sup> r <sup>BA</sup> r <sup>Ba</sup>	21	8095.38	0	0.126
	Slope×SP(U), Rainfall×SP(U)					
$\Psi^A \Psi^B \Psi^{BA}$	Forest×SP(U), Elevation <sup>2</sup> ×SP(U), Rainfall <sup>2</sup> ×SP(U), RAI <sub>dog</sub> ×SP(U), RD×SP	p <sup>A</sup> p <sup>B</sup> r <sup>BA</sup> r <sup>Ba</sup>	21	8095.38	0	0.126
	(U), Slope×SP(U), YearPerc					
$\Psi^A \Psi^B \Psi^{BA}$	Elevation, $RAI_{dog}$ , Slope, Forest×SP(U), Elevation <sup>2</sup> ×SP(U), Rainfall <sup>2</sup> ×SP(U),	p <sup>A</sup> p <sup>B</sup> r <sup>BA</sup> r <sup>Ba</sup>	21	8095.38	0.0001	0.126
	$RD \times SP(U)$ , Rainfall $\times SP(U)$					
$\Psi^{A} \Psi^{B} \Psi^{BA}$	Elevation, Slope, Forest×SP(U), Elevation <sup>2</sup> ×SP(U), Rainfall <sup>2</sup> ×SP(U),	p <sup>A</sup> p <sup>B</sup> r <sup>BA</sup> r <sup>Ba</sup>	21	8095.38	0.0001	0.126
A D DA	$RAI_{dog} \times SP(U), RD \times SP(U), YearPerc$	4 D D4 D-				
$\Psi^{A} \Psi^{B} \Psi^{BA}$	Forest, RAI <sub>dog</sub> , Slope, Elevation×SP(U), Elevation <sup>2</sup> ×SP(U), Rainfall <sup>2</sup> ×SP(U),	p <sup>A</sup> p <sup>B</sup> r <sup>BA</sup> r <sup>Ba</sup>	21	8095.38	0.0001	0.126
	$RD \times SP(U)$ , $Rainfall \times SP(U)$					
$\Psi^{A} \Psi^{B} \Psi^{BA}$	Forest, Slope, Elevation $\times$ SP(U), Elevation $^{2} \times$ SP(U), Rainfall $^{2} \times$ SP(U),	p <sup>A</sup> p <sup>b</sup> r <sup>bA</sup> r <sup>ba</sup>	21	8095.38	0.0001	0.126
	$RAI_{dog} \times SP(U), RD \times SP(U), YearPerc$					
	Elevation, Forest, Rainfall <sup>2</sup> ×SP(U), RAI <sub>dog</sub> ×SP(U), RD×SP(U), Slope×SP(U)		18	8102.28	0.9006	0.081
	Elevation, Slope, Forest×SP(U), Rainfall <sup>2</sup> ×SP(U), RAI <sub>dog</sub> ×SP(U), RD×SP(U)		18	8102.28	0.9006	0.081
Ψ <sup>A</sup> Ψ <sup>b</sup> Ψ <sup>bA</sup>	Forest, Slope, Elevation×SP(U), Rainfall <sup>2</sup> ×SP(U), RAI <sub>dog</sub> ×SP(U), RD×SP(U)	p <sup>A</sup> p <sup>D</sup> r <sup>DA</sup> r <sup>Da</sup>	18	8102.28	0.9006	0.081
Masked palm cive	et-Small Indian civet	A B BA Ba				
$\Psi^{\alpha} \Psi^{\beta} \Psi^{\beta \alpha}$	Elevation, Rainfall <sup>2</sup> , Slope, Forest×SP(U), Elevation <sup>2</sup> ×SP(U), RD×SP(U),	p <sup>A</sup> p <sup>D</sup> r <sup>DA</sup> r <sup>Da</sup>	20	5115.34	0	0.067
A WB WBA	$RAI_{dog} \times SP(C)$	A B BA Ba				
$\Psi^{\mu}\Psi^{\mu}\Psi^{\mu}\Psi^{\mu\nu}$	Forest, Rainfall <sup>2</sup> , Slope, Elevation $\times$ SP(U), Elevation <sup>2</sup> $\times$ SP(U), RD $\times$ SP(U),	p" p" r" r"	20	5115.34	0	0.067
WA WB WBA	RAI <sub>dog</sub> ×SP(C)	A.B.BA.Ba	17	5101 40	0.15	0.000
$\Psi^{A} \Psi^{B} \Psi^{BA}$	Elevation, Forest, RD, Rainfall <sup>2</sup> ×SP(U), $RAI_{dog}$ ×SP(U), Slope×SP(U)	A B BA Ba	17	5121.49	0.15	0.062
$\Psi^{A} \Psi^{B} \Psi^{BA}$	Elevation, RD, Slope, Forest×SP(U), Rainfall <sup>2</sup> ×SP(U), RAI <sub>dog</sub> ×SP(U)	A B BA Ba	17	5121.49	0.15	0.062
$\Psi^{-1} \Psi^{-1} \Psi^{-1}$	Forest, RD, Slope, Elevation×SP(U), Rainfall <sup>-</sup> ×SP(U), RAi <sub>dog</sub> ×SP(U)	A B BA Ba	17	5121.49	0.15	0.062
$\Psi^{-1} \Psi^{-1} \Psi^{-1}$	Elevation, Forest, Rainfall <sup>-</sup> , RAI <sub>dog</sub> ×SP(U), Slope×SP(U)	A B BA Ba	15	5126.15	0.8	0.045
$\Psi \Psi^- \Psi^{}$	Elevation, Forest, Kainfall <sup>-</sup> , KD×SP(U), Slope×SP(U)	p p r r r <sup>Ba</sup>	15	5126.15	0.8	0.045
$\Psi \Psi \Psi^{mA}$	Elevation, Forest, Kainfall, Slope×SP(U), Rainfall×SP(U)	ppr <sup>-</sup> r <sup>-</sup> a	15	5120.15	0.8	0.045
Ψ Ψ Ψ	Elevation, Raman <sup>-</sup> , Slope, Forest×SP(U), RAI <sub>dog</sub> ×SP(U)	p · p- r r	15	5120.15	0.8	0.045

(continued on next page)

# H.-C. Ho et al.

# Table A2 (continued)

0.0000000000000000000000000000000000000	Contractory Contractor <sup>d</sup>	Detection	V	21.00	AAIC	AIC
Occupancy	Occupancy Covariates	Detection	к	-∠ LOg-	ΔAIC	AIC
Model		wodel		Likelihood		wt
$\Psi^A \Psi^B \Psi^{BA}$	Elevation, Rainfall <sup>2</sup> , Slope, Forest $\times$ SP(U), RD $\times$ SP(U)	p <sup>A</sup> p <sup>B</sup> r <sup>BA</sup> r <sup>Ba</sup>	15	5126.15	0.8	0.045
$\Psi^A \Psi^B \Psi^{BA}$	Elevation, Rainfall <sup>2</sup> , Slope, Forest×SP(U), Rainfall×SP(U)	p <sup>A</sup> p <sup>B</sup> r <sup>BA</sup> r <sup>Ba</sup>	15	5126.15	0.8	0.045
$\Psi^A \Psi^B \Psi^{BA}$	Forest Rainfall <sup>2</sup> Slope Elevation $\times$ SP(U) RAL $_{dec} \times$ SP(U)	n <sup>A</sup> n <sup>B</sup> r <sup>BA</sup> r <sup>Ba</sup>	15	5126.15	0.8	0.045
$\Psi^A \Psi^B \Psi^{BA}$	Forest Rainfall <sup>2</sup> Slope Elevation × SP(II) RD× SP(II)	p <sup>A</sup> p <sup>B</sup> r <sup>BA</sup> r <sup>Ba</sup>	15	5126.15	0.8	0.045
$\Psi^{A} \Psi^{B} \Psi^{BA}$	Forest Rainfall <sup>2</sup> Slope Elevation×SP(U) Rainfall×SP(U)	p <sup>A</sup> p <sup>B</sup> r <sup>BA</sup> r <sup>Ba</sup>	15	5126.15	0.8	0.045
WA WB WBA	Flowetion Ecreat Deinfall <sup>2</sup> DAL, SP(U), Raman SP(U), Clones SD(U)	P P I I "A "B "BA "Ba	17	5120.15	0.07	0.043
T T T WA WB WBA	Elevation, Polest, Rallian, RAidog×SP(U), RD×SP(U), Slope×SP(U)	ppii pApBrBArBa	17	5122.51	0.97	0.041
T T T mA mB mBA	Elevation, Kalinan , Stope, Forest×SP(U), KAldog×SP(U), KD×SP(U)	ppii "A"B"BA"Ba	17	5122.51	0.97	0.041
ΨΨΨ wA wB wBA	Forest, Rainian, Stope, Elevation× $SP(U)$ , $RAi_{dog} \times SP(U)$ , $RD \times SP(U)$	рргг А.В.ВА.Ва	17	5122.51	0.97	0.041
$\Psi \Psi \Psi$	Elevation, RD, Slope×SP(U), RAI <sub>dog</sub> ×SP(C)	рргг	15	5126.65	1.3	0.035
$\Psi^{A} \Psi^{B} \Psi^{BA}$	RD, Slope, Elevation×SP(U), $RAl_{dog}$ ×SP(C)	p p r r r	15	5126.65	1.3	0.035
$\Psi^{\mu\nu}\Psi^{\mu\nu}\Psi^{\mu\nu}$	Elevation, Forest, Rainfall <sup>2</sup> ×SP(U), RAI <sub>dog</sub> ×SP(U), RD×SP(U), Slope×SP(U)	p <sup>r</sup> p <sup>s</sup> r <sup>sh</sup> r <sup>sh</sup>	18	5121.15	1.8	0.027
Crab-eating mong	oose-Ferret badger	A D D				
$\Psi^{A} \Psi^{D} \Psi^{DA}$	Forest, Rainfall <sup>2</sup> ×SP(U)	$p^{\Lambda} p^{P} r^{P}$	10	8244.87	0	0.42
$\Psi^A \Psi^B \Psi^{BA}$	Forest×SP(U), Rainfall <sup>2</sup> ×SP(U)	p <sup>A</sup> p <sup>B</sup> r <sup>B</sup>	11	8244.22	1.35	0.21
$\Psi_{A} \Psi_{B} \Psi_{BA}$	Forest, Rainfall <sup>2</sup> ×SP(U)	p <sup>A</sup> p <sup>B</sup> r <sup>BA</sup> r <sup>Ba</sup>	11	8244.46	1.59	0.19
$\Psi^A \Psi^B \Psi^{BA}$	Forest, RD, Rainfall <sup>2</sup> ×SP(U)	p <sup>A</sup> p <sup>B</sup> r <sup>B</sup>	11	8244.59	1.72	0.18
Crab-eating mong	oose-Small Indian civet					
$\Psi^A \Psi^B \Psi^{BA}$	Forest, RD, Slope, Elevation <sup>2</sup> ×SP(U), Rainfall <sup>2</sup> ×SP(U), RAI <sub>dog</sub> ×SP(U)	p <sup>A</sup> p <sup>B</sup> r <sup>B</sup>	16	3107.42	0	0.204
$\Psi^A \Psi^B \Psi^{BA}$	Elevation, Forest, RD, Slope, Rainfall <sup>2</sup> ×SP(U), $RAI_{dog}$ ×SP(U)	p <sup>A</sup> p <sup>B</sup> r <sup>B</sup>	15	3110.63	1.22	0.111
$\Psi^A \Psi^B \Psi^{BA}$	Elevation, Forest, RD, Rainfall <sup>2</sup> ×SP(U), Slope×SP(U), RAI <sub>dog</sub> ×SP(C)	$p^{A} p^{B} r^{B}$	17	3107.1	1.68	0.088
$\Psi^A \Psi^B \Psi^{BA}$	Elevation, RD, Slope, Forest $\times$ SP(U), Rainfall <sup>2</sup> $\times$ SP(U), RAI <sub>dog</sub> $\times$ SP(C)	$p^{A}p^{B}r^{B}$	17	3107.1	1.68	0.088
$\Psi^A \Psi^B \Psi^{BA}$	Forest, RD, Slope, Elevation $\times$ SP(U), Rainfall <sup>2</sup> $\times$ SP(U), RAI <sub>dog</sub> $\times$ SP(C)	$p^{A}p^{B}r^{B}$	17	3107.1	1.68	0.088
$\Psi^A \Psi^B \Psi^{BA}$	Forest logDog Rainfall <sup>2</sup> × SP(U) Slope × SP(U)	$p^{A}p^{B}r^{B}$	13	3115.15	1.73	0.086
$\Psi^A \Psi^B \Psi^{BA}$	Forest RD Rainfall <sup>2</sup> $\times$ SP(II) Slope $\times$ SP(II)	$n^{A}n^{B}r^{B}$	13	3115.15	1 73	0.086
$\Psi^{A} \Psi^{B} \Psi^{BA}$	BAL Slope Forest SP(U) Rainfall <sup>2</sup> SP(U)	$p^{A} p^{B} r^{B}$	13	3115.15	1.73	0.086
w <sup>A</sup> w <sup>B</sup> w <sup>BA</sup>	PD Slope Forest $\times$ SP(II) Painfall <sup>2</sup> $\times$ SP(II)	p p 1 p <sup>A</sup> p <sup>B</sup> r <sup>B</sup>	13	2115.15	1.73	0.086
wA wB wBA	Flavation Forest PD Slope $Painfall^2 \times SD(U)$ $PAL_{L} \times SD(C)$	p p I pA pB rB	15	3110.13	1.75	0.030
I I I Cmall Indian airea	Elevation, Forest, KD, Stope, Kalillan ×Sr(O), KAldog×Sr(C)	p p i	10	5109.51	1.09	0.079
Sman monan cive	Formet is Deletering in DD is DAT (CDCC)	A BB	10	4000.01	0	0.000
$\Psi^{A} \Psi^{B} \Psi^{BA}$	Forest + Rainfall <sup>-</sup> + RD + RAI <sub>dog</sub> ×SP(C)	p <sup>-</sup> p <sup>-</sup> r <sup>-</sup>	13	4883.01	0	0.239
$\Psi^{A} \Psi^{B} \Psi^{BA}$	$Rainfall^{-} + RD + RAI_{dog} \times SP(C)$	p <sup>-</sup> p <sup>-</sup> r <sup>-</sup>	14	4881.1	0.089	0.229
	$RD + RAI_{dog} \times SP(C)$	p <sup>·</sup> p <sup>b</sup> r <sup>b</sup>	15	4879.38	0.37	0.199
	Forest + RD + $RAI_{dog} \times SP(C)$	p^ p <sup>b</sup> r <sup>b</sup>	14	4881.92	0.911	0.151
$\Psi^{A} \Psi^{D} \Psi^{DA}$	Forest + Rainfall <sup>2</sup> + RD×SP(U)	$p^{\Lambda} p^{P} r^{P}$	11	4888.91	1.907	0.092
$\Psi^{A} \Psi^{B} \Psi^{BA}$	$Forest \times SP(U) + Rainfall^2 \times SP(U) + RD \times SP(U)$	p <sup>A</sup> p <sup>B</sup> r <sup>B</sup>	13	4884.95	1.942	0.09
Dog-Ferret badge	r					
$\Psi^A \Psi^B \Psi^{BA}$	Forest×SP(U), Rainfall <sup>2</sup> ×SP(U), RD×SP(U)	p <sup>A</sup> p <sup>B</sup> r <sup>BA</sup> r <sup>Ba</sup>	14	9078.14	0	0.47
$\Psi^A \Psi^B \Psi^{BA}$	Forest×SP(U), Rainfall <sup>2</sup> ×SP(U)	p <sup>A</sup> p <sup>B</sup> r <sup>BA</sup> r <sup>Ba</sup>	12	9083.14	1.01	0.28
$\Psi^A \Psi^B \Psi^{BA}$	Forest×SP(U), Rainfall <sup>2</sup> ×SP(U), RD×SP(U)	p <sup>A</sup> p <sup>B</sup> r <sup>B</sup>	13	9081.36	1.23	0.25
Dog-Masked palm	civet					
$\Psi^{A}\Psi^{B}\Psi^{BA}$	Forest, Elevation <sup>2</sup> , Rainfall <sup>2</sup> ×SP(U), RD×SP(U)	p <sup>A</sup> p <sup>B</sup> r <sup>BA</sup> r <sup>Ba</sup>	13	9273.43	0	0.64
$\Psi^A \Psi^B \Psi^{BA}$	Forest, Rainfall <sup>2</sup> , Elevation <sup>2</sup> ×SP(U), RD×SP(U)	p <sup>A</sup> p <sup>B</sup> r <sup>BA</sup> r <sup>Ba</sup>	14	9272.61	1.18	0.36
$\Psi^A \Psi^B \Psi^{BA}$	Forest, Elevation <sup>2</sup> , $RD \times SP(U)$	p <sup>A</sup> p <sup>B</sup> r <sup>BA</sup> r <sup>Ba</sup>	12	9283.19	1.15	0.22
Dog-Crab-eating	nongoose	r r				
$\Psi^{A} \Psi^{B} \Psi^{BA}$	Forest RD Rainfall <sup>2</sup> SP(II)	p <sup>A</sup> p <sup>B</sup> r <sup>BA</sup> r <sup>Ba</sup>	12	5552 40	0	0.55
$\Psi^A \Psi^B \Psi^{BA}$	RD Forest $\times$ SP(II) Rainfall <sup>2</sup> $\times$ SP(II)	p <sup>A</sup> p <sup>B</sup> r <sup>BA</sup> r <sup>Ba</sup>	13	5552.15	1 72	0.23
$\Psi^{A} \Psi^{B} \Psi^{BA}$	Forest $\text{Painfall}^2 \times \text{SD}(1)$ $\text{RD} \times \text{SD}(1)$	p <sup>A</sup> p <sup>B</sup> r <sup>BA</sup> r <sup>Ba</sup>	12	5552.2	1.72	0.20
r r r Dog Small Indian	i orco, namilali Aor(U), NDAor(U)	РЪГТ	13	3332.30	1.07	0.22
wA wB wBA	Exercit DD Doinfoll <sup>2</sup> (D(1))	A B B	11	2901 71	0	0.20
τ τ τ <sup></sup> wA wB wBA	FULES, RD, Kallilall $\times$ SP(U)	ppr= "A."B."B	11	2891./1	0 00	0.39
Ψ <sup></sup> Ψ <sup></sup> Ψ <sup>BA</sup>	KD, FOREST $\times$ SP(U), Kainfall <sup>-</sup> $\times$ SP(U)	p p r A B BA Ba	12	2890.6	0.89	0.25
$\Psi^{A} \Psi^{B} \Psi^{BA}$	Forest, KD, Kaintall <sup>2</sup> ×SP(U)	p., p. r., r.	12	2891.03	1.32	0.2
$\Psi^{\Lambda} \Psi^{\nu} \Psi^{\nu \Lambda}$	Forest, Rainfall <sup>2</sup> ×SP(U), RD×SP(U)	p^ p <sup>u</sup> r <sup>p</sup>	12	2891.49	1.78	0.16

<sup>a</sup> "RD" refers to road density, "Rainfall" refers to the monthly average rainfall, and "Forest" is the forest coverage. Both the road density and RAI<sub>dog</sub> are logarithmically converted.

# Table A3

The best-performing models of the generalized linear model that estimated temporal niche overlap among native carnivores in Taiwan

Step	Model	AIC	ΔΑΙΟ
	Dog-Ferret badger		
1	Null model	72.254	0
	Dog-Masked palm civet		
1	Null model	82.858	0
	Dog-Crab-eating mongoose		
1	Null model	68.494	0
	Dog-Small Indian civet		
1	Null model	23.135	0
		(c	ontinued on next need)

(continued on next page)

#### Table A3 (continued)

Step	Model	AIC	ΔAIC
	Masked palm civet-Ferret badger		
1	Null model	178.5409	0
	Masked palm civet-Crab-eating mongoose		
1	Null model	51.63195	0
	Masked palm civet-Small Indian civet		
1	Null model	49.62954	0
	Crab-eating Mongoose-Ferret badger		
1	Null model	51.20506	0
	Crab-eating Mongoose-Small Indian civet		
1	Null model	19.38552	0
	Small Indian civet-Ferret badger		
1	Null model	53.24087	0

#### Appendix B. Methods and sources for creating environmental factor layers

Elevation and slope were calculated from a 20-m resolution digital terrain model (Ministry of the Interior, Department of Land Administration, 2020). Monthly average rainfall and annual average temperature were obtained from the Taiwan Climate Change Projection Information Platform (TCCIP) and processed to a resolution of 500 m  $\times$  500 m (Lin et al., 2018). Road layers were downloaded from OpenStreetMap (2022), and we derived the major roads, highway links, and residential roads while excluding minor roads such as sidewalks (Ramm et al., 2014). The waterbody layers were sourced from the river channel layer provided by the Water Resources Agency (2017). The forest cover layers were derived from the results of the fourth forest resources survey conducted by the Council of Agriculture (2017).

When calculating road density and forest coverage, we delineated a buffer zone of  $1 \text{ km}^2$  around each camera, calculated road length and forest area within the buffer zone, and divided it by the buffer area. Additionally, the land cover map released by the Environmental Systems Research Institute (ESRI, 2022) was used as one of the criteria for delineating plots for the estimation of  $\Delta$ . This layer was created using artificial intelligence to identify land use types from satellite images, with a resolution of  $10 \text{ m} \times 10 \text{ m}$ .

#### Data availability

Data will be made available on request.

#### References

Animal Protection Information Network, 2022. Population size estimation of free-roaming dogs in Taiwan, 2022. (https://animal.moa.gov.tw/). accessed 1 June 2024.

Azlan, J.M., Sharma, D.S., 2006. The diversity and activity patterns of wild felids in a secondary forest in Peninsular Malaysia. Oryx 40 (1), 36–41.

Barros, A.L., Raposo, D., Almeida, J.D., Jesus, H., Oliveira, M.A., Fernandes, C.R., MacKenzie, D.I., Santos-Reis, M., 2024. An integrated assessment of niche partitioning reveals mechanisms of coexistence between mesocarnivores. Glob. Ecol. Conserv. 54, e03116.

van Bommel, L., Johnson, C.N., 2016. Livestock guardian dogs as surrogate top predators? How Maremma sheepdogs affect a wildlife community. Ecol. Evol. 6, 6702–6711.

Brook, L.A., Johnson, C.N., Ritchie, E.G., 2012. Effects of predator control on behaviour of an apex predator and indirect consequences for mesopredator suppression. J. Appl. Ecol. 49 (6), 1278–1286.

Burnham, K.P., Anderson, D.R., Burnham, K.P., Anderson, D.R., 1998. Practical use of the information-theoretic approach. Springer, New York, USA. Caravaggi, A., Banks, P.B., Burton, A.C., Finlay, C.M., Haswell, P.M., Hayward, M.W., Rowcliffe, M.J., Wood, M.D., 2017. A review of camera trapping for

conservation behaviour research. Remote Sens. Ecol. Conserv. 3 (3), 109–122.

 $Central \ Weather \ Administration \ of \ Taiwan. \ 2024. \ \langle https://www.cwa.gov.tw/\rangle \ accessed \ 1 \ August \ 2024.$ 

Chang, W.T., 2018. A study on diet variation of the carnivore community in northern Taiwan. Master's thesis, Department of Life Science, National Taiwan Normal University.

Chen, C.C., Pei, J.C., Liao, M.H., Mortenson, J.A., 2008. Canine distemper virus in wild ferret-badgers of Taiwan. J. Wildl. Dis. 44 (2), 440–445.

Chen, H.L., Su, Y.T., Wang, C.H., Pan, Y.C., 2020. Survey of medium and large mammals and birds in Hui-sun Forest Recreation Area. J. Agric. For. 67 (4), 273–288.

Cheng, H.C., Chang Chien, L.W., Lin, R.S., Yang, C.H., Chang, S.W., 2017. The red list of terrestrial mammals in Taiwan. Council of Agriculture, Taipei, Taiwan.

Cheng, H.C., Chang Chien, L.W., 2015. A Guide to the Carnivores of Taiwan. Biodiversity Research Institute, Council of Agriculture, Nantou, Taiwan.

Cheng, Y.S., Yu, H., Chen, H.L., 2021. Survey of medium to large mammals and ground-dwelling birds in Dongshi experimental forest station. College of Agriculture and Natural Resources, National Chung Hsing University.

Chiang, P.J., Pei, J.C., Vaughan, M.R., Li, C.F., 2012. Niche relationships of carnivores in a subtropical primary forest in southern Taiwan. Zool. Stud. 51 (4), 500–511. Chuang, S.A., Lee, L.L., 1997. Food habits of three carnivore species (*Viverricula indica, Herpestes urva*, and *Melogale moschata*) in Fushan Forest, northern Taiwan. J. Zool. 243 (1), 71–79.

Chung,K.F., Shao, K.T., 2022. Catalogue of life in Taiwan. (https://taicol.tw). accessed 1 July 2024.

Cong, W., Li, J., Hacker, C., Li, Y., Zhang, Y., Jin, L., Zhang, Y., Li, D., Xue, Y., Zhang, Y., 2024. Different coexistence patterns between apex carnivores and mesocarnivores based on temporal, spatial, and dietary niche partitioning analysis in Qilian Mountain National Park, China. eLife 13, RP90559. Contreras-Abarca, R., Crespin, S.J., Moreira-Arce, D., Simonetti, J.A., 2022. Redefining feral dogs in biodiversity conservation. Biol. Conserv. 265, 109434.

Council of Agriculture, 2017. Distribution of forest types in the entire island from the fourth forest resource survey. Council of Agriculture, **Taiwan**. (https://data.gov. tw/dataset/57873). accessed 1 April 2022.

Creel, S., 2001. Interspecific competition and the population biology of extinction-prone carnivores. Carniv. Conserv. 35–60. Dahmer, T.D., 2001. Feral dogs and civet mortality on Kau Sai Chau, Sai Kung, Hong Kong. Porcupine! 24, 16–18.

Dobrowski, S., Greenberg, J., Ramirez, C., Ustin, S., 2006. Improving image derived vegetation maps with regression based distribution modeling. Ecol. Model. 192 (1-2), 126–142.

Doherty, T.S., Dickman, C.R., Glen, A.S., Newsome, T.M., Nimmo, D.G., Ritchie, E.G., Vanak, A.T., Wirsing, A.J., 2017. The global impacts of domestic dogs on threatened vertebrates. Biol. Conserv. 210, 56–59.

Donadio, E., Buskirk, S.W., 2006. Diet, morphology, and interspecific killing in Carnivora. Am. Nat. 167 (4), 524–536.

ESRI, 2022. Sentinel-2 10m Land Use/Land Cover Timeseries Downloader. (https://www.esri.com/en-us/home). accessed 1 April 2022.

Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., Carpenter, S.R., Essington, T.E., Holt, R.D., Jackson, J.B., 2011. Trophic downgrading of planet Earth. Science 333 (6040), 301–306.

Ferreiro-Arias, I., Isla, J., Jordano, P., Benítez-López, A., 2021. Fine-scale coexistence between Mediterranean mesocarnivores is mediated by spatial, temporal, and trophic resource partitioning. Ecol. Evol. 11 (22), 15520–15533.

Fiske, I., Chandler, R., 2011. Unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance. J. Stat. Softw. 43, 1–23.

Frey, S., Volpe, J.P., Heim, N.A., Paczkowski, J., Fisher, J.T., 2020. Move to nocturnality not a universal trend in carnivore species on disturbed landscapes. Oikos 129 (8), 1128–1140.

Gálvez, N., Infante, J., Fernandez, A., Díaz, J., Petracca, L., 2021. Land use intensification coupled with free-roaming dogs as potential defaunation drivers of mesocarnivores in agricultural landscapes. J. Appl. Ecol. 58 (12), 2962–2974.

Gompper, M.E., 2014. Free-ranging dogs and wildlife conservation. Oxford University Press, New York, USA.

Guedes, J., Assis, C., Feio, R.N., Quintela, F., 2021. The impacts of domestic dogs (*Canis familiaris*) on wildlife in two Brazilian hotspots and implications for conservation. Anim. Biodivers. Conserv. 44 (1), 45–58.

Hardin, G., 1960. The competitive exclusion principle: an idea that took a century to be born has implications in ecology, economics, and genetics. Science 131 (3409), 1292–1297.

Hayward, M.W., Slotow, R., 2009. Temporal partitioning of activity in large African carnivores: tests of multiple hypotheses. SouthAfr. J. Wildl. Res 39 (2), 109–125. Ho, Y.Y., Chang, H.W., Chang, G.M., Yen, S.C., 2024. Effectiveness of the trap-neuter-return method for free-roaming dog management in an urban protected area: Wildlife cannot wait. Glob. Ecol. Conserv. 53, e02990.

Hsu, Y., Liu Severinghaus, L., Serpell, J.A., 2003. Dog keeping in Taiwan: its contribution to the problem of free-roaming dogs. J. Appl. Anim. Welf. Sci. 6 (1), 1–23. Huang, M.H., 1995. The population and resource use of crab-eating mongooses (*Herpestes urva*) at Fushan. In: Master'S. Thesis. Instituteof Zoology, National Taiwan University.

Hughes, J., Macdonald, D.W., 2013. A review of the interactions between free-roaming domestic dogs and wildlife. Biol. Conserv. 157, 341-351.

Ju, Y.T., 2013. Study on the life history of the special and rare animal (the small Indian civet) in Yangmingshan National Park. Headquarters of Yangmingshan National Park, Taipei, Taiwan.

Keene, O.N., 1995. The log transformation is special. Stat. Med. 14 (8), 811-819.

Kellner, K.F., Smith, A.D., Royle, J.A., Kéry, M., Belant, J.L., Chandler, R.B., 2023. The unmarked R package: twelve years of advances in occurrence and abundance modelling in ecology. Methods Ecol. Evol. 14 (6), 1408–1415.

Kelly, M.J., Holub, E.L., 2008. Camera trapping of carnivores: trap success among camera types and across species, and habitat selection by species, on Salt Pond Mountain, Giles County, Virginia. Northeast. Nat. 15 (2), 249–262.

Kronfeld-Schor, N., Dayan, T., 2003. Partitioning of time as an ecological resource. Annu. Rev. Ecol. Evol. Syst. 34 (1), 153-181.

Lambertucci, S.A., Zamora-Nasca, L.B., Sengupta, A., de la Reta, M., Plaza, P.I., 2024. Evidence-based legislation, strong institutions and consensus needed to mitigate the negative impacts of free-ranging dogs. Ambio 53 (2), 299–308.

Li, C.F., Chytrý, M., Zelený, D., Chen, M.Y., Chen, T.Y., Chiou, C.R., Hsia, Y.J., Liu, H.Y., Yang, S.Z., Yeh, C.L., 2013. Classification of Taiwan forest vegetation. Appl. Veg. Sci. 16 (4), 698–719.

Lijun, C., Wenhong, X., Zhishu, X., 2019. Limitations of relative abundance indices calculated from camera-trapping data. Biodivers. Sci. 27 (3), 243-248.

Lim, P.X., Lin, S.M., Lin, W.L., Tseng, H.Y., 2023. Breeding records, urban habitat, and threats to the masked palm civet in Taiwan. J. Wildl. Manag., e22467

Lin, L.K., Chiang, P.J., Chen, M.T., Chen, C.H., Chang, Y.L., 2008. Ecology and conservation status of protected mammal species in Taiwan, 97-03. Forestry Bureau, Council of Agriculture, Taipei, Taiwan.

Lin, H.Y., Hu, J.M., Chen, T.Y., Hsieh, C.F., Wang, G., Wang, T., 2018. A dynamic downscaling approach to generate scale-free regional climate data in Taiwan. Taiwania 63 (3), 251–266.

- Lin, Y.H., Lin, K.F., Chuang, S.H., Li, K.H., Su, Y.T., Tseng, Y.C., Lin, J.A., Fang, C.S., Chung, H.M., 2020. Camera Trap Survey in Central Taiwan Leopard Cat Research Team. Biodiversity Research Institute, Ministry of Agriculture, TBN Research Management Center. Occurrence Record Dataset. (https://www.tbn.org. tw/dataset/e465aecd-b67f-448b-90e0-46bbaebd0c8e). accessed 7 March 2023.
- Liu, W.T., Chang, Y.C., Chung, K.T., Lin, C.H., Hsu, Y.H., Chen, P.H., Wang, C.A., Hsu, S.H., Huang, Y.P., Huang, Y.C.H., Chen, Y.C., 2023. Observer ecological consultant camera trap data. Biodiversity Research Institute, Ministry of Agriculture, TBN Research Management Center. Occurrence Record Dataset. (https:// www.tbn.org.tw/dataset/3f4b0183-5018-40a0-afbf-c697b7395fc1). accessed 16 May 2022.

Liu, S.S., Fung, H.P., Liu, B.T., Cheng, F.P., 2007. Ovarian cycle of the captive formosan gem-faced civets (*Paguma larvata taivana*). Zoo. Biol.: Publ. Affil. Am. Zoo. Aquar. Assoc. 26 (1), 1–11.

Long, R.A., 2008. Designing effective noninvasive carnivore surveys. In: Long, R.A., Zielinski, W.J., Long, R., MacKay, P., Zielinski, W., Ray, J. (Eds.), Noninvasive survey methods for carnivores. Island Press, Washington, USA, pp. 8–44.

MacArthur, R., Levins, R., 1967. The limiting similarity, convergence, and divergence of coexisting species. Am. Nat. 101 (921), 377-385.

Mackenzie, D.I., 2006. Modeling the probability of resource use: the effect of, and dealing with, detecting a species imperfectly. J. Wildl. Manag. 70 (2), 367–374. MacKenzie, D., Hines, J., 2018. RPresence: R interface for program Presence. R. Package Version 2 47 (13). (https://www.mbr-pwrc.usgs.gov/softw).

MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L.L., Hines, J.E., 2017. Occupancy estimation and modeling: Inferring patterns and dynamics of species occurrence. Elsevier, Amsterdam, Netherlands.

Mahar, N., Habib, B., Hussain, S., 2024. Do we need to unfriend a few friends? Free-ranging dogs affect wildlife and pastoralists in the Indian Trans-Himalaya. Anim. Conserv. 27 (1), 53–64.

Marshall, H.E., Sukumal, N., Ngoprasert, D., Savini, T., 2023. The spatial and temporal displacement of native species by domestic dogs. Glob. Ecol. Conserv. 44, e02504.

Ministry of the Interior, Department of Land Administration, 2020. 2020 version of 20-meter grid digital terrain model (DTM) data for Taiwan and some offshore islands. Ministry of the Interior, Taiwan. (https://data.gov.tw/datasets/search?p=1&size=10&s=\_score\_desc&rtt=2567)accessed 1 March 2022.

Monterroso, P., Rebelo, P., Alves, P.C., Ferreras, P., 2016. Niche partitioning at the edge of the range: a multidimensional analysis with sympatric martens.

J. Mammal. 97 (3), 928–939.

Nayeri, D., Mohammadi, A., Qashqaei, A.T., Vanak, A.T., Gompper, M.E., 2022. Free-ranging dogs as a potential threat to Iranian mammals. Oryx 56 (3), 383–389. OpenStreetMap, 2022. OpenStreetMap Taiwan. (http://osm.tw/).accessed March 2022.

Palomares, F., Caro, T.M., 1999. Interspecific killing among mammalian carnivores. Am. Nat. 153 (5), 492–508.

Pei, J.C., 2004. Present status and conservation of small carnivores at low elevation mountains in Shinchu County and Miaoli County. Forestry Bureau, Council of Agriculture, Taipei, Taiwan.

Ramm, F., Names, I., Files, S., Catalogue, F., Features, P., Features, N., Cars, C., 2014. Open. data Layer. GIS Format (Version 0.6.7).

Read, J.L., Dickman, C.R., Boardman, W.S., Lepczyk, C.A., 2020. Reply to Wolf et al.: why trap-neuter-return (TNR) is not an ethical solution for stray cat management. Animals 10 (9), 1525.

Richmond, O.M., Hines, J.E., Beissinger, S.R., 2010. Two-species occupancy models: a new parameterization applied to co-occurrence of secretive rails. Ecol. Appl. 20 (7), 2036–2046.

Ridout, M.S., Linkie, M., 2009. Estimating overlap of daily activity patterns from camera trap data. J. Agric. Biol. Environ. Stat. 14 (3), 322–337.

Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P., 2014. Status and ecological effects of the world's largest carnivores. Science 343 (6167), 1241484.

Ritchie, E.G., Dickman, C.R., Letnic, M., Vanak, A.T., Gompper, M., 2014. Dogs as predators and trophic regulators. In: Gompper, M.E. (Ed.), Free-ranging dogs and wildlife conservation. Oxford University Press, New York, USA, pp. 55–68.

Ritchie, E.G., Johnson, C.N., 2009. Predator interactions, mesopredator release and biodiversity conservation. Ecol. Lett. 12 (9), 982–998.

Roughgarden, J., Feldman, M., 1975. Species packing and predation pressure. Ecology 56 (2), 489-492.

Schoener, T.W., 1974. Resource partitioning in ecological communities: research on how similar species divide resources helps reveal the natural regulation of species diversity. Science 185 (4145), 27–39.

Schoener, T.W., 1983. Field experiments on interspecific competition. Am. Nat. 122 (2), 240–285.
Sévêque, A., Gentle, L.K., López-Bao, J.V., Yarnell, R.W., Uzal, A., 2020. Human disturbance has contrasting effects on niche partitioning within carnivore communities. Biol. Rev. 95 (6), 1689–1705.

Sévêque, A., Gentle, L.K., Vicente López-Bao, J., Yarnell, R.W., Uzal, A., 2022. Impact of human disturbance on temporal partitioning within carnivore communities. Mammal. Rev. 52 (1), 67–81.

Shanida, S.S., Megantara, E.N., Husodo, T., Mutaqin, A.Z., Kendarto, D.R., Wulandari, I., 2023. Habitat preference of leopard cat (*Prionailurus bengalensis* Kerr. 1792) in the Cisokan Hydropower Development Area, West Java, Indonesia. Biodivers. J. Biol. Divers. 24 (4).

Shepherd, N., 1981. Predation of red kangaroos, Macropus rufus, by the dingo, Canis familiaris dingo (Blumenbach) in north-western New South Wales. Wildl. Res. 8 (2), 255–262.

Shores, C.R., Dellinger, J.A., Newkirk, E.S., Kachel, S.M., Wirsing, A.J., 2019. Mesopredators change temporal activity in response to a recolonizing apex predator. Behav. Ecol. 30 (5), 1324–1335.

Sollmann, R., Mohamed, A., Samejima, H., Wilting, A., 2013. Risky business or simple solution–Relative abundance indices from camera-trapping. Biol. Conserv. 159, 405–412.

Sun, C.M., 2023. 2023 Conservation Action Plan for the Formosan Pangolin (Manis pentadactyla pentadactyla). Council of Agriculture, Taipei, Taiwan.

Sunarto, S., Kelly, M.J., Parakkasi, K., Hutajulu, M.B., 2015. Cat coexistence in central Sumatra: ecological characteristics, spatial and temporal overlap, and implications for management. J. Zool. 296 (2), 104–115.

Taborsky, M., 1988. Kiwis and dog predation: observations in Waitangi State Forest. Notornis 35 (3), 197-202.

Vanak, A.T., Gompper, M.E., 2009a. Dietary niche separation between sympatric free-ranging domestic dogs and Indian foxes in central India. J. Mammal. 90 (5), 1058–1065.

Vanak, A.T., Gompper, M.E., 2009b. Dogs Canis familiaris as carnivores: their role and function in intraguild competition. Mammal. Rev. 39 (4), 265–283.

Vanak, A.T., Gompper, M.E., 2010. Interference competition at the landscape level: the effect of free-ranging dogs on a native mesocarnivore. J. Appl. Ecol. 47 (6), 1225–1232.

Wand, M.P., Jones, M.C., 1994. Kernel smoothing. CRC press, Florida, USA.

Water Resources Agency, 2017. River channels. Ministry of Economic Affairs, Taiwan. (https://data.gov.tw/dataset/25781). accessed 1 March 2022.

Weng, S.Y., 2010. Social structure of crab-eating mongoose (*Herpestes urva*) in Fushan Experimental Forest. Master's thesis, Institute of Ecology and Evolutionary Biology, National Taiwan University.

Weng, K.C., 2021. Optimization and data integration plan for the long-term wildlife monitoring system 1/4. Forestry Bureau, Council of Agriculture, Taiwan, Witten, D., James, G., 2013. An introduction to statistical learning with applications in R. Springer, New York, USA.

Yen, S.C., 2017. Ecological monitoring and intelligent monitoring planning for the rehabilitation of cultivated land in Lianhua Pond. Taroko National Park. Headquarters of Taroko National Park, Hualien City, Taiwan.

Yen, S.C., Ju, Y.T., Shaner, P.J.L., Chen, H.L., 2019. Spatial and temporal relationship between native mammals and free-roaming dogs in a protected area surrounded by a metropolis. Sci. Rep. 9, 8161.

Yen, S.C., Weng, H.M., Kung, M.H., Tseng, C.M., Chang, S.S., Su, Y.C., Lin, C.Y., Ju, Y.T., 2015. Distribution, activity pattern and potential threats faced by small Indian civet in Yangmingshan National Park. J. Natl. Park 25, 58–65.

Yu, Y.R., 2019. Spatial-Temporal Trends and Landscape Characteristics of Rabies Epidemics in Taiwan Ferret Badger (Melogale moschata subaurantiaca), 2013-2018. Master's thesis, Institute of Ecology and Evolutionary Biology, National Taiwan University.