Temporal niche partitioning between carnivores differs depending on the analytical method: comparison between temporal overlap and co-occurrence, and time-to-encounter analyses

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Abstract

Temporal niche partitioning is one of the most important strategies for carnivore coexistence. Camera-trap data has been analyzed through several methods to assess the temporal niche partitioning. When different analytical approaches used to evaluate niche partitioning detect different results, the mechanisms of species coexistence may be misinterpreted. As such, it is important to evaluate the temporal niche partitioning from multiple analytical approaches. In this study, we compared three analytical methods—the temporal overlap, temporal co-occurrence, and time-to-encounter analysis—to evaluate the temporal niche partitioning among sympatric medium-sized carnivores: red foxes, raccoon dogs, and Japanese martens. From May to October 2019 and 2020, we obtained the activity of the target species using camera-traps in northeastern Japan. We analyzed the data with the coefficient of temporal overlap, probabilistic co-occurrence analysis, checkerboard score, and multi-response permutation procedures. The results of the assessment of the niche partitioning differed depending on the analytical methods. Therefore, we conclude that the choice of analytical approach is important for understanding the mechanisms of species coexistence through temporal niche partitioning.

Introduction

The competitive exclusion principle states that two ecologically similar species cannot coexist¹. Thus, multiple sympatric species can partition their niche according to four major factors: food resources, natural enemies, space, and time². Elucidating the mechanisms of species coexistence based on their niche partitioning is important for understanding community diversity and for implementing effective community conservation and management strategies^{3–6}.

It is widely known that interspecific competition can often occur among sympatric carnivores^{7–10}. The extent of their interspecific competition is influenced by taxonomic similarity, dietary overlap, and intermediate body-size differences¹¹. For example, larger coyotes (*Canis latrans*) can exclude smaller swift foxes (*Vulpes velox*) from their home ranges and territories⁹. Similarly, Tsunoda *et al.*¹² suggested that interspecific competition can increase between larger golden jackals (*Canis aureus*) and smaller red foxes (*Vulpes vulpes*) because of their dietary overlaps. To avoid such competition, carnivores coexist sympatrically by shifting their activity time and spaces (e.g.,^{13–15}). In particular, temporal niche partitioning is one of the most important strategies to ensure their coexistence^{5,16,17}.

Currently, temporal niche partitioning among sympatric carnivores is often assessed using camera-trap data⁵, and several studies have demonstrated that temporal niche partitioning is key for their successful sympatry (e.g.,^{18–21}). For example, European badgers (*Meles meles*) and stone martens (*Martes foina*) shifted their diel activity patterns to avoid antagonistic encounters with larger golden jackals in Bulgaria²⁰. Stone martens also tended to be active at different times than larger red foxes and European wildcats (*Felis sylvestris*)²¹. Typically, temporal niche partitioning among carnivores is assessed using time data (i.e., 0:00–23:59) (e.g.,^{18–23}). Among them, the coefficient of temporal overlap of activity

patterns based on the kernel density estimation^{24,25} has been widely used (e.g.,^{5,26–31}). Frey *et al.*⁵ argued that the kernel density estimation has greatly improved the level of knowledge available from camera-trap data.

Furthermore, recent studies have assessed the influence of effective sample size for the accuracy and the statistical power when estimating the temporal overlap^{32,33}. However, measuring the temporal overlap may sometimes be insufficient to assess species interactions correctly, as this method evaluates the overlaps/differences in diel activity patterns between a focal species pair throughout the day, from 0:00 to 23:59, from a dataset pooled during a sampled period. For example, if two species are both nocturnal, a subordinate (i.e., smaller) species may coexist with a dominant species by avoiding direct encounters with the larger competitor at fine time scale (e.g., dozens of minutes or several hours), even if the coefficient of temporal overlap shows a high value³⁴. Nowadays, the spatio-temporal niche partitioning has been measured to assess behavioral avoidance by focusing on the time-to-encounter between individuals of different species (e.g.,^{34–40}). Indeed, Karanth *et al.*³⁴ found a large overlap in diel activity patterns between tigers (*Panthera tigris*) and leopards (*Panthera pardus*), while demonstrating their behavioral avoidance by using the time-to-encounter analysis. Similarly, Paúl *et al.*³⁹ also found a large overlap in diel activity patterns between side-striped jackals (*Canis adustus*) and African wolves (*Canis lupaster*), while indicating the occurrence of some behavioral avoidance using the time-to-encounter analysis, with side-striped jackals taking longer than expected to be detected after the occurrence of African wolves. These results suggest that the evaluation of behavioral avoidance at fine time scales using the time-to-encounter analysis may provide an understanding of the mechanisms of species coexistence that cannot be detected by only estimating the temporal overlap. When different analytical approaches detect different niche partitioning results, the mechanisms of species coexistence may be misinterpreted. To avoid this, it is important to evaluate temporal niche partitioning using multiple analytical approaches. Although a previous study evaluated the detection power of the temporal overlap and the time-to-encounter analysis separately³³, comparative evaluations of multiple analytical methods have not been conducted yet.

To address this methodological issue, we compared multiple analytical methods to accurately evaluate the temporal partitioning among three sympatric mesocarnivores. We used the temporal overlap, temporal co-occurrence analysis, and the time-to-encounter analysis (Fig. 1). Our focal species were red foxes, raccoon dogs (*Nyctereutes procyonoides*), and Japanese martens (*Martes melampus*). Red foxes and genus *Martes* individuals are widespread in the Northern Hemisphere^{41,42}, and raccoon dogs are widely distributed in East Asia and Russian Far East and have also been introduced in Europe⁴³. In addition, the red foxes and raccoon dogs belong to the same family (i.e., Canidae), and differ in body size from the Japanese martens⁴², indicating their potential competitive interactions, according to Donadio & Buskirk¹¹. Therefore, our focal species are ideal to assess the role of temporal partitioning in mesocarnivores sympatry. In this study, we proposed the temporal co-occurrence analysis (Fig. 1b), adapted from the spatial co-occurrence analysis^{44,45}, which is a method used to assess the spatial co-occurrence of multiple species by using presence-absence data (e.g.,^{46–49}). Furthermore, we also

performed the time-to-encounter analysis (Fig. 1c) based on the concept of multi-response permutation procedures, according to Karanth *et al.*³⁴. We performed this analysis in two ways: using multiple time scales which ranged from several minutes to several days or weeks, according to the previous study³⁴, and only using nighttime unit scale to address diel activities of the focal species (for more details see 'Methods').

Methods

Study area

We collected animal images by camera-trapping in the Experimental Forest of Yamagata University in Yamagata Prefecture, northeastern Japan, belonging to a cool temperate climatic zone (38°33'N, 139°51'E; Fig. 2). The annual mean temperature is approximately 10.5°C, and the annual precipitation is approximately 3,300 mm (average from 2019 to 2020). The altitude ranges from approximately 230 to 850 m. The study area has heavy snowfall, with the maximum snow depth exceeding 3 m in winter. Apart from the three focal mesocarnivores in this study, seven other medium- and large-sized mammals were present in the study area: the Japanese hare (*Lepus brachyurus*), Japanese macaque (*Macaca fuscata*), masked palm civet (*Paguma larvata*), Japanese badger (*Meles anakuma*), Asiatic black bear (*Ursus thibetanus*), Japanese weasel (*Mustela itatsi*), and Japanese serow (*Capricornis crispus*)⁵⁰. The major canopy species are beeches (*Fagus crenata*), oaks (*Quercus crispula*), maples (*Aceraceae*), and cedar (*Cryptomeria japonica*) plantations.

Camera trapping

Between May 1 and October 31, 2019 and 2020, we set 18 camera-trap sites using infrared-triggered cameras (models #BTC-6HD-940, Browning, AL, USA and #BTC-6HD-APX, Browning, AL, USA) (Fig. 2; Supplementary Table S1). Previous studies have reported that the effective detection distance of infrared-triggered cameras is shorter with higher vegetation density⁵¹ and that the detection rate of cameras is higher on forest roads than in forests⁵². To mitigate the change in the detection distance due to the increase in vegetation density, and because the detection rates of the three focal species were also high on the forest road in this study area⁵⁰, we installed all cameras on trees along to a forest road, approximately 1.5 m above the ground. We programmed the cameras to capture three images for each trigger, with a 1 min delay between each trigger. We identified the focal species from the three images and recorded the species, camera-trap site, date, and time as a single detection data.

Data analysis

Spatial autocorrelation

Positive spatial autocorrelation can arise because of repeated detections of the species and can affect the assessment of species interactions when cameras are set close together within a small area²¹. To assess the positive spatial autocorrelation, we used the Mantel's correlogram⁵³ before analyzing the temporal niche partitioning. Correlation indices were calculated using 10,000 randomizing simulations based on the number of detections of each target species per day per camera and the longitudinal/latitudinal positions of cameras. According to Tsunoda *et al.*²¹, when we collected consecutive detections of the same species at a camera-trap site within 30 min, we treated it as a single sample. This analysis was performed using the 'vegan' package⁵⁴ in statistical software R⁵⁵ ver. 3.5.2.

Temporal overlap

We first estimated the diel activity patterns of target species as a probability density function using the kernel density estimation²⁴. To determine the interspecific temporal overlap (Fig. 1a), we estimated the coefficient of temporal overlap (D) for each species-pair, which ranged from 0 (no overlap) to 1 (complete overlap)^{24,25}. This is defined as the area under the curve that is formed by taking the minimum of the two density functions at each time point⁵⁶. Ridout & Linkie²⁴ developed three estimation methods (D_1 , D_4 , and D_5) for estimating the overlap of diel activity patterns. According to Meredith & Ridout²⁵, we used the D_4 method because each focal species dataset contained more than 75 samples. We defined the $D \leq 0.5$ as "low", $0.5 < D \leq 0.75$ as "moderate", and $D > 0.75$ as "high", according to Monterroso *et al.*¹⁹. To assess the reliability of the D statistic and its 95% confidence intervals (C), we performed a smoothed bootstrap with 10,000 bootstrap samples²⁵. To reduce duplicate counts of the same individual, when we collected consecutive detections of the same species at a camera-trap site within 30 min, we treated it as a single sample (e.g.,^{19,21,28,30,57}). These analyses were performed using the 'overlap' package²⁵ in R.

Temporal co-occurrence analysis

To assess whether the three target species avoid each other in units of one night, we performed the temporal co-occurrence analysis using a matrix containing the presence-absence data per night at each camera site for each species pair (Fig. 1b). We only analyzed nighttime because the three target species were nocturnal in this study area^{30,57}. We used two methods: the probabilistic co-occurrence analysis⁴⁵ that compares the observed data with simulated data generated by combinatorics, and the checkerboard score⁴⁴ that compares the observed data with simulated data generated through 1,000 randomizations. Both methods determine the probability that the observed frequency of co-occurrence of two species is less than, greater than, or not different from the expected frequency, if the two species occurred independently from each other in units of one night. We defined one night as 60 min before sunset to 60 min after sunrise. We obtained the sunrise and sunset times for each survey day by using the R package 'rSetDayNightAttr'⁵⁸. The analyses were performed using the 'cooccur' and 'vegan' packages^{45,54} in R.

Time-to-encounter analysis

To assess the behavioral avoidance between different species by using the time-to-encounter analysis (Fig. 1c), we used multi-response permutation procedures⁵⁹ (hereafter, MRPP) according to Karanth *et*

*al.*³⁴. To determine competitive dominances among the three target species, we considered the before/after occurrence (e.g. red fox (before) – raccoon dog (after), raccoon dog – red fox) for the detected species when calculating the time-to-encounter across each species pair³⁹. For this procedure, we created matrix of detection records for each species consisting of the camera-trap site, date, and time. For every detection record, we calculated the minimum time to the subsequent detection between species pairs for each camera-trap site in each survey duration (seven sites: May 1–Oct 31, 2019, four sites: Aug 19–Oct 31, 2019, four sites: May 1–Oct 31, 2020, eight sites: Aug 24–Oct 31, 2020). Thus, for each species pair, we obtained a set of observed times-to-encounter. To compare this to a random expectation (i.e., a null model representative of neither segregation nor aggregation), we randomly permuted the detection records of subsequent species among camera-trap sites with the same survey duration. We used this random permutation to re-calculate the time-to-encounter and repeated this process 1,000 times³⁴. Finally, we compared the observed median time-to-encounter and the 1,000 medians of the random permutations. We finally calculated the p -values as the proportion of times the observed median was larger than the medians of the random permutations³⁴. A large p -value indicates spatio-temporal aggregation (i.e., the observed time-to-encounter was shorter than the random expectation) while a small p -value indicates spatio-temporal segregation³⁴. In the previous studies that have conducted time-to-encounter analysis (e.g.,^{34,36}), consecutive detections of the same species less than 1 min apart were collapsed into a single sample. In this study, we set the cameras' interval to 1 min, therefore we used all detection data for this analysis. We used statistical software R for this analysis.

In the MRPP, the time-to-encounter data between two species may span multiple days³⁴. However, our focal species are typically nocturnal^{30,57} and the time-to-encounter data may include daytime when they are inactive or at the resting sites. Considering these factors, we performed the MRPP with an upper limit on the time-to-encounter data to focus on a more detailed scale. To focus on the nocturnal activity time of the target species, we used only the time-to-encounter data within 15 h, and assessed the behavioral avoidance between species using the same calculation method and evaluation criteria in the MRPP described above (hereafter, 15h-MRPP). We defined the time-to-encounter within 15 h as the longest nighttime during the survey period (13 h) with one hour before sunrise and after sunset.

Results

The total number of camera-days at all camera-trap sites was 2,826, excluding the number of days when the angle of the cameras was changed because of bear attacks or when technical issues occurred. We obtained 705, 735, and 289 detection data of red foxes, raccoon dogs, and Japanese martens, respectively.

We found no positive spatial autocorrelation in the first and second proximal distance classes (Supplementary Fig. S1). This result indicated that proximity between cameras did not affect spatial similarities in detected species. Therefore, we showed that the proximal camera-trap placement had little effect on the assessment of species interactions.

Analysis of temporal overlap

The D was higher than 0.75 for all species pairs [red fox–raccoon dog was 0.76 (CI: 0.70–0.80), red fox–Japanese marten was 0.82 (CI: 0.74–0.86), and raccoon dog–Japanese marten was 0.77 (CI: 0.71–0.83)] (Fig. 3). Therefore, the diel activity patterns were largely overlapped among the species.

Temporal co-occurrence analysis

The results of the probabilistic co-occurrence analysis showed that the observed frequency of co-occurrence of red foxes and raccoon dogs and of raccoon dogs and Japanese martens was greater than the expected frequency (Table 1). This indicates that these species pairs significantly co-occurred temporally. The observed frequency of co-occurrence of red foxes and Japanese martens was not different from the expected frequency (Table 1).

Table 1

Results of the probabilistic co-occurrence analysis. Observed cooccurrence is the number of observations in which two species cooccur during one night. Expected cooccurrence represents the expected frequency of two species co-occurring during one night. P_{less} represents the probability that the two species would co-occur at a frequency smaller than the observed frequency, if the two species had occurred randomly (independently). P_{greater} represents the probability that the two species would co-occur at a frequency greater than the observed frequency, if the two species had occurred randomly (independently). The number of presence of data was 479 for red foxes, 460 for raccoon dogs, and 239 for Japanese martens. Asterisk represents $P < 0.05$.

Species	Observed cooccurrence	Expected cooccurrence	P_{less}	P_{greater}
Red fox & Raccoon dog	96	83.0	0.962	0.049*
Red fox & Japanese marten	40	43.1	0.326	0.736
Raccoon dog & Japanese marten	55	41.4	0.993	0.011*

The results of the checkerboard score showed that the observed frequency of co-occurrence of raccoon dogs and Japanese martens was greater than expected frequency (Table 2), indicating that this species pair significantly co-occurred temporally. The observed frequency of co-occurrence of red foxes and raccoon dogs and of red foxes and Japanese martens was not different from the expected frequencies (Table 2).

Table 2

Results of the checkerboard score. Simulated C-score represents the mean and confidence interval of a distribution generated using a randomization algorithm. The positive SES (standardized effect size) indicates an observed co-occurrence at a rate smaller than that expected by chance (partitioning); a negative effect size indicates an observed co-occurrence at a rate greater than that expected by chance (co-occurrence). The number of presence of data was 479 for red foxes, 460 for raccoon dogs, and 239 for Japanese martens. Asterisk represents $P < 0.05$.

Species	Observed C-score	Simulated C-score	SES	<i>P</i>
Red fox & Raccoon dog	0.040	0.042 (CI: 0.039–0.046)	-1.698	0.102
Red fox & Japanese marten	0.025	0.024 (CI: 0.022–0.026)	0.547	0.653
Raccoon dog & Japanese marten	0.021	0.023 (CI: 0.022–0.025)	-2.359	0.023*

Time-to-encounter analysis

As a result of the MRPP, the p -values for all species pairs were greater than 0.92, indicating their spatio-temporal aggregations (Fig. 4).

The results of the 15h-MRPP showed that the observed median time-to-encounter and the medians of the random permutations did not differ substantially for all species pairs (Fig. 5). Although a strong evidence for spatio-temporal segregations among species was not detected, the p -values for the red fox – Japanese marten and raccoon dog – Japanese marten pairs were smaller than those of the other pairs, which were closer to the segregation values than aggregation ($p = 0.243$, $p = 0.285$, Fig. 5).

Discussion

The degree of temporal partitioning differed among the compared analytical methods, which use temporal data differently (Table 3). Although the coefficients of temporal overlap (D) indicated large overlaps in diel activities among all species pairs (Fig. 3), the temporal co-occurrence analyses did not detect co-occurrence nor partitioning between red foxes and Japanese martens (Tables 1 and 2). Further, because of the time-to-encounter analysis, while the MRPP showed spatio-temporal aggregations among all species pairs (Fig. 4), the 15h-MRPP detected marginal segregations in the pairs where martens were detected after the other species (Fig. 5). The coefficient temporal overlap evaluates the overlaps/differences in diel activity patterns between a focal species pair throughout the day, from 0:00 to 23:59, from a dataset pooled during a sampled period. The MRPP evaluates time-to-encounter data with multiple temporal scales that from several hours (i.e., within a night) to several days or weeks (i.e., multiple active and inactive periods). These methods potentially overestimated the temporal niche overlaps, by evaluating longer time periods than their “real” active time. In contrast, both the temporal co-occurrence analysis and the 15h-MRPP evaluated only nighttime data that were consistent with our focal species’ activity patterns. Our results suggest that only using the coefficient of temporal overlap or the

MRPP with multiple-day data was insufficient to accurately determine temporal niche partitioning, specifically when both species show similar activity patterns, such as our focal species. Moreover, the 15h-MRPP evaluates the behavioral avoidances using time-to-encounter data that focused on a finer temporal scale (several hours in a night) than those of the other analytical methods, differentiating the results of temporal niche partitioning from the other analytical methods. Our findings indicated that the evaluation of temporal niche partitioning from multiple analytical methods with different temporal-scale data is necessary.

Table 3

Comparison of all analysis results. + represents a result closer to the overlapping side of the temporal niche and - represents a result closer to the partitioning side of the temporal niche.

Species		Temporal overlap	Probabilistic co-occurrence analysis	Checkerboard score	MRPP	15h-MRPP
Red fox & Raccoon dog	Red fox–Raccoon dog	+	+		+	
	Raccoon dog–Red fox				+	
Red fox & Japanese marten	Red fox–Japanese marten	+			+	-
	Japanese marten–Red fox				+	
Raccoon dog & Japanese marten	Raccoon dog–Japanese marten	+	+	+	+	-
	Japanese marten–Raccoon dog				+	

Although we did not identify which factors were involved, there are several possibilities for the temporal niche overlaps between the target species in this study (Table 3). First, predators typically synchronize their activities with those of their prey, which results in similar activity patterns among predators using the same prey^{60,61}. In Japan, the sympatric red foxes, raccoon dogs, and Japanese martens commonly prey on small mammals⁶². Therefore, the activity patterns of our focal species might be similar due to their synchronization with those of their staple prey species. Second, the timing of the activities of multiple species may coincide with each other due to weather conditions. Hendrichsen & Tyler⁶³ indicated that meteorological factors such as temperature, precipitation, and wind can affect rates of heat loss for wild animals, affecting their activity patterns and narrowing the temporal niche partitioning between species⁶⁴. The results of the 15-MRPP indicated the spatio-temporal avoidance by martens against the

other two species, though the statistical evidence was marginal ($p = 0.243$, $p = 0.285$, Fig. 5). On a more detailed temporal scale, olfactory cues from competitive species provoke behavioral avoidance⁶⁵. Barrull *et al.*⁶⁶ demonstrated that the stone martens rarely appeared within 60 min of the detection of the red foxes and European badgers (*Meles meles*), indicating that smaller martens may detect odors from the larger competitors and avoid them temporally. The Japanese marten is the smallest among our focal mesocarnivores⁴². Odors may have different stimulus residual times that can be perceived by animals depending on the type of sources, such as passing animals, urine, or feces. Therefore, it may be important to set a temporal scale that considers the type of odor sources in assessing species interactions. Our results suggest that factors affecting the assessment of species interactions (i.e., the availability of prey species, weather conditions, and odors) may differ depending on the temporal scales. Therefore, it is important to assess the temporal niche partitioning on temporal scales within which species interactions can be detected.

The temporal co-occurrence analyses in units of one night performed in this study did not detect co-occurrence nor partitioning between red foxes and Japanese martens (Tables 1 and 2), even though their diel activities highly overlapped (Fig. 3). This indicated that the overlaps of diel activity patterns were not always consistent to the temporal niche overlaps. This study suggested that the temporal co-occurrence analysis may be an alternative method to assess the temporal interactions between competitive species that cannot be detected by the overlaps of diel activity patterns. The temporal co-occurrence analyses might have methodological advantages, owing to their use of presence-absence data. For example, presence-absence data are typically available in large amounts of data, compared to those of other methods, such as the MRPP. Indeed, Tattersall *et al.*⁶⁷ indicated that the assessment of the temporal niche partitioning at fine temporal scales required large amounts of the detection data and applied presence-absence data for the assessment. Further, the spatial co-occurrence analysis has been often used in studies focused on spatial niche partitioning and its associated factors (e.g., weather conditions or geo-environmental gradients⁴⁸). Therefore, the knowledge and methodology applied in spatial co-occurrence studies would be applicable to temporal assessments.

In this study, we also assessed the before/after occurrence differences in a species pair (e.g., red fox (before) – raccoon dog (after), and raccoon dog – red fox) in the MRPP and 15h-MRPP analyses; the results differed depending on the species-occurrence order (Figs. 4 and 5). However, many previous studies disregarded the effects of this order^{34,37,38,68} (but also see Paúl *et al.*³⁹). This study suggested the necessity of the time-to-encounter analysis with the species-occurrence order replacement, if the competitive dominances among focal species are not clear. Although the 15h-MRPP analyses indicated the possibility of behavioral avoidances by Japanese martens to the larger species, there were weak evidences in the statistical assessments (Fig. 5), possibly due to the small sample sizes (Fig. 5). Niedballa *et al.*³³ indicated that more than 100 samples per species are needed to perform the time-to-encounter analysis with statistical validations. Our findings suggest that the time-to-encounter analysis with a fine temporal scale dataset may be a powerful tool to assess spatio-temporal partitioning between nocturnal carnivores, when the sample sizes of both species are adequate.

We demonstrated the importance of evaluating the temporal niche partitioning between carnivores on a temporal scale within which species interactions can be detected by using multiple analytical methods with different uses of temporal data. The results of the assessment of the niche partitioning differed depending on the analytical methods, and therefore the choice of analytical approach is important for understanding the mechanisms of species coexistence based on their temporal niche partitioning. Our results suggested that only using the coefficient of temporal overlap to determine the temporal niche partitioning between species is insufficient for assessing species interactions. Therefore, we recommend the use of multiple methods by temporal co-occurrence analysis and/or time-to-encounter analysis in addition to the evaluation by the temporal overlap. Our results also suggest that the factors affecting species interactions may differ depending on the temporal scales. It is important to assess temporal niche partitioning on a detailed temporal scale within which species interactions can be detected by using the time-to-encounter analysis with an upper limit on the time-to-encounter data. Adopting this approach would provide a better understanding of the mechanisms determining species coexistence.

Declarations

Data availability statement

The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

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Author contributions statement

R.W., H.T., and M.U.S. conceived the study and wrote the main text. R.W. collected data, performed analysis, and prepared tables and figures. All authors reviewed the manuscript.

Additional information

Competing Interests

The authors declare no competing interests.

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Figures

Figure 1

Images illustrating the different analytical approaches used in this study.

Figure 2

Study area and locations of camera-trap sites.

Figure 3

Temporal overlap between species. The gray area indicates the overlap between diel activity patterns. The rug at the bottom of the plot indicates the original observations of activity time. The number of samples used for the kernel density estimation was 669 for red foxes, 691 for raccoon dogs, and 282 for Japanese martens.

Figure 4

Results of the time-to-encounter analysis using the MRPP. Red fox-raccoon dog represents that raccoon dogs was detected after red foxes, for example. The dashed vertical lines represent the observed median time-to-encounter between two species. The rug plot represents the 1,000 medians of the random permutations and the curve represents the distribution estimated from them; n represents the number of the observed time-to-encounter. The p-values indicate the proportion of times the observed median was larger than the medians of the random permutations.

Figure 5

Results of the time-to-encounter analysis using the 15-MRPP. Red fox-raccoon dog represents that raccoon dogs was detected after red foxes, for example. The dashed vertical lines represent the observed median time-to-encounter between two species. The rug plot represents the 1,000 medians of the random permutations and the curve represents the distribution estimated from them; n represents the number of the observed time-to-encounter. The p-values indicate the proportion of times the observed median was larger than the medians of the random permutations.

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