



Research Article

Co-occurrence networks analysis to infer avoidance behaviours in coexisting mammalian communities

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Abstract

To complement contemporary techniques for understanding the dynamics that allow the coexistence of species in both conserved and changing environments, the analysis of time intervals (time between records of species) is gaining attention. This study aims to propose a method to measure the time intervals between species, visualise such spatiotemporal co-occurrences in different ecological networks, and compare their topology with seven network measures. We applied the method to 1) two simulated datasets of predator and prey in scenarios varying in their frequencies and day of expected co-occurrences, and 2) detections of mammals from four landscapes differing in the anthropogenic disturbance in tropical southern Mexico. Overall, the method accurately identified the time interval of co-occurrence expected according to simulated data. In the study case, we found prey species occurred several days after predators, suggesting an avoidance behaviour. We found that conventional network measures distinguished small differences between the landscapes because of the similarity in the species composition, but prey-predator relationships differed among landscapes. This approach complements the study of mechanisms in the coexistence patterns of species and can be applied to co-occurrence studies to measure changes within communities. The measures in co-occurrence networks could describe and differentiate behaviour interaction patterns of prey and predators, whilst also displaying the effects of human disturbances on natural habitats.

Introduction

Species interactions are essential for the functioning, dynamic, and stability of ecosystems (García-Callejas et al., 2018; Pilosof et al., 2017; Bairey et al., 2016). Interactions such as amensalism, antagonism, commensalism, and mutualism are crucial for structuring communities in both the short and long-term by influencing colonisation and extinction processes and inducing changes in the characteristics of the interacting populations, thus allowing their coexistence (García-Callejas et al., 2018; Lima and Dill, 1990; Kotler and Holt, 1989). To mitigate the effects of negative interactions (e.g., predation, intraguild competition), species must adapt in one or more dimensions of their niche as a strategy to secure the necessary resources and survive in coexistence (Wiens, 2011). This may involve consuming different foods or utilising different sites or times compared to the dominant competitor or predators (Mendes et al., 2020; Karanth et al., 2017; Fischhoff et al., 2007; Kotler and Holt, 1989).

Studies examining predator-prey relations or intraguild competition have concluded that prey species, or subordinate ones, perceive the risk of encountering predators or dominant competitors, exhibiting temporal or spatial avoidance (a negative association) (Hegab et al., 2015; Bytheway et al., 2013; Vanak et al., 2013; Nersesian et al., 2012). The responses of prey or subordinate competitor have been examined under the Risk Allocation Hypothesis, which postulates that species will

adapt their foraging or movement times (antipredator behaviour) based on the immediate presence or absence of predators or dominant species and previous experiences of their exposure to risk (Smith et al., 2020; Creel et al., 2008). According to the fear theory, both prey and predators are engaged in a dynamic “game” of predation avoidance and seeking predation opportunities, wherein individuals use informative cues to make decisions on the trade-offs between accessing quality resources and avoiding predation (Cornhill and Kerley, 2020; Brown, 2019; Clinchy et al., 2012). According to Lima (2002), in such systems, two conventional ways are recognised in which one species can influence the behaviour of another species. (i.e. behavioural interactions): one is through physical contact, and other is through a third set of entities, such as odours, sounds, or environmental modifications (Hegab et al., 2015; Webster et al., 2012; Apfelbach et al., 2005; Durant, 2000). These agents are not selective, as they may influence multiple species simultaneously (Goudard and Loreau, 2012).

Over the past two decades, temporal and spatial segregation between predator and prey or among competitors has been studied in ground-dwelling animals utilising camera-trap techniques, kernel activity patterns, and multi-species occupancy models (Sollmann, 2018). Kernel analysis assesses the overlap in the circadian activity patterns of pairs of species (Ridout and Linkie, 2009), where a low overlap suggests segregation or avoidance, whereas a high overlap implies potential persecution (Botts et al., 2020; Marinho et al., 2020). Conversely, multi-species occupancy models assess the likelihood of a site being used by

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one species in the presence of another, taking into account the probability of detection influenced by habitat and survey factors (Rota et al., 2016).

In many instances studies have identified overlap between interacting species, indicating either an absence of avoidance or that such activity behaviours remain unaffected by anthropogenic disturbances (Van Scoyoc et al., 2023). Nonetheless, avoidance patterns are anticipated to exist as a coexistence mechanism at the finer scales typical of most studies (Thurman et al., 2019; Fancourt, 2016; Diamond, 1975). For instance, research utilising fine-scale methodologies has identified spatiotemporal avoidance patterns between leopards (*Panthera pardus*) and lions (*Panthera leo*) (Searle et al., 2021; Swanson et al., 2016). Similarly, leopards and caracals (*Caracal caracal*) display mutual avoidance of one another (Müller et al., 2022).

A fine-scale approach to examining avoidance patterns among species using camera-trapping data involves measuring time intervals between detections of pairs of species, addressing the question: How long does it take for species A to appear at a site after the occurrence of species B? (Galindo-Aguilar et al., 2022; Prat-Guitart et al., 2020; Karanth et al., 2017; Parsons et al., 2016). Fine-scale spatiotemporal segregation enables the identification of mechanisms that allow two or more species to coexist in habitats. This approach is increasingly recognised in ecological studies (Rodríguez-Luna et al., 2024; Flores-Martínez et al., 2022). However, the precision of new methods has yet to be verified using simulated datasets with established co-occurrences, and whether these patterns are influenced by anthropogenic activities remains to be determined (Berger-Tal and Saltz, 2019; Caravaggi et al., 2017).

In previous studies, we have presented co-occurrence networks, a type of ecological network, to characterise the time intervals between detections of pairs of species (Galindo-Aguilar et al., 2022). The employment of networks in ecology originated with food webs; this methodology has been extended to represent various types of interactions, including mutualism, predation, and parasitism (Delmas et al., 2019; Bascompte, 2007). Co-occurrence networks were initially introduced as intuitive diagrams that facilitate our understanding of the spatial coexistence of species within communities (Araújo et al., 2011; Gotelli and McCabe, 2002).

Ecological networks of species have been employed to depict multiple interactions (links, directed or not directed) occurring among species (nodes) within communities (Koutrouli et al., 2020; Delmas et al., 2019; García-Callejas et al., 2018; Wells et al., 2014; Hagen et al., 2012). Typically, these networks encompass a broad range of interactions, and their impacts (direct, indirect, weak, or strong) are presented across various temporal and spatial scales (Pilosof et al., 2017). Hence, ecological networks of species serve to understand and represent behavioural interactions straightforwardly, with the capability of facilitating comparisons across communities. These networks have been constructed using adjacency matrices, where interactions among elements are determined by presence/absence, frequency data or potential interactions (Bascompte, 2007). The underlying theory for these representations is graph theory, which ecologists have adapted to employ network measures to characterise and compare networks representing diverse conditions, relationships, communities, periods, and spaces (Koutrouli et al., 2020; Kay et al., 2018; Bascompte, 2007).

In this contribution, we enhanced and assessed the precision of a method for analysing the time intervals between pairs of species within communities, reinforcing the use of ecological networks to illustrate such species co-occurrences, and introducing network measures to qualitatively compare the topology of networks between communities. The method can be useful to elucidate questions about avoidance or prey-tracking in a community context, as well as for comparing variability across communities.

To assess the precision of the proposed method, we generated two *in-silico* datasets, varying in the frequencies of species (one dataset with high frequencies and another with moderate frequencies) and timing of associations among species at sites (ranging from near time to long time between pairs of occurrences). From empirical data across four

landscapes, we anticipated that the time intervals between prey species or subordinate competitors would be longer in sites previously visited by predators or dominant competitors, i.e. antipredator responses would diminish over time (Bytheway et al., 2013; Brook et al., 2012). Among landscapes, we hypothesised that disturbances have affected species behaviours because species react to changes induced by anthropogenic activities, which in turn alter interspecific interactions through increased predation pressure (Prugh, 2023; Van Scoyoc et al., 2023; Smith et al., 2020; Berger-Tal and Saltz, 2019; Gaynor et al., 2019). Specifically, we anticipated structural differences in the topology of the co-occurrence networks; we hypothesised that the most perturbed landscapes would exhibit the nearest co-occurrences between species because species are compelled to visit more hazardous sites to obtain the necessary resources (Morris et al., 2009). Conversely, in the most conserved and continuous landscapes, species are more likely to find resources most widely and will probably avoid risky sites and times (Flores-Martínez et al., 2022; Berger-Tal and Saltz, 2019; Gallo et al., 2019).

The objectives of this contribution are outlined as follows: 1) enhance the previous method for analysing co-occurrences of species to describe the time intervals between pairs of species, thereby inferring avoidance and tracking behaviours in predator-prey systems and intraguild competition; 2) assess the precision of the proposed method with simulated data; 3) introduce topological measures to characterise and compare avoidance and tracking behaviours in co-occurrence networks; and 4) apply the mammal co-occurrence approach to data collected with camera traps in four landscapes in southern Mexico, each with varying disturbance conditions.

Material and methods

The method proposed (mammal co-occurrence approach) involves identifying non-random co-occurrences between pairs of species at sites in a pool of samples. This method can be applied to real data from camera-traps surveys or to datasets generated by simulations (hereafter referred to as the “primary dataset” for both).

Presence/absence matrices

The method requires a table with three sets of data: species names, occurrence dates, and the stations at which the species were recorded. With this table, presence/absence matrices were constructed for each species; consequently, the number of matrices constructed was equal to the number of species included in the dataset. The rows of each matrix represent the total days in the study, and the columns represent the stations. For a given matrix A corresponding to a certain species *z*, in the entry A_{ij} , we put 1 if the species *z* was observed on that day (day *i*) at the given station (station *j*), and we put 0 if the species was not observed, i.e., is a presence/absence matrix. This process was repeated for each species.

Primary association data table

By comparing pairs of matrices, we detected the coincidence of two species at the same station on the same day or days later (time interval); we called associations to these coincidences. Given the matrix A for species *z* and matrix B for species *y*, we proceed as follows: we compared the row of A (day *i*) with the *i*+*t* row of B (*t* days after) with $t=0,1,\dots,20$. If in the column *j*, both matrices have 1, this means that the species *y* appeared *t* days after *z* at the same station; we counted how many times this occurred. That is to say, for $t=0$ we counted how many associations were on the same day, for $t=1$, we counted how many associations occurred one day after, and so on.

We obtained the associations data tables, recording the number of associations for every pair of species each day up to 20 days. We used 20 days as a conservative timeframe during which one animal cues could potentially influence the behaviour of another (Apps et al., 2022). Until this step, we had information about the number of associations for every pair of species from our primary dataset (Fig. 1a).

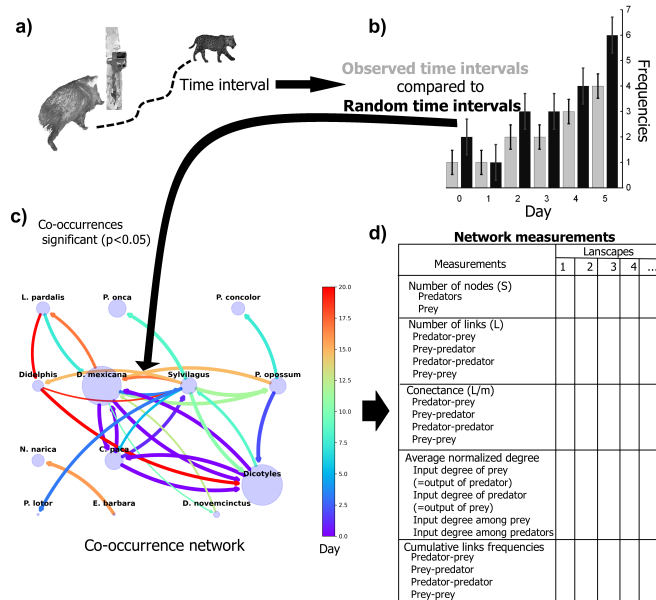


Figure 1 – Framework to analyse spatiotemporal associations between species in communities, depicted with co-occurrences networks, and measures proposed to compare these among landscapes or other conditions. The species node size indicates the relative abundance index.

Resampling bootstrap step

In our method, the next steps were performed to know if randomly we can reproduce the same associations observed in our primary dataset. With this objective, from the primary data, we obtained the time in which the station was operational and the number of records of every species at a particular station. With this information as conditionals, we did a resampling of the presence of the species throughout the days in which the station was active. Since resampling is performed randomly, different occurrence patterns are expected and therefore different species associations. We call this the resampling bootstrap step.

Random data generation

In one run of our programs, the following processes were carried out 100 times: 1) resampling bootstrap for every pair of species and construction of its corresponding presence/absence matrix, and 2) using the presence/absence matrix to create its corresponding association data table (Fig. 1b).

Obtaining the p-value by comparing random data and primary data

Since we constructed 100 random association data tables, for every day we compared how often the number of associations for a pair of species (random associations) from the random data was exceeded the number of associations from the primary data (primary associations). Subsequently, we calculated a one-sided empirical p-value between species z and y , t days later, where t takes integer values between 0 and 20 using the following formula:

$$p(z, y, t) = \frac{1 + \sum H(s \geq s_0)}{N + 1}$$

where s_0 is the number of primary associations between z and y , s is the number of random associations between y and z , $H(s \geq s_0)$ returns if the inequality is satisfied and a 0 if not, $\sum H(s \geq s_0)$ is the number of times the inequality $s \geq s_0$ is satisfied and $N = 100$ (Davison and Hinkley, 1997). That is to say, it counts the number of times that the random associations were greater than the primary associations. If all the times $s \geq s_0$, then $p(z, y, t) = 1$, on the other hand, if all the times $s < s_0$ then $p(z, y, t) = \frac{1}{101}$.

An association between two species y and z is considered significant for a time interval t if $p(z, y, t) \leq 0.05$, which implies that if we observe the distribution of random associations, the primary association value

is at the right extreme part of the distribution, regardless of the form of the distribution.

Until here, we have identified all species pairs and their corresponding time interval where primary associations are not reproduced by random data generation.

Sensitivity of the method

To assess the sensitivity of the method, we generated random data 10 times and obtained the p-value for each iteration. Species y and z are then considered to *co-occur* in the shortest significant time interval t in which they are associated, if for that t and species y and z , $p(z, y, t) \leq 0.05$ in each of all the 10 iterations. In other words, there is a co-occurrence between species y and z whenever $p(z, y, t) \leq 0.05$ in all the 10 iterations. All the processes were programmed in the Octave language Eaton et al. (2007).

Co-occurrence network (CN)

Using the shortest time interval co-occurrences, we build up a co-occurrence network where every node (circle) represents a species, and a directed edge (arrow) represents a co-occurrence between species. The node at the head of the arrow represents the species observed first, and the tail represents the species observed later; the colour of the arrow indicates the time interval. The size of the node represents the relative abundance index (IAR) (Figure 1 c). Programs for visualising the co-occurrence networks were executed in Python (Van Rossum, 1995).

Measures to compare co-occurrence networks

We identified 25 measures to characterising and comparing ecological networks (Koutrouli et al., 2020; Delmas et al., 2019; Kay et al., 2018; Kéfi et al., 2015; Araújo et al., 2011; Junker and Schreiber, 2011; Bascompte et al., 2006; Blüthgen et al., 2006). Metrics involving interactions among more than two species (e.g. nesting, clusterization, Katz centrality, diameter) were discarded, as were those considering the trophic levels (Kéfi et al., 2015). Metrics utilising frequencies such as the index d' and $H2'$, used to measure specialisation based on the strength of the association, were also excluded (Blüthgen et al., 2006).

We selected network measures because they allow us to characterise behavioural interactions between species and facilitate comparisons among different sites, landscapes, or conditions. Initially, six measures were chosen to compare the topology of CNs: the number of nodes, the number of links, connectance, the normalised degree, the average of the normalised degree, and the distribution of the input and output degrees. In addition, we proposed a novel measure: the cumulative frequency of links through time intervals, as a special measure to describe how co-occurrences accumulate over time. After inspection of the results, we noticed that the values of connectance and the average of normalised degrees were equal in all the networks (Mathematical arguments are present in Supplementary material S1), therefore we presented only connectance values. Supplementary material S2 provides a description of the final seven measures chosen, including modifications or derivations of these when it was necessary, and their application in the study of avoidance or tracking behaviours (Fig. 1d).

Simulated scenarios

To demonstrate the applicability and accuracy of the mammal co-occurrence approach, we generate two datasets simulating real camera traps. Each dataset consisted of 12 imaginary prey species, three imaginary predator species, 30 imaginary camera-trap stations, and a span of 35 to 69 days during which species hypothetically occurred. In these two simulated datasets (See Table S1 in Supplementary material, Figure 2), we varied: 1) the timing of associations among species in imaginary cameras (from immediate to extended periods between associations); and 2) species frequencies (from rare to common species). We also included random associations for a set of species (from rare to common random associations of species). In simulated dataset 1, species observation frequencies were higher (range: 10-156 “captures”, coefficient of variation 63.36) compared to simulated dataset 2 (range:

2-101 “captures”; coefficient of variation 70.01). After the simulated process, we obtained 2 datasets of simulated associations between pairs of species.

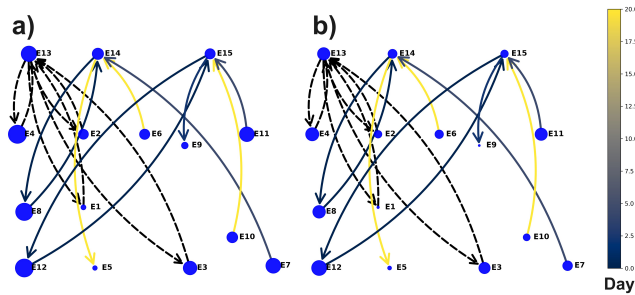


Figure 2 – The networks depict two simulated scenarios: (a) Simulation 1 and (b) Simulation 2. Each scenario includes three predators (*E13*, *E14*, *E15*) and twelve prey species, with varying intervals of days between events. Solid colored arrows indicate fixed day intervals, while dashed arrows denote random intervals. The size of each species node represents its relative abundance. The primary difference between Simulations 1 and 2 is the relative abundances of the species. Notably, the method consistently identified the same interactions regardless of relative abundance of species.

Subsequently, we applied the mammal co-occurrences approach to these primary datasets to identify co-occurrences between pairs of species. For both simulated datasets, we evaluated the accuracy of the method by comparing the detected co-occurrences with respect to those associations proposed in the sceneries.

Case study: co-occurrence networks of mammal species in four landscapes in southern Mexico

We analysed the time intervals between pairs of mammal species in four landscapes located in the Chinantla region, southern Mexico (17.317 and 18.164 N, and -95.567 and -96.699 W), based on their co-occurrence at the same camera trap station with a 1-day interval (24 h). Camera-trapping data were obtained from biodiversity monitoring projects spanning 18 communities in six municipalities (Galindo-Aguilar et al., 2022). The landscapes were categorised into highland areas (predominantly covered by cloud forests) and lowland areas (predominantly covered by tropical rainforests). The four landscapes varied in elevation, type of cover, and agricultural matrix (Fig. 3; details in Table S2 in Supplementary material):

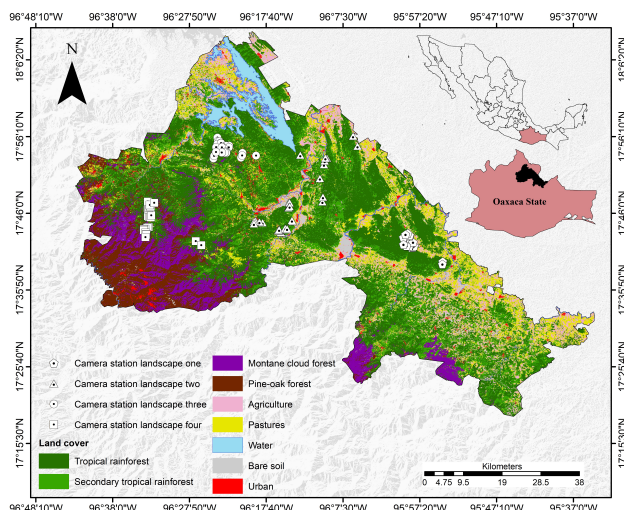


Figure 3 – Localization of landscapes where co-occurrence networks of predator and prey were studied.

- 1) Fragments of undisturbed tropical lowlands forests (landscape 1) consist of patches of a well-conserved tropical rainforest surrounded by agriculture and pasturelands for cattle; there is an elevational range of 100-340 m asl.
- 2) Fragments of slightly disturbed tropical lowlands forests (landscape 2) is a mosaic of tropical rainforest patches interspersed with plots of pasturelands for cattle and agriculture for perennial crops situated between 70 and 900 m asl in the hills along the main highway.
- 3) A large fragment of slightly disturbed tropical highland forest (landscape 3) is covered by semicontinuous tropical rainforests and montane cloud forest, with scattered plots of seasonal agriculture and pasturelands for cattle, spanning elevations from 470 to 1.380 m asl.
- 4) Undisturbed tropical highlands forests (landscape 4) are characterised by continuous well-conserved montane cloud forest and tropical rainforest, situated between 550 and 1.890 m asl, in proximity to human localities.

Based on the level of forest connectivity and surrounding anthropogenic disturbances, we considered landscape 1 to be more conserved than landscape 2 in the lowlands, and landscape 4 more conserved than landscape 3 in the highlands.

A total of 119 camera-trap stations were deployed between 2011 and 2014. The cameras placed in landscape 1 were 26 and the sampling effort was of 1,187 camera traps/day; in landscape 2 were 36 and the sampling effort was of 1,075 camera traps/day; in landscape 3 were 27 and the sampling effort was 677 cameras traps/day; and for landscape 4 were 27 and sampling effort was 1,074 camera traps/day. In the four landscapes, the composition of analysed species was slightly similar, consisting of three species of large and medium-sized predators (*Panthera onca*, *Puma concolor*, and *Leopardus pardalis*) and 11 potential prey species (*Procyon lotor*, *Eira barbara*, *Didelphis* spp., *Philander opossum*, *Nasua narica*, *Mazama temama*, *Dicotyles* spp., *Sylvilagus* spp., *Dasyprocta mexicana*, *Cuniculus paca*, and *Dasybus novemcinctus*). *Mazama temama* was not recorded in landscape 1; *Dicotyles* spp., *Didelphis* spp., *E. barbara*, *P. opossum*, and *P. lotor* were not recorded in landscape 3; and *P. lotor* and *Sylvilagus* spp. were not recorded in landscape 4. The species numbers included in the analyses were 14 for landscape 1, 13 for landscape 2, 9 for landscape 3, and 12 for landscape 4. Prior to analyses, to ensure data independence among adjacent stations, we checked for repeated species associations; in such cases, one of the stations was discarded.

Code to run a spatiotemporal co-occurrence analyses are available at <https://github.com/BeatrizCarelyLuna/Co-occurrence-networks-v2>

Results

Simulations

We found good accuracy of the method based on simulated datasets (90% accuracy for each). In simulation 1 (species with highest IAR), all expected co-occurrences were retrieved except one, where a prey species strongly avoided a predator (*E10* → *E15*). In simulation 2 (species with moderate IAR), the method retrieved all expected co-occurrences excepted one, in which a predator moderately tracked a prey (*E15* → *E9*).

Network measures were calculated for both simulations (Table S3). Overall, we found that the number of links and connectance values were higher in simulation 1 compared to simulation 2. Also, the prey → predator and predator → prey connectance values were slightly higher in simulation 1 than those in simulation 2. However, differences were found in the prey → prey and predator → predator connectance values, almost two-fold higher in simulation 1 than in simulation 2.

Avoidance of prey species and subordinate competitors in four landscapes in southern Mexico

Overall, we found a consistent trend supporting the hypothesis of prey avoidance following predator occurrences across the four landscapes. Further, we found that four potential prey species (*P. opossum*, *D. novemcinctus*, *M. temama*, and *P. lotor*) did not co-occur with predators in any landscape (Fig. 4). Additionally, we found a trend for a moderate number of co-occurrences among prey and predators in both

highland landscapes (five co-occurrences in landscape 3 and four co-occurrences in landscape 4).

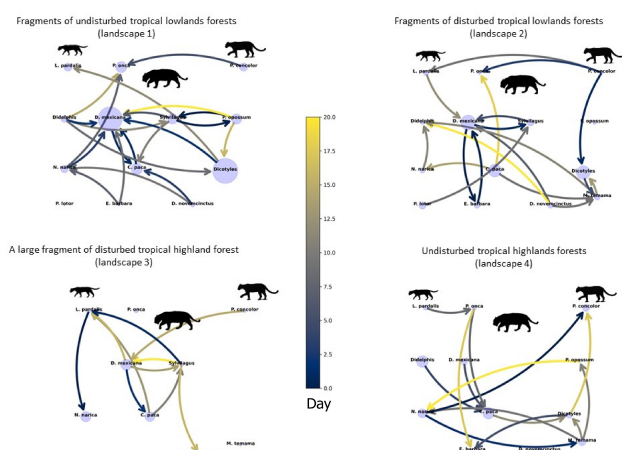


Figure 4 – Co-occurrence networks of predator and prey in four landscapes in southern Mexico: a) landscape one, b) landscape two, c) landscape three, and d) landscape four. On the top, the predators, and below, the prey species. The size of the species nodes corresponds to the relative abundance index; the node at the head of the arrow represents the species observed first and the tail represents the species observed later; the colour of the arrow indicates the time interval between the passage of one and the other. Although some species had no significant co-occurrences (i.e. they are not in or out of a directed edges), we included them in the networks since they are present in the landscapes.

In all landscapes, the time intervals between prey predator co-occurrences were generally equal to or greater than 8 days. Two exceptions cases were observed: *Sylvilagus* spp. occurred two days after *L. pardalis* in landscape 3, and *N. narica* occurred two days after *P. concolor* in landscape 4. On the other hand, predators were observed to occur several days after prey occurrences (equal or greater to 8 days) in the same sites, but *P. concolor*, which occurred one day after *Dicotyles* spp. in landscape 2, and *L. pardalis* one day after *N. narica* in landscape 3 (Fig. 4).

Among predators, co-occurrences were infrequent and typically involved differences of several days. The closest co-occurrence observed was *P. concolor* occurring three days after *P. onca* in landscape 2 (Fig. 4).

Prey species avoiding to co-occur at the same sites as predators were a consistent finding in landscapes. Among the 5–10 prey species in the four landscapes, one or two species occurred after predators, with a maximum of three species (*D. mexicana*, *C. paca*, and *Sylvilagus* spp.) observed after *L. pardalis* in landscape 3. Similarly, we found predators occurred after only a few prey species: two species in landscapes 2, 3 and 4, while predators did not track any prey in landscape 1. Also, co-occurrences among competitors (predators → predators) were rare. In contrast, prey prey co-occurrences exhibited the highest number of links reaching up to 17 co-occurrences in landscape 1 (Fig. 4).

Topological measurements of co-occurrence networks in four landscapes in southern Mexico

We found variations in the topology of the co-occurrence networks among the four landscapes studied. Overall, the lowland landscapes were more diverse with the highest number of nodes and more species co-occurrences (links) compared to the highland landscapes. Even, in landscape 3 (a large fragment of slightly disturbed highland forest), one predator did not co-occur with either prey or another predator.

The low values of the connectance index (L/m) indicated a trend towards spatiotemporal segregation for all landscapes studied (Tab. 1). At the community level, there was no notable differences in the connectance among disturbed and undisturbed landscapes, as the values were very similar (Tab. 1). However, among species groups, the connectance index showed a trend for predators to occur more frequently

in sites where prey species had been observed, particularly in the most perturbed landscapes.

Connectance values among groups were also low or very low, which supports the hypothesis of general avoidance or segregation among species. However, we found connectance values were unrelated to disturbance as disparate trends were obtained. For instance, the connectance value for prey-predator and prey-prey co-occurrences were highest in the undisturbed lowland landscape, whereas the values were lowest in the undisturbed highland landscape (Tab. 1).

The normalised input degrees indicated that most prey species are not actively tracked by predators (index equal to 0). Only five species were found to occur after a predator (each with a normalised input degree = 0.33): *D. mexicana* and *Dicotyles* spp. in landscape 2; *D. mexicana* and *N. narica* in landscapes 3; and *C. paca* and *E. barbara* in landscape 4 (Table S4 in Supplementary material).

Low values in the normalised input degrees for predators and normalised output degrees for prey reinforce the findings of prey avoidance. When co-occurred, prey typically passed after only one of the three predator species (normalised input degree = 0.33 each), such as *N. narica* and *Dicotyles* spp. in both undisturbed landscapes 1 and 4, or *C. paca* in disturbed landscapes 2 and 3 (Table S5 in Supplementary material). It was common that only one prey occurred after predators, except in landscape 3 where *L. pardalis* was followed by half of the prey species (Table S6 in Supplementary material).

Considering normalised input degrees among predators, a segregation pattern was observed, because only one competitor occurred before another: *L. pardalis* in landscape 2, and *P. onca* in landscapes 1, 2 and 4 (normalised input degree = 0.5 each one). *P. concolor* did not exhibit any inputs in any landscape (Table S6 in Supplementary material). Also, we found *L. pardalis* co-occurred after another predator in two landscapes, whereas *P. onca* occurred after another competitor in disturbed lowland landscape 2, and *P. concolor* in undisturbed lowland landscape 1 (Table S6 in Supplementary material).

Overall, predators showed tracking behaviour towards a limited number of prey species. *L. pardalis* and *P. concolor* presented outputs towards prey species in both disturbed lowland and highland landscapes 2 and 3; and *P. onca* had outputs in undisturbed highland landscape 4 (Table S7 in Supplementary material).

Distribution of the input degrees and output degrees

In predator-prey co-occurrences, the input degree 0 was the most frequent in all four landscapes, indicating that predators frequently did not track prey, and prey avoided predators (Figures S2a and S2b in Supplementary material). Also, predators tended to avoid occurring after other competitors, although in the non-conserved lowland landscape 2, two predators exhibited outputs (Figures S2c and S2d in Supplementary material).

In prey-predator co-occurrences, few prey species occurred after predators, with one notable exception where up to 4 prey species occurred after a single predator in the non-conserved highland landscape 3 (Figures S2e and S2f in Supplementary material).

In prey-prey interactions, it was common for prey species to occur after another. It was notable that in landscape 1, up to eight prey species occurred after another (Figures S2g and S2h in Supplementary material).

Cumulative frequency of links through time intervals

Species showed a tendency to co-occur in sites visited by predator or competitor as the days progressed, with slight variations observed among landscapes. Species co-occurrences occurred earliest in the undisturbed lowland landscape 1, whereas in disturbed highland landscape 3, species spend most time to co-occur, resulting in a flattened curve (Figure S3a in Supplementary material). In some cases, species co-occurred in nearest days, such as certain prey species co-occurring shortly after predators in both highland landscapes, whereas in lowland landscapes, prey co-occurred several days later (Figure S3b in Supplementary material). Predators promptly co-occurred after prey in both disturbed landscapes 2 and 3; whereas in the more conserved land-

Table 1 – Measurements obtained from co-occurrence networks describing time intervals between predators and prey in four landscapes in southern Mexico.

Metric	Landscape one	Landscape two	Landscape three	Landscape four
1. Number of nodes (S)	13	14	9	12
Number of prey (Sp)	10	11	6	9
Number of predators (Sd)	3	3	3	3
2. Number of links (L)	21	19	10	14
Links predator-prey ($Ld > p$)	0	2	2	2
Links prey-predator ($Lp > d$)	3	1	3	2
Links prey-prey ($Lp > p$)	17	14	5	9
Links predator-predator ($Ld > d$)	1	2	0	1
Maximum number of co-occurrences (m)	156	182	72	132
3. Connectance (L/m)	0.13	0.10	0.13	0.10
$m = 2(Sp)(Sd) + (Sd)(Sd - 1) + (Sp)(Sp - 1)$				
Connectance predator-prey ($Ld - p/md - p$)	0	0.06	0.11	0.07
$m = (Sp)(Sd)$				
Connectance prey-predator ($Lp - d/mp - d$)	0.10	0.03	0.16	0.07
$m = (Sp)(Sd)$				
Connectance prey-prey ($Lp - p/mp - p$)	0.18	0.12	0.16	0.12
$m = (Sp)(Sp - 1)$				
Connectance predator-predator ($Ld - d/md - d$)	0.16	0.33	0	0.16
$m = (Sd)(Sd - 1)$				

scapes 1 and 4, such co-occurrences were not observed or occurred after several days (Figure S3c in Supplementary material).

For predator \rightarrow predator co-occurrences, all occurred within less than 10 days, except in disturbed highland landscape 3 where no co-occurrence were observed. The earliest predator \rightarrow predator co-occurrences was observed on the fourth day in undisturbed lowland landscape 1 (Figure S3 d) in Supplementary material). Finally, in prey \rightarrow prey co-occurrences, the cumulative frequencies of links suggest that in undisturbed landscapes 1 and 4, prey species tend to co-occurred earlier compared to the other two non-conserved landscapes (Figure S3e in Supplementary material).

Discussion

In this study, we proposed a complementary method to measure spatiotemporal associations among species and represent them in an ecological network. In addition, we introduced measurements to compare these ecological networks. In our method, we incorporated not only spatial associations but also the timing between co-occurrences. We enhanced previous methods (Galindo-Aguilar et al., 2022) by individually analysing camera-trap data and incorporating prey-prey co-occurrences.

It has been demonstrated that the scale influences the direction of associations and the resultant patterns of co-occurrences. For instance, positive spatial associations observed between predators and prey may be counterbalanced by negative temporal associations *in situ* (Blanchet et al., 2020; Thurman et al., 2019). In our system, a coarse-temporal scale revealed significant temporal overlap between predators and among several predators and prey (Galindo-Aguilar et al., 2022). Nonetheless, we have shown that mammal behavioural strategies to mitigate competition and predation can operate at a finer scale (Diamond, 1975). Predators and prey may use the same sites (spatial co-occurrence), but as demonstrated here, through co-occurrence over longer time intervals.

In this work, we proposed network measurements to characterise co-occurrence networks of time intervals and compare them across different conditions, in our case, across landscapes. A plethora of measures are being developed to compare ecological networks; therefore, their selection must be approached with caution (Delmas et al., 2019). In this research, selecting appropriate measurements for co-occurrence networks posed a challenge. From a total of 25 measures identified in the reviewed synthesis works, six were selected (nodes, links, connectance,

distribution, output, and input degree) to compare the topology of CNs and explain the avoidance behaviour of prey towards predators. Earlier studies utilised similar measures plus modularity, species topological role, among-module connectivity, diversity in interactions, and specialisation (H2'), primarily to elucidate how species co-occurrences vary among landscapes and between areas (Corro et al., 2019; Kay et al., 2018; Borthagaray et al., 2014). In addition, we proposed a new measure which describes the dynamics of the cumulative co-occurrences. Rapid accumulation of links suggests lowest avoidance, whereas accumulation of links over several days indicate strong avoidance. The proposed method was applied to simulations and real data, demonstrating its accuracy in inferring behavioural interactions.

Simulations

With simulated data, we observed good accuracy in the method presented here. In only one instance in Simulation 1, the method predicted a co-occurrence in nearer time (2 days) than expected (10 days). Furthermore, in Simulation 2, an expected co-occurrence was not detected at all. Upon examining these co-occurrences in the simulated data, in Simulation 1, the predator species involved were simulated to exhibit a high capture frequency with weak tracking behaviour towards prey, exemplifying the case of a hypothetical common generalist predator. In Simulation 2, the undetected co-occurrence involved a "very rare" prey species. The unexpected co-occurrence in Simulation 1 was influenced by the frequency of the predator species, suggesting that a common generalist predator might frequently co-occur at sites where prey has been recorded, thereby indicating a positive association when there is none. Accordingly, caution is advised in datasets with very frequent predator species, as frequencies may impact the predictions of significant co-occurrences.

In nature, predators are uncommon, and their frequency of detections is low compared to other medium and large-sized mammals (Friedeberg-Gutiérrez et al., 2022; Greenspan et al., 2020). Therefore, the likelihood of detecting a false positive association is generally low, as evidenced by our second simulations, which accurately detect expected positive associations between an uncommon predator and its prey. Instead, attention should be directed towards mesocarnivores, which are commonly found in landscapes and exhibit high frequencies in surveys. Then, if positive associations with potential prey emerge, these should be meticulously evaluated based on known interactions (achieved through direct observations, traits, or analyses of

feeding habits) to determine a true behavioural effect (Clare et al., 2016; Morales-Castilla et al., 2015).

In the case of the simulations, we did not observe an effect of species frequency on network measures in any of the cases. Although the number of links was notably higher in Simulation 1 (highest frequency of species), we observed that links between prey-predator and predator-prey were very similar across simulations. Similarly, the connectance measure was higher in Simulation 1, but prey-predator and predator-prey connectance displayed uncorrelated patterns. These findings indicate that the expected sceneries for predator and prey were minimally influenced by their frequencies; instead, there was a prevalence in the associations expected, demonstrating the robustness of the approach.

Avoidance behaviours of prey and subordinate competitors in four landscapes of southern Mexico

The Chinantla is a relatively well-conserved region with a high richness of mammal species (Briones-Salas et al., 2023). In such resource-abundant regions, prey-predator dynamics align with the risk allocation hypothesis, which posits that species perceive the risk imposed by predators and exhibit antipredator behaviours (Smith et al., 2020; Lima and Bednekoff, 1999). We observed that both prey and subordinate competitors avoid sites previously visited by predators or dominant species, or may not even be present at those sites. Hence, we propose that in well-conserved Neotropical landscapes, prey actively avoid predators, not only spatially but also temporally.

Connectance indices revealed that the number of co-occurrences was low relative to the maximum possible in the networks; such indices were slightly lower for prey-predator co-occurrences than for prey-prey or predator-predator associations, reinforcing evidence of active avoidance. We observed that prey species avoidance behaviour was species-specific, depending on whether the species is a primary prey for the predator. Generally, primary prey co-evolves with their predator, engaging in a survival race where predators may develop strategies to secure food while prey devise strategies to avoid predation (Morris et al., 2009). These relationships are readily observed by interpreting the normalised degree index, which is useful for understanding the importance of individual species in the response of other species. For the largest felids, *P. onca* and *P. concolor*, the proportion of co-occurrences with prey was the lowest, whereas half of the prey species co-occurred after *L. pardalis*; this suggests that prey perceived greater risk associated with large predators than with medium-sized predators. Medium-sized prey species are typically consumed by large predators, whereas *L. pardalis* rarely preys on them, focusing on small mammals, lizards, and birds (Cruz et al., 2022; Emmons, 1987).

The prey species *N. narica*, *M. temama*, *Dicotyles* spp., *D. novemcinctus*, and *C. paca* are considered primary prey for large predators in the Neotropics (Cruz et al., 2022; Foster et al., 2010; De Oliveira, 2002). Our results indicated that these prey remained temporarily distant from sites where predators were detected, possibly as a strategy to reduce the risk of predation. These antipredator behaviours have not been previously described due to the use of a coarse temporal scale. Synchronisation in circadian activity patterns and similar habitat use between prey and predators have been suggested to indicate a positive association, for instance in Bolivia-Peru (Ayala et al., 2021), Costa Rica (Herrera et al., 2018), and Brazil (Foster et al., 2013). Furthermore, in northern Mexico, one of the principal prey species, *Dicotyles* spp., was closely associated with the presence of *P. concolor* and *P. onca* (Gutiérrez-González and López-González, 2017).

However, such associations could be related to scale. As Thurman et al. (2019) noted, current analytical methods used to measure spatial co-occurrence fail to predict empirical trophic interactions. Additionally, in camera-trap studies, devices imperfectly detect animals due to their space use and size, resulting in biased presence/absence records. To address the first challenge, we demonstrated through simulations the accuracy of the co-occurrence method, for example, the method detected instances where a supposed predator actively tracked prey or where prey actively avoided a predator. For the second challenge, it is preferable to use several devices to maximise the number of sites, as well

as to estimate viewable area and distance of individuals to devices to achieve detections close to 1, in order to accurately detect behavioural interactions (Moeller et al., 2023; Kays et al., 2021). In studies with limited equipment resources, conclusions should be restricted to the best detected species, such as large-sized animals (Kays et al., 2021). The use of odorous samples in experimental studies, placed in front of a battery of cameras at the sites, could be useful to better record such animal behaviours.

Kernel estimators and other circular statistics represent a coarse approach that aggregates records for long-term studies into a 24-hour model, thereby displaying the daily activity patterns of species and evaluating their overlap to infer temporal segregation. However, more detailed analyses using time intervals demonstrate how the probability of the presence of prey or subordinate competitors increases as the time interval from the predator's occurrence extends, a mechanism that facilitates their coexistence in landscapes (Harmsen et al., 2009).

An exception to predator avoidance was observed in *Sylvilagus* spp. and *N. narica* which occurred after *L. pardalis* and *P. concolor*, respectively. It is likely that these prey species are employing other anti-predatory strategies not reflected in their movements across habitats and potentially over time. *Sylvilagus* spp. have been documented as a part of the diet of *L. pardalis* (Gómez-Ortiz et al., 2015; Rocha-Mendes et al., 2010; Moreno et al., 2006), whereas *N. narica* is a significant prey item for *P. concolor* (Gómez-Ortiz et al., 2015). Small prey species such as lagomorphs appear not to avoid their main predators; instead, they rely on microhabitat structures for refuge and can escape quickly when they threatened (Wagnon et al., 2020; Gallo et al., 2019; Clare et al., 2016). However, anti-predatory shelter strategies do not account for the co-occurrence of *N. narica* with *P. concolor*; their vigilance behaviours and group living provide security during movement and foraging (Burger, 2001), and an opportunity to defend against any attack (Gómez-Ortiz et al., 2015).

Intraguild coexistence is a characteristic of communities. Its underlying mechanisms have been elucidated through niche segregation in any axis of their niche, for instance, by altering the consumption of food resources (Gómez-Ortiz et al., 2015), or via spatial or temporal segregation (Rodríguez et al., 2021; Breviglieri et al., 2017). Several studies have identified moderate or high circadian overlap between *P. onca*, *P. concolor*, and *L. pardalis* (Argudín-Violante et al., 2023; Galindo-Aguilar et al., 2022; Ayala et al., 2021; Herrera et al., 2018; Santos et al., 2019; Gutiérrez-González and López-González, 2017; Foster et al., 2013; Romero-Muñoz et al., 2010), suggesting that time distribution throughout the day does not constrain their coexistence. However, we demonstrated that although competitors are active during the same day-time hours (high circadian overlap in our study area; Galindo-Aguilar et al., 2022), they avoided sharing the same sites or they occurred with several days of difference. In line with the findings of Harmsen et al. (2009), we highlight that *P. concolor* and *P. onca* tend to avoid using the same site at the same time, illustrating a mechanism of coexistence at a fine temporal or spatial scale (De la Torre et al., 2017; Scognamiglio et al., 2003). A similar pattern of avoidance was observed in the mesocarnivore *L. pardalis* which exhibited a delay of several days before occupying areas recently visited by larger felids, likely as a strategy to avoid intraguild predation (Richards et al., 2023).

Another indicator of the influence of top predators over subordinate ones was the capture rate. For *L. pardalis* it was higher in the most disturbed landscape 2, whereas in the other landscapes, *P. onca* and *P. concolor* exhibited higher capture rates. According to optimal foraging theory, predators select habitats that maximise their hunting success. In the case of *P. concolor*, vegetation cover is crucial to successful capture (Holmes and Laundré, 2006; Laing, 1988; Logan and Irwin, 1985). We concur that mesopredator avoidance of apex predators can occur along two axes: space and time (Brook et al., 2012), as previously highlighted.

Absence of tracking behaviours of predators

To carry out their vital processes, predators seek irregularly dispersed prey (Yahner, 2012). Contrary to our expectations, we did not observe

consistent predator-to-prey tracking behaviour (i.e., selective predation mode); instead, we noted that predators appeared several days after the prey or did not co-occur at all. Similar findings have been observed in other tropical ecosystems, where spatial overlap between predator and prey was low (Vinitpornsawan and Fuller, 2020). This suggests that predators exhibited an opportunistic hunting behaviour, not focusing on a specific prey (Silva-Pereira et al., 2011; Emmons, 1987). Predators likely engage in intermittent food searching, wandering their territory for chance encounters, which allows them to increase chances of encountering different prey species (Galindo-Aguilar et al., 2022). According to Lima (2002), this predatory behaviour may simply represent the optimal strategy to avoid frequent attacks at a specific location and prevent prey from swiftly leaving such risky sites. Moreover, hunting modes are also linked to the influence that predators exert on prey species. For instance, an active predator has a more significant impact on specific prey through consumption than through non-consumptive effects (Middleton et al., 2013). This reinforces the observed anti-predatory spatiotemporal strategy found in prey species in southern Mexico.

In addition, an opportunistic hunting mode could be most successful for predators in areas with high species abundance of prey, such as the Neotropics. Across their distribution *P. onca* and *P. concolor* exhibited a moderate niche breadth (0.43 and 0.45, respectively), which support their opportunistic foraging behaviour of taking whatever is available (De Oliveira, 2002). Although there are site-specific variations, for example, predators may select particular species (Novack et al., 2005), based on availability or habitat conservation conditions (Cruz et al., 2022) or show some preference for large species such as *Dicotyles* spp. (Cruz et al., 2022; Weckel et al., 2006; Emmons, 1987). There is a trend of preying upon a few large-sized species at latitudes farther from the equator (narrower niche breadth) and upon a more diverse pool of species closer to the equator (broader niche breadth) (Gómez-Ortiz et al., 2015).

Measures of the co-occurrence networks in four landscapes in southern Mexico

It has been proposed that species behaviours change almost immediately following environmental changes; therefore behavioural changes are observed more rapidly than changes in population sizes (Morris et al., 2009). Although the co-occurrence networks of the studied landscapes showed variations in their topology, we did not observe a consistent trend in measurements to support our hypothesis. We anticipated that networks in disturbed landscapes would be more connected and have more interactions among species than in the undisturbed ones (Gaynor et al., 2019; Kay et al., 2018). This expectation was based on the premise that in disturbed landscapes, resources might be most limited, forcing prey to co-occur in the same locations as predators. However, we found that the number of links was slightly higher in both undisturbed landscapes (1 and 4), and connectance (an index relating the observed links to the maximum possible links) showed similar values across all four landscapes.

Only for predator-prey co-occurrences was there subtle support for the hypothesis. It was observed that disturbed landscapes 2 and 3 exhibited slightly higher values compared to undisturbed ones, although landscape 1 did not have connectance. Predators in these less conserved landscapes tend to actively seek prey more than in conserved ones. These findings suggest that resources are scarcer in less conserved landscapes, reducing the likelihood of encounters with prey and prompting predators to intensify their search.

In the case of the prey-predator connectance, we observed changes in behaviour patterns, although not in the predicted direction. Disturbed landscapes 2 exhibited the lowest connectivity values, whereas among the highland landscapes (3 and 4), the more conserved showed the lowest connectivity value. This supporting the hypothesis and suggests that prey had a greater chance of avoiding predators in the more conserved landscapes compared to disturbed ones.

We proposed a promising measure to evaluate changes: the cumulative links frequency, a derived measure similar to connectance but

considering only the observed links in the networks and how quickly the links accumulate over time. The slope of these curves allows us to understand the strength of changes in species co-occurrences within communities over time. A faster accumulation indicates that species are more likely to co-occur, showing lower avoidance behaviour compared to species in communities with flattened curves. For instance, in the case of prey-predator interactions, we observed that the few links accumulated rapidly in highland landscapes 3 and 4, suggesting that these prey species exhibited less avoidance behaviour compared to those in lowlands, i.e. in highlands there are a lower avoidance irrespective of the forest conservation condition.

In contrasting habitats, such as agriculture and forests, it has been observed that in more disturbed environments, there is an increased spatial co-occurrence among predators and prey species, as well as among competitors (Kay et al., 2018). However, in less contrasting landscapes, such as those in our study, there were slight differences in the measurements within the co-occurrence networks. It is conceivable that resources and space are sufficient for species, thereby rendering the effects of disturbances on interactions on community interactions not yet observable. It is advisable to explore more sensitive measures, such as using the actual maximum instead of the theoretical maximum (as in connectivity) and incorporating other measurements that involve time.

Limitations

Camera-trapping studies, which are techniques used to study rare or cryptic animals, are not free of bias towards certain species groups, resulting in heterogeneous detection probabilities (Burton et al., 2015). Both the technique and biological parameters must be considered as they influence the network structure and consequently the derived measurements (Hagen et al., 2012). This introduces uncertainty, as the absence of observed time interval between species may stem from factors such as low local abundance, seasonal variations, habitat preference, intensity of the interaction, or the detectability of the species. It has been proposed that population fluctuations in the species could significantly impact network structures, complicating comparisons among networks (Andrade-Ponce et al., 2022; Delmas et al., 2019; Wells et al., 2014; Krishna et al., 2008). Despite such biases, comparisons among sites within the same community, guilds, or group of species in camera-trapping surveys remain feasible by accommodating parameters such as abundance or detectability in models. However, changes in network structures as a consequence of spatial variations and relative species abundances remain as under-explored fields (Hagen et al., 2012).

Similar to other ecological networks, co-occurrence networks provide snapshots that depict community processes (Poisot et al., 2015; Wells et al., 2014). These networks are temporally and spatially dynamic, influenced by various factors such as scale (which determines who dictates the patterns of space use between predators and prey: predators at larger scales and prey at smaller scales; Hammond et al. (2012), local abundances (species must be sufficiently abundant to co-occur), changes in trait distribution (species must share coinciding traits), either attraction or avoidance to the cameras (Meek et al., 2016), and environmental influences on these factors (Poisot et al., 2015). We argue that species abundance affects the structure of the networks, since when species are very abundant, co-occurrence happens randomly.

The network measurements presented here can contribute to understanding spatial and temporal co-occurrence patterns between species. When inferring avoidance behaviours, several considerations must be taken into account. Our threshold for an avoidance effect (20 days) was based on a supposed prolonged impact on prey; however, this threshold may vary across ecosystems or species compositions. For instance, in a review of countermarking studies, Apps et al. (2022) identified durations ranging from 85 hours up to 10 weeks in several mammal species. However, after a few days, cues left by one species may diminish in their effect on another species, and long-time co-occurrences observed may be being governed by different ecological processes (e.g., resources availability, or the presence of a third species). Although experimental studies testing avoidance in medium and large-sized mammals are scarce, they provide data on the duration of cue effects and

reveal a consistent pattern of prey avoidance in response to cues left by predators (Say-Sallaz et al., 2019; Apfelbach et al., 2005). Therefore, inferences about interactions behaviours should focus on those with the shortest time intervals, possibly guided by the cumulative links frequency.

In this study, we employed a novel approach to measure time intervals as a complementary tool for describing and understanding behaviours in predator-prey systems and intraguild competition that facilitate species coexistence. We demonstrate that scale plays a crucial role in the variation of mammal co-occurrence patterns. In our study system in southern Mexico, prey and subordinate competitors avoided large predators, likely to minimise the risk of predation. This avoidance was more pronounced in the primary prey of large carnivores, whereas smaller or social species seem to rely on other anti-predator strategies, such as seeking refuge or staying vigilant. On the other hand, the absence of proximate spatiotemporal predator-prey co-occurrences suggests that, in this highly biodiverse region, predators exhibited an opportunistic hunting mode to increase the likelihood of encounters with a diverse array of prey species scattered across the landscape. We also propose the use of co-occurrence networks for habitat comparisons, enabling the measurement of anthropogenic effects on species behaviour. Although our study did not provide evidence of the impact of anthropized landscapes on co-occurrences, cumulative link frequencies demonstrated potential for exploring temporal, spatial, latitudinal, and elevation patterns in areas affected by natural or anthropogenic disturbances. ☞

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Supplemental information

Additional Supplemental Information may be found in the online version of this article:

- Figure S1** Months in which the camera traps worked in the four landscapes studied.
- Figure S2** Distribution of the input and output degrees.
- Figure S3** Cumulative frequency of links through time intervals.
- Supplement S1** Mathematical arguments demonstrating how connectance and the average of normalised degree give equal values in ecological networks.

- Supplement S2** Description of the final seven measures.
- Table S1** Simulated association scenarios between species A and B.
- Table S2** Characteristics of the camera-trap stations.
- Table S3** Measurements obtained from co-occurrence networks.
- Table S4** Normalised input degree for prey species in four landscapes.
- Table S5** Normalised output degree for prey species in four landscapes.
- Table S6** Normalised input degree for predator species in four landscapes.
- Table S7** Normalised output degree for predator species in four landscapes.