



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.

Keywords: southern Mexico, ground-dwelling mammals, spatiotemporal associations, behavioural interactions, network theory, risk allocation hypothesis.

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24 Introduction

25 Species interactions are essential for the functioning, dynamic, and stability of ecosystems
26 (García-Callejas et al., 2018; Pilosof et al., 2017; Bairey et al., 2016). Interactions such as
27 amensalism, antagonism, commensalism, and mutualism are crucial for structuring
28 communities in both the short and long-term by influencing colonisation and extinction
29 processes and inducing changes in the characteristics of the interacting populations, thus
30 allowing their coexistence (García-Callejas et al., 2018; Lima and Dill, 1990; Kotler and Holt,
31 1989). To mitigate the effects of negative interactions (e.g., predation, intraguild competition),
32 species must adapt in one or more dimensions of their niche as a strategy to secure the necessary
33 resources and survive in coexistence (Wiens, 2011). This may involve consuming different
34 foods or utilising different sites or times compared to the dominant competitor or predators
35 (Mendes et al., 2020; Karanth et al., 2017; Fischhoff et al., 2007; Kotler and Holt 1989).

36 Studies examining predator-prey relations or intraguild competition have concluded that prey
37 species, or subordinate ones, perceive the risk of encountering predators or dominant
38 competitors, exhibiting temporal or spatial avoidance (a negative association) (Hegab et al.,
39 2015; Bytheway et al., 2013; Vanak et al., 2013; Nersesian et al., 2012). The responses of prey
40 or subordinate competitor have been examined under the Risk Allocation Hypothesis, which
41 postulates that species will adapt their foraging or movement times (antipredator behaviour)
42 based on the immediate presence or absence of predators or dominant species and previous
43 experiences of their exposure to risk (Smith et al., 2020; Creel et al., 2008). According to the
44 fear theory, both prey and predators are engaged in a dynamic “game” of predation avoidance
45 and seeking predation opportunities, wherein individuals use informative cues to make
46 decisions on the trade-offs between accessing quality resources and avoiding predation
47 (Cornhill and Kerley 2020; Brown, 2019; Clinchy et al., 2012). According to Lima (2002), in

48 48 such systems, two conventional ways are recognised in which one species can influence the
49 49 behaviour of another species. (i.e. behavioural interactions): one is through physical contact,
50 50 and other is through a third set of entities, such as odours, sounds, or environmental
51 51 modifications (Hegab et al., 2015; Webster et al., 2012; Apfelbach et al., 2005; Durant, 2000).
52 52 These agents are not selective, as they may influence multiple species simultaneously (Goudard
53 53 and Loreau, 2012).

54 54 Over the past two decades, temporal and spatial segregation between predator and prey or
55 55 among competitors has been studied in ground-dwelling animals utilising camera-trap
56 56 techniques, kernel activity patterns, and multi-species occupancy models (Sollmann, 2018).
57 57 Kernel analysis assesses the overlap in the circadian activity patterns of pairs of species (Ridout
58 58 and Linkie, 2009), where a low overlap suggests segregation or avoidance, whereas a high
59 59 overlap implies potential persecution (Botts et al., 2020; Marinho et al., 2020). Conversely,
60 60 multi-species occupancy models assess the likelihood of a site being used by one species in the
61 61 presence of another, taking into account the probability of detection influenced by habitat and
62 62 survey factors (Rota et al., 2016).

63 63 In many instances studies have identified overlap between interacting species, indicating either
64 64 an absence of avoidance or that such activity behaviours remain unaffected by anthropogenic
65 65 disturbances (Van Scoyoc et al., 2023). Nonetheless, avoidance patterns are anticipated to exist
66 66 as a coexistence mechanism at the finer scales typical of most studies (Thurman, 2019;
67 67 Fancourt, 2016; Diamond, 1975). For instance, research utilising fine-scale methodologies has
68 68 identified spatiotemporal avoidance patterns between leopards (*Leopardus pardalis*) and lions
69 69 (*Panthera leo*) (Searle et al., 2021; Swanson et al., 2016). Similarly, leopards and caracals
70 70 (*Caracal caracal*) display mutual avoidance of one another (Müller et al., 2022).

71 71 A fine-scale approach to examining avoidance patterns among species using camera-trapping
72 72 data involves measuring time intervals between detections of pairs of species, addressing the
73 73 question: How long does it take for species A to appear at a site after the occurrence of species
74 74 B? (Galindo-Aguilar et al., 2022; Prat-Guitart et al., 2020; Karanth et al., 2017; Parsons et al.,
75 75 2016). Fine-scale spatiotemporal segregation enables the identification of mechanisms that
76 76 allow two or more species to coexist in habitats. This approach is increasingly recognised in
77 77 ecological studies (Rodríguez-Luna et al., in press; Flores-Martínez et al., 2022). However, the
78 78 precision of new methods has yet to be verified using simulated datasets with established co-
79 79 occurrences, and whether these patterns are influenced by anthropogenic activities remains to
80 80 be determined (Berger-Tal and Saltz, 2019; Caravaggi et al., 2017).

81 81 In previous studies, we have presented co-occurrence networks, a type of ecological network,
82 82 to characterise the time intervals between detections of pairs of species (Galindo-Aguilar et al.,
83 83 2022). The employment of networks in ecology originated with food webs; this methodology
84 84 has been extended to represent various types of interactions, including mutualism, predation,
85 85 and parasitism (Delmas et al., 2019; Bascompte, 2007). Co-occurrence networks were initially
86 86 introduced as intuitive diagrams that facilitate our understanding of the spatial coexistence of
87 87 species within communities (Araújo et al., 2011; Gotelli and McCabe, 2002).

88 88 Ecological networks of species have been employed to depict multiple interactions (links,
89 89 directed or not directed) occurring among species (nodes) within communities (Koutrouli et
90 90 al., 2020; Delmas et al., 2019; García-Callejas et al., 2018; Wells et al., 2014; Hagen et al.,
91 91 2012); Typically, these networks encompass a broad range of interactions, and their impacts
92 92 (direct, indirect, weak, or strong) are presented across various temporal and spatial scales
93 93 (Pilosof et al., 2017). Hence, ecological networks of species serve to understand and represent
94 94 behavioural interactions straightforwardly, with the capability of facilitating comparisons

95 95 across communities. These networks have been constructed using adjacency matrices, where
96 96 interactions among elements are determined by presence/absence, frequency data or potential
97 97 interactions (Bascompte, 2007). The underlying theory for these representations is graph
98 98 theory, which ecologists have adapted to employ network measures to characterise and
99 99 compare networks representing diverse conditions, relationships, communities, periods, and
100 100 spaces (Koutrouli et al., 2020; Kay et al., 2018; Bascompte, 2007).

101 101 In this contribution, we enhanced and assessed the precision of a method for analysing the time
102 102 intervals between pairs of species within communities, reinforcing the use of ecological
103 103 networks to illustrate such species co-occurrences, and introducing network measures to
104 104 qualitatively compare the topology of networks between communities. The method can be
105 105 useful to elucidate questions about avoidance or prey-tracking in a community context, as well
106 106 as for comparing variability across communities.

107 107 To assess the precision of the proposed method, we generated two *in-silico* datasets, varying
108 108 in the frequencies of species (one dataset with high frequencies and another with moderate
109 109 frequencies) and timing of associations among species at sites (ranging from near time to long
110 110 time between pairs of occurrences). From empirical data across four landscapes, we anticipated
111 111 that the time intervals between prey species or subordinate competitors would be longer in sites
112 112 previously visited by predators or dominant competitors, i.e. antipredator responses would
113 113 diminish over time (Bytheway et al., 2013; Brook et al., 2012). Among landscapes, we
114 114 hypothesised that disturbances have affected species behaviours because species react to
115 115 changes induced by anthropogenic activities, which in turn alter interspecific interactions
116 116 through increased predation pressure (Prugh, 2023; Van Scoyoc et al., 2023; Smith et al., 2020;
117 117 Berger-Tal and Saltz, 2019; Gaynor et al., 2019). Specifically, we anticipated structural
118 118 differences in the topology of the co-occurrence networks; we hypothesised that the most

119 119 perturbed landscapes would exhibit the nearest co-occurrences between species because
120 120 species are compelled to visit more hazardous sites to obtain the necessary resources (Morris
121 121 et al., 2009). Conversely, in the most conserved and continuous landscapes, species are more
122 122 likely to find resources most widely and will probably avoid risky sites and times (Flores-
123 123 Martínez et al., 2022; Berger-Tal and Saltz, 2019; Gallo et al., 2019).

124 124 The objectives of this contribution are outlined as follows: 1) enhance the previous method for
125 125 analysing co-occurrences of species to describe the time intervals between pairs of species,
126 126 thereby inferring avoidance and tracking behaviours in predator-prey systems and intraguild
127 127 competition; 2) assess the precision of the proposed method with simulated data; 3) introduce
128 128 topological measures to characterise and compare avoidance and tracking behaviours in co-
129 129 occurrence networks; and 4) apply the mammal co-occurrence approach to data collected with
130 130 camera traps in four landscapes in southern Mexico, each with varying disturbance conditions.

131 131 **Material and methods**

132 132 The method proposed (mammal co-occurrence approach) involves identifying non-random co-
133 133 occurrences between pairs of species at sites in a pool of samples. This method can be applied
134 134 to real data from camera-traps surveys or to datasets generated by simulations (hereafter
135 135 referred to as the “primary dataset” for both).

136 136 *Presence/absence matrices*

137 137 The method requires a table with three sets of data: species names, occurrence dates, and the
138 138 stations at which the species were recorded. With this table, presence/absence matrices were
139 139 constructed for each species; consequently, the number of matrices constructed was equal to
140 140 the number of species included in the dataset. The rows of each matrix represent the total days
141 141 in the study, and the columns represent the stations. For a given matrix A corresponding to a

142 142 certain species z , in the entry A_{ij} , we put 1 if the species z was observed on that day (day i) at
143 143 the given station (station j), and we put 0 if the species was not observed, *i.e.*, A is a
144 144 presence/absence matrix. This process was repeated for each species.

145 145 *Primary association data table*

146 146 By comparing pairs of matrices, we detected the coincidence of two species at the same station
147 147 on the same day or t days later (time interval); we called associations to these coincidences.
148 148 Given the matrix A for species z and matrix B for species y , we proceed as follows: we
149 149 compared the i row of A (day i) with the $i + t$ row of B (t days after) with $t = 0, 1, 2, \dots, 20$
150 150 . If in the column j both matrices have 1, this means that the species y appeared t days after \square
151 151 at the same station; we counted how many times this occurred. That is to say, for $t = 0$ we
152 152 counted how many associations were on the same day, for $t = 1$, we counted how many
153 153 associations occurred one day after, and so on.

154 154 We obtained the associations data tables, recording the number of associations for every pair
155 155 of species each day up to 20 days. We used 20 days as a conservative timeframe during which
156 156 one animal cues could potentially influence the behaviour of another (Apps et al., 2022). Until
157 157 this step, we had information about the number of associations for every pair of species from
158 158 our primary dataset (Figure 1 a).

159 159 *Resampling bootstrap step*

160 160 In our method, the next steps were performed to know if randomly we can reproduce the same
161 161 associations observed in our primary dataset. With this objective, from the primary data, we
162 162 obtained the time in which the station was operational and the number of records of every
163 163 species at a particular station. With this information as conditionals, we did a resampling of the
164 164 presence of the species throughout the days in which the station was active. Since resampling

165 165 is performed randomly, different occurrence patterns are expected and therefore different
166 166 species associations. We call this the resampling bootstrap step.

167 167 *Random data generation*

168 168 In one run of our programs, the following processes were carried out 100 times: 1) resampling
169 169 bootstrap for every pair of species and construction of its corresponding presence/absence
170 170 matrix, and 2) using the presence/absence matrix to create its corresponding association data
171 171 table (Figure 1 b).

172 172 *Obtaining the p-value by comparing random data and primary data*

173 173 Since we constructed 100 random association data tables, for every day we compared how
174 174 often the number of associations for a pair of species (random associations) from the random
175 175 data was exceeded the number of associations from the primary data (primary associations).
176 176 Subsequently, we calculated a one-sided empirical p-value between species z and y , t days later,
177 177 where t takes integer values between 0 and 20 using the following formula:

$$178 \quad 178 \quad p(z, y, t) = (1 + \sum H(s \geq s_0)) / (N + 1)$$

179 179 where s_0 is the number of primary associations between z and y , s is the number of random
180 180 associations between y and z , $H(s \geq s_0)$ returns 1 if the inequality is satisfied and a 0 if not,
181 181 $\sum H(s \geq s_0)$ is the number of times the inequality $s \geq s_0$ is satisfied and $N = 100$ (Davison
182 182 and Hinkley, 1997). That is to say, it counts the number of times that the random associations
183 183 were greater than the primary associations. If all the times $s \geq s_0$, then $p(z, y, t) = 1$, on the

184 184 other hand, if all the times $s \leq s_0$ then $p(z, y, t) = \frac{1}{101}$.

185 185 An association between two species y and z is considered significant for a time interval t if
186 186 $p(z, y, t) \leq 0.05$, which implies that if we observe the distribution of random associations,
187 187 the primary association value is at the right extreme part of the distribution, regardless of the
188 188 form of the distribution.

189 189 Until here, we have identified all species pairs and their corresponding time interval where
190 190 primary associations are not reproduced by random data generation.

191 191 *Sensitivity of the method*

192 192 To assess the sensitivity of the method, we generated random data 10 times and obtained the P
193 193 -value for each iteration. Species y and z are then considered to *co-occur* in the shortest
194 194 significant time interval t in which they are associated, if for that t and species y and z ,
195 195 $p(z, y, t) \leq 0.05$ in each of all the 10 iterations. In other words, there is a co-occurrence
196 196 between species y and z whenever $p(z, y, t) \leq 0.05$ in all the 10 iterations. All the processes
197 197 were programmed in the Octave language (Eaton et al., 2019).

198 198 *Co-occurrence network (CN)*

199 199 Using the shortest time interval co-occurrences, we build up a co-occurrence network where
200 200 every node (circle) represents a species, and a directed edge (arrow) represents a co-occurrence
201 201 between species. The node at the head of the arrow represents the species observed first, and
202 202 the tail represents the species observed later; the colour of the arrow indicates the time interval.
203 203 The size of the node represents the relative abundance index (IAR) (Figure 1 c). Programs for
204 204 visualising the co-occurrence networks were executed in Python (Van Rossum, 1995).

205 205 *Measures to compare co-occurrence networks*

206 206 We identified 25 measures to characterising and comparing ecological networks (Koutrouli et
207 207 al., 2020; Delmas et al., 2019; Kay et al., 2018; Kéfi et al., 2015; Araújo et al., 2011; Junker
208 208 and Schreiber, 2011; Bascompte et al., 2006; Blüthgen et al., 2006). Metrics involving
209 209 interactions among more than two species (e.g. nesting, clusterization, Katz centrality,
210 210 diameter) were discarded, as were those considering the trophic levels (Kefi et al., 2015).
211 211 Metrics utilising frequencies such as the index d' and $H2'$, used to measure specialisation based
212 212 on the strength of the association, were also excluded (Blüthgen et al., 2006).

213 213 We selected network measures because they allow us to characterise behavioural interactions
214 214 between species and facilitate comparisons among different sites, landscapes, or conditions.
215 215 Initially, six measures were chosen to compare the topology of CNs: the number of nodes, the
216 216 number of links, connectance, the normalised degree, the average of the normalised degree,
217 217 and the distribution of the input and output degrees. In addition, we proposed a novel measure:
218 218 the cumulative frequency of links through time intervals, as a special measure to describe how
219 219 co-occurrences accumulate over time. After inspection of the results, we noticed that the values
220 220 of connectance and the average of normalised degrees were equal in all the networks
221 221 (Mathematical arguments are present in Supplementary material S1), therefore we presented
222 222 only connectance values. Supplementary material S2 provides a description of the final seven
223 223 measures chosen, including modifications or derivations of these when it was necessary, and
224 224 their application in the study of avoidance or tracking behaviours (Figure 1 d).

225 225 *Simulated scenarios*

226 226 To demonstrate the applicability and accuracy of the mammal co-occurrence approach, we
227 227 generate two datasets simulating real camera traps. Each dataset consisted of 12 imaginary prey
228 228 species, three imaginary predator species, 30 imaginary camera-trap stations, and a span of 35
229 229 to 69 days during which species hypothetically occurred. In these two simulated datasets (See

230 230 Table S1 in Supplementary material, Figure 2), we varied: 1) the timing of associations among
231 231 species in imaginary cameras (from immediate to extended periods between associations); and
232 232 2) species frequencies (from rare to common species). We also included random associations
233 233 for a set of species (from rare to common random associations of species). In simulated dataset
234 234 1, species observation frequencies were higher (range: 10-156 “captures”, coefficient of
235 235 variation 63.36) compared to simulated dataset 2 (range: 2-101 “captures”; coefficient of
236 236 variation 70.01). After the simulated process, we obtained 2 datasets of simulated associations
237 237 between pairs of species.

238 238 Subsequently, we applied the mammal co-occurrences approach to these primary datasets to
239 239 identify co-occurrences between pairs of species. For both simulated datasets, we evaluated the
240 240 accuracy of the method by comparing the detected co-occurrences with respect to those
241 241 associations proposed in the sceneries.

242 242 *Case study: co-occurrence networks of mammal species in four landscapes in southern Mexico*

243 243 We analysed the time intervals between pairs of mammal species in four landscapes located in
244 244 the Chinantla region, southern Mexico (17.317 and 18.164 N, and -95.567 and - 96.699 W),
245 245 based on their co-occurrence at the same camera trap station with a 1-day interval (24 h).
246 246 Camera-trapping data were obtained from biodiversity monitoring projects spanning 18
247 247 communities in six municipalities (Galindo-Aguilar et al., 2022). The landscapes were
248 248 categorised into highland areas (predominantly covered by cloud forests) and lowland areas
249 249 (predominantly covered by tropical rainforests). The four landscapes varied in elevation, type
250 250 of cover, and agricultural matrix (Figure 3; details in Table S2 in Supplementary material):

251 251 1) Fragments of undisturbed tropical lowlands forests (landscape 1) consist of patches
252 252 of a well-conserved tropical rainforest surrounded by agriculture and pasturelands for cattle;
253 253 there is an elevational range of 100-340 m asl.

254 254 2) Fragments of slightly disturbed tropical lowlands forests (landscape 2) is a mosaic
255 255 of tropical rainforest patches interspersed with plots of pasturelands for cattle and agriculture
256 256 for perennial crops situated between 70 and 900 m asl in the hills along the main highway.

257 257 3) A large fragment of slightly disturbed tropical highland forest (landscape 3) is
258 258 covered by semicontinuous tropical rainforests and montane cloud forest, with scattered plots
259 259 of seasonal agriculture and pasturelands for cattle, spanning elevations from 470 to 1,380 m
260 260 asl.

261 261 4) Undisturbed tropical highlands forests (landscape 4) are characterised by continuous
262 262 well-conserved montane cloud forest and tropical rainforest, situated between 550 and 1,890
263 263 m asl, in proximity to human localities.

264 264 Based on the level of forest connectivity and surrounding anthropogenic disturbances, we
265 265 considered landscape 1 to be more conserved than landscape 2 in the lowlands, and landscape
266 266 4 more conserved than landscape 3 in the highlands.

267 267 A total of 119 camera-trap stations were deployed between 2011 and 2014. The cameras placed
268 268 in landscape 1 were 26 and the sampling effort was of 1,187 camera traps/day; in landscape 2
269 269 were 36 and the sampling effort was of 1,075 camera traps/day; in landscape 3 were 27 and the
270 270 sampling effort was 677 cameras traps/day; and for landscape 4 were 27 and sampling effort
271 271 was 1,074 camera traps/day. In the four landscapes, the composition of analysed species was
272 272 slightly similar, consisting of three species of large and medium-sized predators (*Panthera*
273 273 *onca*, *Puma concolor*, and *Leopardus pardalis*) and 11 potential prey species (*Procyon lotor*,
274 274 *Eira barbara*, *Didelphis* spp., *Philander opossum*, *Nasua narica*, *Mazama temama*, *Dicotyles*
275 275 spp., *Sylvilagus* spp., *Dasyprocta mexicana* and *Cuniculus paca*, and *Dasyopus novemcinctus*).
276 276 *Mazama temama* was not recorded in landscape 1; *Dicotyles* spp., *Didelphis* spp., *E. barbara*,
277 277 *P. opossum*, and *P. lotor* were not recorded in landscape 3; and *P. lotor* and *Sylvilagus* spp.

278 278 were not recorded in landscape 4. The species numbers included in the analyses were 14 for
279 279 landscape 1, 13 for landscape 2, 9 for landscape 3, and 12 for landscape 4. Prior to analyses, to
280 280 ensure data independence among adjacent stations, we checked for repeated species
281 281 associations; in such cases, one of the stations was discarded.

282 282 Code to run a spatiotemporal co-occurrence analyses are available at
283 283 <https://github.com/BeatrizCarelyLuna/Co-occurrence-networks-v2>

284 284 **Results**

285 285 *Simulations*

286 286 We found good accuracy of the method based on simulated datasets (90% accuracy for each).
287 287 In simulation 1 (species with highest IAR), all expected co-occurrences were retrieved except
288 288 one, where a prey species strongly avoided a predator ($E10 \rightarrow E15$). In simulation 2 (species
289 289 with moderate IAR), the method retrieved all expected co-occurrences excepted one, in which
290 290 a predator moderately tracked a prey ($E15 \rightarrow E9$).

291 291 Network measures were calculated for both simulations (Table S3). Overall, we found that the
292 292 number of links and connectance values were higher in simulation 1 compared to simulation 2.
293 293 Also, the prey \rightarrow predator and predator \rightarrow prey connectance values were slightly higher in
294 294 simulation 1 than those in simulation 2. However, differences were found in the prey \rightarrow prey
295 295 and predator \rightarrow predator connectance values, almost two-fold higher in simulation 1 than in
296 296 simulation 2.

297 297 *Avoidance of prey species and subordinate competitors in four landscapes in southern Mexico*

298 298 Overall, we found a consistent trend supporting the hypothesis of prey avoidance following
299 299 predator occurrences across the four landscapes. Further, we found that four potential prey

300 300 species (*P. opossum*, *D. novemcinctus*, *M. temama*, and *P. lotor*) did not co-occur with
301 301 predators in any landscape (Figure 4). Additionally, we found a trend for a moderate number
302 302 of co-occurrences among prey and predators in both highland landscapes (five co-occurrences
303 303 in landscape 3 and four co-occurrences in landscape 4).

304 304 In all landscapes, the time intervals between prey →predator co-occurrences were generally
305 305 equal to or greater than 8 days. Two exceptions cases were observed: *Sylvilagus* spp. occurred
306 306 two days after *L. pardalis* in landscape 3, and *N. narica* occurred two days after *P. concolor* in
307 307 landscape 4. On the other hand, predators were observed to occur several days after prey
308 308 occurrences (equal or greater to 8 days) in the same sites, but *P. concolor*, which occurred one
309 309 day after *Dicotyles* spp. in landscape 2, and *L. pardalis* one day after *N. narica* in landscape 3
310 310 (Figure 4).

311 311 Among predators, co-occurrences were infrequent and typically involved differences of several
312 312 days. The closest co-occurrence observed was *P. concolor* occurring three days after *P. onca*
313 313 in landscape 2 (fragments of slightly disturbed lowlands forests) (Figure 4).

314 314 Prey species avoiding to co-occur at the same sites as predators were a consisting finding in
315 315 landscapes. Among the 5-10 prey species in the four landscapes, one or two species occurred
316 316 after predators, with a maximum of three species (*D. mexicana*, *C. paca*, and *Sylvilagus* spp.)
317 317 observed after *L. pardalis* in landscape 3. Similarly, we found predators occurred after only a
318 318 few prey species: two species in landscapes 2, 3 and 4, while predators did not track any prey
319 319 in landscape 1. Also, co-occurrences among competitors (predators →predators) were rare. In
320 320 contrast, prey →prey co-occurrences exhibited the highest number of links reaching up to 17
321 321 co-occurrences in landscape 1 (Figure 4).

322 322 *Topological measurements of co-occurrence networks in four landscapes in southern Mexico*

323 323 We found variations in the topology of the co-occurrence networks among the four landscapes
324 324 studied. Overall, the lowland landscapes were more diverse with the highest number of nodes
325 325 and more species co-occurrences (links) compared to the highland landscapes. Even, in
326 326 landscape 3 (a large fragment of slightly disturbed highland forest), one predator did not co-
327 327 occur with either prey or another predator.

328 328 The low values of the connectance index (L/m) indicated a trend towards spatiotemporal
329 329 segregation for all landscapes studied (Table 1). At the community level, there was no notable
330 330 differences in the connectance among disturbed and undisturbed landscapes, as the values were
331 331 very similar (Table 1). However, among species groups, the connectance index showed a trend
332 332 for predators to occur more frequently in sites where prey species had been observed,
333 333 particularly in the most perturbed landscapes.

334 334 Connectance values among groups were also low or very low, which supports the hypothesis
335 335 of general avoidance or segregation among species. However, we found connectance values
336 336 were unrelated to disturbance as disparate trends were obtained. For instance, the connectance
337 337 value for prey-predator and prey-prey co-occurrences were highest in the undisturbed lowland
338 338 landscape, whereas the values were lowest in the undisturbed highland landscape (Table 1).

339 339 The normalised input degrees indicated that most prey species are not actively tracked by
340 340 predators (index equal to 0). Only five species were found to occur after a predator (each with
341 341 a normalised input degree = 0.33): *D. mexicana* and *Dicotyles* spp. in landscape 2 (fragments
342 342 of slightly disturbed lowlands forests); *D. mexicana* and *N. narica* in landscapes 3 (a large
343 343 fragment of slightly disturbed highland forest); and *C. paca* and *E. barbara* in landscape 4
344 344 (undisturbed highlands forests) (Table S4 in Supplementary material).

345 345 Low values in the normalised input degrees for predators and normalised output degrees for
346 346 prey reinforce the findings of prey avoidance. When co-occurred, prey typically passed after

347 347 only one of the three predator species (normalised input degree = 0.33 each), such as *N. narica*
348 348 and *Dicotyles* spp. in both undisturbed landscapes 1 and 4, or *C. paca* in disturbed landscapes
349 349 2 and 3 (Table S5 in Supplementary material). It was common that only one prey occurred after
350 350 predators, except in landscape 3 where *L. pardalis* was followed by half of the prey species
351 351 (Table S6 in Supplementary material).

352 352 Considering normalised input degrees among predators, a segregation pattern was observed,
353 353 because only one competitor occurred before another: *L. pardalis* in landscape 2, and *P. onca*
354 354 in landscapes 1, 2 and 4 (normalised input degree = 0.5 each one). *P. concolor* did not exhibit
355 355 any inputs in any landscape (Table S6 in Supplementary material). Also, we found *L. pardalis*
356 356 co-occurred after another predator in two landscapes, whereas *P. onca* occurred after another
357 357 competitor in disturbed lowland landscape 2, and *P. concolor* in undisturbed lowland landscape
358 358 1 (Table S6 in Supplementary material).

359 359 Overall, predators showed tracking behaviour towards a limited number of prey species. *L.*
360 360 *pardalis* and *P. concolor* presented outputs towards prey species in both disturbed lowland and
361 361 highland landscapes 2 and 3; and *P. onca* had outputs in undisturbed highland landscape 4
362 362 (Table S7 in Supplementary material).

363 363 *Distribution of the input degrees and output degrees*

364 364 In predator →prey co-occurrences, the input degree 0 was the most frequent in all four
365 365 landscapes, indicating that predators frequently did not track prey, and prey avoided predators
366 366 (Figures S2a and S2b in Supplementary material). Also, predators tended to avoid occurring
367 367 after other competitors, although in the non-conserved lowland landscape 2, two predators
368 368 exhibited outputs (Figures S2c and S2d in Supplementary material).

369 369 In prey →predator co-occurrences, few prey species occurred after predators, with one notable
370 370 exception where up to 4 prey species occurred after a single predator in the non-conserved
371 371 highland landscape 3 (Figures S2e and S2f in Supplementary material).

372 372 In prey →prey interactions, it was common for prey species to occur after another. It was
373 373 notable that in landscape 1, up to eight prey species occurred after another (Figures S2g and
374 374 S2h in Supplementary material).

375 375 *Cumulative frequency of links through time intervals*

376 376 Species showed a tendency to co-occur in sites visited by predator or competitor as the days
377 377 progressed, with slight variations observed among landscapes. Species co-occurrences
378 378 occurred earliest in the undisturbed lowland landscape 1, whereas in disturbed highland
379 379 landscape 3, species spend most time to co-occur, resulting in a flattened curve (Figure S3a in
380 380 Supplementary material). In some cases, species co-occurred in nearest days, such as certain
381 381 prey species co-occurring shortly after predators in both highland landscapes, whereas in
382 382 lowland landscapes, prey co-occurred several days later (Figure S3b in Supplementary
383 383 material). Predators promptly co-occurred after prey in both disturbed landscapes 2 and 3;
384 384 whereas in the more conserved landscapes 1 and 4, such co-occurrences were not observed or
385 385 occurred after several days (Figure S3c in Supplementary material).

386 386 For predator →predator co-occurrences, all occurred within less than 10 days, except in
387 387 disturbed highland landscape 3 where no co-occurrence were observed. The earliest predator
388 388 →predator co-occurrences was observed on the fourth day in undisturbed lowland landscape 1
389 389 (Figure S3 d) in Supplementary material). Finally, in prey →prey co-occurrences, the
390 390 cumulative frequencies of links suggest that in undisturbed landscapes 1 and 4, prey species
391 391 tend to co-occurred earlier compared to the other two non-conserved landscapes (Figure S3e
392 392 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 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

417 417 measures plus modularity, species topological role, among-module connectivity, diversity in
418 418 interactions, and specialisation (H_2'), primarily to elucidate how species co-occurrences vary
419 419 among landscapes and between areas (Corro et al., 2019; Kay et al., 2018; Borthagaray et al.,
420 420 2014). In addition, we proposed a new measure which describes the dynamics of the cumulative
421 421 co-occurrences. Rapid accumulation of links suggests lowest avoidance, whereas accumulation
422 422 of links over several days indicate strong avoidance. The proposed method was applied to
423 423 simulations and real data, demonstrating its accuracy in inferring behavioural interactions.

424 424 *Simulations*

425 425 With simulated data, we observed good accuracy in the method presented here. In only one
426 426 instance in Simulation 1, the method predicted a co-occurrence in nearer time (2 days) than
427 427 expected (10 days). Furthermore, in Simulation 2, an expected co-occurrence was not detected
428 428 at all. Upon examining these co-occurrences in the simulated data, in Simulation 1, the predator
429 429 species involved were simulated to exhibit a high capture frequency with weak tracking
430 430 behaviour towards prey, exemplifying the case of a hypothetical common generalist predator.
431 431 In Simulation 2, the undetected co-occurrence involved a “very rare” prey species. The
432 432 unexpected co-occurrence in Simulation 1 was influenced by the frequency of the predator
433 433 species, suggesting that a common generalist predator might frequently co-occur at sites where
434 434 prey has been recorded, thereby indicating a positive association when there is none.
435 435 Accordingly, caution is advised in datasets with very frequent predator species, as frequencies
436 436 may impact the predictions of significant co-occurrences.

437 437 In nature, predators are uncommon, and their frequency of detections is low compared to other
438 438 medium and large-sized mammals (Friedeberg-Gutiérrez et al., 2022; Greenspan et al., 2020).
439 439 Therefore, the likelihood of detecting a false positive association is generally low, as evidenced
440 440 by our second simulations, which accurately detect expected positive associations between an

441 441 uncommon predator and its prey. Instead, attention should be directed towards mesocarnivores,
442 442 which are commonly found in landscapes and exhibit high frequencies in surveys. Then, if
443 443 positive associations with potential prey emerge, these should be meticulously evaluated based
444 444 on known interactions (achieved through direct observations, traits, or analyses of feeding
445 445 habits) to determine a true behavioural effect (Clare et al., 2016; Morales-Castilla et al., 2015).

446 446 In the case of the simulations, we did not observe an effect of species frequency on network
447 447 measures in any of the cases. Although the number of links was notably higher in Simulation
448 448 1 (highest frequency of species), we observed that links between prey-predator and predator-
449 449 prey were very similar across simulations. Similarly, the connectance measure was higher in
450 450 Simulation 1, but prey-predator and predator-prey connectance displayed disparate patterns.
451 451 These findings indicate that the expected sceneries for predator and prey were minimally
452 452 influenced by their frequencies; instead, there was a prevalence in the associations expected,
453 453 demonstrating the robustness of the approach.

454 454 *Avoidance behaviours of prey and subordinate competitors in four landscapes of southern*
455 455 *Mexico*

456 456 The Chinantla is a relatively well-conserved region with a high richness of mammal species
457 457 (Briones-Salas et al., 2023). In such resource-abundant regions, prey-predator dynamics align
458 458 with the risk allocation hypothesis, which posits that species perceive the risk imposed by
459 459 predators and exhibit antipredator behaviours (Smith et al., 2020; Lima and Bednekoff, 1999).
460 460 We observed that both prey and subordinate competitors avoid sites previously visited by
461 461 predators or dominant species, or may not even be present at those sites. Hence, we propose
462 462 that in well-conserved Neotropical landscapes, prey actively avoid predators, not only spatially
463 463 but also temporally.

464 464 Connectance indices revealed that the number of co-occurrences was low relative to the
465 465 maximum possible in the networks; such indices were slightly lower for prey-predator co-
466 466 occurrences than for prey-prey or predator-predator associations, reinforcing evidence of active
467 467 avoidance. We observed that prey species avoidance behaviour was species-specific,
468 468 depending on whether the species is a primary prey for the predator. Generally, primary prey
469 469 co-evolves with their predator, engaging in a survival race where predators may develop
470 470 strategies to secure food while prey devise strategies to avoid predation (Morris, 2009). These
471 471 relationships are readily observed by interpreting the normalised degree index, which is useful
472 472 for understanding the importance of individual species in the response of other species. For the
473 473 largest felids, *P. onca* and *P. concolor*, the proportion of co-occurrences with prey was the
474 474 lowest, whereas half of the prey species co-occurred after *L. pardalis*; this suggests that prey
475 475 perceived greater risk associated with large predators than with medium-sized predators.
476 476 Medium-sized prey species are typically consumed by large predators, whereas *L. pardalis*
477 477 rarely preys on them, focusing on small mammals, lizards, and birds (Cruz et al., 2022;
478 478 Emmons, 1987).

479 479 The prey species *N. narica*, *M. temama*, *Dicotyles* spp., *D. novemcinctus*, and *C. paca* are
480 480 considered primary prey for large predators in the Neotropics (Cruz et al., 2022; Foster et al.,
481 481 2010; De Oliveira, 2002). Our results indicated that these prey remained temporarily distant
482 482 from sites where predators were detected, possibly as a strategy to reduce the risk of predation.
483 483 These antipredator behaviours have not been previously described due to the use of a coarse
484 484 temporal scale. Synchronisation in circadian activity patterns and similar habitat use between
485 485 prey and predators have been suggested to indicate a positive association, for instance in
486 486 Bolivia-Peru (Ayala et al., 2021), Costa Rica (Herrera et al., 2018), and Brazil (Foster et al.,
487 487 2013). Furthermore, in northern Mexico, one of the principal prey species, *Dicotyles* spp., was

488 488 closely associated with the presence of *P. concolor* and *P. onca* (Gutiérrez-González and
489 489 López-González, 2017).

490 490 However, such associations could be related to scale. As Thurman (2019) noted, current
491 491 analytical methods used to measure spatial co-occurrence fail to predict empirical trophic
492 492 interactions. Additionally, in camera-trap studies, devices imperfectly detect animals due to
493 493 their space use and size, resulting in biased presence/absence records. To address the first
494 494 challenge, we demonstrated through simulations the accuracy of the co-occurrence method, for
495 495 example, the method detected instances where a supposed predator actively tracked prey or
496 496 where prey actively avoided a predator. For the second challenge, it is preferable to use several
497 497 devices to maximise the number of sites, as well as to estimate viewable area and distance of
498 498 individuals to devices to achieve detections close to 1, in order to accurately detect behavioural
499 499 interactions (Moeller et al., 2023; Kays et al., 2021). In studies with limited equipment
500 500 resources, conclusions should be restricted to the best detected species, such as large-sized
501 501 animals (Kays et al., 2021). The use of odorous samples in experimental studies, placed in front
502 502 of a battery of cameras at the sites, could be useful to better record such animal behaviours.

503 503 Kernel estimators and other circular statistics represent a coarse approach that aggregates
504 504 records for long-term studies into a 24-hour model, thereby displaying the daily activity
505 505 patterns of species and evaluating their overlap to infer temporal segregation. However, more
506 506 detailed analyses using time intervals demonstrate how the probability of the presence of prey
507 507 or subordinate competitors increases as the time interval from the predator's occurrence
508 508 extends, a mechanism that facilitates their coexistence in landscapes (Harmsen et al., 2009).

509 509 An exception to predator avoidance was observed in *Sylvilagus* spp. and *N. narica* which
510 510 occurred after *L. pardalis* and *P. concolor*, respectively. It is likely that these prey species are
511 511 employing other anti-predatory strategies not reflected in their movements across habitats and

512 512 potentially over time. *Sylvilagus* spp. have been documented as a part of the diet of *L. pardalis*
513 513 (Gómez-Ortiz et al., 2015; Rocha-Mendes et al., 2010; Moreno et al., 2006), whereas *N. narica*
514 514 is a significant prey item for *P. concolor* (Gómez-Ortiz et al., 2015). Small prey species such
515 515 as lagomorphs appear not to avoid their main predators; instead, they rely on microhabitat
516 516 structures for refuge and can escape quickly when they threatened (Wagnon et al., 2020; Gallo
517 517 et al., 2019; Clare et al., 2016). However, anti-predatory shelter strategies do not account for
518 518 the co-occurrence of *N. narica* with *P. concolor*; their vigilance behaviours and group living
519 519 provide security during movement and foraging (Burger, 2001), and an opportunity to defend
520 520 against any attack (Gómez-Ortiz et al., 2015).

521 521 Intraguild coexistence is a characteristic of communities. Its underlying mechanisms have been
522 522 elucidated through niche segregation in any axis of their niche, for instance, by altering the
523 523 consumption of food resources (Gómez-Ortiz et al., 2015), or via spatial or temporal
524 524 segregation (Rodríguez et al., 2021; Breviglieri et al., 2017). Several studies have identified
525 525 moderate or high circadian overlap between *P. onca*, *P. concolor*, and *L. pardalis* (Argudín-
526 526 Violante et al., 2023; Galindo-Aguilar et al., 2022; Ayala et al., 2021; Herrera et al., 2018;
527 527 Santos et al., 2019; Gutiérrez-González and López-González, 2017; Foster et al., 2013;
528 528 Romero-Muñoz et al., 2010), suggesting that time distribution throughout the day does not
529 529 constrain their coexistence. However, we demonstrated that although competitors are active
530 530 during the same daytime hours (high circadian overlap in our study area; Galindo et al., 2022),
531 531 they avoided sharing the same sites or they occurred with several days of difference. In line
532 532 with the findings of Harmsen et al. (2009), we highlight that *P. concolor* and *P. onca* tend to
533 533 avoid using the same site at the same time, illustrating a mechanism of coexistence at a fine
534 534 temporal or spatial scale (de la Torre et al., 2017; Scognamillo et al., 2003). A similar pattern
535 535 of avoidance was observed in the mesocarnivore *L. pardalis* which exhibited a delay of several

536 536 days before occupying areas recently visited by larger felids, likely as a strategy to avoid
537 537 intraguild predation (Richards et al., 2023).

538 538 Another indicator of the influence of top predators over subordinate ones was the capture rate.
539 539 For *L. pardalis* it was higher in the most disturbed landscape 2, whereas in the other landscapes,
540 540 *P. onca* and *P. concolor* exhibited higher capture rates. According to optimal foraging theory,
541 541 predators select habitats that maximise their hunting success. In the case of *P. concolor*,
542 542 vegetation cover is crucial to successful capture (Holmes and Laundré, 2006; Laing, 1988;
543 543 Logan and Irwin, 1985). We concur that mesopredator avoidance of apex predators can occur
544 544 along two axes: space and time (Brook et al., 2012), as previously highlighted.

545 545 *Absence of tracking behaviours of predators*

546 546 To carry out their vital processes, predators seek irregularly dispersed prey (Yahner, 2012).
547 547 Contrary to our expectations, we did not observe consistent predator-to-prey tracking
548 548 behaviour (i.e., selective predation mode); instead, we noted that predators appeared several
549 549 days after the prey or did not co-occur at all. Similar findings have been observed in other
550 550 tropical ecosystems, where spatial overlap between predator and prey was low
551 551 (Vinitpornsawan and Fuller, 2020). This suggests that predators exhibited an opportunistic
552 552 hunting behaviour, not focusing on a specific prey (Silva-Pereira et al., 2011; Emmons, 1987).
553 553 Predators likely engage in intermittent food searching, wandering their territory for chance
554 554 encounters, which allows them to increase chances of encountering different prey species
555 555 (Galindo-Aguilar et al., 2022). According to Lima (2002), this predatory behaviour may simply
556 556 represent the optimal strategy to avoid frequent attacks at a specific location and prevent prey
557 557 from swiftly leaving such risky sites. Moreover, hunting modes are also linked to the influence
558 558 that predators exert on prey species. For instance, an active predator has a more significant
559 559 impact on specific prey through consumption than through non-consumptive effects

560 560 (Middleton et al., 2013). This reinforces the observed anti-predatory spatiotemporal strategy
561 561 found in prey species in southern Mexico.

562 562 In addition, an opportunistic hunting mode could be most successful for predators in areas with
563 563 high species abundance of prey, such as the Neotropics. Across their distribution *P. onca* and
564 564 *P. concolor* exhibited a moderate niche breadth (0.43 and 0.45, respectively), which support
565 565 their opportunistic foraging behaviour of taking whatever is available (De Oliveira, 2002).
566 566 Although there are site-specific variations, for example, predators may select particular species
567 567 (Novack et al., 2005), based on availability or habitat conservation conditions (Cruz et al.,
568 568 2022) or show some preference for large species such as *Dicotyles* spp. (Cruz et al., 2022;
569 569 Weckel et al., 2006; Emmons, 1987). There is a trend of preying upon a few large-sized species
570 570 at latitudes farther from the equator (narrower niche breadth) and upon a more diverse pool of
571 571 species closer to the equator (broader niche breadth) (Gómez-Ortiz et al., 2015).

572 572 *Measures of the co-occurrence networks in four landscapes in southern Mexico*

573 573 It has been proposed that species behaviours change almost immediately following
574 574 environmental changes; therefore behavioural changes are observed more rapidly than changes
575 575 in population sizes (Morris et al., 2009). Although the co-occurrence networks of the studied
576 576 landscapes showed variations in their topology, we did not observe a consistent trend in
577 577 measurements to support our hypothesis. We anticipated that networks in disturbed landscapes
578 578 would be more connected and have more interactions among species than in the undisturbed
579 579 ones (Gaynor et al., 2019; Kay et al., 2018). This expectation was based on the premise that in
580 580 disturbed landscapes, resources might be most limited, forcing prey to co-occur in the same
581 581 locations as predators. However, we found that the number of links was slightly higher in both
582 582 undisturbed landscapes (1 and 4), and connectance (an index relating the observed links to the
583 583 maximum possible links) showed similar values across all four landscapes.

584 584 Only for predator-prey co-occurrences was there subtle support for the hypothesis. It was
585 585 observed that disturbed landscapes 2 and 3 exhibited slightly higher values compared to
586 586 undisturbed ones, although landscape 1 did not had connectance. Predators in these less
587 587 conserved landscapes tend to actively seek prey more than in conserved ones. These finding
588 588 suggest that resources are scarcer in less conserved landscapes, reducing the likelihood of
589 589 encounters with prey and prompting predators to intensify their search.

590 590 In the case of the prey-predator connectance, we observed changes in behaviour patterns,
591 591 although not in the predicted direction. Disturbed landscapes 2 exhibited the lowest
592 592 connectivity values, whereas among the highland landscapes (3 and 4), the more conserved
593 593 showed the lowest connectivity value. This supporting the hypothesis and suggests that prey
594 594 had a greater chance of avoiding predators in the more conserved landscapes compared to
595 595 disturbed ones.

596 596 We proposed a promising measure to evaluate changes: the cumulative links frequency, a
597 597 derived measure similar to connectance but considering only the observed links in the networks
598 598 and how quickly the links accumulate over time. The slope of these curves allows us to
599 599 understand the strength of changes in species co-occurrences within communities over time. A
600 600 faster accumulation indicates that species are more likely to co-occur, showing lower avoidance
601 601 behaviour compared to species in communities with flattened curves. For instance, in the case
602 602 of prey-predator interactions, we observed that the few links accumulated rapidly in highland
603 603 landscapes 3 and 4, suggesting that these prey species exhibited less avoidance behaviour
604 604 compared to those in lowlands, i. e. in highlands there are a lower avoidance irrespective of the
605 605 forest conservation condition.

606 606 In contrasting habitats, such as agriculture and forests, it has been observed that in more
607 607 disturbed environments, there is an increased spatial co-occurrence among predators and prey

608 608 species, as well as among competitors (Kay et al., 2018). However, in less contrasting
609 609 landscapes, such as those in our study, there were slight differences in the measurements within
610 610 the co-occurrence networks. It is conceivable that resources and space are sufficient for species,
611 611 thereby rendering the effects of disturbances on interactions on community interactions not yet
612 612 observable. It is advisable to explore more sensitive measures, such as using the actual
613 613 maximum instead of the theoretical maximum (as in connectivity) and incorporating other
614 614 measurements that involve time.

615 615 *Limitations*

616 616 Camera-trapping studies, which are techniques used to study rare or cryptic animals, are not
617 617 free of bias towards certain species groups, resulting in heterogeneous detection probabilities
618 618 (Burton et al., 2015). Both the technique and biological parameters must be considered as they
619 619 influence the network structure and consequently the derived measurements (Hagen et al.,
620 620 2012). This introduces uncertainty, as the absence of observed time interval between species
621 621 may stem from factors such as low local abundance, seasonal variations, habitat preference,
622 622 intensity of the interaction, or the detectability of the species. It has been proposed that
623 623 population fluctuations in the species could significantly impact network structures,
624 624 complicating comparisons among networks (Andrade-Ponce et al., 2022; Delmas et al., 2019;
625 625 Wells et al., 2014; Krishna et al., 2008). Despite such biases, comparisons among sites within
626 626 the same community, guilds, or group of species in camera-trapping surveys remain feasible
627 627 by accommodating parameters such as abundance or detectability in models. However, changes
628 628 in network structures as a consequence of spatial variations and relative species abundances
629 629 remain as under-explored fields (Hagen et al., 2012).

630 630 Similar to other ecological networks, co-occurrence networks provide snapshots that depict
631 631 community processes (Poisot et al., 2015; Wells et al., 2014). These networks are temporally

632 632 and spatially dynamic, influenced by various factors such as scale (which determines who
633 633 dictates the patterns of space use between predators and prey: predators at larger scales and
634 634 prey at smaller scales; Hammond et al., 2012), local abundances (species must be sufficiently
635 635 abundant to co-occur), changes in trait distribution (species must share coinciding traits), either
636 636 attraction or avoidance to the cameras (Meek et al., 2016), and environmental influences on
637 637 these factors (Poisot et al., 2015). We argue that species abundance affects the structure of the
638 638 networks, since when species are very abundant, co-occurrence happens randomly.

639 639 The network measurements presented here can contribute to understanding spatial and
640 640 temporal co-occurrence patterns between species. When inferring avoidance behaviours,
641 641 several considerations must be taken into account. Our threshold for an avoidance effect (20
642 642 days) was based on a supposed prolonged impact on prey; however, this threshold may vary
643 643 across ecosystems or species compositions. For instance, in a review of countermarking
644 644 studies, Apps et al. (2022) identified durations ranging from 85 hours up to 10 weeks in several
645 645 mammal species. However, after a few days, cues left by one species may diminish in their
646 646 effect on another species, and long-time co-occurrences observed may be being governed by
647 647 different ecological processes (e. g., resources availability, or the presence of a third species).
648 648 Although experimental studies testing avoidance in medium and large-sized mammals are
649 649 scarce, they provide data on the duration of cue effects and reveal a consistent pattern of prey
650 650 avoidance in response to cues left by predators (Say-Sallaz et al., 2019; Apfelbach et al., 2005).
651 651 Therefore, inferences about interactions behaviours should focus on those with the shortest
652 652 time intervals, possibly guided by the cumulative links frequency.

653 653 In this study, we employed a novel approach to measure time intervals as a complementary
654 654 tool for describing and understanding behaviours in predator-prey systems and intraguild
655 655 competition that facilitate species coexistence. We demonstrate that scale plays a crucial role

656 656 in the variation of mammal co-occurrence patterns. In our study system in southern Mexico,
657 657 prey and subordinate competitors avoided large predators, likely to minimise the risk of
658 658 predation. This avoidance was more pronounced in the primary prey of large carnivores,
659 659 whereas smaller or social species seem to rely on other anti-predator strategies, such as seeking
660 660 refuge or staying vigilant. On the other hand, the absence of proximate spatiotemporal predator-
661 661 prey co-occurrences suggests that, in this highly biodiverse region, predators exhibited an
662 662 opportunistic hunting mode to increase the likelihood of encounters with a diverse array of prey
663 663 species scattered across the landscape. We also propose the use of co-occurrence networks for
664 664 habitat comparisons, enabling the measurement of anthropogenic effects on species behaviour.
665 665 Although our study did not provide evidence of the impact of anthropized landscapes on co-
666 666 occurrences, cumulative link frequencies demonstrated potential for exploring temporal,
667 667 spatial, latitudinal, and elevation patterns in areas affected by natural or anthropogenic
668 668 disturbances.

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- 1019 1019 **List of tables**
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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.

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.

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

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 ($IAR \neq 0$).

1049 1049 **Supplementary material**

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1051 1051 **Supplementary material S1.** Mathematical arguments demonstrating how connectance and
1052 1052 the average of normalised degree give equal values in ecological networks.

1053 1053 **Supplementary material S2.** Description of the final seven measures, their modifications, or
1054 1054 their derivations when it was necessary, and their application in the study of
1055 1055 avoidance or tracking behaviours.

1056 1056 **Table S1.** Simulated association scenarios between species A and B, to assess the accuracy of
1057 1057 the approach to infer co-occurrence behaviour in mammal communities. Species A
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1059 1059 **Table S2.** Characteristics of the camera-trap stations in four landscapes in southern Mexico,
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1066 1066 Mexico.

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1070 1070 **Figure S1.** Months (white) in which the camera traps worked in the four landscapes studied
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1072 1072 vertically the stations.

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1075 1075 predator arrows; d) output degrees for predator→predator arrows; e) input degrees for
1076 1076 prey→predator arrows; f) output degrees for predator→prey arrows; g) input degrees
1077 1077 for prey→prey arrows; and h) output degrees for prey→prey arrows.

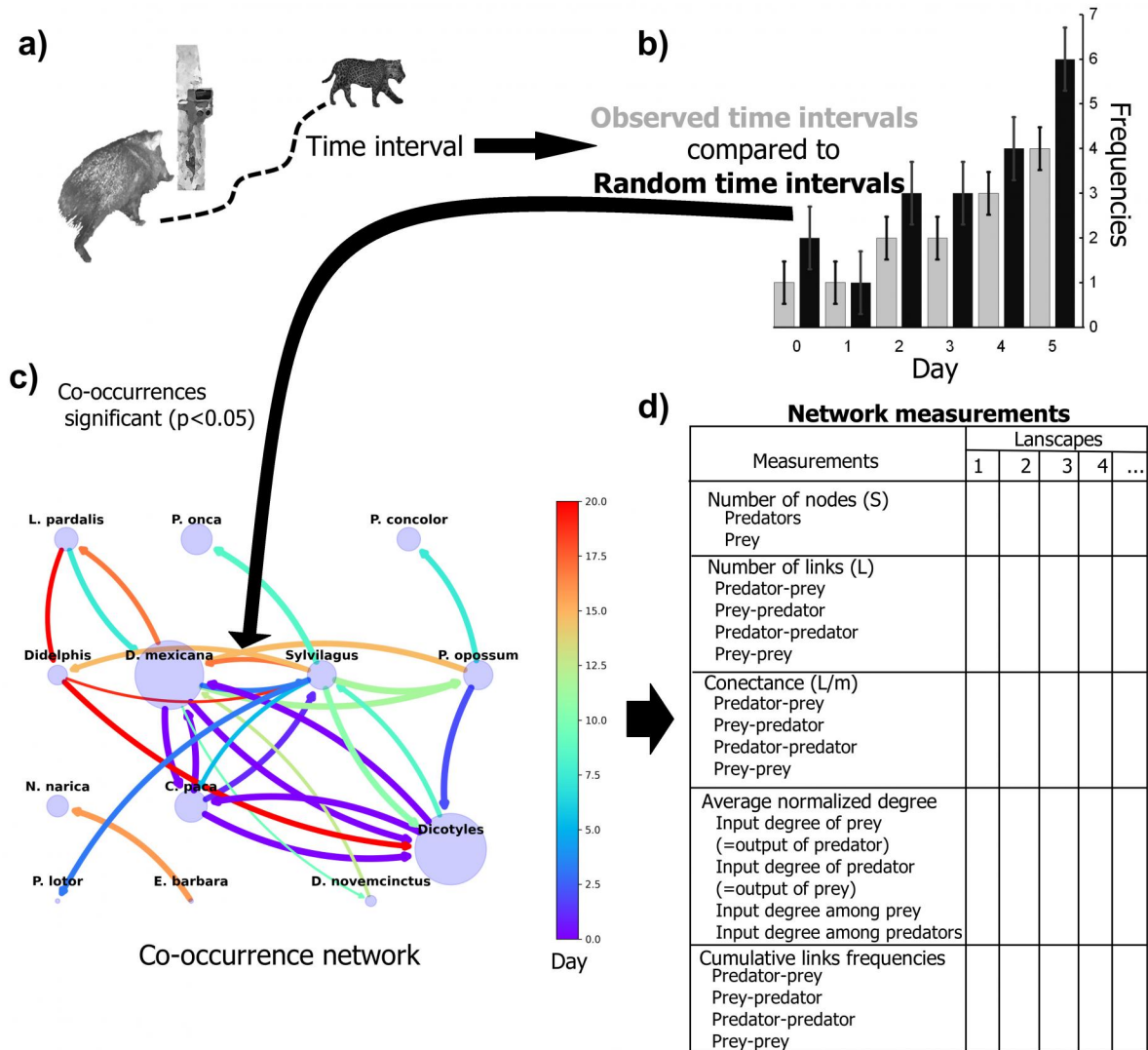
1078 1078 **Figure S3.** Cumulative frequency of links through time intervals: a) co-occurrences in the
1079 1079 complete community; b) prey→predator co-occurrences; c) prey→prey co-
1080 1080 occurrences; d) predator→prey co-occurrences; and e) predator→predator co-
1081 1081 occurrences.

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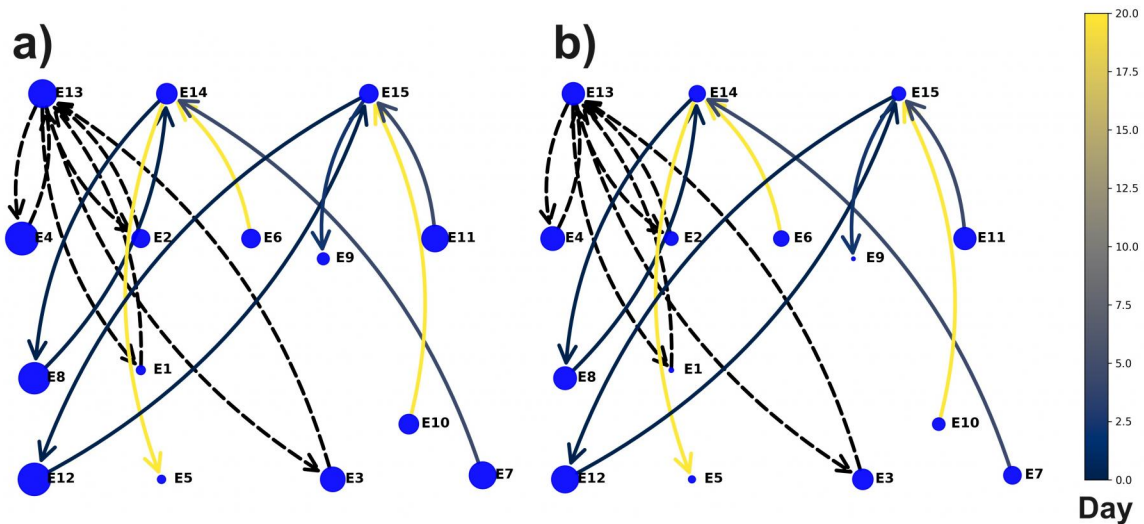
Table 1. Measurements obtained from co-occurrence networks describing interval times between predators and prey in four landscapes in southern Mexico.

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 ($Ld-p/m d-p$)	0	0.06	0.11	0.07
$m=(Sp)(Sd)$				

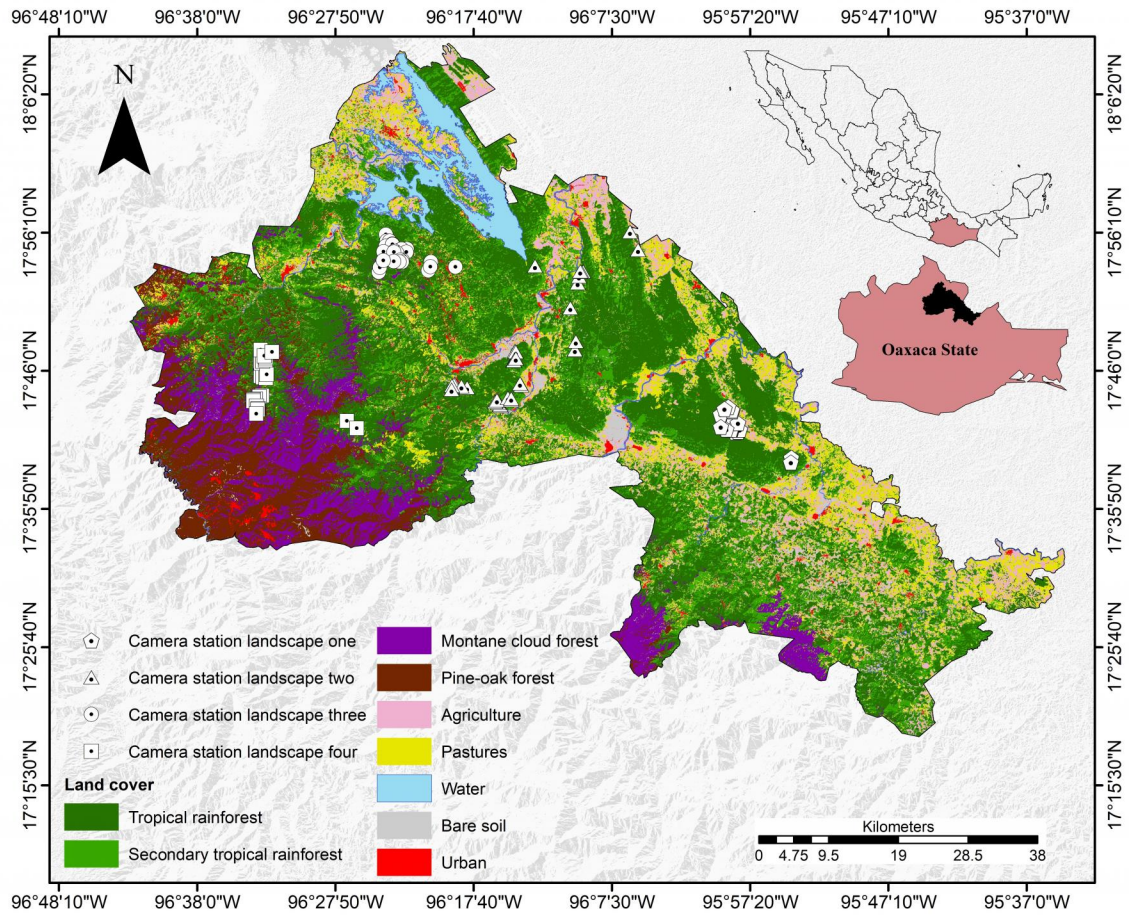
Connectance prey-predator <i>Lp-d/m p-d</i> $m=(Sp)(Sd)$	0.10	0.03	0.16	0.07
Connectance prey-prey <i>(Lp-p/m p-p)</i> $m=(Sp)(Sp-1)$	0.18	0.12	0.16	0.12
Connectance predator-predator <i>(Ld-d/m d-d)</i> $m=(Sd)(Sd-1)$	0.16	0.33	0	0.16



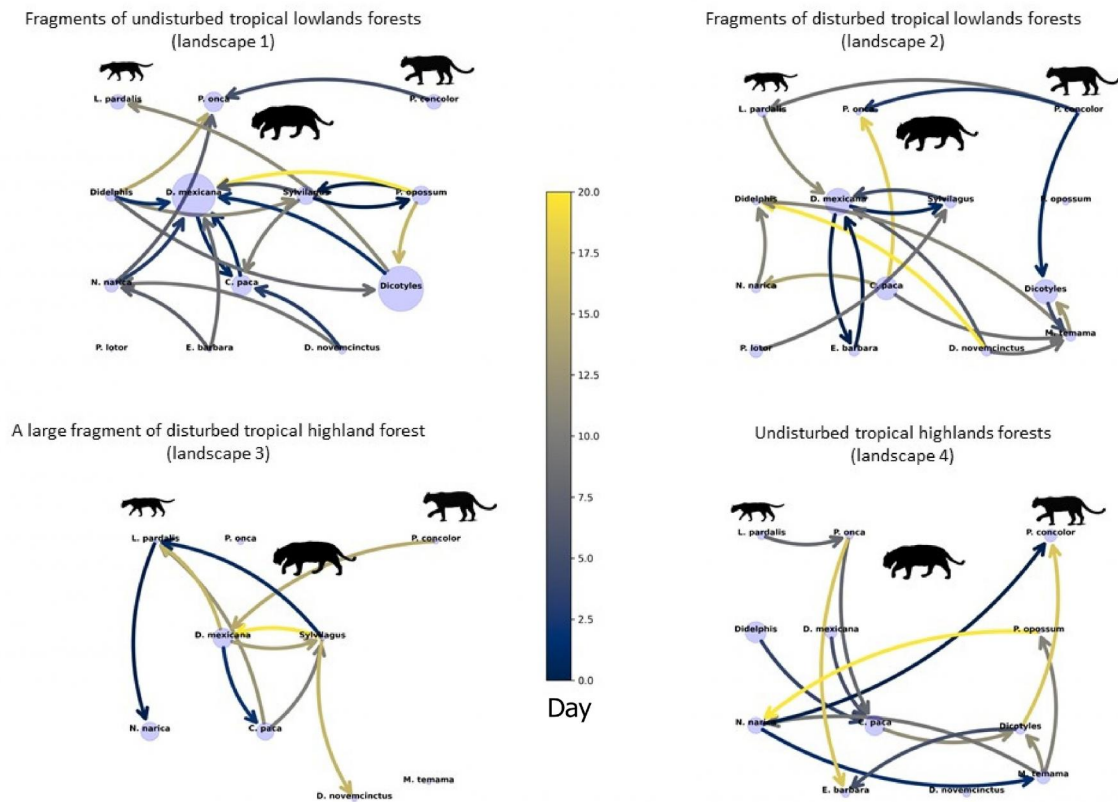
Framework to analyse spatiotemporal associations between species in communities, depicted with co-occurrences networks, and measures proposed to compare these among landscapes or other conditions. The species node size indicates the relative abundance index.



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.



Localization of the landscapes where co-occurrence networks of predator and prey were studied.



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.

Manuscript body

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

Figures

Figure 1 - [Download source file \(2.79 MB\)](#)

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.

Figure 2 - [Download source file \(915.45 kB\)](#)

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.

Figure 3 - [Download source file \(10.95 MB\)](#)

Localization of the landscapes where co-occurrence networks of predator and prey were studied.

Figure 4 - [Download source file \(830.81 kB\)](#)

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.

Supplementary Online Material

File 1 - [Download source file \(156.87 kB\)](#)

Mathematical arguments demonstrating how connectance and the average of normalised degree give equal values in ecological networks.

File 2 - [Download source file \(241.81 kB\)](#)

Description of the final seven measures, their modifications, or their derivations when it was necessary, and their application in the study of avoidance or tracking behaviours.

File 3 - [Download source file \(16.16 kB\)](#)

Simulated association scenarios between species A and B, to assess the accuracy of the approach to infer co-occurrence behaviour in mammal communities. Species A passed in the same station before species B.

File 4 - [Download source file \(15.76 kB\)](#)

Characteristics of the camera-trap stations in four landscapes in southern Mexico, where co-occurrence networks of predators and prey were studied.

File 5 - [Download source file \(16.27 kB\)](#)

Measurements obtained from co-occurrence networks describing interval times between simulated predators and prey.

File 6 - [Download source file \(16.31 kB\)](#)

Normalised output degree for prey species in four landscapes in southern Mexico.

File 7 - [Download source file \(15.93 kB\)](#)

Normalised input degree for predator species in four landscapes in southern Mexico.

File 8 - [Download source file \(15.73 kB\)](#)

Normalised output degree for predators in four landscapes in southern Mexico.

File 9 - [Download source file \(4.03 MB\)](#)

Months (white) in which the camera traps worked in the four landscapes studied in La Chinantla region, southern Mexico. Horizontally we have every year and vertically the stations.

File 10 - [Download source file \(549.49 kB\)](#)

Distribution of the input and output degrees: a) input degrees for predator-prey arrows; b) output degrees for prey-predator arrows; c) input degrees for predator-predator arrows; d) output degrees for predator-predator arrows; e) input degrees for prey-predator arrows; f) output degrees for predator-prey arrows; g) input degrees for prey-prey arrows; and h) output degrees for prey-prey arrows.

File 11 - [Download source file \(553.92 kB\)](#)

Cumulative frequency of links through time intervals: a) co-occurrences in the complete community; b) prey-predator co-occurrences; c) prey-prey co-occurrences; d) predator-prey co-occurrences; and e) predator-predator co-occurrences.