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1 **Title:** The spatial scaling of species interaction networks

2
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35

36 Abstract

37

38 Species-Area Relationships (SARs) are pivotal to understand the distribution of biodiversity
39 across spatial scales. We know little, however, about how the network of biotic interactions
40 in which biodiversity is embedded changes with spatial extent. Here we develop a new
41 theoretical framework which enables us to explore how different assembly mechanisms and
42 theoretical models affect multiple properties of ecological networks across space. We
43 present a number of testable predictions on network-area relationships (NARs) for multi-
44 trophic communities. Network structure changes as area increases because of (1) the
45 existence of different SARs across trophic levels, (2) the preferential selection of generalist
46 species at small spatial extents, and (3) the effect of dispersal limitation promoting beta-
47 diversity. Developing an understanding of NARs will complement the growing body of
48 knowledge on SARs with potential applications in conservation ecology. Specifically,
49 combined with further empirical evidence, NARs can generate predictions of potential
50 effects on ecological communities of habitat loss and fragmentation in a changing world.

51 The species-area relationship (SAR) is amongst the most widely recognised ecological
52 patterns¹⁻³. The larger the geographical area sampled, the richer is the ecological
53 community²⁻⁴. SARs have been used extensively to estimate species richness in a given
54 region^{2,4,5}, and to predict species extinctions due to habitat loss⁶⁻⁸. Yet, for several logistic
55 reasons, most studies of species-area relationships have been traditionally limited to
56 particular taxa and functional groups. SARs for multi-trophic communities are just starting to
57 be documented⁹⁻¹¹ along with the role played by biotic interactions in shaping these
58 relationships^{10,12}.

59 Biotic interactions modulate the outcomes of community assembly and disassembly.
60 Different spatial processes in turn determine which interactions will be realized, ultimately
61 regulating community dynamics¹³⁻¹⁶. For example, higher dispersal rates of species at the
62 top of the food web can increase the proportion of top predators in local communities and
63 in turn enhance top-down regulation^{14,17}. The relationship between area and biodiversity is
64 thus inherently affected by the way ecological interactions and the emerging network
65 structure of multispecies communities change according to the location and size of the area
66 sampled. Unveiling the mechanisms underlying the relationship between area and biotic
67 interactions will provide insights on ecosystem organization across spatial scales^{10,15,18-21}.

68 Gaining a deeper understanding of network-area relationships (NARs) is arguably as
69 important as the knowledge we have on SARs. Indeed, understanding the mechanistic basis
70 of the spatial scaling of network properties is essential to predict the effects of disturbances
71 such as habitat loss and fragmentation on the organisation of multispecies communities,
72 ultimately affecting their persistence and functioning. Disentangling how network structure
73 changes with spatial scale is crucial to interpret empirical data on ecological networks. If the
74 spatial scale affects network structure, then comparative studies should explicitly consider
75 the area sampled as well as the environmental conditions to generate meaningful
76 conclusions, as it is systematically done on studies on diversity distribution patterns²².

77 Here we propose NARs as a theoretical and predictive framework to study the variation of
78 the properties of ecological networks (e.g., connectivity, trophic level composition, trophic
79 chain length) across spatial scales; from small to large areas. We first showcase a number of
80 spatial processes (e.g., dispersal) that could generate different types of NARs. Then we
81 present three simple theoretical models to understand and test how NARs could emerge
82 given specific processes of spatial assembly of multi-trophic communities. As such, we
83 provide new insights on the role of spatial processes on community assembly and structure

84 and explain how this can be used to predict not only the effects of habitat loss and
85 fragmentation on species richness across trophic levels, but also on the structure of biotic
86 interactions. Last, we propose further theoretical and empirical research avenues, stemming
87 from our NARs framework, which could contribute to a unified theory of the spatial scaling
88 of ecological communities.

89 **Mechanisms behind Network-Area Relationships**

90 There are several possible mechanisms responsible for changes of network structure across
91 spatial scales. Box 1 provides a synthesis of the ones analysed here, our expectations for the
92 emergence of NARs based on three mechanisms, and the theoretical models used to
93 evaluate our expectations.

94 1. The first mechanism is derived from the SAR. There is an associated increase in the
95 number of interactions (links) with the increase of species richness with area. Two major
96 hypotheses have been proposed to account for the variation of the number of links with
97 species richness in food webs. Both hypotheses do not explicitly account for species-area
98 relationships. The 'link-species scaling law'²³ states that species interact with a constant
99 number of species independently of species richness^{24,25}. In contrast, the 'constant
100 connectance hypothesis'²⁶ states that the fraction of potential interactions realized (i.e., the
101 number of trophic links L , standardized by the number of potential interactions S^2) is
102 constant across food webs, irrespective of species richness. Empirical evidence suggests that
103 link-species richness relationships lay in between the two hypotheses^{27,28}. If we introduce
104 area within these link-species scaling hypotheses, given that S increases with area, and L
105 scales with S , we expect changes in food web structure with area simply emerging from SAR
106 which are in turn shaped by the specific link-species relationship in place. Brose and
107 colleagues¹⁸ proposed a scaling of trophic links with area by combining species–area and the
108 link–species scaling theories mentioned above. Following their approximation, we generated
109 trophic communities of different sizes (i.e., different number of species) with the *Trophic*
110 *Sampling* model. This model randomly subsamples species from the metaweb (i.e., food web
111 of 200 species generated with the niche model²⁹, see Supplementary Methods and
112 Supplementary Table 1 for a full description), which conforms the regional pool of species,
113 with the only constraint that each consumer needs at least one prey to be selected (Box 1).
114 We expect different shapes of the species richness-area relationships at each trophic level
115 emerging from this trophic constraint. If the spatial scaling of species richness differs among
116 trophic levels, different facets of network structure are expected to change with area. As a

117 consequence, the proportion of species belonging to each trophic level (e.g., basal,
118 intermediate, and top species) will be different at each spatial scale, triggering further
119 consequences on community structure^{9,10,30}. We explore the combination of both
120 mechanisms (i.e. the scaling of the number of links with species richness and the variation of
121 SARs across trophic levels) with the *Trophic Sampling* model (Box1; Supplementary
122 Methods).

123 2. The second mechanism arises from the scaling of colonization-extinction dynamics in
124 multi-trophic communities with area. This was first considered in the Theory of Island
125 Biogeography⁴ (hereafter *TIB*) and its extension to trophic interactions^{16,30-32} (Trophic Theory
126 of Island Biogeography, *TTIB*). The *TIB* predicts the richness of local assemblages from the
127 equilibrium between colonisation and extinction processes. It assumes that the closer the
128 island is to the mainland the larger the colonisation rate⁴, and that the larger the island size
129 the lower the extinction rate due to the increase in population sizes^{33,34}. The *TTIB*
130 incorporates a trophic constraint not considered in the *TIB*: consumers must have a prey on
131 the islands they colonize to be able to establish and persist. Therefore, the richness of the
132 local assemblage and their biotic interactions are defined by the equilibrium between
133 colonisation and extinction processes where species that are diet generalists and/or belong
134 to lower trophic level species are preferentially selected given that they are less affected by
135 the trophic constraint. Generalist species have been shown to be faster colonizers than
136 specialists, ultimately shifting community structure through time^{16,35}. We expect stronger
137 impact of this trophic constraint at smaller areas, where the number of species is smaller. As
138 area increases, the number of species also increases, which in turn increases the opportunity
139 for consumers to find a prey, and therefore not only generalist species will be able to
140 colonize, but also specialists, ultimately promoting changes in network structure as area
141 changes. We use the *TTIB* model¹⁶ to generate islands of different sizes based on different
142 colonisation/extinction ratios where colonization rate is fixed to analyse the network
143 structure resulting from the assembly process for each island size (Box 1; Supplementary
144 Methods).

145 3. The last mechanism arises from the spatial variability in community composition, i.e.,
146 spatial turnover of species. Clumping of species underlies beta-diversity and SARs^{36,37}. Its
147 effect on the variation of network structure with area is driven by the increase in the
148 number of species and their interactions as area increases. The spatial turnover of species
149 composition can be explained by several processes³⁸. Here we focus on the spatial

150 configuration and connectivity of the landscape, which ultimately determines the rates of
151 dispersal of organisms between sites. In fragmented landscapes with major dispersal
152 barriers, species turnover is higher than in homogeneous and continuous environments³⁹.
153 Changes in network structure with area are likely to be mediated by dispersal limitation
154 through its effects on spatial turnover. Larger beta-diversity values will generate larger
155 changes in network structure with area because the number of different species
156 encountered as the area sampled increases will be larger. To test the effects of this process
157 we employ a multi-trophic meta-community model, extending the above-mentioned *TTIB* to
158 entire landscapes, where we control species dispersal between local patches (Box 1;
159 Supplementary Methods).

160

161 **Multi-trophic community assembly models**

162 We explore the effects of each process on the spatial scaling of food web structure with the
163 three models of multi-trophic community assembly mentioned above. We then analyse
164 several network properties at different spatial scales, which allows us to characterize a suite
165 of NARs (see Supplementary Methods for a full description of the assembly models and the
166 network properties used). In this section, we first present the emergence of the mechanisms
167 tested for each assembly model and its effects on the spatial scaling of food web structure.
168 We then provide a comparison between the predictions emerging from each model.

169

170 ***Trophic Sampling model***

171 *Mechanisms.* The number of links scales exponentially with species richness
172 (Slope= 1.91 ± 0.003 -95% confidence interval- in log-log space; Figure 1a). Although the
173 relationship falls between the two link scaling hypotheses (link-species scaling law -Slope ≈ 1
174 in log-log space- and constant connectance hypothesis -Slope ≈ 2 in log-log space-), our
175 results better support the latter. Additionally, we observe different SARs across trophic
176 levels (Figure 1b). The number of intermediate species increases significantly faster with
177 area than the number of top and basal species (See Supplementary Table 2 for statistical
178 analyses). Taken together, these results show that both mechanisms suggested as possible
179 drivers of NARs: (i) link scaling and (ii) different shape of the SARs across trophic levels, are
180 at play in the *Trophic Sampling* model. As expected, these mechanisms trigger changes in
181 network structure from local to regional scales.

182

183 *NARs*. Network complexity properties smoothly increase with area (Figure 2a,
184 Supplementary Figure 1 and Supplementary Table 3). Whereas number of species, links per
185 species, mean indegree and mean outdegree (i.e., mean generality and mean vulnerability,
186 respectively) show a pronounced sub-linear increase quickly approaching the asymptotic
187 value set by the regional network, total number of links increases linearly with area. As a
188 consequence, due to its quadratic relationship with the number of species ($C=L/S^2$),
189 connectance decays sharply with area. That is, network complexity increases with area
190 because larger areas have more species, more links and more links per species. However,
191 given the faster rate of increase in the number of species than in the number of links, we
192 observe a decrease in connectance. Network vertical diversity properties increase with area
193 (Figure 2b, Supplementary Figure 1 and Supplementary Table 3). Mean food chain length
194 (MFCL), fraction of omnivory, and fraction of intermediate species increase sharply with
195 area, reaching the asymptote corresponding to the regional values at relatively small areas.
196 This, in turn, decreases asymptotically the fraction of basal and top species with area. Notice
197 however that the fraction of herbivores (included within the category of intermediate
198 species) decreases asymptotically with area, in parallel to the decrease on the fraction of
199 basal species (Supplementary Figure 2).

200

201 Unexpectedly, network modularity and the distribution of food web motifs do not show
202 strong variations across spatial scales (Figure 2d and Supplementary Figure 1). Modularity,
203 the proportion of simple chains, and apparent competition slightly decrease with area while
204 the proportion of exploitative competition shows a small increase with area.

205

206 ***Trophic Theory of Island Biogeography (TTIB) model***

207 *Mechanisms*. The proportion of specialist species increases with area (Figure 3a and 3b). This
208 indicates that species feeding on a larger number of prey do persist better in small patches
209 than specialist species. Potential indegree distributions (quantified as the species indegree in
210 the metaweb) are consequently shifted towards smaller values with increasing area (Figure
211 3b). Interestingly, this preferential selection of generalist species at smaller scales does not
212 affect the shape of the realized cumulative indegree distributions of the local networks
213 (Figure 3c). Independently of island size, indegree distributions are skewed, i.e., there are
214 more specialist than generalist species in all networks regardless of area. However, it is
215 important to notice that the most specialized species (pointed with arrows in Figure 3c) on
216 small islands have more prey (i.e., they are more generalist) than the most specialized

217 species on large islands. In other words, at smaller areas, we observe a preferential selection
218 of species that are generalists in the regional pool. As area increases, more specialized
219 species are able to persist, which manifests both in a reduction on mean potential indegree
220 and higher specialisation of the most specialised species.

221

222 *NARs*. *TTIB* predictions do not differ qualitatively from the *Trophic Sampling* model. All facets
223 of network complexity increase with area sub-linearly (Supplementary Figure 3 and
224 Supplementary Table 3), except from connectance, which decreases with area. As for the
225 *Trophic Sampling* model, the faster rate of increase in the number of species than in the
226 number of links, causes the decrease in network connectance even though the number of
227 links per species also increases. In terms of vertical diversity, we observe a sharp increase in
228 omnivory, mean food chain length, and fraction of intermediate species (but see
229 Supplementary Figure 2), whereas the fraction of basal and top species show a drastic drop
230 with increasing area (Supplementary Figure 3 and Supplementary Table 3). Network
231 properties of communities assembled with the *TTIB* model show more abrupt changes with
232 area than the *Trophic Sampling* model, with asymptotes of all food web properties reached
233 at smaller areas. The difference between the *TTIB* and the *Trophic Sampling* models lays on
234 the complexity of the assembly process. The stochastic nature of the community assembly
235 enforced by the *TTIB* model, which is the result of colonisation-extinction dynamics, favours
236 the persistence over time of generalist consumers. Specialist consumers that depend on a
237 single resource are more prone to become secondarily extinct given the trophic constraint: if
238 their only resource goes stochastically extinct, they go extinct too. In contrast, the *Trophic*
239 *Sampling* model only searches for possible configurations of a given number of species
240 where every consumer needs to have a resource, without subjecting the selected
241 community to additional stochastic extinctions. Therefore, the effects of the trophic
242 constraint become more evident in the *TTIB*.

243

244 The modular structure and the distribution of motifs of the communities are again not
245 strongly affected by the spatial scale (Supplementary Figure 3 and Supplementary Table 3).
246 Modularity is constant across spatial scales. However, the proportion of simple chains and
247 apparent competition slightly decrease with area while the proportion of exploitative
248 competition increases.

249

250 ***Trophic Meta-community model***

251 *Mechanisms.* Dispersal limitation among local patches affects the turnover of species
252 composition in our meta-communities. Beta-diversity decreases with dispersal rate
253 (Supplementary Figure 4), having further consequences for the spatial scaling of network
254 structure. High dispersal rates increase local diversity (i.e., scaled area 0) and reduces beta-
255 diversity (Supplementary Figure 4), making food webs more similar across the landscape.
256 This implies that the amount of change in network structure is smaller, and that the
257 asymptote that corresponds to regional network properties is reached at even smaller areas
258 than for low values of dispersal. As a consequence, for high values of dispersal, we need to
259 aggregate a smaller number of local communities to recover the structure of the large
260 metaweb than with low dispersal rates and with the *TTIB*.

261

262 *NARs.* At low dispersal rates, network-area relationships are similar to those observed for
263 the *TTIB*. Both network complexity and vertical diversity change with area at a smaller rate
264 than compared with the high dispersal scenario (Supplementary Figure 5 and Supplementary
265 Table 3). High levels of dispersal among local communities weaken the scale-dependency of
266 network structure: increasing the area sampled has less effect on network properties at high
267 levels of dispersal because the values of the properties of the regional network (i.e., the
268 asymptote) are reached earlier. Dispersal increases food web complexity (i.e. more species,
269 links and links per species) and its vertical diversity at both local and regional scales
270 (Supplementary Figure 5 and Supplementary Table 3).

271

272 As for the previous two models, network modularity and the distribution of motifs show
273 small variations across spatial scales for both dispersal levels, being slightly less pronounced
274 for high dispersal levels (Supplementary Figure 5). Network modularity, the proportion of
275 simple chains and apparent competition show a marginally decrease with area while the
276 proportion of exploitative competition shows a small increase.

277

278 ***Comparison between models***

279 We found both quantitative and qualitative differences among NARs resulting from the
280 three models (Figure 4, Supplementary Table 3 and Supplementary Figure 6). Qualitatively,
281 the *Trophic Sampling* model shows smooth changes in network structure with area. The
282 changes in network structure observed with the *TTIB* will be more abrupt as area increases
283 reaching the asymptote faster. Similarly, the *Trophic Meta-community* model with low
284 dispersal leads to abrupt changes in network structure with area. However, important

285 qualitative differences exist between the two that allow for determining the most likely
286 mechanism behind empirical patterns of network scaling (Box 2, Supplementary Figure 6).
287 Finally, the *Trophic Meta-community* model with high dispersal shows the smallest change in
288 network structure with area reaching the asymptote for the regional network very small
289 spatial scales.

290 Quantitatively, the *Trophic Sampling* model shows the lowest rate of growth (g , measured as
291 the steepness of a bounded exponential fitted to the data; Supplementary Table 3) for all
292 complexity properties, followed by the *Trophic Meta-community* model with low dispersal,
293 the *TTIB* and lastly the *Trophic Meta-community* model with high dispersal. This implies that
294 increasing the area sampled has a less abrupt effect for NARs in the *Trophic Sampling* model,
295 but this effect is manifested over a larger range of areas sampled. At the other extreme of
296 the spectrum, the *Trophic Meta-community* model with high dispersal shows a rapid change
297 in network structure at relatively small spatial scales. Hence, the scale-dependency of
298 network structure depends on whether we focus on the rate of change of a given network
299 property for a given increase in area, or on the range of areas across which the property
300 changes.

301

302 The *Trophic Meta-community* model with low dispersal has the lowest growth rate for most
303 vertical diversity properties, followed by the *Trophic Sampling* model. Whereas the *TTIB*
304 shows the highest growth rate for the proportion of basal and intermediate species, the
305 *Trophic Meta-community* model with high dispersal shows the highest values for the
306 proportion of top species and MFCL (Supplementary Table 3). We compared each model
307 with its non-trophic constrained version in Supplementary Figure 7. The comparison shows a
308 faster initial increase in complexity for communities assembled using the unconstrained
309 versions of the *TTIB* and the *Trophic Meta-community* model with a levelling off for larger
310 areas, while the unconstrained version of the *Trophic Sampling* model only shows
311 differences for vertical diversity metrics (Supplementary Figure 7).

312

313 **Testable predictions**

314 We presented a theoretical framework predicting the existence of a number of network-
315 area relationships (NARs) in spatial multi-trophic communities, arising from different
316 assembly processes. Although we obtained some universal predictions independent of the
317 particularities of the assembly process used, we found differences in regards to the exact
318 shapes of the specific NAR under scrutiny. This allows for specific predictions emerging from

319 each model to be tested with empirical data (Boxes 2 and 3). In particular, we showed that
320 the existence of different SARs across trophic levels has consequences for the variation of
321 network structure with increasing area, that the preferential selection of generalist species
322 at small areas causes drastic changes on network structure in space, and that dispersal
323 limitation is a key process influencing trophic interactions across spatial scales. Here we
324 summarize and discuss a number of empirically testable predictions emerging from our
325 framework (Boxes 2 and 3), and provide suggestions on where to focus future research
326 efforts to better understand the causes and consequences of the variation of network
327 structure across spatial scales.

328

329 **Beyond single trophic levels: multi-trophic SARs and NARs**

330 The spatial scaling of network structure cannot be fully explained by the increase in species
331 richness with area. It is well established that species richness affects several food web
332 properties. In many cases, differences in network properties simply result from differences
333 in species richness between the communities studied^{40–43}. However, the spatial scaling of
334 species richness is likely to vary across trophic levels^{9,10,30}. This differential scaling has further
335 consequences for the variation of trophic network structure with area^{10,12,30}. Recently, Roslin
336 and colleagues¹⁰ showed that the slope of the species-area relationship steepens from plants
337 to herbivores and from primary to secondary parasitoids. This in turn triggers a decrease in
338 food chain length from large to small islands. In contrast, our *Trophic Sampling* model
339 showed the steepest species-area slope for intermediate species (Figure 1b). This
340 contrasting result can be attributed to the fact that parasitoids tend to have exceptionally
341 narrow diet breadths when compared with other top predators, being classified as a
342 separate category within food webs in comparative analyses²⁸. We considered wider diet
343 breadths for top predators, which allowed them to overcome the trophic constraint^{9,30}, and
344 therefore, reduce the slope of their SARs by being selected locally even when the number of
345 species was small. The *Trophic Sampling* model thus shows that, in the absence of spatial
346 structure, and in totally homogeneous communities, different SARs across trophic levels will
347 emerge and will bias NARs towards higher fractions of intermediate species and longer food
348 chains.

349 In the theoretical work developed by Brose and colleagues¹⁸, where they derived the
350 spatial scaling of trophic links with area by combining the species–area relationship and the
351 link–species relationship, they predicted the effect of having different SARs across trophic

352 levels for the scaling of the number of links with area. Here we extended the analyses of this
353 effect to many other aspects of network structure beyond the number of links (e.g. degree
354 distributions, mean food chain length or modularity). By using a mechanistic approach to
355 understand the spatial scaling of network structure we can determine the specific effects of
356 each process tested and generate specific and testable predictions on how network
357 structure will change with area depending on the spatial scenario and the processes in
358 operation.

359 In agreement with our expectations, the *TTIB* model exhibited a strong variation of
360 network structure with area, mediated by the preferential selection of generalist species
361 that emerges from the trophic constraint (Figure 3). The effect of this constraint on species
362 occupancy decreases with area because the total number of species increases, whereby the
363 chances of finding a suitable prey also increase. Thus, colonisation-extinction dynamics
364 favoured greater occupancy of generalist consumers in small areas, where fewer prey are
365 available. The occupancy for a given colonisation and extinction rate is predicted to reach an
366 asymptote with increasing prey species richness, because for larger diet breadths,
367 consumers are no longer constrained to find their prey^{16,35}. The comparison between the
368 *TTIB* and its non-constrained *TIB* version, shows a faster initial increase in complexity (i.e.,
369 species and links/species) for communities assembled using the *TIB* with a levelling off for
370 larger areas, illustrating the loss of importance of the trophic constraint as area increases
371 (Supplementary Figure 7). Therefore, as the area sampled increases, the proportion of
372 specialist species also increases (Figure 3a and 3b).

373 Food web degree distributions are usually skewed (many specialists, few
374 generalists)⁴⁴⁻⁴⁶. In spite of the fact that smaller islands host species with larger potential
375 diet breadth (i.e., species indegree in the metaweb; Figure 3a and 3b), the indegree
376 distributions of the realized food webs kept this characteristic skewness (Figure 3c). Given
377 the importance of the degree distribution to community robustness to species loss, this
378 suggests that food web robustness is preserved across spatial scales. The *TTIB* thus suggests
379 that important features of network structure might reflect those present in the regional pool
380 and are maintained across spatial scales, as it is shown for the degree distribution.

381 **Dispersal in multi-trophic metacommunities and NARs relationships**

382 Dispersal is a key process driving species-area relationships^{4,47,48}. Competitive meta-
383 community models, for instance, have shown that moderate to intermediate levels of

384 dispersal reduce local competitive exclusion, increasing local diversity via colonization-
385 competition trade-offs⁴⁸⁻⁵¹ or by enhancing source-sink dynamics when resources are
386 heterogeneously distributed in space^{47,52}. However, high levels of dispersal would
387 homogenize local communities, leading to regional competitive exclusion and to reductions
388 of the overall diversity^{47,53}.

389 The *Trophic Meta-community* model also predicts that local diversity increases with
390 dispersal, reducing differences between patches (i.e., lower beta-diversity) and leading to a
391 more homogeneous meta-community (Supplementary Figure 4). The higher the dispersal
392 rate, and thus the lower spatial beta-diversity, the smaller the effect of increasing area on
393 network properties because sampling a small number of local communities is enough to
394 capture the structure and composition of the regional community (Supplementary Figure 5).
395 However, given the absence of direct competitive interactions in our models, both regional
396 and local diversity will increase until they reach the maximum number of species in the
397 regional pool. This observation may differ in presence of top-down regulation. Our models
398 used a bottom-up sequential food web assembly, with the food chain consistently increasing
399 with the addition of new species. Future explorations of the effect of dispersal on the
400 structure and composition of multi-trophic communities should integrate the trophic
401 constraints used here together with indirect competitive interactions.

402 Pillai and colleagues²⁰ used a meta-community model to explain the emergence of
403 complex food webs through the linkages between patches provided by omnivorous and
404 generalist species. In our models, consumer's diet specialization constrains the probability of
405 finding a required resource, and hence, disfavour the presence of specialist consumers in
406 local communities. Given that generalist and omnivorous consumers have more potential
407 resources, they are more likely to persist, which allows for the emergence of network
408 complexity (i.e. higher species richness with more links and links per species) in space when
409 local patches are aggregated. Yet, the role of generalists for the spatial scaling of network
410 complexity depends on dispersal. Under dispersal limitation, where a lower number of
411 species coexist locally, generalists are key for the spatial scaling of food web complexity
412 because they are the ones spatially connecting patches. However, in the absence of
413 dispersal limitation, a higher number of species coexist in local communities, increasing the
414 probability of specialists encountering their required prey, and thus, generalists are no
415 longer key contributors to the increase of food web complexity in space. This increase in
416 complexity enhanced by dispersal, at both local and regional scales, might have important

417 implications for the study of the stabilising effect of space on ecological communities^{14,17,54}.

418 **On the need to incorporate the spatial scale in comparative network studies**

419 Empirical characterizations of species interaction networks often fail to acknowledge the
420 spatial scale at which these networks are observed. The restricted number of empirical
421 studies that have done so support our theoretical predictions for several network-area
422 relationships. The variation in food-chain length with ecosystem size (e.g., lake volume) is an
423 example. Although ecosystem productivity can modulate this variation⁵⁵, ecosystem size on
424 its own is a good predictor of food-chain length⁵⁶. Our models agree with this empirical
425 observation, showing that mean food chain length increases with area.

426 Our predictions of NARs suggest caution must be exercised in comparative studies of
427 network properties. If network properties vary systematically across spatial scales, then
428 comparative network studies that fail to acknowledge the spatial scale at which the study
429 was performed will wrongly estimate the causes of variation of the structure of ecological
430 networks.

431 The variability observed in food web properties often disappears when species
432 richness is controlled for⁴⁰⁻⁴³. Then, as area also affects species richness, a key question is to
433 what extent comparative studies addressing variation in network properties need to control
434 additionally for the area sampled, or if the effects of area on network properties are solely
435 driven by richness. In our models, area not only determines the number of species but also
436 their identity based on their feeding traits (i.e., more or less generalists) and where they are
437 placed within the food web (i.e., across trophic levels). Regardless of area, for a given
438 number of species, we observe differences across models in terms of other network
439 properties (Figure 4b and 4c), suggesting that each spatial process has different effects on
440 structuring communities. While network complexity metrics are highly correlated with
441 species (i.e., for a given S , there is no variation across models), vertical diversity properties
442 are not fully explained by the number of species. For instance, network mean indegree (i.e.
443 mean generality) (Figure 4b) shows little variation between models once controlled by the
444 number of species; and this variation disappears when we additionally control by
445 connectance²¹. However, the proportion of species at each trophic level (Figure 4c) is
446 difficult to predict solely from the number of species, given that each spatial process affects
447 these proportions differently. This suggests that controlling for both species richness and
448 connectance will account for most of the variation in complexity properties across spatial
449 scales, and hence it would suffice in comparative studies, but it would not explain all the

450 variation observed in vertical diversity properties. Therefore, incorporating the spatial scale
451 of sampling in comparative studies would provide additional key information on the scaling
452 of certain network properties.

453

454 Moreover, we cannot disregard the effects of habitat size in more complex
455 environments. Our models and the few empirical NARs available mostly concern
456 communities from relatively homogeneous environments. In more heterogeneous
457 landscapes, other processes are at work, such as species sorting (i.e., species have different
458 preferences for different habitats within a given area) and priority effects. Intense species
459 sorting would likely create compartments and result in modular or compartmented
460 webs^{57,58}. Food webs are compartmented when interactions between species are either
461 more numerous or stronger within the compartment and few or weak between
462 compartments^{57,58}. Our results show very little variation on the modular structure of the
463 communities across spatial scales, but this prediction is likely to be affected when
464 environmental heterogeneity is considered, revealing a potential effect of area on network
465 properties independent of species richness and connectance.

466 **Implications for conservation**

467 Habitat destruction is the primary cause of the erosion of biodiversity⁵⁹⁻⁶¹. SARs have been
468 extensively used to estimate species loss due to habitat loss⁶⁻⁸. Understanding its effects on
469 the structure of ecological networks is crucial to better preserve ecosystem structure and
470 functioning⁶²⁻⁶⁶. Our results provide insights into how habitat loss and fragmentation would
471 lead to network simplification, reducing not only species richness, but also, and perhaps
472 more importantly, their interactions. Nonetheless it is important to distinguish the effect of
473 losing habitat (i.e., moving across the x-axis in Figures 2 and 4a) from the effect of limiting
474 species dispersal (i.e., different dispersal scenarios in Figure 4a and Supplementary Figure 5)
475 by, for example, habitat fragmentation. Our results suggest that habitat loss should reduce
476 the number of links per species (L/S), the proportion of omnivorous species, and shorten
477 food chains (MFCL). Additionally, we observe that fragmented communities with higher
478 dispersal limitation should be less complex across spatial scales, with e.g. less species and
479 less links per species. In general, our framework shows that fragmented communities should
480 be expected to be less resistant to habitat loss showing dramatic changes in food web
481 structure even for small habitat reductions (Figure 4a and Supplementary Figure 5).

482

483 **Limitations and future research**

484 Species interactions can experience spatial turnover by themselves, correlated or
485 uncorrelated with species composition turnover⁶⁷. Even if two species co-occur in space,
486 they may not interact if the environment is not favourable enough⁶⁸, if one of them is rare⁶⁹,
487 or if they experienced phenological mismatches⁷⁰. Also, we have assumed dispersal
488 constancy across trophic levels. Different scales of movement across trophic levels^{13,17}, may
489 also promote variation in network structure across space. Incorporating such processes into
490 theoretical frameworks like the one presented here could increase the accuracy of our
491 predictions.

492 Despite the realization that the effect of area on network properties is intimately
493 related to that of richness or connectance, NARs open new possibilities to explore network
494 stability and functioning across spatial scales. Several aspects of food web structure and
495 complexity have been studied locally and related to community stability and functioning,
496 such as the importance of diversity⁷¹, the presence of stabilising modules like the
497 omnivorous loop structures^{72,73} or the predominance of weak interactions^{74,75}. Scaling up in
498 space alters network properties suggesting that community stability and functioning might
499 also vary across spatial scales. Assessing network structure at different spatial scales can,
500 therefore, provide new insights to analyse and understand community stability and
501 functioning in relation to the different processes that are at play at each spatial scale.

502 **Code Availability**

503 Custom code used to develop the theoretical models is available upon request.

504 **Data Availability**

505 Data sharing not applicable to this article as no datasets were generated or analysed during
506 the current study.

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514 **Competing financial interests:**

515 The authors declare no competing financial interests.

516

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Boxes

Box 1. A mechanistic approach to understand Network-Area relationships (NARs).

Model used	Trophic Sampling	Trophic Theory of Island Biogeography	Trophic Meta-community
Process tested	The effect of Species-Area Relationship (SAR) on the spatial scaling of network structure.	Extinction probability (<i>e</i>) decreases with Area size promoting a general increase in species richness.	Dispersal limitation increases spatial heterogeneity in species composition (i.e., beta-diversity).
Underlying mechanisms for NARs	The added effect of the scaling of the number of links with species richness and the variation of SARs across trophic levels.	Larger species richness in larger areas favours the opportunity for all consumers (not only generalists) to find a prey. This promotes a preferential selection of generalist species in smaller areas that will generate changes in network structure across spatial scales.	The higher the heterogeneity in species composition across space, the stronger dependency of network structure with area: increasing the area sampled increases the number of new species sampled and has a stronger effect on network properties.

“INSERT FIGURE HERE”

Model description	The <i>Trophic Sampling model</i> subsamples species randomly from the regional pool of 200 species (metaweb). It uses the species – area relationship ($S = kA^z$; with $k = 10$ and $z = 0.27$) to obtain the number of species expected for a given area and, therefore, to construct food webs of different sizes that correspond to different areas. Local community assembly is only constrained by trophic interactions, i.e., consumers need a prey to be selected.	The <i>Trophic Theory of Island Biogeography</i> assumes that species from the mainland (metaweb) can colonise the island with a fixed colonisation probability (<i>c</i>) and can go extinct with a range of extinction probabilities (<i>e</i>). Stochastic colonisation-extinction dynamics are trophically constrained. That is, consumers need to have a prey on the island to be able to colonize, and they go extinct if their last prey goes extinct. Area is determined by the ratio between colonization and extinction (c/e).	It consists in 75 local patches connected to the mainland (metaweb) and connected to themselves depending on the distance. Species can arrive to each local patch from the metaweb with a fixed colonisation probability and can go extinct with a fixed probability. Species can disperse between connected local patches according to different dispersal values. Stochastic colonisation-extinction dynamics and dispersal are trophically constrained. Area is determined by the aggregation of local communities (patches) in an ever-increasing fashion from 1 to the maximum number of communities (75).
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678

679 **Box 2. Empirical data and testable predictions.**

680 Each model used could be represented by a different empirical dataset. The *Trophic*
681 *Sampling* model (a) corresponds to random subsamples of different area sizes all included
682 within a larger homogeneous area. The *Trophic Theory of Island Biogeography* model (b)
683 corresponds to independent and isolated islands (or patches) of different sizes (e.g., an
684 archipelago). The *Trophic Metacommunity* model (c) corresponds to independent local
685 communities (e.g., patches, islands) of the same size connected through dispersal, where the
686 spatial scaling of network structure is given by the progressive aggregation of different
687 localities.

688

689 “INSERT FIGURE HERE”

690

691 We can predict a different scaling of network structure in space emerging from each type of
692 data (Figure 4 and Supplementary Figure 6). When area is subsampled randomly, network
693 structure will smoothly change as we increase the size of the area sampled. In isolated
694 islands, where each island constitutes one fully assembled community, changes in network
695 structure will be more abrupt as area increases reaching the asymptote faster. In
696 metacommunities, the spatial scaling of network structure will be determined by the spatial
697 heterogeneity in species composition. In fully connected metacommunities (i.e., high
698 dispersal), changes in network structure with area will be minimal because the complexity
699 and the vertical diversity of the regional network are already reached at small spatial scales.
700 In poorly connected metacommunities (i.e., low dispersal), the spatial scaling of the majority
701 of the network properties will be qualitatively similar the one observed in isolated islands.
702 However, two fundamental network properties can elucidate the difference between the
703 two types of data: connectance and the percentage of basal species. In highly fragmented
704 metacommunities with low dispersal, network connectance and the percentage of basal
705 species will be higher through the entire range of areas (Supplementary Figure 6), suggesting
706 that the trophic constraint is having a strong effect across spatial scales. In isolated islands,
707 connectance and the percentage of basal species drop drastically with a minimal increase of
708 area, indicating a relief of the trophic constraint with area.

709

710

711 **Box 3. Universal predictions.**

712 **Network Complexity**

713 *Network Degree distribution preserves its skewness across spatial scales, but specialism*
714 *increases with area.*

715 Indegree distributions are skewed regardless of area, i.e., there are more specialist than
716 generalist species in all networks irrespective of the spatial scale (Figure 3c). The preferential
717 selection of generalist species at smaller scales affects the starting point of the distribution -
718 determined by the most specialized species- but not its shape. The most specialized species
719 have more prey at smaller than at larger spatial scales.

720

721 **Network Vertical diversity**

722 *Species-Area Relationships (SARs) vary across trophic levels.*

723 In food webs, the number of intermediate species increases faster with area than the
724 number of top and basal species (Figure 1b). This results in steeper slopes of SARs for
725 intermediate species. Networks where top predators are heavily specialized, i.e., host-
726 parasitoid networks, should be an exception, with steeper slopes as trophic level increases.

727

728 *The proportion of omnivorous links increases with area promoting an increase of food chain*
729 *length.*

730 The faster increase in the number of intermediate species with area facilitates the growth of
731 the number of links among intermediate species (e.g., intraguild predation) generating an
732 increase of food chain length.

733

734 **Network Modules**

735 *Network modularity is constant across spatial scales in homogeneous landscapes.*

736 Heterogeneous landscapes, however, are likely to promote the emergence of network
737 compartments due to, for example, the effect of species sorting. This will likely generate an
738 increase of modularity with area, as more compartments will be captured as the area
739 sampled increases.

740

741

742

743 **Figures**

744 **Figure 1.** Mechanisms underlying NARs. a) Scaling of the number of links with species
745 richness. Orange line: Constant Connectance Hypothesis (CCH; that is, the number of links in
746 a web increases approximately as the square of the number of trophic species: $L \approx S^2$);
747 Green line: Links Species Scaling Law (LSSL; the number of links per species in a web is
748 constant and scale invariant at roughly two: $L \approx 2S$); Grey line: links-species relationship for
749 the *Trophic Sampling* model. b) Species-Area relationships (SARs) per trophic level for the
750 *Trophic Sampling* model. Area values close to -4 correspond to local communities and values
751 close to 0 correspond to regional communities. Notice that area was rescaled to fall in the
752 range between 0 and 1, where 0 is the smallest local scale and 1 is the largest regional scale
753 and these are the log-transformed values of area. Black line: basal species; Dashed line:
754 intermediate species; Dotted line: top species. Shaded areas correspond to 95% confidence
755 intervals.

756

757 **Figure 2.** Network-Area relationships (NAR) for the *Trophic Sampling* model. Area values
758 close to 0 correspond to local communities and values close to 1 correspond to regional
759 communities. Relationship of (a) the Number of Species, (b) the Number of links per species,
760 (c) Mean food Chain Length and (d) Modularity with Area. Notice that the Species-Area
761 relationship shown in (a) is given by $S = kA^z$, with $k = 10$ and $z = 0.27$. Lines represent a
762 GAM fit to data points.

763

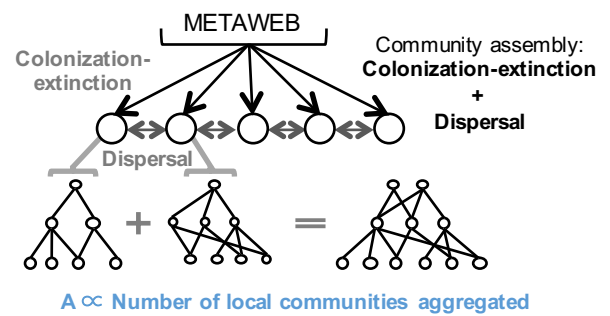
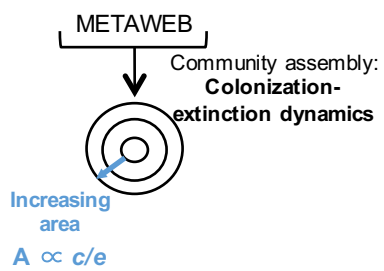
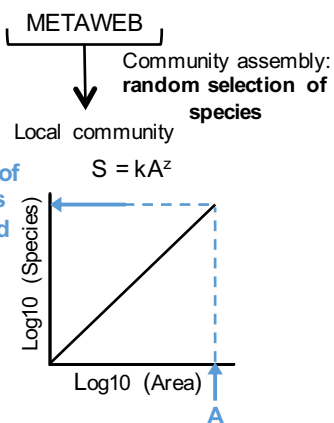
764 **Figure 3.** Specialism across spatial scales. a) Variation of food web mean potential indegree -
765 quantified as the species indegree (i.e. generality) in the metaweb- with area for the *TTIB*
766 model. Area values close to 0 correspond to local communities and values close to 1
767 correspond to regional communities. Shaded areas show 95% confidence intervals. b)
768 Species potential indegree distributions for islands of different sizes simulated as the ratio
769 between colonisation and extinction rates, with higher ratios representing larger island
770 areas. Colonisation rate is fixed at 0.2 and each colour represents a different value of
771 extinction (i.e., red and purple correspond to the largest and the smallest area respectively).
772 c) Realised indegree distributions across spatial scales for the *TTIB* model. The cumulative
773 probabilities $P_c(k)$, for $\geq k$, where $P(k)$ is the probability a species has k prey in the network,
774 is represented normalized by the mean number of links per species in the network. Coloured

775 arrows show the starting point of the distribution for each island size. Colours correspond to
776 the same area sizes as in b.

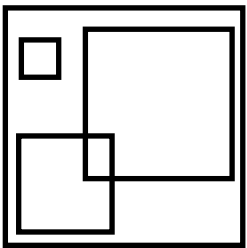
777

778 **Figure 4.** Comparison between models. In (a) variation of the number of links with area for
779 the three different models of community assembly. Area values close to 0 correspond to
780 local communities and values close to 1 correspond to regional communities. In (b) and (c)
781 comparison between models controlling by the number of species. For a given number of
782 species, differences in network properties between models. Blue line: *Trophic Sampling*
783 model; Green line: *Trophic theory of Island Biogeography*; Red line: *Trophic Meta-community*
784 model $d=0.01$; Orange line: *Trophic Meta-community* model $d=0.1$. Notice that high dispersal
785 rates in the *Trophic Meta-community* model increase local diversity resulting in local
786 communities with more than 70 species. Lines represent a GAM fit to data points. Shaded
787 areas show 95% confidence intervals.

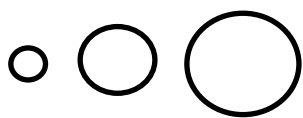
788



a.



b.



c.

