

1 Ecological network complexity scales with area

2 Núria Galiana^{1,2*}, Miguel Lurgi^{1,3}, Vinicius A. G. Bastazini^{1,4}, Jordi Bosch⁵, Luciano Cagnolo⁶, Kevin
3 Cazelles⁷, Bernat Claramunt-López^{5,8}, Carine Emer^{9,10}, Marie-Josée Fortin¹¹, Ingo Grass¹², Carlos
4 Hernández-Castellano^{5,8}, Frank Jauker¹³, Shawn J. Leroux¹⁴, Kevin McCann⁷, Anne M. McLeod¹⁴, Daniel
5 Montoya^{1,15,16}, Christian Mulder¹⁷, Sergio Osorio-Canadas^{5,18}, Sara Reverté⁵, Anselm Rodrigo^{5,8}, Ingolf
6 Steffan-Dewenter¹⁹, Anna Traveset²⁰, Sergi Valverde^{21,22}, Diego P. Vázquez^{23,24}, Spencer A. Wood²⁵,
7 Dominique Gravel²⁶, Tomas Roslin^{27,28}, Wilfried Thuiller²⁹ and José M. Montoya¹.

8 Affiliations:

- 9 1. Centre for Biodiversity Theory and Modelling, Theoretical and Experimental Ecology Station, CNRS,
10 2 route du CNRS, 09200 Moulis, France.
- 11 2. Institut de Ciència i Tecnologia Ambientals, Universitat Autònoma de Barcelona, Barcelona, Spain.
- 12 3. Department of Biosciences, Swansea University, Singleton Park, SA1 8PP, UK.
- 13 4. Rui Nabeiro Biodiversity Chair, MED - Mediterranean Institute for Agriculture, Environment and
14 Development, University of Évora. Casa Cordovil 2º Andar, Rua Dr. Joaquim Henrique da Fonseca,
15 7000 – 890 Évora, Portugal.
- 16 5. CREAf, Bellaterra (Cerdanyola del Vallès), E08193, Catalonia, Spain.
- 17 6. Institute for Multidisciplinary Plant Biology (IMBIV), Faculty of Exact, Physical and Natural
18 Sciences, National University of Cordoba and CONICET, Avenida Vélez Sarsfield 1611, 5000
19 Córdoba, Argentina.
- 20 7. Department of Integrative Biology, University of Guelph, Guelph, ON, Canada.
- 21 8. Universitat Autònoma de Barcelona, Bellaterra (Cerdanyola del Vallès), E08193, Catalonia, Spain.
- 22 9. Departament of Ecology, Institute of Bioscience, São Paulo State University (UNESP), CP 199,
23 13506-900, Rio Claro - SP, Brazil.
- 24 10. Department of Botany, University of Pernambuco (UFPE), CP 199, 13506-900, Recife - PE, Brazil.
- 25 11. Department of Ecology & Evolutionary Biology, University of Toronto, Ontario, Canada.
- 26 12. Ecology of Tropical Agricultural Systems, University of Hohenheim, Garbenstrasse 13, 70599
27 Stuttgart, Germany.
- 28 13. Department of Animal Ecology, Justus Liebig University Giessen, Heinrich-Buff-Ring 26-32,
29 Giessen, 35392 Germany.
- 30 14. Department of Biology, Memorial University of Newfoundland, St. John's, Newfoundland and
31 Labrador, Canada.
- 32 15. Basque Centre for Climate Change (BC3), Edificio Sede 1, Planta 1, Parque Científico UPV-EHU,
33 Barrio Sarriena, Leioa, Spain
- 34 16. IKERBASQUE, Basque Foundation for Science, Bilbao, Spain
- 35 17. Department of Biological, Geological and Environmental Sciences, University of Catania, 95124
36 Catania, Italy.
- 37 18. Departamento de Ecología de la Biodiversidad, Instituto de Ecología, Universidad Nacional
38 Autónoma de México, AP 70-275, CP 04510, México City, México.
- 39 19. Department of Animal Ecology and Tropical Biology, Biocenter, University of Würzburg, Am
40 Hubland, 97074 Würzburg, Germany.
- 41 20. Global Change Research Group, Inst. Mediterrani d'Estudis Avançats (CSIC-UIB).
- 42 21. Evolution of Technology Laboratory, Institute of Evolutionary Biology, CSIC–Universitat Pompeu
43 Fabra, Barcelona, Spain.
- 44 22. European Centre for Living Technology, Venice, Italy.
- 45 23. Argentine Institute for Dryland Research, CONICET & National University of Cuyo, Avenida Ruiz
46 Leal s/n, 5500 Mendoza Argentina.
- 47 24. Faculty of Exact and Natural Sciences, National University of Cuyo, Padre Jorge Contreras 1300,
48 M5502JMA Mendoza Argentina.
- 49 25. eScience Institute, University of Washington, Seattle, WA, USA.
- 50 26. Département de Biologie, Université de Sherbrooke, Sherbrooke, Quebec, Canada.
- 51 27. Department of Ecology, Swedish University of Agricultural Sciences, P.O. Box 7044, SE-750 07
52 Uppsala Sweden.
- 53 28. Department of Agricultural Sciences, University of Helsinki, PO Box 27, (Latokartanonkaari 5), FI-
54 00014 Helsinki Finland.
- 55 29. Univ. Grenoble Alpes, Univ. Savoie Mont Blanc, CNRS, LECA, F-38000 Grenoble, France.
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57 **Larger geographical areas contain more species –an observation raised to a law in ecology.**
58 **Less explored is whether biodiversity changes are accompanied by a modification of**
59 **interaction networks. We use data from 32 spatial interaction networks from different**
60 **ecosystems to analyse how network structure changes with area. We find that basic**
61 **community structure descriptors (number of species, links, and links per species) increase**
62 **with area following a power-law. Yet, the distribution of links per species varies little with**
63 **area, indicating that the fundamental organization of interactions within networks is**
64 **conserved. Our null model analyses suggest that the spatial scaling of network structure is**
65 **determined by factors beyond species richness and the number of links. We demonstrate**
66 **that biodiversity–area relationships can be extended from species counts to higher levels of**
67 **network complexity. Therefore, the consequences of anthropogenic habitat destruction**
68 **may extend from species loss to wider simplification of natural communities.**

69

70 **INTRODUCTION**

71 Research on the spatial scaling of biodiversity has historically focused on the increase of species
72 richness with area¹⁻³ and on other components of biodiversity, such as functional or
73 phylogenetic diversity⁴⁻⁶. The Species Area Relationship (SAR) is essential to estimate species
74 richness in a region and species loss following habitat destruction and range contraction⁷⁻⁹.
75 Ecological communities are, however, more than disconnected collections of species. Instead,
76 they can be represented as networks, with species as nodes and interactions among species as
77 links¹⁰. Ecological interactions are fundamental to predict ecosystem responses to environmental
78 changes¹¹⁻¹³ and to sustain important ecosystem functions¹⁴⁻¹⁶. Understanding how the structure
79 of interaction networks changes with area is, thus, crucial to fully characterize the spatial scaling
80 of biodiversity and to predict ecosystem responses to human activities.

81 The influence of spatial processes on the organization of interaction networks has long
82 interested ecologists¹⁷⁻¹⁹. However, research on the spatial scaling of network structure has been
83 scarce²⁰⁻²². This scaling concerns two hierarchical levels: the number of building blocks within

84 communities (species and their interactions) and the relationships between them. The scaling of
85 the number of links (i.e., biotic interactions) with area has been previously predicted²⁰ by
86 unifying the SAR with the well-established scaling of the number of links with species
87 richness^{23–26}. Similarly, recent theoretical research has shown that a number of network–area
88 relationships (NARs) can emerge from different spatial mechanisms and assembly processes,
89 such as different SARs across trophic levels or dispersal limitation²¹. Yet, empirically
90 documenting the specific shape of these relationships and assessing their potential universality
91 across biomes, interaction types, and spatial domains remains a major challenge.

92 The power function of the form $S \sim cA^z$ has been found to describe the increase in
93 species richness with area A across all ecosystem types^{1,27}, with parameter z varying
94 substantially with the spatial extent studied^{27–29}. Whether other aspects of network complexity
95 can be captured by the same functional form, and how the parameters of such scaling vary with
96 network properties and spatial extent, are questions of fundamental importance for
97 characterizing the effects of area loss on biodiversity. Similarly, as many aspects of network
98 structure can change with species diversity and network connectance^{30–33} (i.e., the proportion of
99 realised interactions among all potential ones), it is important to determine whether the spatial
100 scaling of network structure is a trivial consequence of the increase of species richness with
101 area, or whether such scaling of network properties follow rules beyond those applying to
102 species richness.

103 We compiled 32 datasets from different ecosystems across the globe describing
104 interaction networks (including both mutualistic and antagonistic interactions) within two
105 spatial domains: regional and biogeographical. The regional domain represents communities for
106 which sampling was conducted locally in a replicated fashion within narrow spatial extents (i.e.,
107 maximum spatial extent of ca. 1000 km²). The biogeographical spatial domain includes datasets
108 for which the sampling units span much broader areas, encompassing multiple biomes (see
109 Methods and Supplementary Text 1). Thus, biogeographical data comprise communities
110 exposed to larger environmental heterogeneity, stronger dispersal barriers and historical

111 contingencies, which combine to produce diversity patterns at large spatial scales. Hence, we
112 expected *a priori* the scaling relationships for the biogeographical domain to be steeper than
113 those for the regional domain, as within the biogeographical domain, species assemblages can
114 be evolutionary less related and exhibit greater turnover of species and links. Each dataset
115 contained interaction data, using different methodologies to document pairwise interactions. To
116 characterise changes in network properties with changes in area, we sequentially aggregated the
117 sampling units available, scoring the structure of the network at each step of the aggregation
118 procedure (see Methods).

119 RESULTS & DISCUSSION

120 **Links or species: which one is gained faster?**

121 We found that network complexity increased with area at all levels: at the level of the number of
122 building blocks (species and links) and at the level of their combinations (links per species;
123 Figure 1; Table 1 and Supplementary Table 1). For all datasets, the relationships followed a
124 power-law function, regardless of the spatial extent of observation or interaction type. Within
125 both the regional and biogeographical domain, we found that an extended power function best
126 describes the scaling of network complexity with area (see Methods and Supplementary Table
127 1). This function has the form $N = cA^{(zA^{-d})}$, where N is a given network property, A is area,
128 and c , z and d are fitted parameters, where z represents the slope of a given NAR in log-log
129 space (i.e., the scaling exponent) and d controls the strength of the asymptotic flattening.

130 We found systematic differences in the shape of the scaling relationships between the
131 regional and biogeographical domains. All measures of network complexity followed a linear-
132 concave increase with area size in the regional domain (i.e. $z \gg d > 0$) while in the
133 biogeographical domain, the increase was convex for most datasets ($z > 0 > d$) (but see
134 Supplementary Figure 7 and Supplementary Figure 8). The biogeographic domain also showed
135 larger variability across datasets than the regional domain, suggesting lower predictability at
136 larger spatial extents (Supplementary Table 3).

137 The number of links increased faster with area than the number of species, within both
138 the regional and biogeographical domains. Importantly, whether links increase faster than
139 species with area will depend on how the number of links scales with species richness^{20,21}.
140 Previous empirical studies^{23–26} have used a power function to relate the increase of the number
141 of links with species richness, and found the value of the scaling exponents to lie between 1 and
142 2^{25,26} – coining the expressions of the “link-species scaling law”³⁴ versus “constant connectance
143 hypothesis”²⁴, respectively. Consistent with previous work, we found the increase in the number
144 of links with an increase in species richness to follow a power law in all data sets (Figure 2,
145 Supplementary Table 2). The exponents were larger for the biogeographical (mean \pm SD: $z =$
146 1.78 ± 0.20) than for the regional domain ($z = 1.60 \pm 0.20$). For both spatial domains, the
147 scaling exponents of the links-per-species relationship were thus clustered between 1.5 and 2,
148 but with substantial variability in specific values (Figure 2, Supplementary Table 2). The high
149 variation observed suggests that the species richness of a community may carry little
150 information on how the number of links will change with area. Instead, the scaling of the
151 number of links with species richness may need to be established on a network-specific basis²⁰.

152 **The unpredictability of vertical diversity**

153 Within a network, the links can be organized in multiple ways. In our dataset, the mean number
154 of resources used by a consumer (i.e. mean indegree: $\text{Links}/\text{Species}_{\text{consumer}}$) increased with area.
155 The general shape of the relationship was similar to that of the other complexity measures
156 analysed, i.e. linear-concave in the regional domain and convex in the biogeographical domain
157 (Figure 3, Supplementary Table 1). Still, compared to the relationships observed for other
158 network properties, we observed greater variability in indegree-area relationships within spatial
159 domains (Supplementary Table 3). This variability is partially driven by the variability in
160 changes in consumer to resource ratios with area observed across datasets (Supplementary Table
161 1). Although previous studies have shown a consistent increase of the slope of SARs with
162 trophic level^{35,36}, we did not observe any consistent increase nor decrease of the
163 consumer:resource richness ratio with area at any of the spatial domains (Supplementary Table

164 1). These findings suggest that the spatial scaling of vertical diversity properties, such as the
165 proportion of species per trophic level, might be system-specific.

166 **The scale-invariance of degree distributions**

167 Beyond the network properties considered above, other network properties were more consistent
168 across scales. The degree distribution of ecological networks is typically highly skewed, with
169 many specialist species and few generalists^{37,38}. This skewness may influence the stability and
170 robustness of communities³⁸ and it is tightly linked to widely studied network properties, such
171 as nestedness^{39,40}, (i.e. the degree to which specialist species interact with subsets of the species
172 interacting with generalists). Previous theoretical work has suggested that the skewness of
173 ecological networks is preserved across spatial scales²¹, an expectation borne out in our data.
174 Despite variability in the degree distribution across datasets, the same function provided a good
175 fit to the degree distribution of most ecological networks across the full range of areas (see
176 Methods and Figure 3). Although we observed variation in the parameters of the functions
177 (Supplementary Figure 4), the consistency in the fundamental shape suggests that community
178 robustness to species loss (independently of whether it is high or low) may be maintained across
179 spatial scales.

180 **Disentangling the effect of species richness**

181 Given the influence of species richness and network connectance on many aspects of network
182 structure³⁰⁻³³, we aimed to investigate whether network structure changes with area beyond
183 those changes associated to the increase in species richness and links with area. To do so, we
184 generated random networks with two different null models, as reflecting the case where the
185 spatial scaling of network structure emanates from the spatial scaling of species richness alone
186 (with no change in links per species), or the spatial scaling of both species richness and links,
187 respectively. In both models, we started from the metaweb (i.e. the overall network pooled
188 across all original networks within each specific study), then randomly drew the same number
189 of species as observed in the original, local networks. In null model 1, local random networks
190 were drawn as random subsets of the metaweb, picked to have the same species richness as the

191 observed local networks. In other words, after randomly selecting a given number of species
192 from the metaweb, we only kept interactions among this subset of species, thereby determining
193 the number of links of the network generated. Thus, this procedure mimics a scenario where
194 random local networks have the same number of species as the observed local networks, but the
195 number of links and the associated network properties may differ. In null model 2, we preserved
196 both species richness and the number of interactions observed in the original networks, but
197 distributed the links randomly among the species (see Methods). Accordingly, null model 2
198 mimics a scenario where a change in area causes a potential change in indegree and network
199 degree distribution, while not affecting either the number of species or links. For each of the
200 100 randomizations under each scenario, we then scored each of the complexity metrics defined
201 above: species, links, links per species, indegree and network degree distribution.

202 The observed spatial scaling of network structure in the original networks differed
203 significantly from the results generated by the null models. The number of links in empirical
204 networks increased more slowly with an increase in the number of species than expected from a
205 random sample of species from the metaweb (i.e. null model 1) (Supplementary Figure 5). This
206 slower increase is driven by the fact that local original networks show greater complexity (i.e.
207 more links per species) than random networks. This result suggests that the scaling of the
208 number of links is shaped by factors beyond the species richness of a community, such as
209 evolutionary constraints, phenological matching or competition. In contrast, other structural
210 properties, such as mean indegree and degree distributions, are consistent with the pattern
211 derived from null model 1 (Supplementary Figure 5 and Supplementary Figure 6;
212 Supplementary Table 5 and Supplementary Table 6). The latter consistency indicates that these
213 particular network properties might be inherited from the metaweb, and that the particular co-
214 occurrence structure of species in the empirical data is not meaningfully impacting the degree
215 distribution. This interpretation is supported by patterns observed under null model 2. When
216 links are reshuffled randomly amongst selected species from the metaweb, the pattern is
217 substantially different from the observed one: here, both the mean indegree and network degree

218 distributions of the randomized networks strongly deviate from that of their original
219 counterparts (Supplementary Figure 5 and Supplementary Figure 6; Supplementary Table 5 and
220 Supplementary Table 6). Similarly, the observed spatial scaling of the consumer:resource ratio
221 was poorly predicted by both null models.

222 Overall, our null model analyses suggest that the spatial scaling of network structure is
223 determined by factors beyond species richness and the number of links. With a change in area,
224 we see changes in important features of ecological networks – such as vertical diversity,
225 consumer specialisation, and degree distribution – well beyond those expected if changes were
226 driven by the number of species and/or links alone.

227 **The fragility of biotic interactions**

228 In conclusion, our analyses of multiple interaction networks from different biomes,
229 interaction types, and spatial domains allowed us to explore the generality in the spatial scaling
230 of several structural properties of ecological networks. Our results demonstrate how previously-
231 established biodiversity–area relationships can be extended from species counts^{2,3,27} to higher
232 levels of network complexity. The increase in the number of interactions in which each species
233 is involved when area increases indicates that trophic interactions might be more vulnerable to
234 habitat loss than species richness^{41,42}. Therefore, the consequences of anthropogenic habitat
235 destruction may extend from species loss to wider simplification of natural communities^{43–45},
236 with further consequences for the functioning of ecosystems^{14–16,46,47}. The systematic scaling of
237 network complexity with area suggests that trophic interactions will be lost with habitat
238 destruction in a predictable manner, and describing the factors shaping this sequence allows us
239 to better anticipate the effects for ecosystem functioning. Importantly, the scaling of the number
240 of interactions with species richness proved variable across datasets, and our null model
241 analysis indicated that other complexity metrics cannot be predicted from species richness
242 alone. Both of these patterns suggest that we need network-specific knowledge on the
243 relationship between links and species to accurately predict the effects of habitat loss on

244 network complexity. To estimate the spatial scaling of the number of links, a general
245 understanding of the species-area relationship may still suffice, if it is supplemented by
246 informed assumptions regarding the scaling exponent of the links-species relationship. For such
247 assumptions, our current results will form a useful point of departure, given their foundation in a
248 wide set of scales and biomes.

249 Future studies should put effort towards unravelling the potential ecological
250 mechanisms affecting the slopes of NARs, as well as disentangling the importance of the
251 methodological aspects (Supplementary Figure 7 and Supplementary Figure 8; Supplementary
252 Table 7), as has been widely done for SARs²⁷. Explicitly investigating the effect of habitat
253 heterogeneity, for instance, would help elucidate the effect of area, not only on network size and
254 the number of links, but also on its modular structure. Such insight is urgently needed, given
255 that heterogeneous landscapes are likely to promote the emergence of compartments within
256 networks^{48,49}. Similarly, it is important to investigate how our observations could inform
257 predictions about the effects of habitat loss caused, for instance, by link extinction debt or
258 changes in trophic regulation^{41,42}. Yet, it is also fundamental to understand how our predictions
259 of the effects of habitat loss on network structure would resemble those obtained by direct
260 experiments of habitat destruction. Gaining a deeper understanding of the mechanisms behind
261 NARs will allow us to not only anticipate the potential consequences of habitat loss, but to also
262 provide management recommendations with a solid foundation in the structure and functioning
263 of natural ecosystems.

264 **METHODS**

265 To measure network-area relationships (NARs) for ecological communities from different
266 biomes across the world, we used 32 empirical datasets comprising species recorded in different
267 localities, and with different types of interactions. This is the most comprehensive synthesis of
268 spatial interaction network datasets to date. Depending on the study, local observations span
269 either a regional or biogeographical spatial extent. Our analysis allowed us to identify
270 universalities in the ways that network properties change with area, for datasets comprising

271 different interaction types. To evaluate whether there are universalities in the ways that
272 networks of ecological interactions scale across space, we quantified the exponents of the
273 relationships between all network properties analysed with area when fitted to a power function.
274 The spatial scaling of network degree distributions was assessed by fitting four different
275 distributions at each spatial domain and comparing the best fit across the entire range of areas.
276 Additionally, we used two different null models to disentangle the effects of the spatial scaling
277 of species richness on the patterns observed in other complexity metrics.

278

279 ***Data classification***

280 32 datasets comprising species distributions and their interactions were obtained from different
281 sources and classified into two categories according to the geographical extent covered: regional
282 or biogeographical spatial domains. The main features of the type of data considered in each
283 category, including sampling method, location, and interaction types, are briefly described
284 below. Additional details about each dataset can be found in Supplementary Text 1.

285

286 *Regional spatial domain.* Datasets in this category are distinguished from biogeographical
287 networks by their geographical extent and sampling methods. Regional-domain data were
288 collected with locally replicated samples over relatively narrow spatial extents up to ca. 1000
289 km². Sample units are generally the same size or a series of localities of roughly equal size. A
290 total of 19 datasets were considered in the regional domain, covering different ecosystems and
291 geographical locations across the globe. The datasets are: networks describing plant-pollinator
292 interactions and host-parasitoid interactions from Mediterranean scrublands located in Garraf (3
293 datasets^{50,51}), and forests located in the Natural Parks of Montseny (1 dataset⁵²) and Olot (1
294 dataset⁵³) in Catalonia, Spain; host-parasite interactions networks describing insect herbivores
295 (gallers and leaf miners) of the Pedunculate Oak (*Quercus robur*) and their parasites in a
296 temperate forest in Finland (1 dataset⁵⁴); plant-pollinator interactions from a temperate forest in
297 Argentinian Patagonia (1 dataset⁵⁵); soil food webs from agroecosystems across The
298 Netherlands (7 datasets⁵⁶); terrestrial food webs within small islands of a temperate saltmarsh

299 mudflat in south-eastern England (1 dataset⁵⁷); intertidal food webs from the Northeastern
300 Pacific in Alaska, USA (1 dataset⁵⁸); networks of plant-pollinator interactions and host-
301 parasitoid interactions in fragmented calcareous grasslands in central Germany (2 datasets⁵⁹);
302 and networks of plant-leafminer-parasitoid interactions from forest fragments embedded in an
303 agricultural matrix landscape in central Argentina (1 dataset⁶⁰).

304

305 *Biogeographical spatial domain.* Datasets from this category span broad (i.e. biogeographical)
306 spatial extents. There are two types of biogeographical datasets: can be comprised of either (1)
307 datasets where local communities are built based on the information of the presence of all
308 species found in each location and where the interactions between species have been inferred
309 from literature review and expert knowledge; and (2) datasets where local communities are built
310 based on direct observations of ecological interactions at each locality. The datasets of type (1)
311 comprise: the European terrestrial vertebrate trophic network (food web, ⁶¹) divided among 10
312 biogeographical regions that characterise each region according to its climatic conditions. Local
313 communities for this dataset are defined at the 10km × 10km grid level (10 datasets); and the
314 terrestrial vertebrate food web of the Catalan Pyrenees (1 dataset;¹²), where local communities
315 are also defined at the 10km × 10km grid level. The datasets of type (2) comprise networks of
316 plant-herbivore interactions and herbivore-parasitoid interaction sampled from plants of the
317 genus *Salix* and spanning a large latitudinal gradient from Italy to northern Norway (2
318 datasets;⁶²).

319

320 ***Building network-area relationships***

321 To analyse the spatial scaling of network structure we built NARs for each dataset described
322 above. The procedure to generate NARs was slightly different between spatial domains.

323

324 *Regional spatial domain.* The spatial extent was rescaled for each dataset. The smallest spatial
325 scale considered was a single sampling unit. The spatial scaling of network structure was
326 defined by sequentially aggregating each of the sampling units available until all replicated

327 samples were considered. The aggregated sampling units are not contiguous, given that the
328 specific location of each of them was not considered. We analysed network structure at each
329 step of the aggregation procedure. Given that the order in which sampling units (i.e. local
330 communities) are aggregated might generate a bias in the aggregation procedure, we replicated
331 the procedure 100 times for each dataset where the aggregation order was randomly generated
332 without replacement.

333

334 *Biogeographical spatial domain.* The fundamental difference between the two spatial domains
335 considered is that biogeographical data span large spatial extents, thus comprising communities
336 exposed to large environmental gradients. This environmental heterogeneity suggests potential
337 differences in scaling patterns, when compared to communities sampled regionally, which cover
338 smaller geographical extents. Due to the large spatial extent covered by these datasets, an
339 aggregation procedure where each aggregated sampling unit is randomly selected in space,
340 independently of its location, would generate a fast accumulation of species and links at small
341 areas due to the large heterogeneity among the sampling units (Supplementary Figure 8 and
342 Supplementary Table 7), generating a fast accumulation of species and links at small areas. For
343 this reason, we employ an aggregation method based on neighbouring cells, while still
344 preserving the statistical power of randomising across replicated aggregation instances (here, we
345 refer the reader to Supplementary Figure 8 and Supplementary Table 7 for results based on the
346 random aggregation of sites). Two types of data comprise this category: those for which species
347 presences and their interactions were recorded in the field from single georeferenced locations
348 across the latitudinal gradient⁶²; and those where species presences were extracted from species
349 distributions maps and interactions were inferred based on the joint condition of species co-
350 occurrence in space and an indication that the two species interact, as extracted from the
351 literature⁶¹. The latter datasets, therefore, include all potential interactions between species,
352 which are not necessarily realised locally. Local sampling units of these latter datasets were
353 defined as the 10×10 km cells on a gridded map. The spatial scaling of network structure is thus
354 simulated by merging adjacent cells of the map in an increasing manner. Starting from a

355 randomly chosen cell, subsequent communities occupying larger areas were defined as
356 collections of neighbouring cells forming increasingly larger clusters of cells, chosen in counter-
357 clockwise fashion from the starting cell (i.e., spiral fashion). Thus, the sampling units that are
358 aggregated are contiguous. We measured network properties at each step of the aggregation
359 procedure. We repeated the aggregation procedure 100 times. For datasets with georeferenced
360 locations, the spatial scaling of network structure was defined by sequentially aggregating the
361 closest communities (in terms of Euclidean distance) to the starting point.

362

363 *Network properties*

364 We analysed the spatial scaling of network complexity at both spatial scales measuring the
365 number of species (S), the total number of links (i.e. biotic interactions; L) present in the
366 network and the number of links per species (L/S). We also quantified the relationship between
367 species richness and the total number of links in the network (i.e. links-species scaling).
368 Specialisation was measured at the network level by computing the mean in-degree (mean
369 number of resources utilized by a consumer; L/S_c) of the community (also known as generality
370 or diet breadth in food webs).

371

372 To further assess how the structure of ecological networks scales across space in different
373 ecosystems, we examined their degree distribution. The degree distribution $P(k)$ of a network is
374 defined as the probability of finding a species that has k links to resources in the network.

375 Degree distributions provide a notion of how links are structured across the network, and their
376 shape has been related to different aspects of community stability^{46,63–65}. In particular, scale-free
377 degree distributions are considered the hallmark of network organisation; conferring stability
378 properties to ecological communities. We fitted four different functions that have been
379 identified as typical of the shapes observed in degree distributions in ecological networks:
380 power law, truncated power law, lognormal and exponential^{63,66}. After fitting these distributions
381 to the network of interactions built for each spatial scale analysed, for each dataset, the most
382 parsimonious one as measured by Akaike Information Criterion (AIC) was recorded as the best

383 representation of the data. We did that for each replicate of each dataset, selecting the
384 distribution that was best ranked in most of the replicates. Looking at whether the top-ranked
385 distribution (i.e., the lowest AIC) changes with area provides insights into the scale invariance
386 of this network property. Additionally, we looked at the changes of the parameters involved in
387 each function with area (Supplimentary Figure 4).

388

389 *Network-Area relationships fitting*

390 After constructing NARs based on the 100 replicates for each dataset, we analysed the scaling
391 relationships by fitting a suite of functions that have traditionally been used to quantify species-
392 area relationships^{67,68} (see Supplementary Table 4 for the full set of functions tested). These
393 scaling functions incorporate in different ways the network property as the response variable
394 and area as the predictor variable, using a characteristic exponent, or a variation of it, to define
395 the relationship of network properties to area size. For example, the power law ($N = cA^z$),
396 relates N (a network property), to area (A) using a constant c and a scaling exponent (z).

397 Similarity in the fitted parameters obtained for different datasets was then used to evaluate
398 universalities in NARs. Scaling functions in Supplementary Table 4 were fitted to each dataset
399 (after network properties were calculated at each spatial extent) using the *sar* package in R⁶⁸.

400 We used R^2 and p -values to assess goodness of fit. Comparison across models and selection of
401 the best supported model was done with AIC. Amongst all fitted functions, we focused on the
402 top five models that were best supported and selected (if possible) the best ranked model from
403 the power family to facilitate comparisons among datasets. We note that the functions were
404 fitted to the original data in arithmetic space and that the re-scaling of the properties to start at 0
405 was performed for visualisation purposes alone.

406

407 *Null models*

408 To understand the contribution of species richness and the number of links for the spatial
409 scaling of the associated network properties analysed we used two null models. For null model
410 1, we checked for each dataset the number of species present in each spatial unit and we

411 randomly picked the same number of species from the corresponding metaweb. We then built
412 the network for those species taking from the metaweb all the interactions present between the
413 selected species. Thus, the resulting assemblages can differ from the original networks in the
414 number of links between species and, in turn, in the associated network properties analysed. In
415 contrast, for null model 2, we checked that the number of species is present in each spatial unit
416 but also the number of links present and randomly distributed those links between the selected
417 species. While networks built with null model 1 can potentially preserve part of the structure
418 from each metaweb given that the selected species preserve the links they have in the metaweb,
419 networks built with null model 2 can be considered random networks given that there is no
420 inherited structure from the metaweb. Thus, null model 1 allows us to determine the
421 contribution of the identity of the species (with their respective links) to the observed patterns,
422 while null model 2, allows us to further test whether there is any contribution of area into
423 network structure beyond species richness and the number of links. For both null models, we
424 generated networks of different sizes by adding the number of species of the subsequent spatial
425 units of each dataset. At each step of species addition, we calculated all network metrics. We
426 replicated the procedure 100 times for each dataset. We evaluate the resulting network-area
427 relationships (where area is the number of spatial units from which we extracted the number of
428 species) by fitting a power function, as we did for the original networks. We finally compared
429 the spatial scaling of network properties with those obtained in the original networks
430 (Supplementary Figure 5 and Supplementary Figure 6; Supplementary Table 5 and
431 Supplementary Table 6).

432 **Code availability.** Custom code used to perform the analyses are available online here:
433 <https://doi.org/10.5061/dryad.zcrjdfndg⁶⁹>, here: <https://github.com/nuriagaliana/Ecological->
434 [network-complexity-scales-with-area](https://github.com/nuriagaliana/Ecological-network-complexity-scales-with-area) or here: <https://github.com/mlurgi/global-network-area>.

435 **Data availability.** All datasets analysed during the current study are available online here:
436 <https://doi.org/10.5061/dryad.zcrjdfndg⁶⁹>, here: <https://github.com/nuriagaliana/Ecological->
437 [network-complexity-scales-with-area](https://github.com/nuriagaliana/Ecological-network-complexity-scales-with-area) or here: <https://github.com/mlurgi/global-network-area>.

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439

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453

454 **Author contributions**

455 NG, JMM and ML designed research with contributions from all co-authors. NG and ML
456 conducted research and analysed the data. JB, LC, BC-L, CE, IG, CH-C, FJ, DM, CM, SO-C,
457 SR, AR, IS-D, AT, DPV, SAW, TR and WT contributed the data. JMM, VAGB, KC, M-JF,
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460 **Competing interests**

461 The authors declare no competing interests.

462 **Additional information**

463 Supplementary information is available for this paper.

464 **Correspondence and requests for materials** should be addressed to NG
465 (galiana.nuria@gmail.com)

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471 **Table 1.** Parameter estimates for the fit of the extended power model ($N = cA^{(zA^{-d})}$) to the
 472 network properties analysed. Mean and standard deviation of d and z are shown for each
 473 network property analysed in both spatial domains. The model fit was performed on the original
 474 data in arithmetic space and not on the rescaled properties.

Network property	Parameter	Spatial Domain	
		Regional	Biogeographical
Species	d	0.08 ± 0.03	-0.38 ± 0.78
	z	0.48 ± 0.12	0.05 ± 0.41
Links	d	0.07 ± 0.03	-0.19 ± 0.13
	z	0.72 ± 0.10	0.41 ± 0.63
Links/Species	d	0.05 ± 0.11	-0.31 ± 0.57
	z	0.26 ± 0.10	0.08 ± 0.11
Indegree	d	0.04 ± 0.12	-0.27 ± 0.22
	z	0.31 ± 0.13	0.07 ± 0.19

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492 **Figures**

493 **Fig 1. Spatial scaling of network complexity.** The relationship of species (a,d), links (b,e), and
494 links/species (c,f) with area for regional (top) versus biogeographical (bottom) networks. For
495 each dataset, each point represents the mean value of the analysed network property across the
496 total amount of replicates in the aggregation procedure, for a given area. For all datasets, all
497 network properties have been re-scaled to start at 0 for visualisation purposes. In the
498 biogeographical domain, three datasets show a linear-concave increase of the number of species,
499 network links and links per species with area, similar to those observed in the regional domain;
500 these differences may be explained by differences in sampling methods among datasets (see
501 Methods and Discussion; Supplementary Text 1).

502

503 **Fig 2. Scaling of the number of links with species richness.** For networks spanning both
504 regional (a) and biogeographical (b) spatial domains, the number of links scales with species
505 following a power law (Supplementary Table 2). Each point represents the mean values across
506 all replicates in the aggregation procedure. Note that for visualisation purposes, all x - and y -
507 values in all datasets have been re-scaled to start at 0. To allow convenient comparison with the
508 constant connectance hypothesis and the link–species scaling law, the slope of each log-log
509 relationship is provided in Supplementary Table 2. Note that for constant connectance, the slope
510 equals 2, as the number of links in a web increases approximately as the square of the number of
511 trophic species: $L \approx S^2$. For the link–species scaling law, the slope equals 1, as the number of
512 links per species in a web is constant and scale invariant at roughly two: $L \approx 2S$.

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514 **Fig 3. Spatial scaling of mean indegree and network degree distribution.** The mean number
515 of resources per consumer (i.e., mean indegree) increases with area within both regional (left)
516 and biogeographical (right) spatial domains (a-b). Each point represents the mean value across
517 every replicate in the aggregation procedure at a given area. Note that for visualisation purposes,
518 all x - and y -values in all datasets have been re-scaled to start at 0. The shape of the network

519 degree distributions is consistent across area at both regional and biogeographical domains. In
520 (c-d) two datasets are shown as illustration: *Garraf-PP* and *Galpar*, respectively (see
521 Supplementary Text 1). The cumulative probabilities of finding a species in the network that
522 has k links to resources in the network, are normalized by the mean number of links per species
523 in the network. One replicate for a subset of areas is shown for each dataset to facilitate
524 visualization. Each colour represents network degree distribution for a given area. From dark
525 blue, representing the smallest area (i.e. 1 spatial unit), to yellow, representing the largest area
526 for each dataset (40 spatial units for *Garraf-PP* and 373 spatial units for *Galpar*). Notice that
527 the starting point of each distribution changes with area, indicating that at smaller spatial scales,
528 the most specialized species of the network have more interacting partners than at larger spatial
529 scales. Yet, the shape of the degree distribution is preserved. The top-ranked model describing
530 the degree distribution of each ecological network across the area range (e-f). Although the
531 degree distribution of most ecological networks was characterised by the same function along
532 the range of areas, the specific shape of each function changed with area (see Supplementary
533 Figure 4). Area values were re-scaled between 0 and 1.

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References

1. Arrhenius, O. Species and area. *J. Ecol.* **9**, 95–99 (1921).
2. MacArthur, R. H. & Wilson, E. O. *The theory of island biogeography*. (Princeton University Press, 1967).
3. Rosenzweig, M. L. *Species diversity in space and time*. (Cambridge University Press, 1995).
4. Smith, A. B., Sandel, B., Kraft, N. J. B. & Carey, S. Characterizing scale-dependent community assembly using the functional-diversity–area relationship. *Ecology* **94**, 2392–2402 (2013).
5. Mazel, F. *et al.* Multifaceted diversity-area relationships reveal global hotspots of mammalian species, trait and lineage diversity. *Glob. Ecol. Biogeogr.* **23**, 836–847 (2014).
6. Dias, R. A. *et al.* Species richness and patterns of overdispersion, clustering and randomness shape phylogenetic and functional diversity–area relationships in habitat islands. *J. Biogeogr.* **00**, 1– 11 (2020).
7. Pereira, H. M. *et al.* Scenarios for global biodiversity in the 21st century. *Science (80-.)*. **330**, 1496–1501 (2010).
8. Pimm, S. L., Russell, G. J., Gittleman, J. L. & Brooks, T. M. The future of biodiversity. *Science (80-.)*. **269**, 347 (1995).
9. Simberloff, D. Do species-area curves predict extinction in fragmented forest. *Trop. deforestation species extinction* 75–89 (1992).
10. Jordano, P. Chasing ecological interactions. *PLoS Biol.* **14**, e1002559 (2016).
11. Montoya, J. M., Woodward, G., Emmerson, M. C. & Solé, R. V. Press perturbations and indirect effects in real food webs. *Ecology* **90**, 2426–33 (2009).
12. Lurgi, M., López, B. C., Montoya, J. M. & Lopez, B. C. Novel communities from climate change. *Philos. Trans. R. Soc. B Biol. Sci.* **367**, 2913–2922 (2012).
13. Tylianakis, J. M., Tscharntke, T. & Lewis, O. T. Habitat modification alters the structure of tropical host–parasitoid food webs. *Nature* **445**, 202–205 (2007).
14. Montoya, J. M., Rodríguez, M. Á., Hawkins, B. A. & Montoya, J. M., Rodríguez, M. A. & Hawkins, B. A. Food web complexity and higher-level ecosystem services. *Ecol. Lett.* **6**, 587–593 (2003).
15. Reiss, J., Bridle, J. R., Montoya, J. M. & Woodward, G. Emerging horizons in biodiversity and ecosystem functioning research. *Trends Ecol. Evol.* **24**, 505–514 (2009).
16. Thompson, R. M. *et al.* Food webs: reconciling the structure and function of biodiversity. *Trends Ecol. Evol.* **27**, 689–697 (2012).
17. Cohen, J. E. & Newman, C. M. Community area and food-chain length: theoretical predictions. *Am. Nat.* **138**, 1542–1554 (1991).
18. Schoener, T. W. Food webs from the small to the large: the Robert H. MacArthur Award Lecture. *Ecology* **70**, 1559–1589 (1989).
19. Post, D. M., Pace, M. L. & Hairston, N. G. Ecosystem size determines food-chain length in lakes. *Nature* **405**, 1047–1049 (2000).
20. Brose, U., Ostling, A., Harrison, K. & Martinez, N. D. Unified spatial scaling of species and their trophic interactions. *Nature* **428**, 167–171 (2004).
21. Galiana, N. *et al.* The spatial scaling of species interaction networks. *Nat. Ecol. Evol.* **2**, 782–790 (2018).
22. Wood, S. A., Russell, R., Hanson, D., Williams, R. J. & Dunne, J. A. Effects of spatial scale of sampling on food web structure. *Ecol. Evol.* **5**, 3769–3782 (2015).
23. Pimm, S. L., Lawton, J. H., Cohen, J. E. & Pimm, S. L., Lawton, J. H. & Cohen, J. E. Food web patterns and their consequences. *Nat.* 350,669–674 **350**, 669–674 (1991).
24. Martinez, N. D. Constant connectance in community food webs. *Am. Nat.* **139**, 1208–1218 (1992).
25. Ings, T. C. *et al.* Ecological networks–beyond food webs. *J. Anim. Ecol.* **78**, 253–69 (2009).
26. Montoya, J. M. & Solé, R. V. Topological properties of food webs: from real data to

- 593 community assembly models. *Oikos* **102**, 614–622 (2003).
- 594 27. Drakare, S., Lennon, J. J. & Hillebrand, H. The imprint of the geographical, evolutionary
595 and ecological context on species–area relationships. *Ecol. Lett.* **9**, 215–227 (2006).
- 596 28. Preston, F. W. Time and space and the variation of species. *Ecology* **41**, 611–627 (1960).
- 597 29. Turner, W. R. & Tjørve, E. Scale-dependence in species-area relationships. *Ecography*
598 (*Cop.*) **6**, 721–730 (2005).
- 599 30. Bengtsson, J. Confounding variables and independent observations in comparative
600 analyses of food webs. *Ecology* **75**, 1282–1288 (1994).
- 601 31. Vermaat, J. E., Dunne, J. A. & Gilbert, A. J. Major dimensions in food-web structure
602 properties. *Ecology* **90**, 278–282 (2009).
- 603 32. Dunne, J. A. *et al.* Parasites affect food web structure primarily through increased
604 diversity and complexity. *PLoS Biol.* **11**, e1001579 (2013).
- 605 33. Poisot, T. & Gravel, D. When is an ecological network complex? Connectance drives
606 degree distribution and emerging network properties. *PeerJ* **2**, e251 (2014).
- 607 34. Cohen, J. E. & Briand, Fredeiri. Trophic links of community food webs. *Proc. Natl.*
608 *Acad. Sci.* **81**, 4105–4109 (1984).
- 609 35. Roslin, T., Várkonyi, G., Koponen, M., Vikberg, V. & Nieminen, M. Species-area
610 relationships across four trophic levels - decreasing island size truncates food chains.
611 *Ecography (Cop.)* **37**, 443–453 (2014).
- 612 36. Holt, R. D., Lawton, J. H., Polis, G. A. & Martinez, N. D. Trophic rank and the species–
613 area relationship. *Ecology* **80**, 1495–1504 (1999).
- 614 37. Dunne, J. A., Williams, R. J. & Martinez, N. D. Food-web structure and network theory:
615 The role of connectance and size. *Proc. Natl. Acad. Sci. U. S. A.* **99**, 12917–22 (2002).
- 616 38. Montoya, J. M., Pimm, S. L. & Solé, R. V. Ecological networks and their fragility.
617 *Nature* **442**, 259–64 (2006).
- 618 39. James, A., Pitchford, J. W. & Plank, M. J. Disentangling nestedness from models of
619 ecological complexity. *Nature* **487**, 227–30 (2012).
- 620 40. Valverde, S. *et al.* The architecture of mutualistic networks as an evolutionary spandrel.
621 *Nat. Ecol. Evol.* **2**, 94–99 (2018).
- 622 41. Valiente-Banuet, A. *et al.* Beyond species loss: the extinction of ecological interactions
623 in a changing world. *Funct. Ecol.* **29**, 299–307 (2015).
- 624 42. Janzen, D. H. The deflowering of central America. (1971).
- 625 43. Mendoza, M. & Araújo, M. B. Climate shapes mammal community trophic structures
626 and humans simplify them. *Nat. Commun.* **10**, 1–9 (2019).
- 627 44. Emer, C. *et al.* Seed dispersal networks in tropical forest fragments: Area effects,
628 remnant species, and interaction diversity. *Biotropica* **52**, 81–89 (2020).
- 629 45. McWilliams, C., Lurgi, M., Montoya, J. M., Sauve, A. & Montoya, D. The stability of
630 multitrophic communities under habitat loss. *Nat. Commun.* **10**, 1–11 (2019).
- 631 46. McCann, K. S. The diversity–stability debate. *Nature* **405**, 228–233 (2000).
- 632 47. Fig, T., Mccann, K., Hastings, A. & Huxel, G. R. Weak trophic interactions and the
633 balance of nature. **395**, 794–798 (1998).
- 634 48. Pimm, S. L. & Lawton, J. H. Are food webs divided into compartments? *J. Anim. Ecol.*
635 **49**, 879–898 (1980).
- 636 49. Macfadyen, S., Gibson, R. H., Symondson, W. O. C. & Memmott, J. Landscape
637 structure influences modularity patterns in farm food webs: consequences for pest
638 control. *Ecol. Appl.* **21**, 516–524 (2011).
- 639 50. Reverté, S. *et al.* Spatial variability in a plant–pollinator community across a continuous
640 habitat: high heterogeneity in the face of apparent uniformity. *Ecography (Cop.)* **42**,
641 1558–1568 (2019).
- 642 51. Torné-Noguera, A., Arnan, X., Rodrigo, A. & Bosch, J. Spatial variability of hosts,
643 parasitoids and their interactions across a homogeneous landscape. *Ecol. Evol.* **10**, 3696–
644 3705 (2020).
- 645 52. Hernández-Castellano, C. *et al.* A new native plant in the neighborhood: effects on
646 plant–pollinator networks, pollination, and plant reproductive success. *Ecology* **101**,
647 e03046 (2020).

- 648 53. Osorio, S., Arnan, X., Bassols, E., Vicens, N. & Bosch, J. Local and landscape effects in
649 a host–parasitoid interaction network along a forest–cropland gradient. *Ecol. Appl.* **25**,
650 1869–1879 (2015).
- 651 54. Kaartinen, R. & Roslin, T. Shrinking by numbers: landscape context affects the species
652 composition but not the quantitative structure of local food webs. *J. Anim. Ecol.* **80**, 622–
653 631 (2011).
- 654 55. Vázquez, D. P. & Simberloff, D. Changes in interaction biodiversity induced by an
655 introduced ungulate. *Ecol. Lett.* **6**, 1077–1083 (2003).
- 656 56. Mulder, C., Den Hollander, H. A. & Hendriks, A. J. Aboveground herbivory shapes the
657 biomass distribution and flux of soil invertebrates. *PLoS One* **3**, e3573 (2008).
- 658 57. Montoya, D., Yallop, M. L. & Memmott, J. Functional group diversity increases with
659 modularity in complex food webs. *Nat. Commun.* **6**, 1–9 (2015).
- 660 58. Wood, S. A., Russell, R., Hanson, D., Williams, R. J. & Dunne, J. A. Effects of spatial
661 scale of sampling on food web structure. *Ecol. Evol.* **5**, 3769–3782 (2015).
- 662 59. Grass, I., Jauker, B., Steffan-Dewenter, I., Tschardtke, T. & Jauker, F. Past and potential
663 future effects of habitat fragmentation on structure and stability of plant–pollinator and
664 host–parasitoid networks. *Nat. Ecol. Evol.* (2018). doi:10.1038/s41559-018-0631-2
- 665 60. Cagnolo, L., Salvo, A. & Valladares, G. Network topology: patterns and mechanisms in
666 plant–herbivore and host–parasitoid food webs. *J. Anim. Ecol.* **80**, 342–51 (2011).
- 667 61. Maiorano, L., Montemaggiore, A., Ficetola, G. F., O’Connor, L. & Thuiller, W. TETRA-
668 EU 1.0: A species-level trophic metaweb of European tetrapods. *Glob. Ecol. Biogeogr.*
669 (2020).
- 670 62. Kopelke, J. *et al.* Food-web structure of willow-galling sawflies and their natural
671 enemies across Europe. *Ecology* **98**, 1730 (2017).
- 672 63. Montoya, J. M., Pimm, S. L. & Solé, R. V. Ecological networks and their fragility.
673 *Nature* **442**, 259–264 (2006).
- 674 64. Dunne, J. A., Williams, R. J. & Martinez, N. D. Food-web structure and network theory:
675 the role of connectance and size. *Proc. Natl. Acad. Sci.* **99**, 12917–12922 (2002).
- 676 65. Sole, R. V. & Montoya, M. Complexity and fragility in ecological networks. *Proc. R.*
677 *Soc. London B Biol. Sci.* **268**, 2039–2045 (2001).
- 678 66. Broido, A. D. & Clauset, A. Scale-free networks are rare. *Nat. Commun.* **10**, 1017
679 (2019).
- 680 67. Guilhaumon, F., Mouillot, D. & Gimenez, O. mmSAR: An R-package for multimodel
681 species–area relationship inference. *Ecography (Cop.)*. **33**, 420–424 (2010).
- 682 68. Matthews, T. J., Triantis, K. A., Whittaker, R. J. & Guilhaumon, F. sars: an R package
683 for fitting, evaluating and comparing species–area relationship models. *Ecography*
684 *(Cop.)*. 1446–1455 (2019). doi:10.1111/ecog.04271
- 685 69. Galiana, N. Ecological network complexity scales with area, Dryad, Dataset,
686 <https://doi.org/10.5061/dryad.zcrjdfndg>. (2021).
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