



**HAL**  
open science

## Ecological network complexity scales with area

Núria Galiana, Miguel Lurgi, Vinicius Bastazini, Jordi Bosch, Luciano Cagnolo, Kevin Cazelles, Bernat Claramunt-López, Carine Emer, Marie-Josée Fortin, Ingo Grass, et al.

► **To cite this version:**

Núria Galiana, Miguel Lurgi, Vinicius Bastazini, Jordi Bosch, Luciano Cagnolo, et al.. Ecological network complexity scales with area. *Nature Ecology & Evolution*, 2022, 6 (3), pp.307-314. 10.1038/s41559-021-01644-4 . hal-03765314

**HAL Id: hal-03765314**

**<https://hal.science/hal-03765314>**

Submitted on 31 Aug 2022

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

## 1 Ecological network complexity scales with area

2 Núria Galiana<sup>1,2\*</sup>, Miguel Lurgi<sup>1,3</sup>, Vinicius A. G. Bastazini<sup>1,4</sup>, Jordi Bosch<sup>5</sup>, Luciano Cagnolo<sup>6</sup>, Kevin  
3 Cazelles<sup>7</sup>, Bernat Claramunt-López<sup>5,8</sup>, Carine Emer<sup>9,10</sup>, Marie-Josée Fortin<sup>11</sup>, Ingo Grass<sup>12</sup>, Carlos  
4 Hernández-Castellano<sup>5,8</sup>, Frank Jauker<sup>13</sup>, Shawn J. Leroux<sup>14</sup>, Kevin McCann<sup>7</sup>, Anne M. McLeod<sup>14</sup>, Daniel  
5 Montoya<sup>1,15,16</sup>, Christian Mulder<sup>17</sup>, Sergio Osorio-Canadas<sup>5,18</sup>, Sara Reverté<sup>5</sup>, Anselm Rodrigo<sup>5,8</sup>, Ingolf  
6 Steffan-Dewenter<sup>19</sup>, Anna Traveset<sup>20</sup>, Sergi Valverde<sup>21,22</sup>, Diego P. Vázquez<sup>23,24</sup>, Spencer A. Wood<sup>25</sup>,  
7 Dominique Gravel<sup>26</sup>, Tomas Roslin<sup>27,28</sup>, Wilfried Thuiller<sup>29</sup> and José M. Montoya<sup>1</sup>.

## 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. Department 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.
- 56

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 **Biotic interactions, the missing link**

72 Research on the spatial scaling of biodiversity has historically focused on the increase of species  
73 richness with area<sup>1-3</sup> and on other components of biodiversity, such as functional or  
74 phylogenetic diversity<sup>4-6</sup>. The Species Area Relationship (SAR) is essential to estimate species  
75 richness in a region and species loss following habitat destruction and range contraction<sup>7-9</sup>.  
76 Ecological communities are, however, more than disconnected collections of species. Instead,  
77 they can be represented as networks, with species as nodes and interactions among species as  
78 links<sup>10</sup>. Ecological interactions are fundamental to predict ecosystem responses to environmental  
79 changes<sup>11-13</sup> and to sustain important ecosystem functions<sup>14-16</sup>. Understanding how the structure  
80 of interaction networks changes with area is, thus, crucial to fully characterize the spatial scaling  
81 of biodiversity and to predict ecosystem responses to human activities.

82         The influence of spatial processes on the organization of interaction networks has long  
83 interested ecologists<sup>17-19</sup>. However, research on the spatial scaling of network structure has been

84 scarce<sup>20–22</sup>. This scaling concerns two hierarchical levels: the number of building blocks within  
85 communities (species and their interactions) and the relationships between them. The scaling of  
86 the number of links (i.e., biotic interactions) with area has been previously predicted<sup>20</sup> by  
87 unifying the SAR with the well-established scaling of the number of links with species  
88 richness<sup>23–26</sup>. Similarly, recent theoretical research has shown that a number of network–area  
89 relationships (NARs) can emerge from different spatial mechanisms and assembly processes,  
90 such as different SARs across trophic levels or dispersal limitation<sup>21</sup>. Yet, empirically  
91 documenting the specific shape of these relationships and assessing their potential universality  
92 across biomes, interaction types, and spatial domains remains a major challenge.

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

#### 104 **A unique dataset across ecosystems and biomes**

105         We compiled 32 datasets from different ecosystems across the globe describing  
106 interaction networks (including both mutualistic and antagonistic interactions) within two  
107 spatial domains: regional and biogeographical. The regional domain represents communities for  
108 which sampling was conducted locally in a replicated fashion within narrow spatial extents (i.e.,  
109 maximum spatial extent of ca. 1000 km<sup>2</sup>). The biogeographical spatial domain includes datasets  
110 for which the sampling units span much broader areas, encompassing multiple biomes (see

111 Methods and Supplementary Text 1). Thus, biogeographical data comprise communities  
112 exposed to larger environmental heterogeneity, stronger dispersal barriers and historical  
113 contingencies, which combine to produce diversity patterns at large spatial scales. Hence, we  
114 expected *a priori* the scaling relationships for the biogeographical domain to be steeper than  
115 those for the regional domain, as within the biogeographical domain, species assemblages can  
116 be evolutionary less related and exhibit greater turnover of species and links. Each dataset  
117 contained interaction data, using different methodologies to document pairwise interactions. To  
118 characterise changes in network properties with changes in area, we sequentially aggregated the  
119 sampling units available, scoring the structure of the network at each step of the aggregation  
120 procedure (see Methods).

## 121 RESULTS & DISCUSSION

### 122 **Links or species: which one is gained faster?**

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

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

137 larger variability across datasets than the regional domain, suggesting lower predictability at  
138 larger spatial extents (Supplementary Table 3).

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

#### 154 **The unpredictability of vertical diversity**

155 Within a network, the links can be organized in multiple ways. In our dataset, the mean number  
156 of resources used by a consumer (i.e. mean indegree:  $\text{Links}/\text{Species}_{\text{consumer}}$ ) increased with area.  
157 The general shape of the relationship was similar to that of the other complexity measures  
158 analysed, i.e. linear-concave in the regional domain and convex in the biogeographical domain  
159 (Figure 3, Supplementary Table 1). Still, compared to the relationships observed for other  
160 network properties, we observed greater variability in indegree-area relationships within spatial  
161 domains (Supplementary Table 3). This variability is partially driven by the variability in  
162 changes in consumer to resource ratios with area observed across datasets (Supplementary Table  
163 1). Although previous studies have shown a consistent increase of the slope of SARs with

164 trophic level<sup>35,36</sup>, we did not observe any consistent increase nor decrease of the  
165 consumer:resource richness ratio with area at any of the spatial domains (Supplementary Table  
166 1). These findings suggest that the spatial scaling of vertical diversity properties, such as the  
167 proportion of species per trophic level, might be system-specific.

### 168 **The scale-invariance of degree distributions**

169 Beyond the network properties considered above, other network properties were more consistent  
170 across scales. The degree distribution of ecological networks is typically highly skewed, with  
171 many specialist species and few generalists<sup>37,38</sup>. This skewness may influence the stability and  
172 robustness of communities<sup>38</sup> and it is tightly linked to widely studied network properties, such  
173 as nestedness<sup>39,40</sup>, (i.e. the degree to which specialist species interact with subsets of the species  
174 interacting with generalists). Previous theoretical work has suggested that the skewness of  
175 ecological networks is preserved across spatial scales<sup>21</sup>, an expectation borne out in our data.  
176 Despite variability in the degree distribution across datasets, the same function provided a good  
177 fit to the degree distribution of most ecological networks across the full range of areas (see  
178 Methods and Figure 3). Although we observed variation in the parameters of the functions  
179 (Supplementary Figure 4), the consistency in the fundamental shape suggests that community  
180 robustness to species loss (independently of whether it is high or low) may be maintained across  
181 spatial scales.

### 182 **Disentangling the effect of species richness**

183 Given the influence of species richness and network connectance on many aspects of network  
184 structure<sup>30-33</sup>, we aimed to investigate whether network structure changes with area beyond  
185 those changes associated to the increase in species richness and links with area. To do so, we  
186 generated random networks with two different null models, as reflecting the case where the  
187 spatial scaling of network structure emanates from the spatial scaling of species richness alone  
188 (with no change in links per species), or the spatial scaling of both species richness and links,  
189 respectively. In both models, we started from the metaweb (i.e. the overall network pooled  
190 across all original networks within each specific study), then randomly drew the same number

191 of species as observed in the original, local networks. In null model 1, local random networks  
192 were drawn as random subsets of the metaweb, picked to have the same species richness as the  
193 observed local networks. In other words, after randomly selecting a given number of species  
194 from the metaweb, we only kept interactions among this subset of species, thereby determining  
195 the number of links of the network generated. Thus, this procedure mimics a scenario where  
196 random local networks have the same number of species as the observed local networks, but the  
197 number of links and the associated network properties may differ. In null model 2, we preserved  
198 both species richness and the number of interactions observed in the original networks, but  
199 distributed the links randomly among the species (see Methods). Accordingly, null model 2  
200 mimics a scenario where a change in area causes a potential change in indegree and network  
201 degree distribution, while not affecting either the number of species or links. For each of the  
202 100 randomizations under each scenario, we then scored each of the complexity metrics defined  
203 above: species, links, links per species, indegree and network degree distribution.

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



218 links are reshuffled randomly amongst selected species from the metaweb, the pattern is  
219 substantially different from the observed one: here, both the mean indegree and network degree  
220 distributions of the randomized networks strongly deviate from that of their original  
221 counterparts (Supplementary Figure 5 and Supplementary Figure 6; Supplementary Table 5 and  
222 Supplementary Table 6). Similarly, the observed spatial scaling of the consumer:resource ratio  
223 was poorly predicted by both null models.

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

### 229 **The fragility of biotic interactions**

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

244 alone. Both of these patterns suggest that we need network-specific knowledge on the  
245 relationship between links and species to accurately predict the effects of habitat loss on  
246 network complexity. To estimate the spatial scaling of the number of links, a general  
247 understanding of the species-area relationship may still suffice, if it is supplemented by  
248 informed assumptions regarding the scaling exponent of the links-species relationship. For such  
249 assumptions, our current results will form a useful point of departure, given their foundation in a  
250 wide set of scales and biomes.

251 Future studies should put effort towards unravelling the potential ecological  
252 mechanisms affecting the slopes of NARs, as well as disentangling the importance of the  
253 methodological aspects (Supplementary Figure 7 and Supplementary Figure 8; Supplementary  
254 Table 7), as has been widely done for SARs<sup>27</sup>. Explicitly investigating the effect of habitat  
255 heterogeneity, for instance, would help elucidate the effect of area, not only on network size and  
256 the number of links, but also on its modular structure. Such insight is urgently needed, given  
257 that heterogeneous landscapes are likely to promote the emergence of compartments within  
258 networks<sup>48,49</sup>. Similarly, it is important to investigate how our observations could inform  
259 predictions about the effects of habitat loss caused, for instance, by link extinction debt or  
260 changes in trophic regulation<sup>41,42</sup>. Yet, it is also fundamental to understand how our predictions  
261 of the effects of habitat loss on network structure would resemble those obtained by direct  
262 experiments of habitat destruction. Gaining a deeper understanding of the mechanisms behind  
263 NARs will allow us to not only anticipate the potential consequences of habitat loss, but to also  
264 provide management recommendations with a solid foundation in the structure and functioning  
265 of natural ecosystems.

## 266 **METHODS**

267 To measure network-area relationships (NARs) for ecological communities from different  
268 biomes across the world, we used 32 empirical datasets comprising species recorded in different  
269 localities, and with different types of interactions. This is the most comprehensive synthesis of  
270 spatial interaction network datasets to date. Depending on the study, local observations span

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

280

### 281 ***Data classification***

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

287

288 *Regional spatial domain.* Datasets in this category are distinguished from biogeographical  
289 networks by their geographical extent and sampling methods. Regional-domain data were  
290 collected with locally replicated samples over relatively narrow spatial extents up to ca. 1000  
291 km<sup>2</sup>. Sample units are generally the same size or a series of localities of roughly equal size. A  
292 total of 19 datasets were considered in the regional domain, covering different ecosystems and  
293 geographical locations across the globe. The datasets are: networks describing plant-pollinator  
294 interactions and host-parasitoid interactions from Mediterranean scrublands located in Garraf (3  
295 datasets<sup>50,51</sup>), and forests located in the Natural Parks of Montseny (1 dataset<sup>52</sup>) and Olot (1  
296 dataset<sup>53</sup>) in Catalonia, Spain; host-parasite interactions networks describing insect herbivores  
297 (gallers and leaf miners) of the Pedunculate Oak (*Quercus robur*) and their parasites in a  
298 temperate forest in Finland (1 dataset<sup>54</sup>); plant-pollinator interactions from a temperate forest in

299 Argentinian Patagonia (1 dataset<sup>55</sup>); soil food webs from agroecosystems across The  
300 Netherlands (7 datasets<sup>56</sup>); terrestrial food webs within small islands of a temperate saltmarsh  
301 mudflat in south-eastern England (1 dataset<sup>57</sup>); intertidal food webs from the Northeastern  
302 Pacific in Alaska, USA (1 dataset<sup>58</sup>); networks of plant-pollinator interactions and host-  
303 parasitoid interactions in fragmented calcareous grasslands in central Germany (2 datasets<sup>59</sup>);  
304 and networks of plant-leafminer-parasitoid interactions from forest fragments embedded in an  
305 agricultural matrix landscape in central Argentina (1 dataset<sup>60</sup>).

306

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

321

### 322 ***Building network-area relationships***

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

325

326 *Regional spatial domain.* The spatial extent was rescaled for each dataset. The smallest spatial  
327 scale considered was a single sampling unit. The spatial scaling of network structure was  
328 defined by sequentially aggregating each of the sampling units available until all replicated  
329 samples were considered. The aggregated sampling units are not contiguous, given that the  
330 specific location of each of them was not considered. We analysed network structure at each  
331 step of the aggregation procedure. Given that the order in which sampling units (i.e. local  
332 communities) are aggregated might generate a bias in the aggregation procedure, we replicated  
333 the procedure 100 times for each dataset where the aggregation order was randomly generated  
334 without replacement.

335

336 *Biogeographical spatial domain.* The fundamental difference between the two spatial domains  
337 considered is that biogeographical data span large spatial extents, thus comprising communities  
338 exposed to large environmental gradients. This environmental heterogeneity suggests potential  
339 differences in scaling patterns, when compared to communities sampled regionally, which cover  
340 smaller geographical extents. Due to the large spatial extent covered by these datasets, an  
341 aggregation procedure where each aggregated sampling unit is randomly selected in space,  
342 independently of its location, would generate a fast accumulation of species and links at small  
343 areas due to the large heterogeneity among the sampling units (Supplementary Figure 8 and  
344 Supplementary Table 7), generating a fast accumulation of species and links at small areas. For  
345 this reason, we employ an aggregation method based on neighbouring cells, while still  
346 preserving the statistical power of randomising across replicated aggregation instances (here, we  
347 refer the reader to Supplementary Figure 8 and Supplementary Table 7 for results based on the  
348 random aggregation of sites). Two types of data comprise this category: those for which species  
349 presences and their interactions were recorded in the field from single georeferenced locations  
350 across the latitudinal gradient<sup>62</sup>; and those where species presences were extracted from species  
351 distributions maps and interactions were inferred based on the joint condition of species co-  
352 occurrence in space and an indication that the two species interact, as extracted from the  
353 literature<sup>61</sup>. The latter datasets, therefore, include all potential interactions between species,

354 which are not necessarily realised locally. Local sampling units of these latter datasets were  
355 defined as the 10×10 km cells on a gridded map. The spatial scaling of network structure is thus  
356 simulated by merging adjacent cells of the map in an increasing manner. Starting from a  
357 randomly chosen cell, subsequent communities occupying larger areas were defined as  
358 collections of neighbouring cells forming increasingly larger clusters of cells, chosen in counter-  
359 clockwise fashion from the starting cell (i.e., spiral fashion). Thus, the sampling units that are  
360 aggregated are contiguous. We measured network properties at each step of the aggregation  
361 procedure. We repeated the aggregation procedure 100 times. For datasets with georeferenced  
362 locations, the spatial scaling of network structure was defined by sequentially aggregating the  
363 closest communities (in terms of Euclidean distance) to the starting point.

364

### 365 *Network properties*

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

373

374 To further assess how the structure of ecological networks scales across space in different  
375 ecosystems, we examined their degree distribution. The degree distribution  $P(k)$  of a network is  
376 defined as the probability of finding a species that has  $k$  links to resources in the network.  
377 Degree distributions provide a notion of how links are structured across the network, and their  
378 shape has been related to different aspects of community stability<sup>46,63–65</sup>. In particular, scale-free  
379 degree distributions are considered the hallmark of network organisation; conferring stability  
380 properties to ecological communities. We fitted four different functions that have been  
381 identified as typical of the shapes observed in degree distributions in ecological networks:

382 power law, truncated power law, lognormal and exponential<sup>63,66</sup>. After fitting these distributions  
383 to the network of interactions built for each spatial scale analysed, for each dataset, the most  
384 parsimonious one as measured by Akaike Information Criterion (AIC) was recorded as the best  
385 representation of the data. We did that for each replicate of each dataset, selecting the  
386 distribution that was best ranked in most of the replicates. Looking at whether the top-ranked  
387 distribution (i.e., the lowest AIC) changes with area provides insights into the scale invariance  
388 of this network property. Additionally, we looked at the changes of the parameters involved in  
389 each function with area (Supplementary Figure 4).

390

### 391 *Network-Area relationships fitting*

392 After constructing NARs based on the 100 replicates for each dataset, we analysed the scaling  
393 relationships by fitting a suite of functions that have traditionally been used to quantify species-  
394 area relationships<sup>67,68</sup> (see Supplementary Table 4 for the full set of functions tested). These  
395 scaling functions incorporate in different ways the network property as the response variable  
396 and area as the predictor variable, using a characteristic exponent, or a variation of it, to define  
397 the relationship of network properties to area size. For example, the power law ( $N = cA^z$ ),  
398 relates  $N$  (a network property), to area ( $A$ ) using a constant  $c$  and a scaling exponent ( $z$ ).  
399 Similarity in the fitted parameters obtained for different datasets was then used to evaluate  
400 universalities in NARs. Scaling functions in Supplementary Table 4 were fitted to each dataset  
401 (after network properties were calculated at each spatial extent) using the *sar* package in R<sup>68</sup>.  
402 We used  $R^2$  and  $p$ -values to assess goodness of fit. Comparison across models and selection of  
403 the best supported model was done with AIC. Amongst all fitted functions, we focused on the  
404 top five models that were best supported and selected (if possible) the best ranked model from  
405 the power family to facilitate comparisons among datasets. We note that the functions were  
406 fitted to the original data in arithmetic space and that the re-scaling of the properties to start at 0  
407 was performed for visualisation purposes alone.

408

### 409 *Null models*

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

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

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



440

441

442 **Acknowledgements**

443 We thank J.-F. Arnoldi, M. Barbier and Y. Zelnik for numerous discussions which improved the  
444 quality of this paper. We also thank Steffano Allesina for his criticism and suggestions. This work  
445 was supported by the TULIP Laboratory of Excellence (ANR-10-LABX-41 and 394 ANR-11-  
446 IDEX-002-02) to JMM, by a Region Midi-Pyrenees project (CNRS 121090) to JMM, and by the  
447 FRAGCLIM Consolidator Grant (726176) to JMM from the European Research Council under  
448 the European Union's Horizon 2020 Research and Innovation Program. The study was also  
449 supported by Spanish MICINN projects CGL2009-12646, CSD2008-0040 and CGL2013-41856  
450 to JB and AR. CE was funded through the São Paulo Research Foundation (FAPESP 2015/15172-  
451 7). VAGB was funded by National Funds through FCT - Foundation for Science and Technology  
452 under the Project UIDB/05183/2020. WT received funding from the ERA-Net BiodivERsA -  
453 Belmont Forum, with the national funder Agence National pour la Recherche (FutureWeb: ANR-  
454 18-EBI4-0009 & BearConnect: ANR-16-EBI3-0003).

455

456 **Author contributions**

457 NG, JMM and ML designed research with contributions from all co-authors. NG and ML  
458 conducted research and analysed the data. JB, LC, BCL, CE, IG, CHC, FJ, DM, CM, SOC, SR,  
459 AR, ISD, AT, DV, SW, TR and WT contributed the data. JMM, VAB, KC, MJF, SL, KM, AM,  
460 DG, TR, SV and WT supported research. NG and JMM wrote the manuscript with substantial  
461 contributions from DG, TR and WT, and feedback from all co-authors.

462 **Competing interests**

463 The authors declare no competing interests.

464 **Additional information**

465 Supplementary information is available for this paper.

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

468

469

470

471

472

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

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

477  
 478  
 479  
 480  
 481  
 482  
 483  
 484  
 485  
 486  
 487  
 488  
 489  
 490  
 491  
 492

493

## 494 **Figures**

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

504

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

515

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

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

536

537

538

539

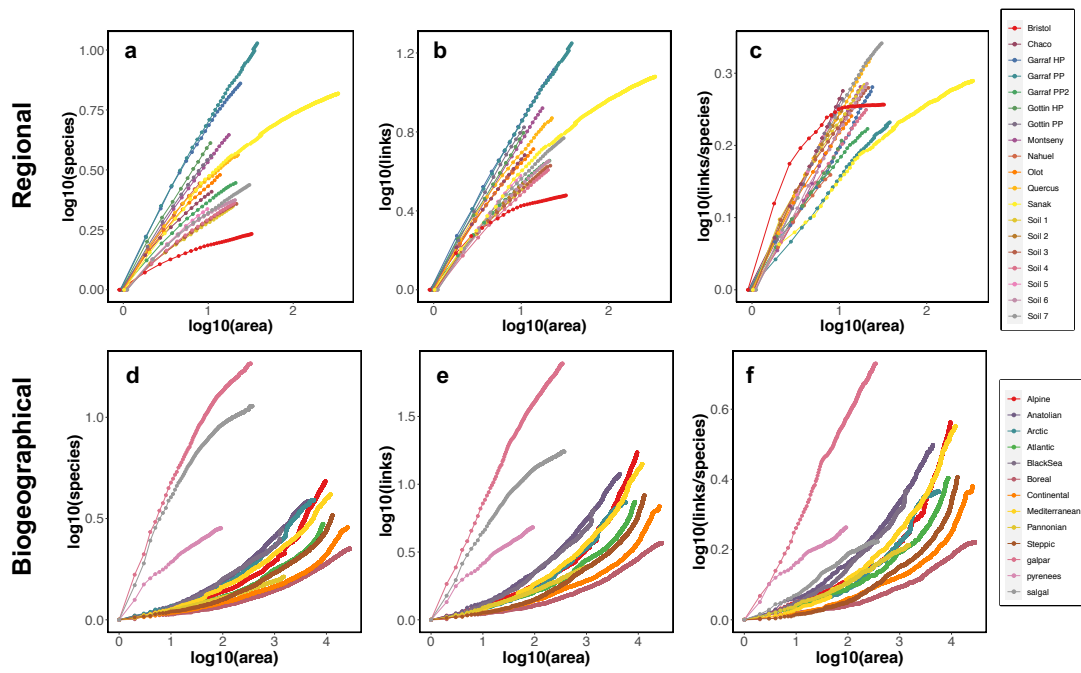
540 **References**

- 541
- 542 1. Arrhenius, O. Species and area. *J. Ecol.* **9**, 95–99 (1921).
- 543 2. MacArthur, R. H. & Wilson, E. O. *The theory of island biogeography*. (Princeton
- 544 University Press, 1967).
- 545 3. Rosenzweig, M. L. *Species diversity in space and time*. (Cambridge University Press,
- 546 1995).
- 547 4. Smith, A. B., Sandel, B., Kraft, N. J. B. & Carey, S. Characterizing scale-dependent
- 548 community assembly using the functional-diversity–area relationship. *Ecology* **94**, 2392–
- 549 2402 (2013).
- 550 5. Mazel, F. *et al.* Multifaceted diversity-area relationships reveal global hotspots of
- 551 mammalian species, trait and lineage diversity. *Glob. Ecol. Biogeogr.* **23**, 836–847
- 552 (2014).
- 553 6. Dias, R. A. *et al.* Species richness and patterns of overdispersion, clustering and
- 554 randomness shape phylogenetic and functional diversity–area relationships in habitat
- 555 islands. *J. Biogeogr.* **00**, 1– 11 (2020).
- 556 7. Pereira, H. M. *et al.* Scenarios for global biodiversity in the 21st century. *Science (80-. )*.
- 557 **330**, 1496–1501 (2010).
- 558 8. Pimm, S. L., Russell, G. J., Gittleman, J. L. & Brooks, T. M. The future of biodiversity.
- 559 *Science (80-. )*. **269**, 347 (1995).
- 560 9. Simberloff, D. Do species-area curves predict extinction in fragmented forest. *Trop.*
- 561 *deforestation species extinction* 75–89 (1992).
- 562 10. Jordano, P. Chasing ecological interactions. *PLoS Biol.* **14**, e1002559 (2016).
- 563 11. Montoya, J. M., Woodward, G., Emmerson, M. C. & Solé, R. V. Press perturbations and
- 564 indirect effects in real food webs. *Ecology* **90**, 2426–33 (2009).
- 565 12. Lurgi, M., López, B. C., Montoya, J. M. & Lopez, B. C. Novel communities from
- 566 climate change. *Philos. Trans. R. Soc. B Biol. Sci.* **367**, 2913–2922 (2012).
- 567 13. Tylianakis, J. M., Tscharntke, T. & Lewis, O. T. Habitat modification alters the structure
- 568 of tropical host–parasitoid food webs. *Nature* **445**, 202–205 (2007).
- 569 14. Montoya, J. M., Rodríguez, M. Á., Hawkins, B. A. & Montoya, J. M., Rodríguez, M. A.
- 570 & Hawkins, B. A. Food web complexity and higher-level ecosystem services. *Ecol. Lett.*
- 571 **6**, 587–593 (2003).
- 572 15. Reiss, J., Bridle, J. R., Montoya, J. M. & Woodward, G. Emerging horizons in
- 573 biodiversity and ecosystem functioning research. *Trends Ecol. Evol.* **24**, 505–514 (2009).
- 574 16. Thompson, R. M. *et al.* Food webs: reconciling the structure and function of
- 575 biodiversity. *Trends Ecol. Evol.* **27**, 689–697 (2012).
- 576 17. Cohen, J. E. & Newman, C. M. Community area and food-chain length: theoretical
- 577 predictions. *Am. Nat.* **138**, 1542–1554 (1991).
- 578 18. Schoener, T. W. Food webs from the small to the large: the Robert H. MacArthur Award
- 579 Lecture. *Ecology* **70**, 1559–1589 (1989).
- 580 19. Post, D. M., Pace, M. L. & Hairston, N. G. Ecosystem size determines food-chain length
- 581 in lakes. *Nature* **405**, 1047–1049 (2000).
- 582 20. Brose, U., Ostling, A., Harrison, K. & Martinez, N. D. Unified spatial scaling of species
- 583 and their trophic interactions. *Nature* **428**, 167–171 (2004).
- 584 21. Galiana, N. *et al.* The spatial scaling of species interaction networks. *Nat. Ecol. Evol.* **2**,
- 585 782–790 (2018).
- 586 22. Wood, S. A., Russell, R., Hanson, D., Williams, R. J. & Dunne, J. A. Effects of spatial
- 587 scale of sampling on food web structure. *Ecol. Evol.* **5**, 3769–3782 (2015).
- 588 23. Pimm, S. L., Lawton, J. H., Cohen, J. E. & Pimm, S. L., Lawton, J. H. & Cohen, J. E.
- 589 Food web patterns and their consequences. *Nat.* 350,669–674 **350**, 669–674 (1991).
- 590 24. Martinez, N. D. Constant connectance in community food webs. *Am. Nat.* **139**, 1208–
- 591 1218 (1992).
- 592 25. Ings, T. C. *et al.* Ecological networks--beyond food webs. *J. Anim. Ecol.* **78**, 253–69
- 593 (2009).
- 594 26. Montoya, J. M. & Solé, R. V. Topological properties of food webs: from real data to

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

- 650 53. Osorio, S., Arnan, X., Bassols, E., Vicens, N. & Bosch, J. Local and landscape effects in  
651 a host–parasitoid interaction network along a forest–cropland gradient. *Ecol. Appl.* **25**,  
652 1869–1879 (2015).
- 653 54. Kaartinen, R. & Roslin, T. Shrinking by numbers: landscape context affects the species  
654 composition but not the quantitative structure of local food webs. *J. Anim. Ecol.* **80**, 622–  
655 631 (2011).
- 656 55. Vázquez, D. P. & Simberloff, D. Changes in interaction biodiversity induced by an  
657 introduced ungulate. *Ecol. Lett.* **6**, 1077–1083 (2003).
- 658 56. Mulder, C., Den Hollander, H. A. & Hendriks, A. J. Aboveground herbivory shapes the  
659 biomass distribution and flux of soil invertebrates. *PLoS One* **3**, e3573 (2008).
- 660 57. Montoya, D., Yallop, M. L. & Memmott, J. Functional group diversity increases with  
661 modularity in complex food webs. *Nat. Commun.* **6**, 1–9 (2015).
- 662 58. Wood, S. A., Russell, R., Hanson, D., Williams, R. J. & Dunne, J. A. Effects of spatial  
663 scale of sampling on food web structure. *Ecol. Evol.* **5**, 3769–3782 (2015).
- 664 59. Grass, I., Jauker, B., Steffan-Dewenter, I., Tscharrntke, T. & Jauker, F. Past and potential  
665 future effects of habitat fragmentation on structure and stability of plant–pollinator and  
666 host–parasitoid networks. *Nat. Ecol. Evol.* (2018). doi:10.1038/s41559-018-0631-2
- 667 60. Cagnolo, L., Salvo, A. & Valladares, G. Network topology: patterns and mechanisms in  
668 plant–herbivore and host–parasitoid food webs. *J. Anim. Ecol.* **80**, 342–51 (2011).
- 669 61. Maiorano, L., Montemaggiore, A., Ficetola, G. F., O’Connor, L. & Thuiller, W. TETRA-  
670 EU 1.0: A species-level trophic metaweb of European tetrapods. *Glob. Ecol. Biogeogr.*  
671 (2020).
- 672 62. Kopelke, J. *et al.* Food-web structure of willow-galling sawflies and their natural  
673 enemies across Europe. *Ecology* **98**, 1730 (2017).
- 674 63. Montoya, J. M., Pimm, S. L. & Solé, R. V. Ecological networks and their fragility.  
675 *Nature* **442**, 259–264 (2006).
- 676 64. Dunne, J. A., Williams, R. J. & Martinez, N. D. Food-web structure and network theory:  
677 the role of connectance and size. *Proc. Natl. Acad. Sci.* **99**, 12917–12922 (2002).
- 678 65. Sole, R. V & Montoya, M. Complexity and fragility in ecological networks. *Proc. R.*  
679 *Soc. London B Biol. Sci.* **268**, 2039–2045 (2001).
- 680 66. Broido, A. D. & Clauset, A. Scale-free networks are rare. *Nat. Commun.* **10**, 1017  
681 (2019).
- 682 67. Guilhaumon, F., Mouillot, D. & Gimenez, O. mmSAR: An R-package for multimodel  
683 species–area relationship inference. *Ecography (Cop.)*. **33**, 420–424 (2010).
- 684 68. Matthews, T. J., Triantis, K. A., Whittaker, R. J. & Guilhaumon, F. sars: an R package  
685 for fitting, evaluating and comparing species–area relationship models. *Ecography*  
686 *(Cop.)*. 1446–1455 (2019). doi:10.1111/ecog.04271
- 687  
688  
689  
690  
691  
692  
693

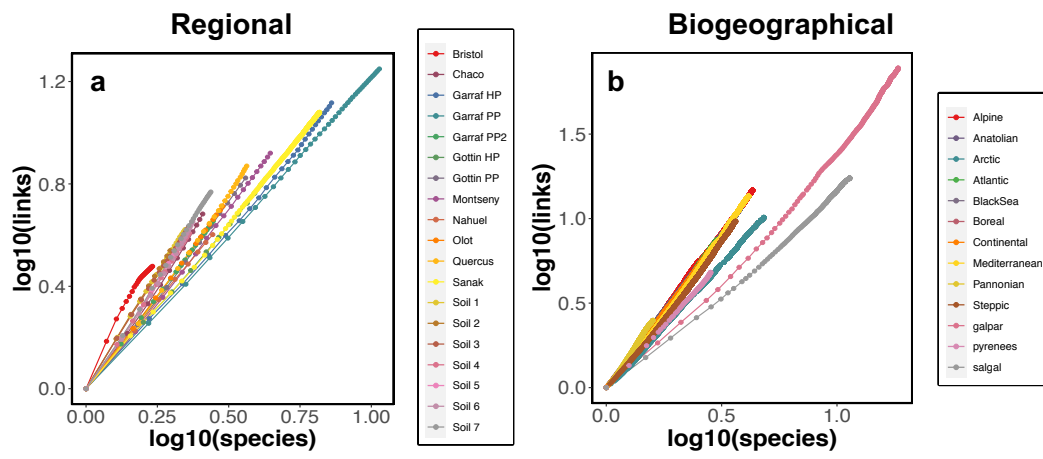




694  
695

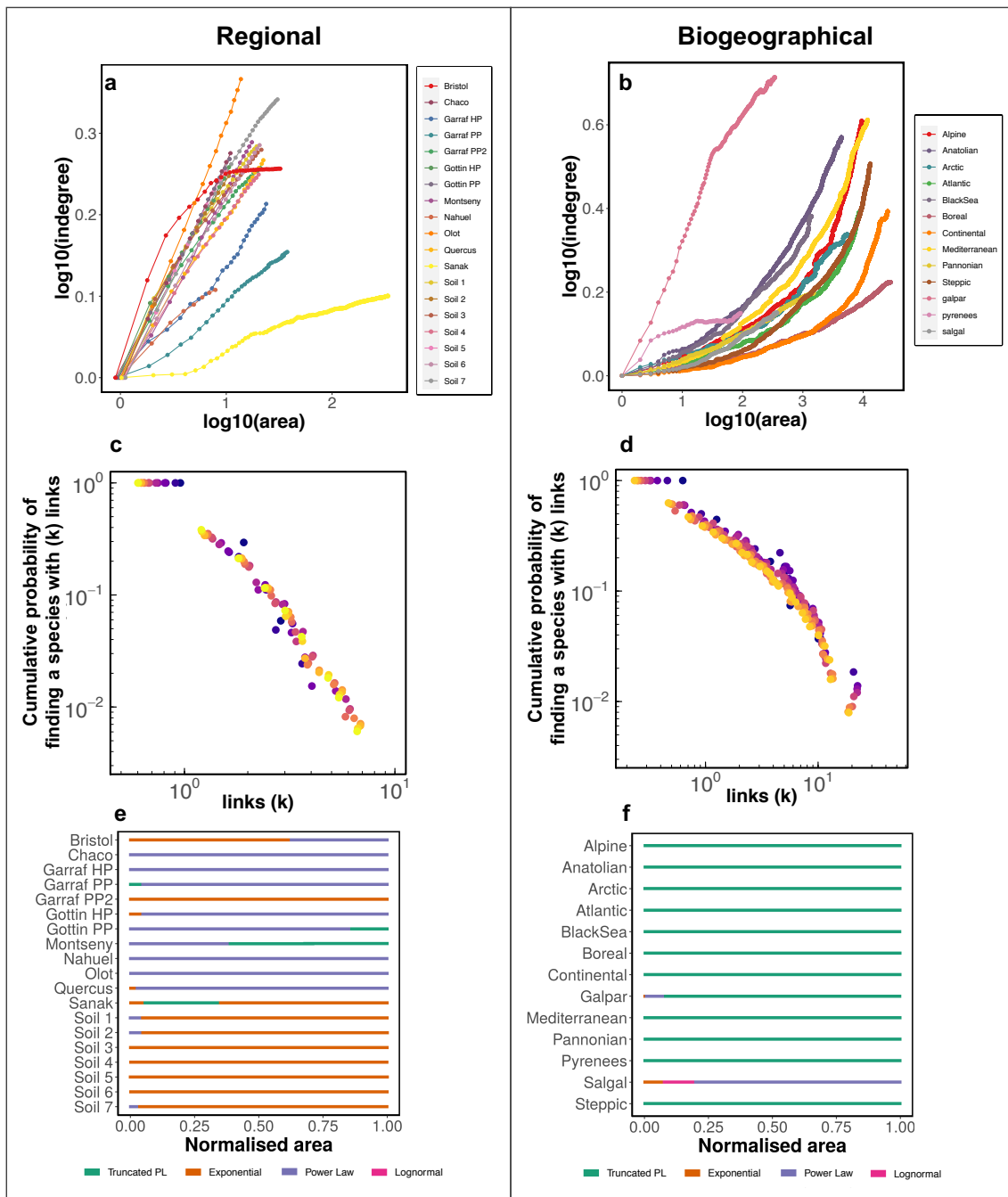
Figure 1

696



697  
698  
699

Figure 2



700  
701

Figure 3