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1 econullnetr: an R package using null models to analyse the structure of  
2 ecological networks and identify resource selection

3

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13

14

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17

18

19 **Summary**

- 20 1. Network analysis is increasingly widespread in ecology, with frequent questions asking  
21 which nodes (typically species) interact with one another and how strong are the  
22 interactions. Null models are a way of addressing these questions, helping to distinguish  
23 patterns driven by neutral mechanisms or sampling effects (e.g. relative abundance of  
24 different taxa, sampling completeness) from deterministic biological mechanisms (e.g.  
25 resource selection and avoidance), but few ‘off the shelf’ tools are available.
- 26 2. We present `econullnetr`, an R package combining null modelling and plotting  
27 functions for networks, with data-export tools to facilitate its use alongside existing  
28 network analysis packages. It models resource choices made by individual consumers,  
29 enabling it to capture individual-level heterogeneity and generalising to a wider range of  
30 data types and scenarios than models applied directly to network matrices. The outputs  
31 can be analysed from the level of individual links to whole networks.
- 32 3. We describe the main functions and provide two short examples, along with the results of  
33 a benchmarking exercise to provide guidance about the statistical power and error rates.  
34 Our hope is that `econullnetr` provides a basis for more widespread use of null  
35 modelling to assist ecological network interpretation.

36

37

38 Key words: food webs; plant-pollinator networks; prey choice; resource selection

39

## 40 **Introduction**

41 Network analysis is being used with increasing frequency in ecology, primarily for the  
42 analysis of food webs, and mutualistic and social networks. A common aim is to understand  
43 patterns of interactions – among nodes usually defined as species – and their strength – often  
44 approximated by interaction frequency – as this allows deeper insight into network assembly,  
45 functioning and response to disturbance (Allesina *et al.*, 2008). Related research questions  
46 ask whether particular species are specialists or generalists, and which taxa they interact with  
47 most strongly (e.g. Vázquez & Aizen, 2003).

48

49 In addressing these research themes with empirical data, null models can highlight network  
50 structures that cannot be accounted for by neutral mechanisms or sampling artefacts. A  
51 simple null hypothesis is that interaction frequencies between consumers and resources are a  
52 consequence of the relative abundances of the potential resources i.e. more common  
53 resources are utilised more heavily than rarer resources because they are encountered more  
54 often (Agusti *et al.*, 2003). This neutral mechanism has been applied in a series of studies,  
55 affording valuable insights into network structure and the behaviour of consumers (e.g.  
56 Agusti *et al.*, 2003; Vázquez & Aizen, 2003; Ibanez 2012). One of the main advantages is  
57 that, by holding characteristics of the observed data constant (e.g. sample size), null models  
58 can reduce the influence of sampling effects on network interpretation (Blüthgen *et al.*,  
59 2008).

60

61 Here we present an R package, `econullnetr`, comprising functions for null modelling and  
62 interpretation of a wide range of networks, including bipartite and more complex networks.  
63 The model was developed to identify prey choices by predators (Agusti *et al.* 2003; King *et*  
64 *al.*, 2010; Davey *et al.*, 2013), but generalises to any network with one or more consumer

65 species. By operating at the level of individual consumers, rather than data already  
66 summarised at the node level in network matrices (e.g. Dormann *et al.*, 2008), it can account  
67 for additional sources of heterogeneity in the data (e.g. intra-specific heterogeneity) or the  
68 need to combine spatially and/or temporally distinct samples into an overall network.  
69 Furthermore, this individual-level approach generalises to complex interaction data, where: i)  
70 individual consumers may interact with multiple resources, ii) data could range from a list of  
71 species an individual interacted with, to actual quantities (e.g. number of prey eaten by a  
72 predator), and iii) “forbidden links” may need to be specified. Rather than fixing network  
73 properties (e.g. overall network size) *a priori*, network structure emerges from individual  
74 behaviour, which can lead to more robust models (Grimm & Berger, 2016).

75

76 We describe the null model and report on a benchmarking exercise to provide guidance about  
77 its power and error rate (Gotelli & Ulrich, 2012). We then describe the functions in  
78 `econullnetr` and provide two short examples. For simplicity, and in line with long-  
79 established conventions in ecological network analysis, we refer to the nodes as “species”,  
80 each of which comprises one or more individuals: in reality, nodes vary in their taxonomic  
81 resolution or may represent different entities altogether (e.g. functional groups), and  
82 `econullnetr` can be applied in these cases too.

83

#### 84 **Overview of the null model**

85 Resource selection is modelled for each individual consumer in turn (see below), after which  
86 interaction strengths are summarised for each pair of consumer and resource species to  
87 produce the interaction matrix, from which a range of statistics can be calculated. Iterations  
88 of the model build sampling distributions for the selected statistics, from which  $1-\alpha\%$   
89 confidence limits can be calculated using the  $1-\alpha/2$  percentiles from the frequency

90 distribution (Manly 2006). If the value of the statistic from the observed network falls outside  
91 the confidence interval, it can be considered to be significantly greater or less than expected  
92 based on random resource use (i.e. resources used in proportion to their abundance). The  
93 mean value for the statistic across the iterations of the model provides an estimate of the  
94 expected value to which the observed value can be compared.

95

96 Interaction data may be nominal or quantitative at the level of individual consumers, prior to  
97 being aggregated to species level in the interaction matrix (Table 1). To model resource  
98 selection with nominal interaction data, the same number of resource species are selected as  
99 were originally recorded (i.e. an individual's degree is held constant), using sampling without  
100 replacement: the probabilities of different resources being selected are proportional to their  
101 relative abundance (Agusti *et al.*, 2003). Direct measures of resource availability (e.g. flower  
102 abundance in quadrats or transects) are required by `econullnetr` (cf. using marginal totals  
103 of a network matrix e.g. Dormann 2009). For count data, the same number of interactions are  
104 allocated (e.g. prey items eaten or flowers visited by an individual), allowing repeated use of  
105 the same resource species (i.e. sampling with replacement). When interactions are quantities  
106 such as biomass, the proportions are drawn from a Dirichlet distribution with shape  
107 parameters determined by the relative abundance of the different resources (Ainsworth *et al.*,  
108 2010). For both types of quantitative data (Table 1), the degree can either be held constant  
109 within each individual or resources drawn from the full range of species.

110

111 An important stage in null model development is investigating Type I and II error rates,  
112 respectively the frequency of erroneously identifying patterns in random data and failing to  
113 identify features in the data, using synthetic data with known properties (Gotelli & Ulrich,  
114 2012). We subjected `econullnetr` to >100 benchmark tests capturing a range of sample

115 sizes (10–100 individuals per consumer species), data types (nominal and quantitative) and  
116 strengths of resource selection by consumers, the latter ranging from no selection (‘perfect  
117 generalists’) to only interacting with one preferred resource (‘perfect specialists’).  
118 Performance was examined for individual links, whole species and the complete network.  
119 Full details of the testing process and the results are provided in Appendix S1. In summary,  
120 Type I error rates were consistently around 5%, as expected for 95% confidence limits,  
121 except for the combination of multinomial data with three out of the five network-level  
122 statistics (linkage density, weighted connectance and interaction evenness), for which Type I  
123 error >10% (Table S2). No problems were evident at link- or species-level (Table S2). The  
124 ability to detect preferences was strongly related to the strength of a consumer’s preferences  
125 and secondarily to sample size: very strong preferences (e.g. focusing on a single resource  
126 species) were detected in almost all situations, even at small sample sizes, whilst weak  
127 preferences were hard to detect, irrespective of sample size (Tables S3 & S4; Figs S2 & S3).  
128 The tests provide confidence that strong patterns of resource preference should be detected  
129 and results not compromised by frequent spurious test results.

130

### 131 **The `econullnetr` package**

132 The package comprises six functions and three data sets (Table 2). We briefly illustrate some  
133 of the features using the `Silene` (flower visitation) and `Broadstone` (food web) data sets:  
134 `econullnetr`’s help files and vignette provide full details and code to reproduce the  
135 examples.

136

137 The main function, `generate_null_net`, uses two data frames and an optional third: i)  
138 interaction data, where rows represent individual consumers, columns the resource species  
139 and the elements either the presence/absence of an interaction, the number of interactions or

140 the quantity; ii) the relative abundance of the resource species; and iii) optionally, a table of  
141 resource weights, one set for each consumer species, which are multiplied by the relative  
142 resource abundances to modulate the probabilities of different resources species being  
143 selected. This is primarily to specify ‘forbidden’ links for each consumer (weight = 0). Where  
144 data from different time points or locations are combined to produce an overall network, this  
145 can be specified in the call to `generate_null_net`, running the model separately in each  
146 sub-unit before combining them.

147

#### 148 *The Silene network*

149 For bipartite networks, a wide range of statistics can be calculated for the observed and null  
150 networks using `bipartite_stats` (Table 2). *Silene* shows significantly lower linkage  
151 density, connectance and interaction evenness than expected (Table 3), consistent with  
152 preferences among the pollinator community. For any network, `test_interactions`  
153 generates a table comparing the observed and expected link strengths for all interactions in  
154 the network. Only 6% of links in *Silene* were inconsistent with the null model (Fig 1),  
155 including preferences for *Senecio* by two of the commonest pollinators (*Eristalis tenax* and  
156 *Rhagonycha fulva*), and fewer visits than expected to *Hypericum* by *Episyrphus balteatus*  
157 (Fig 1).

158

159 Whilst network plots are valuable for revealing where preferences occur, they are less  
160 effective at conveying the strength of preferences: instead, `plot_preferences` provides  
161 a detailed comparison of observed and predicted link strengths for individual consumer taxa  
162 (King *et al.*, 2010). One pollinator, the hoverfly *Sphaerophoria scripta*, showed a near four-  
163 fold preference for *Silene* at the expense of *Senecio*, which was only visited around 20% as  
164 often as predicted: visitation to the other flower species was consistent with the null model



165 (Fig 2). In a conservation context, the apparent specialisation of this hoverfly, coupled with  
166 its abundance, highlights its potential importance for managing *Silene* (Gibson *et al.* 2006).

167

### 168 *The Broadstone Stream network*

169 For more complex networks, a range of network packages, such as `igraph` (Csardi &  
170 Nepusz 2006) or `cheddar` (Hudson *et al.*, 2013), may be useful for calculating network  
171 statistics and visualising the data. The function `generate_edgelist` exports the  
172 observed and expected link strengths in a format that is readily imported into other packages.  
173 Here, we used the `cheddar` package in combination with `econullnetr`.

174

175 Eighteen percent of links in the Broadstone food web were inconsistent with the null  
176 model (Fig 3 a & b), with all but one of the predators displaying evidence of prey preferences  
177 (positive or negative; Fig 3a). Combining `cheddar`'s  
178 `NodeQuantitativeDescriptors` function with `generate_null_net`, revealed  
179 one predator (*Cordulegaster*) showed higher generality than expected, two (*Trissopelopia*  
180 and *Macropelopia*) demonstrated dietary specialisation, whilst the remainder were consistent  
181 with the null model (Fig 3b). The preferences fitted the well-known size structuring of the  
182 Broadstone food web (Woodward *et al.* 2005). *Cordulegaster*, the largest invertebrate  
183 predator, consumed small, abundant taxa less often than expected and larger, less abundant  
184 taxa more often than expected, leading to its more general diet than predicted by the model  
185 (Fig 3c). This reflects mouthparts that allow it to take larger prey and the relative  
186 inaccessibility of small prey in fine interstitial spaces. *Trissopelopia* (*Macropelopia* was  
187 similar, but not shown) was one of the smallest predators, and showed strong preference for  
188 *Heterotrissocladius*, a small chironomid midge that occupies similar interstitial  
189 microhabitats, with most other taxa consistent with the null model or eaten less often than

190 expected (e.g. *Zavreliomyia*), leading to the more specialised diet (Fig 3d). Large, mobile taxa  
191 (towards the bottom of the y-axis) were rarely consumed by this small and relatively  
192 sedentary predator.

193

#### 194 **Concluding remarks**

195 The `econullnetr` package provides simple tools for revealing structures within networks.  
196 It ignores dynamics, only considering networks at a point in time, and uses simple proxies of  
197 interaction strength (e.g. interaction frequency) that may limit insight into network behaviour  
198 (Berlow *et al.*, 2004). Nevertheless, `econullnetr` covers the types of data most frequently  
199 collected, and should aid basic network interpretation. The model cannot explain the  
200 mechanisms underpinning ‘selection’, which may be an active choice (e.g. based on prey size  
201 or flower morphology) or a passive process (e.g. spatio-temporal separation), but provides a  
202 way to highlight interactions for further investigation. It has good Type I error properties  
203 under a wide range of conditions and, with sufficient consumers sampled ( $\gg 10$  individuals),  
204 good power to recover resource preferences.

205

206 As networks become large and contain many links, multiple significance testing is likely to  
207 become important. Currently, `econullnetr` does not attempt to control for this, but issues  
208 a reminder about Type I error when `test_interactions` is run. Based on our  
209 benchmark testing, Type I error rates were low and could be reduced by selecting a more  
210 stringent testing criterion (e.g.  $\alpha=0.01$ ). For larger networks, some form of false discovery  
211 rate procedure is likely to be valuable for controlling Type I errors (e.g. the local false  
212 discovery rate, Gotelli & Ulrich 2010), and we hope to add this in a future version.

213

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218 `econullnetr` was supported by a Cardiff University Research Leave Fellowship awarded  
219 to IPV.

220

### 221 **Accessibility**

222 `econullnetr` is freely available under the open source MIT licence. A stable version is  
223 available from the CRAN archive (<https://CRAN.R-project.org/package=econullnetr>), whilst  
224 the development version is hosted on GitHub (<https://github.com/ivaughan/econullnetr>),  
225 where feature requests and bug reports can be posted.

226

### 227 **Author contributions**

228 IPV designed the null model, wrote the R package and the first draft of the paper. NJG helped  
229 to design the benchmarking tests and advised on aspects of the null model. JM, CEP and GW  
230 contributed data sets and ideas on model applications. WOCS provided applications for the  
231 initial development of the model and helped to design the plotting functions. All authors were  
232 involved in preparing the final manuscript.

233

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**Table 1.** The four types of interaction data handled by `econullnetr`.

Data recorded for individual consumers	Examples
<i>Nominal</i>	
One resource species recorded per consumer	<ul style="list-style-type: none"><li>• Ants carrying individual seeds</li><li>• Pollinators recorded on the flower species where they were observed</li></ul>
Varying numbers of resource species per consumer	<ul style="list-style-type: none"><li>• List of flower species visited by a pollinator during a fixed observation period</li><li>• Molecular gut contents analysis identifying prey species, but without quantifying the amount of prey tissue</li></ul>
<i>Quantitative</i>	
Counts of interactions with each resource species by individual consumers	<ul style="list-style-type: none"><li>• Number of visits to each flower species by a pollinator during a fixed observation period</li><li>• Visual gut contents analysis, counting the number of individuals of each prey species based on identification of hard parts</li></ul>
Biomass, or equivalent quantitative measurement	<ul style="list-style-type: none"><li>• Proportion of gut contents comprised by different food sources</li><li>• Number of pollen grains of different flower species on a pollinator's body</li></ul>

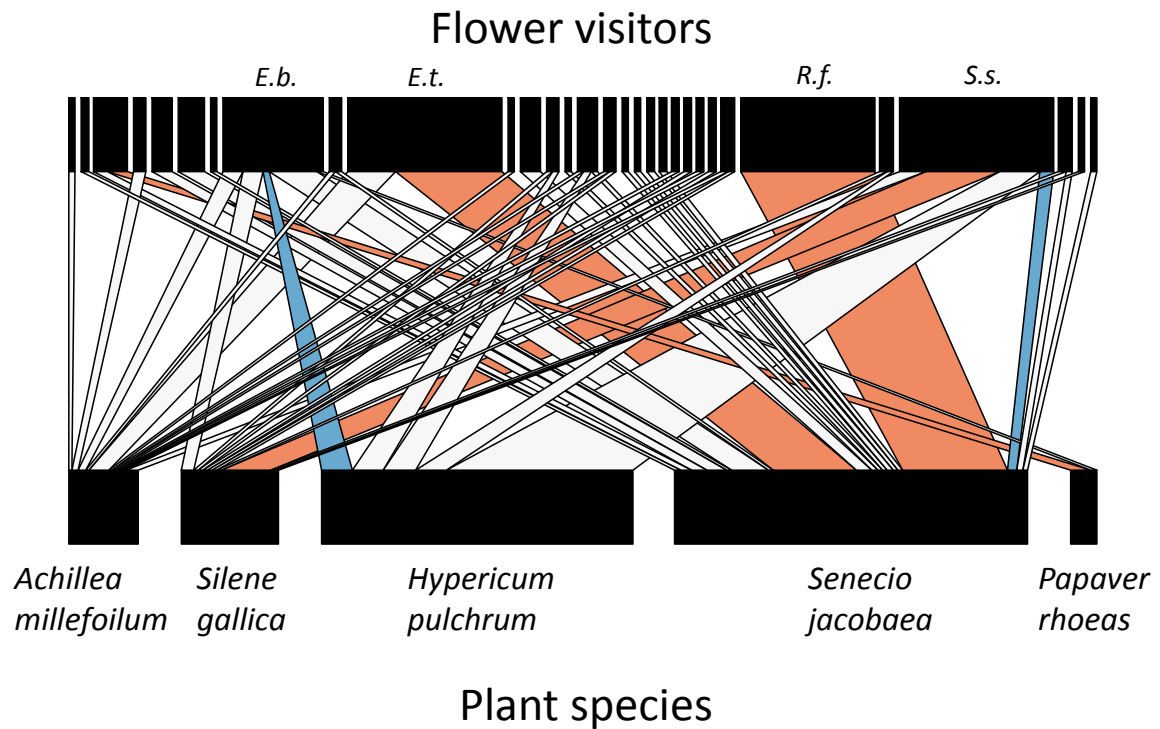
**Table 2.** Overview of `econullnetr`'s functions and data sets

Name	Description
<i>Functions</i>	
<code>generate_null_net</code>	Specify and run the null model.
<code>test_interactions</code>	Compare observed interaction strengths to those generated by the null model
<code>plot_preferences</code>	Plot observed and modelled interaction strengths for individual consumer species
<code>bipartite_stats</code>	Compare network metrics between the observed and null bipartite networks. A wrapper for the <code>bipartite</code> package's <code>networklevel</code> , <code>grouplevel</code> and <code>specieslevel</code> functions (Dormann <i>et al.</i> , 2008, 2009).
<code>plot_bipartite</code>	A wrapper for <code>bipartite</code> 's <code>plotweb</code> function (Dormann <i>et al.</i> , 2008), colour coding interactions according to their consistency with the null model
<code>generate_edgelist</code>	Export null model results in a format compatible with other network analysis packages
<i>Data sets</i>	
Broadstone	Part of the highly-resolved Broadstone Stream food web (Woodward <i>et al.</i> , 2005).
Silene	Flower visitation network, notable for the presence of small-flowered catchfly <i>Silene gallica</i> , a rare arable weed in the UK (Gibson <i>et al.</i> 2006)
WelshStreams	Part of a macroinvertebrate food web from upland streams in south Wales, UK, focusing on two abundant predators

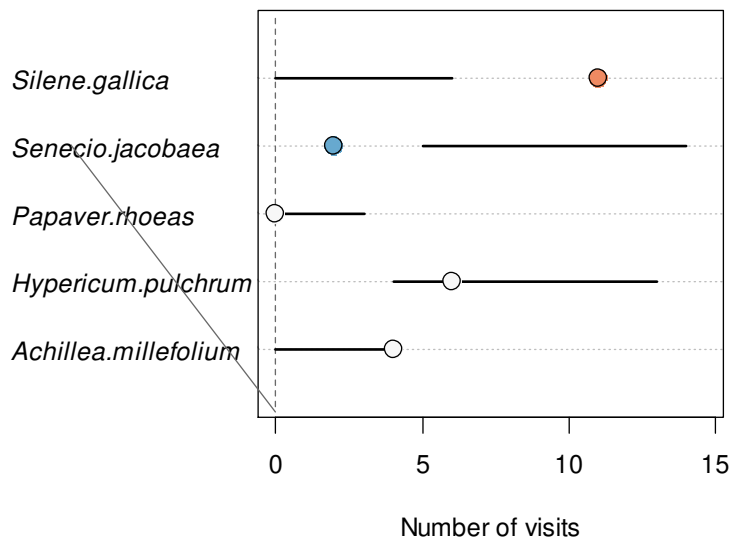


**Table 3.** Network-level statistics for *Silene*, comparing observed values to the 95% confidence limits from the null model and including the standardised effect size (SES).

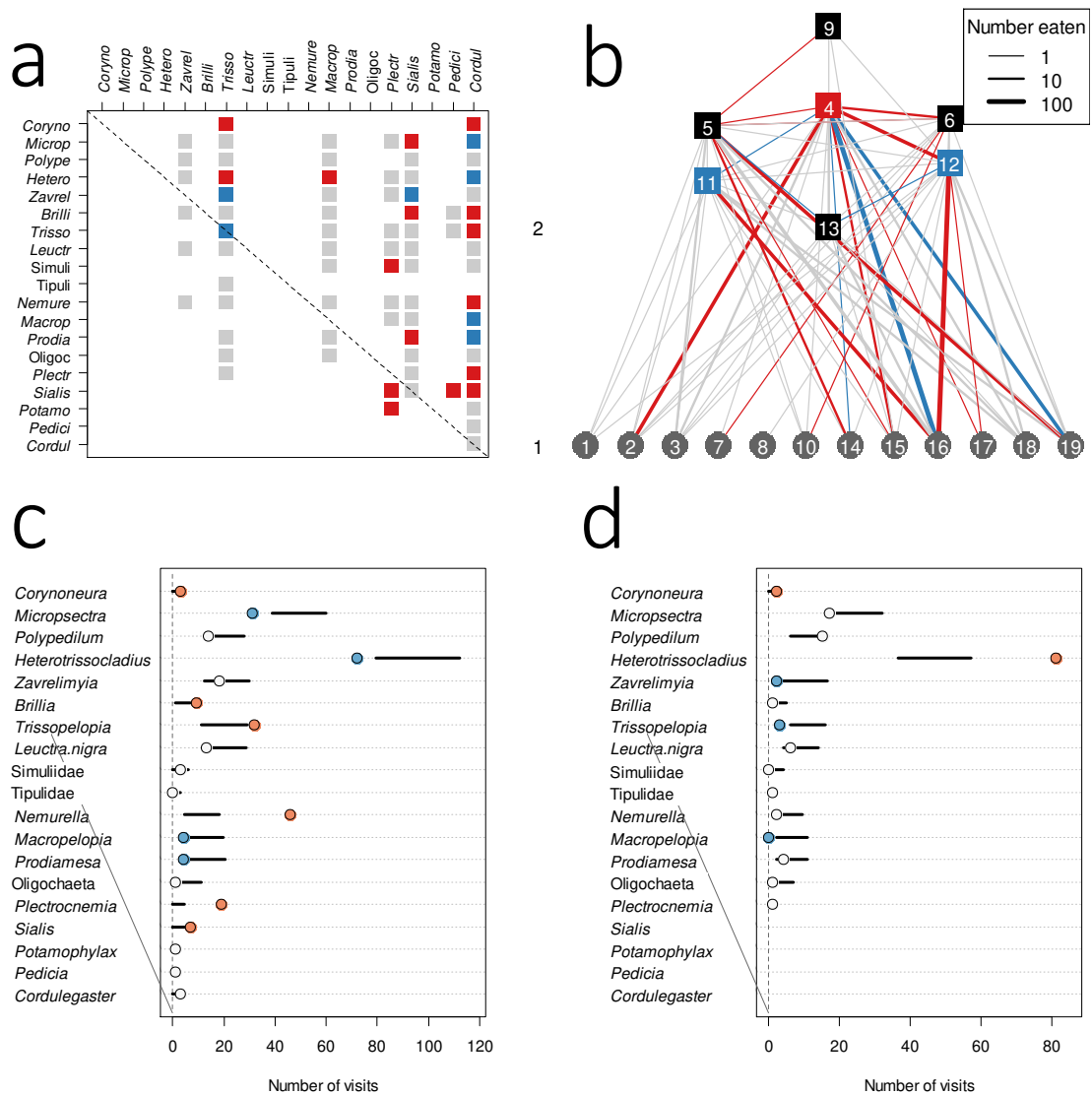
Metric	Observed	Null	Lower.CL	Upper.CL	Test	SES
linkage density	5.096	6.687	6.166	7.230	Lower	-5.830
Connectance (weighted)	0.142	0.186	0.171	0.201	Lower	-5.740
Nestedness (weighted)	0.518	0.569	0.369	0.744	ns	-0.535
Interaction evenness	0.849	0.897	0.880	0.913	Lower	-5.763



**Figure 1.** Flower visitation network for *Silene* using `plot_bipartite`: for simplicity, individual pollinator species are not labelled. Link widths represent the observed frequency of interactions, with red links stronger than expected under the null model and blue links weaker than expected. Bar widths at the two levels indicate the relative abundances of different plants and flower visitors. Four pollinator species mentioned in the test are highlighted: *E.b.* = *Episyrphus balteatus*, *E.t.* = *Eristalis tenax*, *R.f.* = *Rhagonycha fulva* and *S.s.* = *Sphaerophoria scripta*.



**Figure 2.** Preference plot for the hoverfly *Sphaerophoria scripta* in the *Silene* network, comparing the observed interaction frequencies (dots) to the 95% confidence intervals from the null model (bars). The red dot denotes an interaction that was stronger than expected under the null model, the blue dot weaker than expected, and white dots consistent with the null model.



**Figure 3.** Null modelling results for Broadstone: (a) the predation matrix, with taxa ranked in increasing size order (left to right); grey symbols indicate links consistent with the null model, blue = significantly weaker, red = significantly stronger and white = interaction not observed; (b) alternative plot of the web, with the mean trophic level of each species on the y-axis; links colour coded as for (a), with thickness indicative of predation frequency; predators in black = consistent with the null model, red = more general diet than expected, blue = more specialised; (c) preferences of *Cordulegaster* (predator 4 in (b)) and (d) *Trissopelopia* (predator 12 in (b)); interpretation of (c) and (d) as for Figure 2.

300 **Supporting information**

301

302 **Appendix S1.** Full methods and results from benchmark testing of the null model.

303

304