

An *a posteriori* measure of network modularity

TIMOTHÉE POISOT^{1,2,*}

¹*Département de biologie, chimie et géographie, Université du Québec à Rimouski, 300 Allée des Ursulines, Rimouski (QC), G5L 3A1, Canada*

²*Québec Centre for Biodiversity Sciences, Stewart Biological Sciences Building, 1205 Dr. Penfield Avenue, Montréal (QC), H3A 1B1, Canada*

**email: timothee.poisot@uqar.ca*

Abstract

Measuring modularity is important to understand the structure of networks, and has an important number of real-world implications. Several measures exist to assess modularity, which when applied to the same network, can return both different modularity values and different module compositions. In this article, I propose an *a posteriori* measure of modularity, which is simply defined as the ratio of interactions between members of the same modules *vs.* members of different modules. I apply this measure to a large dataset of 290 ecological networks representing host–parasite (bipartite) and predator–prey (unipartite) interactions, to show how the results are easy to interpret, and can reveal new features about modularity.

1 Introduction

Modularity, the fact that groups of nodes within a network interact more frequently with themselves than with other nodes, is an important property of several systems, including genetic [1, 2], informatics [3], ecological [4], and socio-economic [5] interactions, as well as biogeographic patterns [6, 7] and disease spread management [8].

6 Because of the relevance of modularity for network properties, it is important to as-
7 sess it correctly. There exists several methods to measure network modularity, some
8 of which rely on the optimization of a given criterion [9, 10], label propagation [11], or
9 combination of these approaches [12, 13]. These methods return two elements. The
10 first is a value of modularity for the networks, most often within the 0–1 interval.
11 Each method often has a threshold value, above which a network is considered to be
12 modular. Increasing values reflect and increasingly modular structure. The second
13 element is a “community partition”, *i.e.* the attribution of each node to a module.

14 Recently, Thébault [7] showed that different measures of modularity tailored
15 to presence/absence matrices (*i.e.* networks in which links have no weight), gave
16 roughly equal estimates of the significance of modularity, but differed in the com-
17 munity partition they returned (*i.e.* the identity of nodes composing each module
18 varied). In such situations, one might look for a way to choose which community
19 partition should be used. As the criterion that is optimized by each method is dif-
20 ferent, one possible way to compare the different community partitions is to use
21 an *a posteriori* measure to quantify modularity, which can be applied to a network
22 regardless of the method used to obtain the community partition.

23 An important feature of modular networks is the occurrence of interactions be-
24 tween nodes of different modules. They contribute to the propagation of disturbances
25 [4], flow of information [14, 15], and cross- regulation of biological processes [16], *in-*
26 *ter alia* [17]. In addition to measuring how modular the network is, determining
27 to what extent modules are connected, and to identify nodes and edges responsible
28 for connecting modules, is thus valuable information. In this article, I propose an

29 *a posteriori* measure of the proportion of interactions established between modules,
 30 *i.e.* edges connecting different communities. I apply this measure to the community
 31 partition identified by the Louvain method on 290 ecological networks, and show
 32 that it behaves in a similar way to other modularity measures.

33 2 The measure

34 In this contribution I define the *realized modularity*, termed Q_R . Q_R measures the
 35 extent to which edges, within a network, are established between nodes belonging to
 36 the same module. For E edges in a network, if W of them are established between
 37 members of the same module, then

$$Q_R = \frac{W}{E}. \quad (1)$$

38 When there are no between-module links, then $W = 0$ and Q_R takes the maximal
 39 value of 0. When between-module interactions are as numerous as within-modules
 40 interactions, then $W = E/2$, and Q_R takes the minimal value of 1/2. To express the
 41 *realized modularity* as a value between 0 and 1, it is expressed as:

$$Q'_R = 2 \times Q_R - 1. \quad (2)$$

42 The main advantage of Q_R is that it is agnostic with regard to the measure used
 43 to optimize modularity (and even to the method by which the nodes were assigned to
 44 modules, which can be arbitrary), as it acts *a posteriori*, *i.e.* after nodes have been
 45 attributed to modules. It can therefore be used to select the community detection

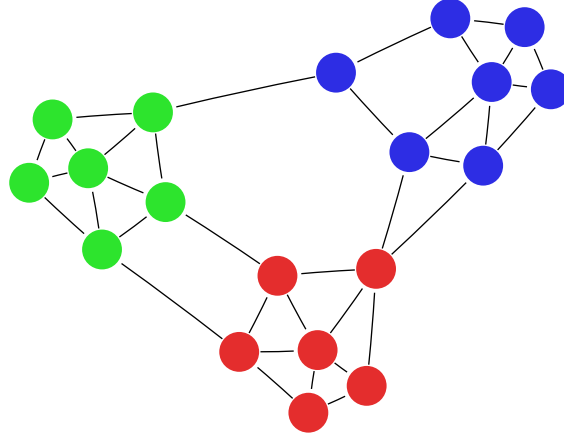


Figure 1: A cartoon depiction of a modular network with links between modules. Nodes of the same modules are identified by different colors. This network has a modularity (Louvain method) of $Q = 0.527$. Out of the 36 interactions, 31 are established within modules, and 5 between modules. This gives a Q_R value of 0.86, and $Q'_R = 0.72$.

method maximizing modularity. This measure works on most type of networks, as it makes no difference if links are directional, or if the networks are bipartite/unipartite. An illustration of this measure is given in Figure 1. This measure is purposefully simple, (i) so that it makes no assumption about what modularity is, or how it should be optimized, and (ii) because it is not meant to be used to optimize modularity, but to either compare the outcome of different methods, or present the value of modularity in a way that is straightforward to interpretate.

A python implementation of this measure, using the `networkx` package, is proposed at <https://gist.github.com/tpoisot/4947006>. It reads data in the edge list format, and offers additional functions to generate null networks, as detailed in the following section.

3 Example application: realized modularity in ecological networks

In this section, I analyze the modular structure of a large dataset of 290 ecological networks (187 food webs and 113 host-parasite networks) published in previous meta-analyses [18, 19]. Modularity is an important feature of ecological interaction networks, which is linked to their resilience [20, 21], stability [7], biogeographic structure [22], functioning [23], and to the evolutionary mechanisms involved in their assembly [24]. Notably, the occurrence of interactions between and within modules plays a central role in the structure of pollination networks [4], and help buffer the effect of species extinctions [21].

The existence of interactions in ecological systems involves a large family of processes, ranging from abundance related [25, 26] (abundant species are more likely to interact together) to trait related [27] (pollination depends on the flower and insect having compatible morphologies, predators are constrained by the body-size of their preys). The interaction within these different families of mechanisms will drive heterogeneity in interaction strength [28]. Yet, the analysis of binary matrices (is there an interaction between a pair of species, or not), still has relevance to identify properties that are conserved across systems [29], especially given that one could argue that quantitative information on interaction strength is an additional level of information. The systems analyzed in this section are represented by their adjacency matrix, describing the presence or absence of an interaction.

78 3.1 Data and analysis

79 I used the Louvain method [30] to detect modules, due to its rapidity and efficiency
80 on large networks. The Louvain method works in two steps: first it optimizes mod-
81 ularity *locally*, through clustering of neighboring nodes. These clusters are, in the
82 second steps, aggregated together, until modularity ceases to increase. This method
83 is known to give values of modularity comparable to what is found using *e.g.* sim-
84 ulated annealing, and has been observed to give modules that have a functional
85 relevance [30]. Once the partition is returned by the Louvain method, I recorded its
86 realized modularity Q'_R , and its modularity Q (using the Newman and Girvan [31]
87 measure).

88 For each network, I compared the values of Q and Q'_R on the empirical networks
89 to their random estimate using a network null model. Because random networks will
90 by chance display a modular (among other) structure, it is important to confront
91 the empirical measures of Q and Q'_R to their random expectations. The null model
92 is defined as follows. For each node n of the network, I measured its degree d_n , its
93 number of successors (the number of node it links to, or generality in ecological terms,
94 as *per* [32]) g_n , and its number of predecessors (the number of nodes that link to
95 it, or vulnerability) v_n . In each random network, for each pair of nodes (i, j) , the
96 probability that i interacts with j is given by

$$P(i \rightarrow j) = \frac{1}{2} \left(\frac{g_i}{d_i} + \frac{v_j}{d_j} \right), \quad (3)$$

97 and conversely for $P(j \rightarrow i)$. This null model allowed the generation of pseudo-

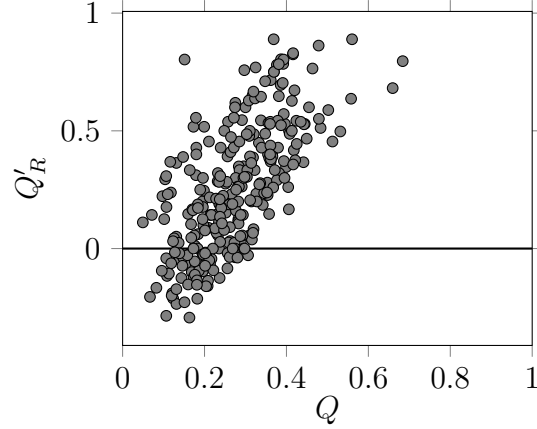


Figure 2: Relationship between the modularity of the best partition using the Louvain method and the *a posteriori* realized modularity. There exists a strong, positive relationship between the two variables. Worth noting is that fact that, for some networks, the best partition resulted in *negative* versions of Q'_R , *i.e.* there were more interactions between than within modules. Each dot correspond to a network.

98 random networks through a Bernoulli process (in each replicate, the occurrence of a
99 link is randomly determined), with the same connectance, and the same distribution
100 of degrees, generality, and vulnerability, as the original one (these properties are also
101 conserved at the *node* level). For each of the 290 networks, 1000 pseudo-random
102 replicates are generated. For each of them, the average value of Q_R and Q'_R are
103 estimated along with their 90% confidence interval. When the empirical value lies
104 outside the confidence interval, it can be assumed that the modular structure of the
105 network is different than expected by chance.

106 3.2 Results

107 There is a strong, positive relationship, between the values of Q'_R and the values of Q
 108 (Pearsons's product-moment correlation coefficient, as implemented in R 2.15 [33],
 109 $\rho = 0.64$, 288 d.f., $p < 10^{-6}$), *i.e.* networks for which a high modularity is detected
 110 tend to have relatively few between-module links (Figure 2). It is worth noting
 111 that some Q'_R values were negative: in some cases, the best community division
 112 resulted in more interactions between than within modules. This result highlights
 113 why using an *a posteriori* measure is useful: other measures of modularity do not
 114 reveal the fact that there were more interactions between than within modules. In
 115 the dataset examined, most of the networks with a modularity lower than 0.2 had a
 116 negative realized modularities. This result suggests that discussing the modularity
 117 of such networks makes little sense, as their modules are not more densely linked
 118 than other random collections of nodes within the graph. Q and Q'_R have different
 119 relationships with connectance (Figure 3). Increased connectance values resulted in
 120 lower modularity ($\rho = -0.61$, 288 d.f., $p < 10^{-6}$), but had no impact on Q'_R . This
 121 is a desirable property, as it allows easy comparison with the Q'_R values of networks
 122 with extremely different connectances.

123 There is a linear relationship between the deviation from random expectation of
 124 Q and Q'_R ($\rho = 0.78$, 288 d.f., $p < 10^{-6}$ – Figure 4). The deviations (respectively
 125 ΔQ and $\Delta Q'_R$) are calculated as the empirical value, minus the average of the values
 126 on the networks generated by the null model. As an example, a ΔQ less than
 127 zero indicates that the empirical network is less modular than expected by chance.
 128 Confidence intervals for the average of the null models were typically very narrow

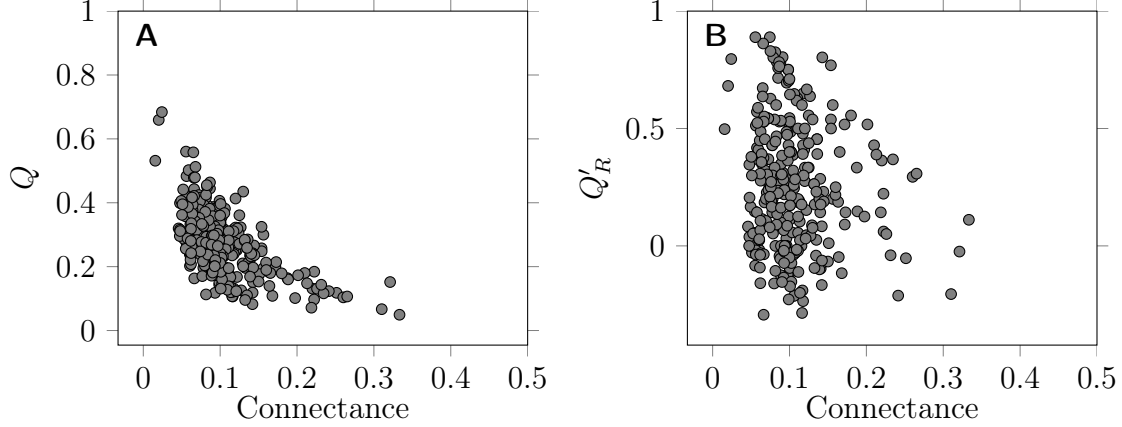


Figure 3: Relationship between the two measures of modularity and network connectance. **A.** Q is negatively affected by connectance, *i.e.* densely connected networks are more likely not to be modular. **B.** Q'_R is not affected by connectance, allowing to use it to compare different networks. Each dot correspond to a network.

129 (not represented in the figure to avoid cluttering – see associated original dataset),
 130 probably owing to the fact that the null model is restrictive on the type of networks
 131 which are generated. It is worth noting that for some networks, the diagnostic of the
 132 null model analysis conflicted. In a vast majority of the situations, this corresponds
 133 to networks having a lower modularity than expected by chance, yet having a higher
 134 realized modularity (dots in the upper left corner of Fig. 4). Depending on whether
 135 the true modularity, or the realized modularity, is the most relevant metric of the
 136 processes studied, the interpretation of the null models for these networks will be
 137 different.

138 Finally, for the unipartite network dataset, I compare the results of three alterna-
 139 tive methods of community detection (the walktrap, spinglass, and edge betweenness
 140 methods, as implemented in the *igraph* library). For each of the unipartite networks,

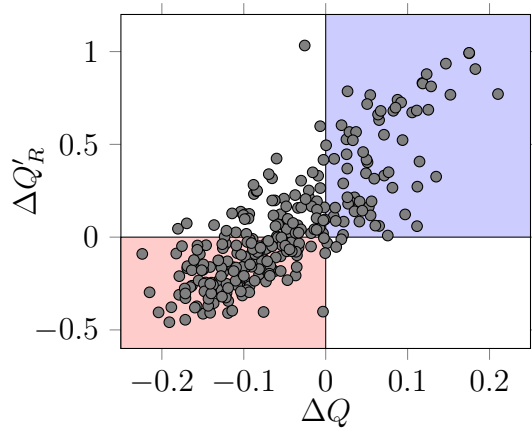


Figure 4: Linear relationship between the deviation from random expectation in Q and Q'_R . Networks in the red area are detected as being less modular than expected both by Q'_R and Q , while networks in the blue area are detected as being more modular. Although the agreement between the two measures is good (see main text for statistics), some networks are detected as having a higher than expected realized modularity Q'_R , despite a lower than expected modularity Q . Each dot correspond to a network.

141 I computed the value of Barber’s Q , and Q'_R , on the best partition found. The strong
 142 correlation between Q and Q'_R were observed for the spinglass method ($r = 0.61$, df
 143 $= 165$, $t = 10.02$), and the weakest for the edge-betweenness method ($r = 0.04$,
 144 non-significant at $\alpha = 0.05$). The walktrap algorithm gave results in between ($r =$
 145 0.489 , $df = 165$, $t = 7.20$). For both the walktrap and edge-betweenness methods, sev-
 146 eral networks had negative values of Q'_R , which indicates that the “best” community
 147 partition had more links between than within modules. The spinglass method had,
 148 by contrast, less than 8% of all networks with values of Q'_R lower than 0, meaning
 149 that this algorithm should be preferred when one wants to group nodes in densely
 150 connected clusters.

151 4 Conclusions

152 The Q'_R measure presented here allows the estimation of the proportion of inter-
 153 actions established between different modules in a network. This measure can be
 154 analyzed much in the same way as other measures of modularity, but is applied *a*
 155 *posteriori*. As such, it can help choose the “best” community partition according to
 156 the property of the network that one wants to maximize. For example, choosing
 157 the partition giving the lowest Q'_R can help identify which species are more likely to
 158 act as connectors between different modules. Ultimately, this information may have
 159 some practical relevance as a decision tool. Saavedra et al. [5] showed that different
 160 nodes contribute differently to overall network properties. In a context in which net-
 161 works are increasingly being used as management tools to adress *e.g.* conservation or

162 pest management [8], knowing the realized modularity, and developping methods to
163 estimate which species have the highest impact on it, can allow the design of efficient
164 policies to maximize, or decrease, the ability of network modules to interact.

165 Competing interests

166 No competing interests were disclosed.

167 Grant information

168 TP is funded by a PBEEE-FQRNT post-doctoral scholarship, and thanks the EEC
169 Canada Research Chair for providing computational support.

170 **Acknowledgements:** Thanks are due to the maintainers and contributors of
171 the free textttnetworkx, textttscipy, and textttnumpy packages used in this project,
172 and to Scott Chamberlain for discussions.

173 References

- 174 [1] Carlos Espinosa-Soto and Andreas Wagner. “Specialization can drive the evo-
175 lution of modularity”. In: *PLoS Computational Biology* 6.3 (2010), e1000719.
- 176 [2] A. Bauer-Mehren et al. “Gene-Disease Network Analysis Reveals Functional
177 Modules in Mendelian, Complex and Environmental Diseases”. In: *PLoS One*
178 6.6 (2011), e20284.

- 179 [3] M. A. Fortuna, J. A. Bonachela, and S. A. Levin. “Evolution of a modular
180 software network”. In: *Proceedings of the National Academy of Sciences of the
181 United States of America* 108.50 (Nov. 2011), 19985–19989.
- 182 [4] Jens M Olesen et al. “The modularity of pollination networks”. In: *Proceedings
183 of the National Academy of Sciences of the United States of America* 104.50
184 (2007), 19891–19896.
- 185 [5] Serguei Saavedra et al. “Strong contributors to network persistence are the
186 most vulnerable to extinction”. In: *Nature* 478.7368 (Sept. 2011), 233–235.
- 187 [6] Daniel W. Carstensen et al. “Biogeographical modules and island roles: a com-
188 parison of Wallacea and the West Indies”. In: *Journal of Biogeography* (Nov.
189 2011), no–no.
- 190 [7] Elisa Thébault. “Identifying compartments in presence-absence matrices and
191 bipartite networks: insights into modularity measures”. In: *Journal of Biogeog-
192 raphy* (Nov. 2012). Ed. by Joseph Veech, n/a–n/a.
- 193 [8] Iadine Chadès et al. “General rules for managing and surveying networks
194 of pests, diseases, and endangered species.” In: *Proceedings of the National
195 Academy of Sciences of the United States of America* 108.20 (May 2011),
196 8323–8328.
- 197 [9] Mark E J Newman. “Modularity and community structure in networks.” In:
198 *Proceedings of the National Academy of Sciences of the United States of Amer-
199 ica* 103.23 (June 2006), 8577–82.

- 200 [10] Xiang-Sun Zhang and Rui-Sheng Wang. “Optimization analysis of modular-
201 ity measures for network community detection”. In: *The Second International*
202 *Symposium on Optimization and Systems Biology*. Lijiang, China, 2008, 13–20.
- 203 [11] Michael Barber. “Modularity and community detection in bipartite networks”.
204 In: *Physical Review E* 76.6 (Dec. 2007).
- 205 [12] Xin Liu and Tsuyoshi Murata. “Community detection in large-scale bipartite
206 networks”. In: *Transactions of the Japanese Society for Artificial Intelligence*.
207 Vol. 5. 2010, 184–192.
- 208 [13] Flavia Maria Darcie Marquitti et al. *MODULAR: Software for the Autonomous*
209 *Computation of Modularity in Large Network Sets*. arXiv e-print 1304.2917.
210 Apr. 2013.
- 211 [14] Gio Wiederhold. “Mediators in the architecture of future information systems”.
212 In: *The IEEE Computer Magazine* (1992), 1–36.
- 213 [15] Jure Leskovec et al. “Statistical properties of community structure in large
214 social and information networks”. In: *Proceeding of the 17th international con-*
215 *ference on World Wide Web - WWW '08*. New York, New York, USA: ACM
216 Press, 2008, p. 695.
- 217 [16] L H Hartwell et al. “From molecular to modular cell biology.” In: *Nature*
218 402.6761 Suppl (Dec. 1999), C47–52.
- 219 [17] Martin Rosvall and CT Bergstrom. “Maps of random walks on complex net-
220 works reveal community structure”. In: *Proceedings of the National \ldots* 105.4
221 (Jan. 2008), 1118–23.

- 222 [18] Dominique Gravel et al. “Trophic theory of island biogeography.” In: *Ecology*
223 *Letters* 14.10 (Oct. 2011), 1010–1016.
- 224 [19] Timothée Poisot et al. “The dissimilarity of species interaction networks.” In:
225 *Ecology Letters* 15.12 (Sept. 2012), 1353–1361.
- 226 [20] Miguel Angel Fortuna et al. “Nestedness versus modularity in ecological net-
227 works: two sides of the same coin?” In: *Journal of Animal Ecology* 78 (2010),
228 811–817.
- 229 [21] Daniel B Stouffer and Jordi Bascompte. “Compartmentalization increases food-
230 web persistence.” In: *Proceedings of the National Academy of Sciences of the*
231 *United States of America* 108.9 (Feb. 2011), 3648–3652.
- 232 [22] Cesar O Flores, Sergi Valverde, and Joshua S Weitz. “Multi-scale structure
233 and geographic drivers of cross-infection within marine bacteria and phages”.
234 In: *The ISME Journal* (Nov. 2012), 1–13.
- 235 [23] Elisa Thébault and Michel Loreau. “Food-web constraints on biodiversity–ecosystem
236 functioning relationships”. In: *Proceedings of the National Academy of Sciences*
237 *of the United States of America* 100.25 (2003), 14949–14954.
- 238 [24] Cesar O Flores et al. “Statistical structure of host-phage interactions.” In: *Pro-*
239 *ceedings of the National Academy of Sciences of the United States of America*
240 108.28 (June 2011), E288–297.
- 241 [25] Nico Blüthgen, Florian Menzel, and Nils Blüthgen. “Measuring specialization
242 in species interaction networks.” In: *BMC ecology* 6 (Jan. 2006), p. 9.

- 243 [26] Elsa Canard et al. “Emergence of Structural Patterns in Neutral Trophic Net-
244 works”. In: *PLoS ONE* 7.8 (Aug. 2012), e38295.
- 245 [27] Ignasi Bartomeus. “Understanding Linkage Rules in Plant-Pollinator Networks
246 by Using Hierarchical Models That Incorporate Pollinator Detectability and
247 Plant Traits”. In: *PLoS ONE* 8.7 (July 2013), e69200.
- 248 [28] E.L. Berlow et al. “Quantifying variation in the strengths of species interac-
249 tions”. In: *Ecology* 80.7 (1999), 2206–2224.
- 250 [29] Jennifer A Dunne. “The Network Structure of Food Webs”. In: *Ecological net-
251 works: Linking structure and dynamics*. Ed. by Jennifer A Dunne and Mercedes
252 Pascual. Oxford University Press, 2006, 27–86.
- 253 [30] Vincent D Blondel et al. “Fast unfolding of communities in large networks”. In:
254 *Journal of Statistical Mechanics: Theory and Experiment* 2008.10 (Oct. 2008),
255 P10008.
- 256 [31] MEJ Newman and M Girvan. “Finding and evaluating community structure in
257 networks”. In: *Physical review E* (2004).
- 258 [32] Thomas W Schoener. “Food webs from the small to the large”. In: *Ecology* 70.6
259 (1989), 1559–1589.
- 260 [33] R. Development Core Team. *R: A Language and Environment for Statistical
261 Computing*. Vienna, Austria, 2008.