

Should we build a macro-scale theory for coevolution? Nope.

Timothée Poisot

Daniel B. Stouffer

Oct. 31, 2014

1 **Coevolutionary dynamics acting on both species and their interactions are a key**
2 **driving force behind the structure of ecological communities. The Geographic**
3 **Mosaic Theory of Coevolution (GMTC) provides a spatial perspective to these**
4 **dynamics by proposing the existence of feedbacks between local and regional**
5 **scales. It remains unclear, however, how the structure of communities at larger**
6 **spatial scales either influences or is influenced by local coevolutionary processes.**
7 **Despite this, ecological networks are known to have an ecological structure, which**
8 **suggest that coevolution may play a role in their evolutionary dynamics. Here**
9 **we show that the coevolutionary significance of individual interactions is main-**
10 **tained when moving between the local and regional scale. Importantly, this oc-**
11 **curs despite the fact that community variation at the local scale tends to weaken**
12 **or remove community-wide coevolutionary signal. This apparent mismatch be-**
13 **tween our interaction-level and community-level results strongly suggests that**
14 **interactions provide the correct scale to study coevolution at small spatial scales**
15 **while communities are the relevant scale only at larger spatial extents. We pro-**
16 **vide a new perspective on the interplay between coevolutionary theory and com-**
17 **munity ecology, by establishing the organisational scales at which the different**

1 theories have relevance. Although it has been tempting so far to understand how
2 coevolution relates to network structure, our results suggest that the way for-
3 ward is to understand how network structure may affect coevolution over space
4 instead.

5 Ecological interactions introduce selective pressures on the species involved. At
6 large organisational scales, this results in taxonomic boundaries delineating groups
7 of interacting species¹, invariant structures in some ecological communities², and
8 conservatism of both the distribution of community modules⁴ and the role of species
9 occupy within them⁵. Although the evolutionary dynamics for a pair of interacting
10 species has been well described^{???}, attempts to understand how these mechanisms
11 cascade up to generate species diversity observed in large ecological networks have
12 been inconclusive^{6,7}, despite the well known effect of antagonistic coevolution on
13 genomic diversification^{8,9}. The scales at which these diversities happen are hard
14 to reconcile: coevolution is expressed within patches connected by gene-flow¹⁰⁻¹²,
15 whereas the species diversity of complex networks is typically observed at spatial
16 scales matching the species distribution^{13,14}. Because these scales differ by orders
17 of magnitude, one must question the relevance of previous calls to scale the theory
18 on coevolution up to multi-species systems covering large spatial extents^{???}.

19 Network-based approaches^{15,16}, on the other hand, were designed to study and
20 describe species-rich systems. Previous empirical findings revealed the impact of
21 evolutionary dynamics on overall network structure in food webs^{1,17}, pollination
22 networks^{18,19}, and host-parasite networks^{20,21}. Both micro^{3,22} and macro^{23,24} evo-
23 lutionary dynamics have been measured or modelled in species-rich communities,
24 but there is no understanding of how, or even of whether, local/micro-evolutionary

1 and regional/macro-evolutionary feedback into one another. Another layer of com-
2 plexity is that ecological networks are known to vary in their structure over time and
3 space²⁵: the same two species will not interact in a consistent way locally, either be-
4 cause of local environmental contingencies, by chance, or because their phenolo-
5 gies do not positively covary in space²⁶. As a consequence, *locally*, the evolutionary
6 signal on network structure is expected to be buried under much ecological noise,
7 and the effect of coevolution can only be inferred *regionally*.

8 In multi-species systems that typically span a large taxonomic range, coevolution is
9 often measured as the matching between the phylogenies of two sets of interacting
10 organisms^{20,27}. This build on the century-old ideas that extant species interact in a
11 way similar to the way their ancestors did²⁸. “Coevolved” systems should (i) have
12 approximately similar phylogenetic trees and (ii) species at matching positions in
13 either trees should interact. It is not clear, however, how this idea relates to dynam-
14 ics occurring at smaller scales²⁹: many ecological and evolutionary processes that
15 occur locally, or over small spatial scales, can disturb this expected structure. No-
16 tably, it has been shown that species interactions are not consistent through space
17 ^{25,30}. Local loss of both interactions and species from the regional pool is most likely
18 to result in observed communities that do not appear to have been shaped by co-
19 evolution.

20 We use data on ectoparasites of rodents from Western to Eastern Europe³¹ to test
21 the following four hypotheses. First, local species assemblages do not show evi-
22 dence of coevolution even though the system as a whole does. Second, interaction-
23 level coevolutionary signal is conserved. Third, interaction-level coevolutionary
24 signal does not predict the spatial consistency of interactions. We do so by coupling

1 two novel methods: the *PACO* algorithm for detection of phylogenetic congruence
2 ³², and a general framework for the variation of ecological networks ³⁰.

3 Local observations on the 51 localities (*Supp. Mat. 1*) are aggregated into a regional
4 metanetwork ³⁰. The two phylogenetic trees have been rendered ultrametric. We
5 use *PACO* ³² to measure the congruence between trees knowing the matrix of inter-
6 action. *PACO* yields a network-level significance value for the likelihood that hosts
7 and parasites have coevolved. For each local network, we measure the strength of
8 coevolution using (i) only local observations and (ii) all possible interactions be-
9 tween local species (as known from the regional aggregation of all local networks).
10 This allows us to separate the effect of species sorting (regional interactions) and
11 interaction sorting (local interactions). At the regional scale, coevolutionary signal
12 is extremely strong ($p \leq 10^{-4}$), as established by previous analysis of this system ³³.
13 Most local networks, on the other hand, show very little evidence of phylogenetic
14 congruence. Out of 51 local networks, 35 show no signal of coevolution, 11 show
15 coevolution when using the regional interactions, and 12 show coevolution using
16 the local interactions (see *Supp. Mat. 1* for network-level significance values). **Fig-**
17 **ure?**.

18 This suggests that macro-evolutionary processes (such as co-diversification) have
19 consequences at the macro-ecological level ³⁴, but may not be detected at finer spa-
20 tial scales due to a stronger effect of ecological processes locally. *PACO* permits the
21 analysis of *how strongly* each interaction contribute to coevolution, in a way that
22 is as independent as possible from other interactions. As interactions vary only in-
23 sofar that there are some locations in which they *do not* happen, we expect that
24 the overall contribution of interactions will be the same in the local and regional

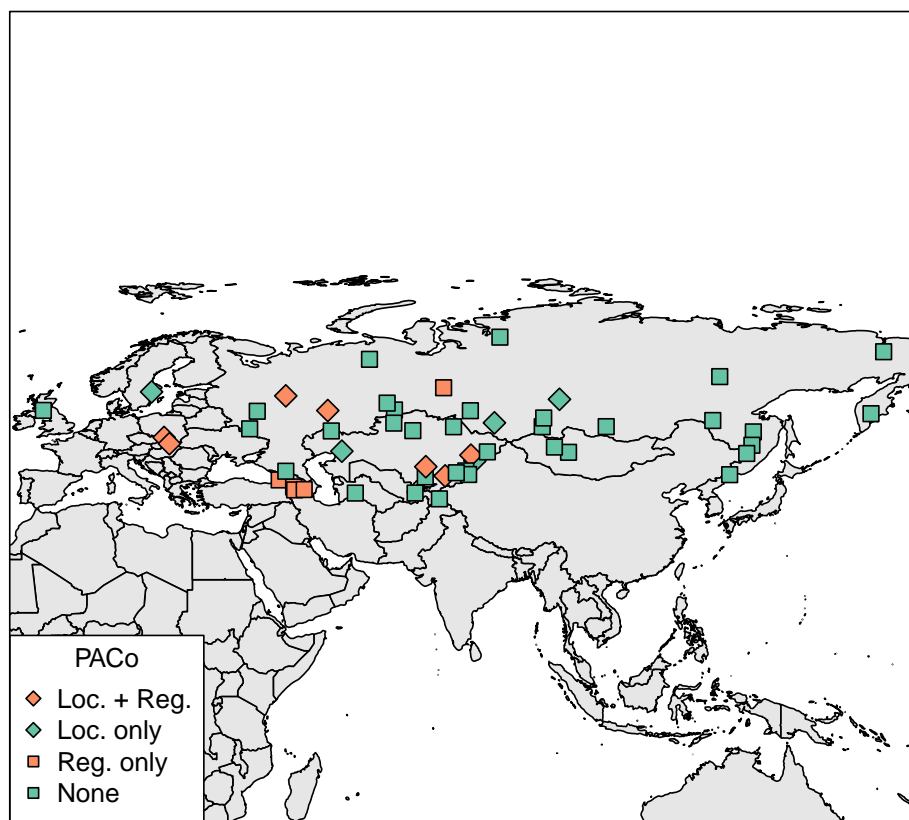


Figure 1: figure1

1 networks. For the 5 networks that show evidences of coevolution accounting both
2 for species and interactions sorting, we measured the contribution of each inter-
3 action locally, and compared it to its contribution to the regional network. Results
4 are presented in **FIG.**

5 **Point 2 – Interactions respond locally to micro-processes**

- 6 • Review of mechanisms involved in interactions locally: neutrality and trait-
7 based mechanisms
- 8 • Key refs: Oikos paper, Canard, Olesen, Combes
- 9 • These mechanism can only *filter* from a pool of regional interactions
- 10 • Key refs: Biol Lett paper, Olito & Fox, Lounnas, ...
- 11 • Key points: i) even though they will change the network-level signal, con-
12 tribution of interactions should not vary locally vs. regionally ii) this is the
13 expectation because (a) past knowledge about motifs/evolution and (b) in-
14 teractions are the unit in which selection takes place, not networks
- 15 • Illustration: distribution of the significance in each interaction locally (mea-
16 sured vs. metaweb) vs. in the regional network.

17 **Point 3 – The spatial replication of networks is imperfect**

- 18 • Ecological processes = sorting of interactions + species

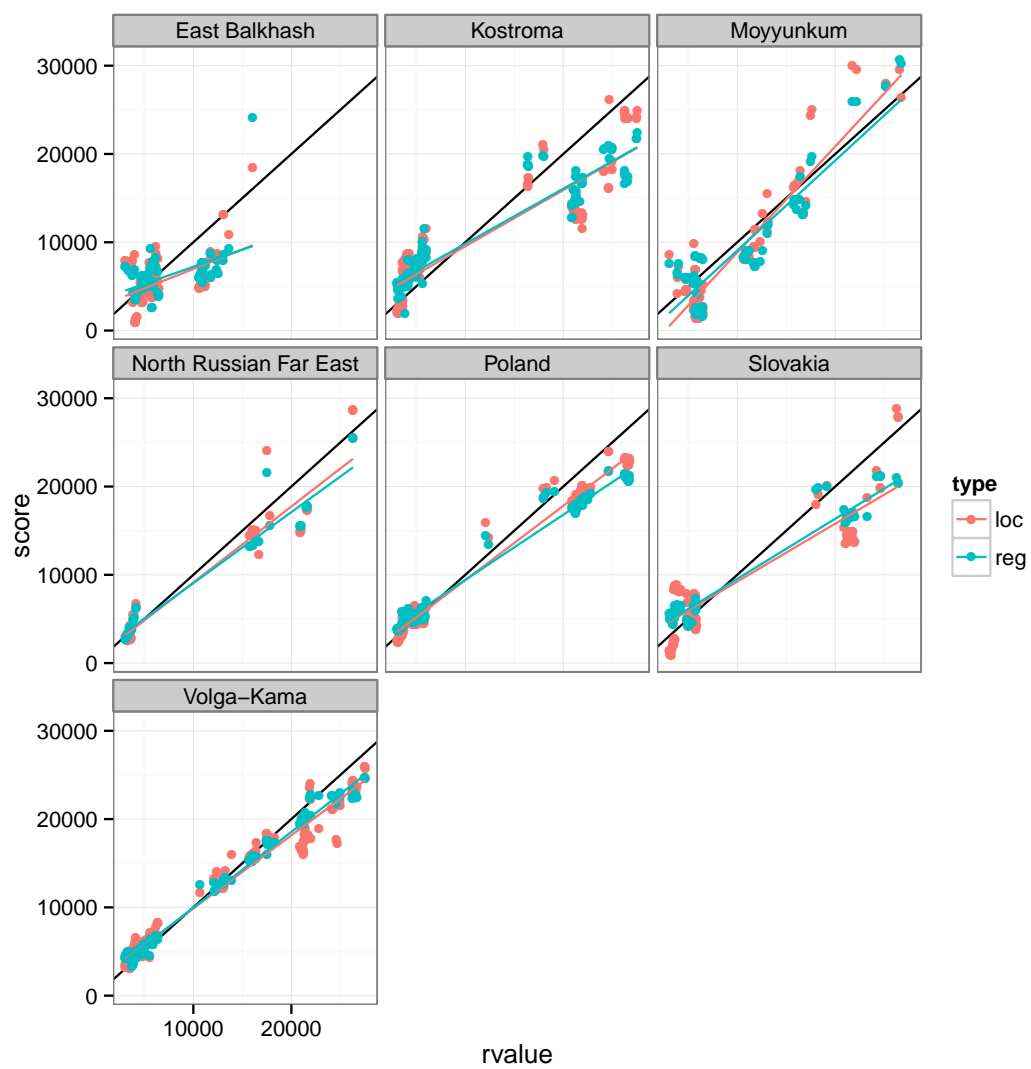


Figure 2: figure2

- 1 • Key refs: Ecol Lett -div
- 2 • Key points: observation of interactions result from filtering through two pro-
- 3 cesses, and not clear they are related to past coevolution = we expect a loss
- 4 of signal locally
- 5 • Illustration: jackknife score vs. observed/possible : there is no relationship
- 6 between how important an interaction is (coevo) and how frequent it will be.
- 7 suggests that ecological >> evolutionary drivers of local network structure
- 8 • This is caused by local ecological processes, but also influences local evolu-
- 9 tionary dynamics
- 10 • Key refs: Gomulkiewicz, Hochberg, Benkman, Siepilski
- 11 • Key points: i) Opportunity to integrate more network theory to understand
- 12 between-sites differences ii) Even though coevo theory recognized variation
- 13 in effects, very little attention to variation in presence/absence of int and its
- 14 implications

15 **Conclusions**

- 16 • Need to bridge ecological networks with co-evolution (understand the im-
- 17 pact of ecology vs. evolution in the local observations)
- 18 • Main advance: coevolutionary dynamics are important at the continental/regional
- 19 scale, much less at the local scale

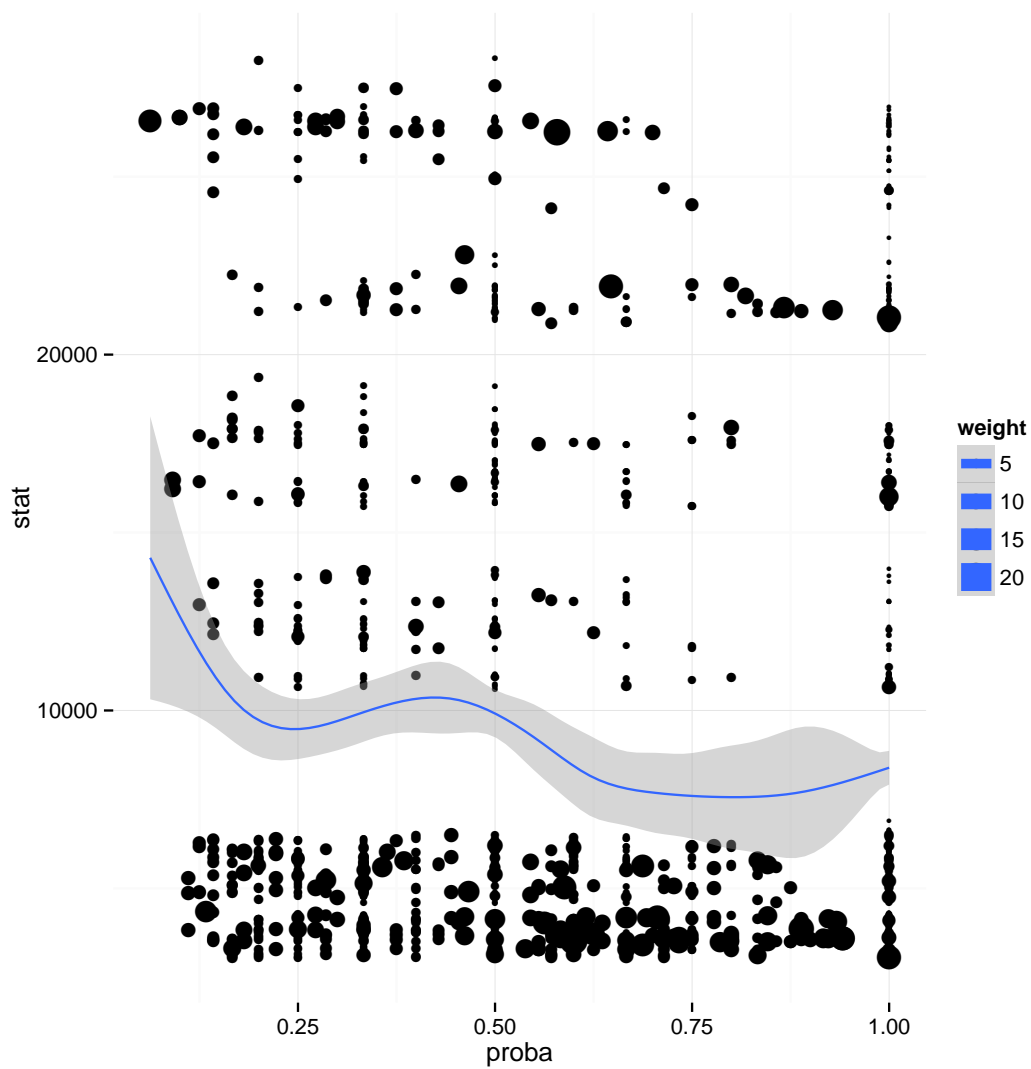


Figure 3: figure3

- 1 • Focus on datasets that are spatially replicated, with as good as possible phy-
 - 2 logenies. Ref Buckley, Harkel.
 - 3 • Currently local variability is not accounted for by statistical methods, need to
 - 4 do a better job. See Desdevises chapter on ParaFit 2.0.
- 5 1.Eklof, A., Helmus, M. R., Moore, M., Allesina, S. & Eklöf, A.*et al.* Relevance of
 - 6 evolutionary history for food web structure. *Proc. R. Soc. B Biol. Sci.* **279**, 1588–
 - 7 1596 (2011).
 - 8 2.Nuismer, S. L., Jordano, P. & Bascompte, J.*et al.* Coevolution and the architecture
 - 9 of mutualistic networks. *Evolution* **67**, 338–354 (2013).
 - 10 3.Jordano, P., Bascompte, J. & Olesen, J. M.*et al.* Invariant properties in coevolu-
 - 11 tionary networks of plant-animal interactions. *Ecol. Lett.* **6**, 69–81 (2003).
 - 12 4.Stouffer, D. B., Camacho, J., Guimera, R., Ng, C. A. & Amaral, L. A. N.*et al.* Quan-
 - 13 titative patterns in the structure of model and empirical food webs. *Ecology* **86**,
 - 14 1301–1311 (2005).
 - 15 5.Stouffer, D. B., Sales-Pardo, M., Sirer, M. I. & Bascompte, J.*et al.* Evolutionary Con-
 - 16 servation of Species' Roles in Food Webs. *Science* **335**, 1489–1492 (2012).
 - 17 6.Hembry, D. H., Yoder, J. B. & Goodman, K. R.*et al.* Coevolution and the Diversifi-
 - 18 cation of Life. *The American Naturalist* **184**, 425–438 (2014).
 - 19 7.Yoder, J. B. & Nuismer, S. L. *et al.* When does coevolution promote diversification?
 - 20 *Am. Nat.* **176**, 802–817 (2010).
 - 21 8.Paterson, S. *et al.* Antagonistic coevolution accelerates molecular evolution. *Na-*
 - 22 *ture* **464**, 275–278 (2010).

- 1 9. Buckling, A., Wei, Y., Massey, R. C., Brockhurst, M. A. & Hochberg, M. E. *et al.* An-
2 tagonistic coevolution with parasites increases the cost of host deleterious muta-
3 tions. *Proc. R. Soc. B* **273**, 45–49 (2006).
- 4 10. Brockhurst, M. A., Buckling, A., Poullain, V. & Hochberg, M. E. *et al.* The impact
5 of migration from parasite-free patches on antagonistic host-parasite coevolution.
6 *Evolution* **61**, 1238–1243 (2007).
- 7 11. Nuismer, S. L., Thompson, J. N. & Gomulkiewicz, R. *et al.* Coevolution between
8 hosts and parasites with partially overlapping geographic ranges. *J. Evol. Biol.* **16**,
9 1337–1345 (2003).
- 10 12. Benkman, C. W., Parchman, T. L., Favis, A. & Siepielski, A. M. *et al.* Reciprocal
11 selection causes a coevolutionary arms race between crossbills and lodgepole pine.
12 *Am. Nat.* **162**, 182–194 (2003).
- 13 13. Havens, K. *et al.* Scale and structure in natural food webs. *Science* **257**, 1107–
14 1109 (1992).
- 15 14. Bascompte, J. *et al.* Disentangling the Web of Life. *Science* **325**, 416–419 (2009).
- 16 15. Proulx, S., Promislow, D. & Phillips, P. *et al.* Network thinking in ecology and evo-
17 lution. *Trends Ecol. Evol.* **20**, 345–353 (2005).
- 18 16. Dunne, J. A. *et al.* in *Ecological networks: Linking structure and dynamics* (eds.
19 Dunne, J. A. & Pascual, M.) 27–86 (Oxford University Press, 2006).
- 20 17. Stouffer, D. B., Camacho, J., Jiang, W. & Amaral, L. A. N. *et al.* Evidence for the
21 existence of a robust pattern of prey selection in food webs. *Proc. R. Soc. B Biol.*
22 *Sci.* **274**, 1931–40 (2007).
- 23 18. Chamberlain, S. A. *et al.* Traits and phylogenetic history contribute to network

- 1 structure across Canadian plant–pollinator communities. *Oecologia* 1–12 (2014).
- 2 19.Vamosi, J. C., Armbruster, W. S. & Renner, S. S.*et al.* Evolutionary ecology of
3 specialization: insights from phylogenetic analysis. *Proc. R. Soc. B* **281**, 20142004
4 (2014).
- 5 20.Desdevises, Y., Morand, S., Jousson, O. & Legendre, P.*et al.* Coevolution between
6 *Lamellodiscus* (Monogenea: Diplectanidae) and Sparidae (Teleostei): the study of
7 a complex host-parasite system. *Evolution* **56**, 2459–2471 (2002).
- 8 21.Hafner, M. S. & Page, R. D. M. *et al.* Molecular phylogenies and host-parasite
9 cospeciation: gophers and lice as a model system. *Philos. Trans. R. Soc. B Biol. Sci.*
10 **349**, 77–83 (1995).
- 11 22.Hall, A. R., Scanlan, P. D. & Buckling, A.*et al.* Bacteria-Phage coevolution and the
12 emergence of generalist pathogens. *Am. Nat.* **177**, 44–53 (2010).
- 13 23.Roopnarine, P. D. & Angielczyk, K. D. *et al.* The evolutionary palaeoecology of
14 species and the tragedy of the commons. *Biol. Lett.* **8**, 147–50 (2012).
- 15 24.Dunne, J. a, Williams, R. J., Martinez, N. D., Wood, R. a & Erwin, D. H.*et al.* Com-
16 pilation and network analyses of cambrian food webs. *PLoS Biol.* **6**, e102 (2008).
- 17 25.Poisot, T., Stouffer, D. B. & Gravel, D.*et al.* Beyond species: why ecological inter-
18 action networks vary through space and time. *Oikos* (2014).
- 19 26.Devictor, V. *et al.* Differences in the climatic debts of birds and butterflies at a
20 continental scale. *Nat. Clim. Change* **2**, 121–124 (2012).
- 21 27.Legendre, P., Desdevises, Y. & Bazin, E.*et al.* A statistical test for host-parasite
22 coevolution. *Syst. Biol.* **51**, 217–234 (2002).

- 1 28.Fahrenholz, H. *et al.* Ectoparasiten und abstammungslehre. *Zool. Anz.* **41**, 371–
2 374 (1913).
- 3 29.Poisot, T. *et al.* in *Evolutionary Ecology of Host-Parasite Systems* (eds. Morand,
4 S., Littlewood, D. T. & Poulin, R.) (Cambridge University Press, 2015).
- 5 30.Poisot, T., Canard, E., Mouillot, D., Mouquet, N. & Gravel, D.*et al.* The dissimi-
6 larity of species interaction networks. *Ecol. Lett.* **15**, 1353–1361 (2012).
- 7 31.Data from: Phylogenetic signal in module composition and species connectivity
8 in compartmentalized host-parasite networks. (2012).
- 9 32.Balbuena, J. A., Míguez-Lozano, R. & Blasco-Costa, I.*et al.* PACo: A Novel Pro-
10 crustes Application to Cophylogenetic Analysis. *PLoS ONE* **8**, e61048 (2013).
- 11 33.Krasnov, B. R. *et al.* Phylogenetic signal in module composition and species
12 connectivity in compartmentalized host-parasite networks. *Am. Nat.* **179**, 501–
13 11 (2012).
- 14 34.Price, P. W. *et al.* *Macroevolutionary Theory on Macroecological Patterns*. (Cam-
15 bridge University Press, 2003).