

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
2 are a key driving force behind the structure of ecological communi-
3 ties. The Geographic Mosaic Theory of Coevolution (GMTC) provides
4 a spatial perspective to these dynamics by proposing the existence of
5 feedbacks between local and regional scales. It remains unclear, how-
6 ever, how the structure of communities at larger spatial scales either in-
7 fluences or is influenced by local coevolutionary processes. Despite this,
8 ecological networks are known to have an ecological structure, which
9 suggest that coevolution may play a role in their evolutionary dynamics.
10 Here we show that the coevolutionary significance of individual interac-
11 tions is maintained when moving between the local and regional scale.
12 Importantly, this occurs despite the fact that community variation at
13 the local scale tends to weaken or remove community-wide coevolution-
14 ary signal. This apparent mismatch between our interaction-level and
15 community-level results strongly suggests that interactions provide the
16 correct scale to study coevolution at small spatial scales while commu-
17 nities are the relevant scale only at larger spatial extents. We provide

1 a new perspective on the interplay between coevolutionary theory and
2 community ecology, by establishing the organisational scales at which
3 the different theories have relevance. Although it has been tempting
4 so far to understand how coevolution relates to network structure, our
5 results suggest that the way forward is to understand how network
6 structure may affect coevolution over space instead.

7 Ecological interactions introduce selective pressures on the species involved. At
8 large organisational scales, this results in taxonomic boundaries delineating groups
9 of interacting species ¹, invariant structures in some ecological communities ², and
10 conservatism of both the distribution of community modules ⁴ and the role of
11 species occupy within them ⁵. Although the evolutionary dynamics for a pair of
12 interacting species has been well described ^{???}, attempts to understand how these
13 mechanisms cascade up to generate species diversity observed in large ecological
14 networks have been inconclusive ^{6,7}, despite the well known effect of antagonistic
15 coevolution on genomic diversification ^{8,9}. The scales at which these diversities
16 happen are hard to reconcile: coevolution is expressed within patches connected
17 by gene-flow ¹⁰⁻¹², whereas the species diversity of complex networks is typically
18 observed at spatial scales matching the species distribution ^{13,14}. Because these
19 scales differ by orders of magnitude, one must question the relevance of previous
20 calls to scale the theory on coevolution up to multi-species systems covering large
21 spatial extents ^{???}.

22 Network-based approaches ^{15,16}, on the other hand, were designed to study and
23 describe species-rich systems. Previous empirical findings revealed the impact
24 of evolutionary dynamics on overall network structure in food webs ^{1,17}, pollina-

tion networks ^{18,19}, and host-parasite networks ^{20,21}. Both micro ^{3,22} and macro ^{23,24} evolutionary dynamics have been measured or modelled in species-rich communities, but there is no understanding of how, or even of whether, local/micro-evolutionary and regional/macro-evolutionary feedback into one another. Another layer of complexity is that ecological networks are known to vary in their structure over time and space ²⁵: the same two species will not interact in a consistent way locally, either because of local environmental contingencies, by chance, or because their phenologies do not positively covary in space ²⁶. As a consequence, *locally*, the evolutionary signal on network structure is expected to be buried under much ecological noise, and the effect of coevolution can only be inferred *regionally*.

In multi-species systems that typically span a large taxonomic range, coevolution is often measured as the matching between the phylogenies of two sets of interacting organisms ^{20,27}. This build on the century-old ideas that extant species interact in a way similar to the way their ancestors did ²⁸. “Coevolved” systems should (i) have approximately similar phylogenetic trees and (ii) species at matching positions in either trees should interact. It is not clear, however, how this idea relates to dynamics occurring at smaller scales ²⁹: many ecological and evolutionary processes that occur locally, or over small spatial scales, can disturb this expected structure. Notably, it has been shown that species interactions are not consistent through space ^{25,30}. Local loss of both interactions and species from the regional pool is most likely to result in observed communities that do not appear to have been shaped by coevolution.

We use data on ectoparasites of rodents from Western to Eastern Europe ³¹ to test the following four hypotheses. First, local species assemblages do not

1 show evidence of coevolution even though the system has a whole does. Second,
2 interaction-level coevolutionary signal is conserved. Third, interaction-level co-
3 evolutionary signal does not predict the spatial consistency of interactions. We
4 do so by coupling two novel methods: the *PACO* algorithm for detection of phy-
5 logenetic congruence ³², and a general framework for the variation of ecological
6 networks ³⁰.

7 Local observations on the 51 localities (*Supp. Mat. 1*) are aggregated into a
8 regional metanetwork ³⁰, and the two phylogenetic trees have been rendered ul-
9 trametric (see *Suppl. Methods*). We use *PACO* ³² to measure the congruence
10 between trees knowing the interactions. *PACO* yields a network-level significance
11 value for the likelihood that hosts and parasites have coevolved. For each local
12 network, we measure the strength of coevolution using (i) only local observations
13 and (ii) all possible interactions between local species (as known from the regional
14 aggregation of all local networks). This allows us to separate the effect of species
15 sorting (regional interactions) and interaction sorting (local interactions). At the
16 regional scale, coevolutionary signal is extremely strong ($p \leq 10^{-4}$), as established
17 by previous analysis of this system ³³. Most local networks, on the other hand,
18 show very little evidence of phylogenetic congruence. Out of 51 local networks,
19 35 show no signal of coevolution, 11 show coevolution when using the regional
20 interactions, and 12 show coevolution using the local interactions (see *Supp. Mat.*
21 *1* for network-level significance values). **Figure?**

22 This suggests that macro-evolutionary processes (such as co-diversification) have
23 consequences at the macro-ecological level ³⁴, but may not be detected at finer
24 spatial scales due to a stronger effect of ecological processes locally. *PACO* per-

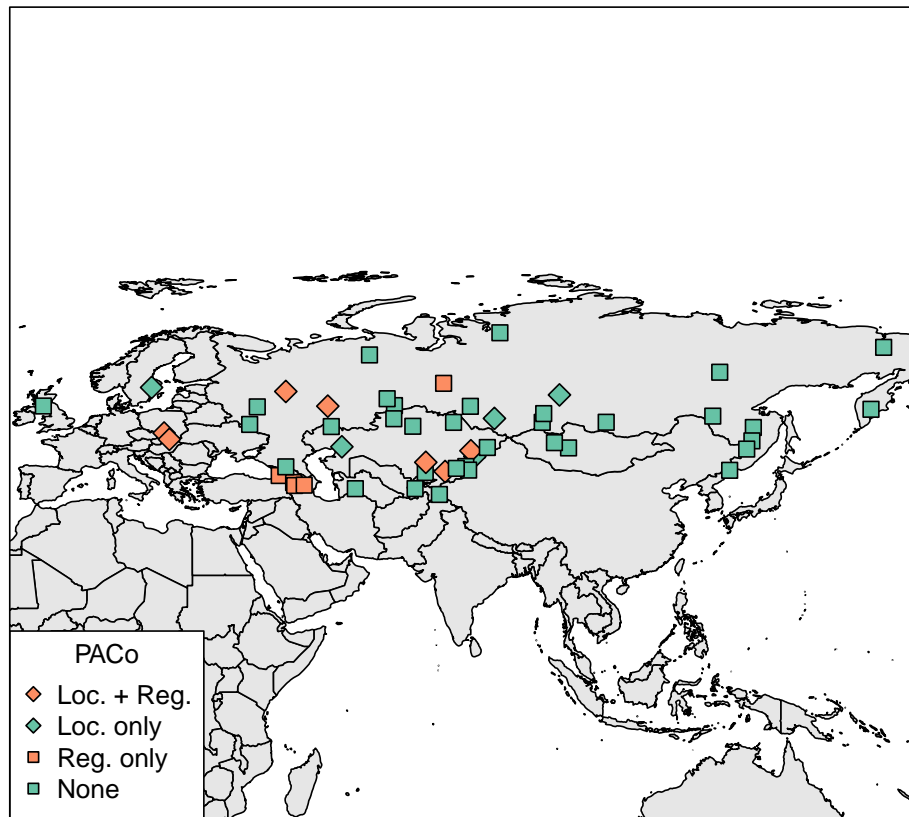


Figure 1: figure1

mits the analysis of *how strongly* each interaction contribute to coevolution, in a way that is as independent as possible from other interactions. As interactions vary only insofar that there are some locations in which they *do not* happen, we expect that the overall contribution of interactions will be the same in the local and regional networks. For the 5 networks that show evidences of coevolution accounting both for species and interactions sorting, we measured the contribution of each interaction locally, and compared it to its contribution to the regional network. Results are presented in **FIG. one-sentence summary**. This is a key result, as it establishes that although coevolution does not leave an imprint on local networks, it is still detectable in *interactions*. This is in line with recent results that established that, although networks are composed of interactions, both objects seem to have uncoupled behaviors ³⁵.

Species interactions vary in a way that is independent from species distribution ³⁰. One possible explanation is that species that have a strong (coevolutionary) relationship would either co-distribute more, or interact more frequently when they co-occur. Should it be true, we would expect that *coevolved species pairs*, or in other words, species involved in an interaction contributing strongly to the community-wide coevolution, should be interacting frequently. This would result in a positive association between the frequency of the interaction (the number of observations of a particular interaction divided by the number of observations of the two species together), and its overall importance for coevolution (here measured in the *regional* network). As we report in **FIGURE**, we do not find this relationship – how strongly an interaction contributes to overall coevolution does not predict how frequently it will be realized when the two species are put together.

1 Our results, that (i) local networks show no signal of coevolution and (ii) the
2 strength of coevolution between two species does not predict how frequently they
3 interact, fall when in line with recent conclusions about the spatial dynamics
4 of species interactions. Species interactions vary according to ecological mecha-
5 nisms²⁵: local population abundance³⁶, local mis-matches of phenologies³⁷, local
6 micro-environmental conditions³⁸. And even though network composition varies,
7 the overall network *structure* remains constant over time³⁹, suggesting either (i)
8 higher-order constraints or (ii) replacement of species by functionally equivalents
9 from the regional pool. These result show that our current understanding of co-
10 evolution in multi-species interactions does not scale well to ecological questions
11 – although phylogenetic structure and interaction show a strong agreement at
12 the regional scale, the structure of local communities remains largely driven by
13 ecological constraints. The analysis of ecological networks has often focused on
14 emerging properties⁴⁰ rather than on the building blocks of the networks, that is
15 species and interactions. As we report that interactions retain their coevolution
16 signal at either the local or regional scale, we suggest that they should be the
17 focus of community ecologists in the future.

18 References

- 19 1.Eklof, A., Helmus, M. R., Moore, M., Allesina, S. & Eklöf, A.*et al.* Relevance
20 of evolutionary history for food web structure. *Proc. R. Soc. B Biol. Sci.* **279**,
21 1588–1596 (2011).
- 22 2.Nuismer, S. L., Jordano, P. & Bascompte, J.*et al.* Coevolution and the archi-

1 tecture of mutualistic networks. *Evolution* **67**, 338–354 (2013).

2 3.Jordano, P., Bascompte, J. & Olesen, J. M.*et al.* Invariant properties in coevo-
3 lutionary networks of plant-animal interactions. *Ecol. Lett.* **6**, 69–81 (2003).

4 4.Stouffer, D. B., Camacho, J., Guimera, R., Ng, C. A. & Amaral, L. A. N.*et al.*
5 Quantitative patterns in the structure of model and empirical food webs. *Ecology*
6 **86**, 1301–1311 (2005).

7 5.Stouffer, D. B., Sales-Pardo, M., Sirer, M. I. & Bascompte, J.*et al.* Evolutionary
8 Conservation of Species’ Roles in Food Webs. *Science* **335**, 1489–1492 (2012).

9 6.Hembry, D. H., Yoder, J. B. & Goodman, K. R.*et al.* Coevolution and the
10 Diversification of Life. *The American Naturalist* **184**, 425–438 (2014).

11 7.Yoder, J. B. & Nuismer, S. L. *et al.* When does coevolution promote diversifi-
12 cation? *Am. Nat.* **176**, 802–817 (2010).

13 8.Paterson, S. *et al.* Antagonistic coevolution accelerates molecular evolution.
14 *Nature* **464**, 275–278 (2010).

15 9.Buckling, A., Wei, Y., Massey, R. C., Brockhurst, M. A. & Hochberg, M. E.*et*
16 *al.* Antagonistic coevolution with parasites increases the cost of host deleterious
17 mutations. *Proc. R. Soc. B* **273**, 45–49 (2006).

18 10.Brockhurst, M. A., Buckling, A., Poullain, V. & Hochberg, M. E.*et al.* The
19 impact of migration from parasite-free patches on antagonistic host-parasite co-
20 evolution. *Evolution* **61**, 1238–1243 (2007).

21 11.Nuismer, S. L., Thompson, J. N. & Gomulkiewicz, R.*et al.* Coevolution be-
22 tween hosts and parasites with partially overlapping geographic ranges. *J. Evol.*
23 *Biol.* **16**, 1337–1345 (2003).

- 1 12.Benkman, C. W., Parchman, T. L., Favis, A. & Siepielski, A. M.*et al.* Recip-
2 rocal selection causes a coevolutionary arms race between crossbills and lodgepole
3 pine. *Am. Nat.* **162**, 182–194 (2003).
- 4 13.Havens, K. *et al.* Scale and structure in natural food webs. *Science* **257**,
5 1107–1109 (1992).
- 6 14.Bascompte, J. *et al.* Disentangling the Web of Life. *Science* **325**, 416–419
7 (2009).
- 8 15.Proulx, S., Promislow, D. & Phillips, P.*et al.* Network thinking in ecology and
9 evolution. *Trends Ecol. Evol.* **20**, 345–353 (2005).
- 10 16.Dunne, J. A. *et al.* in *Ecological networks: Linking structure and dynamics*
11 (eds. Dunne, J. A. & Pascual, M.) 27–86 (Oxford University Press, 2006).
- 12 17.Stouffer, D. B., Camacho, J., Jiang, W. & Amaral, L. A. N.*et al.* Evidence for
13 the existence of a robust pattern of prey selection in food webs. *Proc. R. Soc. B*
14 *Biol. Sci.* **274**, 1931–40 (2007).
- 15 18.Chamberlain, S. A. *et al.* Traits and phylogenetic history contribute to network
16 structure across Canadian plant–pollinator communities. *Oecologia* 1–12 (2014).
- 17 19.Vamosi, J. C., Armbruster, W. S. & Renner, S. S.*et al.* Evolutionary ecology
18 of specialization: insights from phylogenetic analysis. *Proc. R. Soc. B* **281**,
19 20142004 (2014).
- 20 20.Desdevises, Y., Morand, S., Jousson, O. & Legendre, P.*et al.* Coevolution
21 between *Lamellodiscus* (Monogenea: Diplectanidae) and Sparidae (Teleostei): the
22 study of a complex host-parasite system. *Evolution* **56**, 2459–2471 (2002).
- 23 21.Hafner, M. S. & Page, R. D. M. *et al.* Molecular phylogenies and host-parasite

- 1 cospeciation: gophers and lice as a model system. *Philos. Trans. R. Soc. B Biol.*
2 *Sci.* **349**, 77–83 (1995).
- 3 22.Hall, A. R., Scanlan, P. D. & Buckling, A.*et al.* Bacteria-Phage coevolution
4 and the emergence of generalist pathogens. *Am. Nat.* **177**, 44–53 (2010).
- 5 23.Roopnarine, P. D. & Angielczyk, K. D. *et al.* The evolutionary palaeoecology
6 of species and the tragedy of the commons. *Biol. Lett.* **8**, 147–50 (2012).
- 7 24.Dunne, J. a, Williams, R. J., Martinez, N. D., Wood, R. a & Erwin, D. H.*et*
8 *al.* Compilation and network analyses of cambrian food webs. *PLoS Biol.* **6**, e102
9 (2008).
- 10 25.Poisot, T., Stouffer, D. B. & Gravel, D.*et al.* Beyond species: why ecological
11 interaction networks vary through space and time. *Oikos* (2014).
- 12 26.Devictor, V. *et al.* Differences in the climatic debts of birds and butterflies at
13 a continental scale. *Nature Clim. Change* **2**, 121–124 (2012).
- 14 27.Legendre, P., Desdevises, Y. & Bazin, E.*et al.* A statistical test for host-
15 parasite coevolution. *Syst. Biol.* **51**, 217–234 (2002).
- 16 28.Fahrenholz, H. *et al.* Ectoparasiten und abstammungslehre. *Zool. Anz.* **41**,
17 371–374 (1913).
- 18 29.Poisot, T. *et al.* in *Evolutionary Ecology of Host-Parasite Systems* (eds. Morand,
19 S., Littlewood, D. T. & Poulin, R.) (Cambridge University Press, 2015).
- 20 30.Poisot, T., Canard, E., Mouillot, D., Mouquet, N. & Gravel, D.*et al.* The
21 dissimilarity of species interaction networks. *Ecol. Lett.* **15**, 1353–1361 (2012).
- 22 31.Data from: Phylogenetic signal in module composition and species connectivity
23 in compartmentalized host-parasite networks. (2012).

1 32.Balbuena, J. A., Míguez-Lozano, R. & Blasco-Costa, I.*et al.* PACo: A Novel
2 Procrustes Application to Cophylogenetic Analysis. *PLoS ONE* **8**, e61048 (2013).

3 33.Krasnov, B. R. *et al.* Phylogenetic signal in module composition and species
4 connectivity in compartmentalized host-parasite networks. *Am. Nat.* **179**, 501–
5 11 (2012).

6 34.Price, P. W. *et al.* *Macroevolutionary Theory on Macroecological Patterns*.
7 (Cambridge University Press, 2003).

8 35.Olito, C. & Fox, J. W. *et al.* Species traits and abundances predict metrics of
9 plant–pollinator network structure, but not pairwise interactions. *Oikos* n/a–n/a
10 (2014).

11 36.Canard, E. F. *et al.* Empirical evaluation of neutral interactions in host–
12 parasite networks. *Am. Nat.* **183**, 468–479 (2014).

13 37.Olesen, J. M. *et al.* Missing and forbidden links in mutualistic networks. *Proc.*
14 *R. Soc. B* **278**, 725–732 (2011).

15 38.Poisot, T., Lepennetier, G., Martinez, E., Ramsayer, J. & Hochberg, M. E.*et*
16 *al.* Resource availability affects the structure of a natural bacteria-bacteriophage
17 community. *Biol. Lett.* **7**, 201–204 (2011).

18 39.Dupont, Y. L., Padrón, B., Olesen, J. M. & Petanidou, T.*et al.* Spatio-temporal
19 variation in the structure of pollination networks. *Oikos* **118**, 1261–1269 (2009).

20 40.Blüthgen, N. *et al.* Why network analysis is often disconnected from commu-
21 nity ecology: A critique and an ecologist’s guide. *Basic and Applied Ecology* **11**,
22 185–195 (2010).