

# Coevolution is detected regionally but not locally in ecological communities

Timothée Poisot

Daniel B. Stouffer

Oct. 31, 2014

1 Coevolutionary dynamics acting on both species and their interactions are  
2 a key driving force behind the structure of ecological communities. The  
3 Geographic Mosaic Theory of Coevolution (GMTC) provides a spatial per-  
4 spective to these dynamics by proposing the existence of feedbacks between  
5 local and regional scales. It remains unclear, however, how the structure  
6 of communities at larger spatial scales either influences or is influenced  
7 by local coevolutionary processes. Despite this, ecological networks are  
8 known to have an ecological structure, which suggest that coevolution may  
9 play a role in their evolutionary dynamics. Here we show that the coevo-  
10 lutionary significance of individual interactions is maintained when mov-  
11 ing between the local and regional scale. Importantly, this occurs despite  
12 the fact that community variation at the local scale tends to weaken or re-  
13 move community-wide coevolutionary signal. This apparent mismatch be-  
14 tween our interaction-level and community-level results strongly suggests  
15 that interactions provide the correct scale to study coevolution at small spa-  
16 tial scales while communities are the relevant scale only at larger spatial ex-

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

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

22 Network-based approaches <sup>17,18</sup>, 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 <sup>1,19</sup>, pol-

1 lination networks <sup>20,21</sup>, and host-parasite networks <sup>22,23</sup>. Both micro <sup>3,24</sup> and  
2 macro <sup>25,26</sup> evolutionary dynamics have been measured or modelled in species-  
3 rich communities, but there is no understanding of how, or even of whether,  
4 local/micro-evolutionary and regional/macro-evolutionary feedback into one  
5 another. Another layer of complexity is that ecological networks are known to  
6 vary in their structure over time and space <sup>27</sup>: the same two species will not  
7 interact in a consistent way locally, either because of local environmental con-  
8 tingencies, by chance, or because their phenologies do not positively covary in  
9 space <sup>28</sup>. As a consequence, *locally*, the evolutionary signal on network struc-  
10 ture is expected to be buried under much ecological noise, and the effect of  
11 coevolution can only be inferred *regionally*.

12 In multi-species systems that typically span a large taxonomic range, coevo-  
13 lution is often measured as the matching between the phylogenies of two sets  
14 of interacting organisms <sup>22,29</sup>. This build on the century-old ideas that ex-  
15 tant species interact in a way similar to the way their ancestors did <sup>30</sup>. “Coe-  
16 volved” systems should (i) have approximately similar phylogenetic trees and  
17 (ii) species at matching positions in either trees should interact. It is not clear,  
18 however, how this idea relates to dynamics occurring at smaller scales <sup>31</sup>: many  
19 ecological and evolutionary processes that occur locally, or over small spatial  
20 scales, can disturb this expected structure. Notably, it has been shown that  
21 species interactions are not consistent through space <sup>27,32</sup>. Local loss of both  
22 interactions and species from the regional pool is most likely to result in ob-  
23 served communities that do not appear to have been shaped by coevolution.

24 We use data on ectoparasites of rodents from Western to Eastern Europe <sup>33</sup> to

1 test the following four hypotheses. First, local species assemblages do not show  
2 evidence of coevolution even though the system as a whole does. Second,  
3 interaction-level coevolutionary signal is conserved. Third, interaction-level  
4 coevolutionary signal does not predict the spatial consistency of interactions.  
5 We do so by coupling two novel methods: the *PACO* algorithm for detection  
6 of phylogenetic congruence <sup>34</sup>, and a general framework for the variation of  
7 ecological networks <sup>32</sup>.

8 Local observations on the 51 localities (*Supp. Mat. 1*) are aggregated into a  
9 regional metanetwork <sup>32</sup>, and the two phylogenetic trees have been rendered  
10 ultrametric (see Suppl. Methods). We use *PACO* <sup>34</sup> to measure the congruence  
11 between trees knowing the interactions. *PACO* yields a network-level signif-  
12 icance value for the likelihood that hosts and parasites have coevolved. For  
13 each local network, we measure the strength of coevolution using (i) only local  
14 observations and (ii) all possible interactions between local species (as known  
15 from the regional aggregation of all local networks). This allows us to sepa-  
16 rate the effect of species sorting (regional interactions) and interaction sorting  
17 (local interactions). At the regional scale, coevolutionary signal is extremely  
18 strong ( $p \leq 10^{-4}$ ), as established by previous analysis of this system <sup>35</sup>. Most  
19 local networks, on the other hand, show very little evidence of phylogenetic  
20 congruence. Out of 51 local networks, 35 show no signal of coevolution, 11  
21 show coevolution when using the regional interactions, and 12 show coevolu-  
22 tion using the local interactions (see *Supp. Mat. 1* for network-level significance  
23 values). **Figure?**

24 This suggests that macro-evolutionary processes (such as co-diversification)

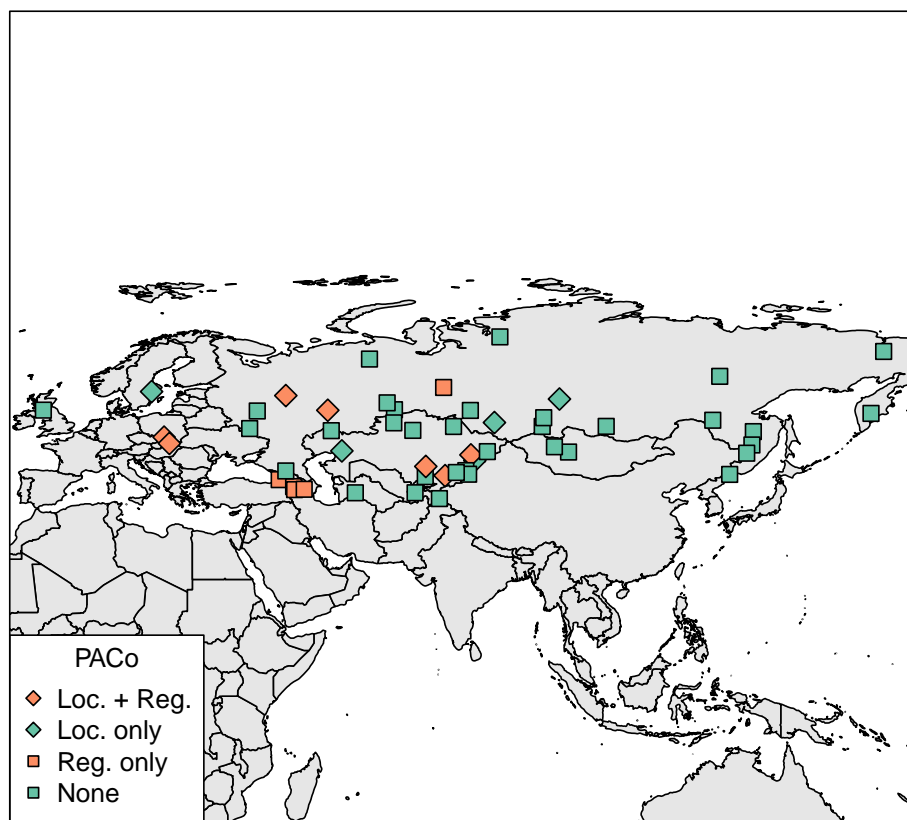


Figure 1: figure1

1 have consequences at the macro-ecological level <sup>36</sup>, but may not be detected  
 2 at finer spatial scales due to a stronger effect of ecological processes locally.  
 3 *PACO* permits the analysis of *how strongly* each interaction contribute to coevo-  
 4 lution, in a way that is as independent as possible from other interactions. As  
 5 interactions vary only insofar that there are some locations in which they *do not*  
 6 happen, we expect that the overall contribution of interactions will be the same  
 7 in the local and regional networks. For the 5 networks that show evidences of  
 8 coevolution accounting both for species and interactions sorting, we measured  
 9 the contribution of each interaction locally, and compared it to its contribution  
 10 to the regional network. Results are presented in **FIG. one-sentence summary**.  
 11 This is a key result, as it establishes that although coevolution does not leave  
 12 an imprint on local networks, it is still detectable in *interactions*. This is in line  
 13 with recent results that established that, although networks are composed of  
 14 interactions, both objects seem to have uncoupled behaviors <sup>37</sup>.

15 Species interactions vary in a way that is independent from species distribution  
 16 <sup>32</sup>. One possible explanation is that species that have a strong (coevolutionary)  
 17 relationship would either co-distribute more, or interact more frequently when  
 18 they co-occur. Should it be true, we would expect that *coevolved species pairs*, or  
 19 in other words, species involved in an interaction contributing strongly to the  
 20 community-wide coevolution, should be interacting frequently <sup>38</sup>. This would  
 21 result in a positive association between the frequency of the interaction (the  
 22 number of observations of a particular interaction divided by the number of  
 23 observations of the tow species together), and its overall importance for coevo-  
 24 lution (here measured in the *regional* network). As we report in **FIGURE**, we do  
 25 not find this relationship – how strongly an interaction contributes to overall

1 coevolution does not predict how frequently it will be realized when the two  
2 species are put together.

3 Our results, that (i) local networks show no signal of coevolution and (ii) the  
4 strength of coevolution between two species does not predict how frequently  
5 they interact, fall in line with recent conclusions about the spatial dy-  
6 namics of species interactions. Species interactions vary according to ecological  
7 mechanisms <sup>27</sup>: local population abundance <sup>39</sup>, local mis-matches of phenolo-  
8 gies <sup>40</sup>, local micro-environmental conditions <sup>41</sup>. And even though network  
9 composition varies, the overall network *structure* remains constant over time  
10 <sup>42</sup>, suggesting either (i) higher-order constraints or (ii) replacement of species  
11 by functionally equivalents from the regional pool. These results show that our  
12 current understanding of coevolution in multi-species interactions does not  
13 scale well to ecological questions – although phylogenetic structure and in-  
14 teraction show a strong agreement at the regional scale, the structure of local  
15 communities remains largely driven by ecological constraints. The analysis of  
16 ecological networks has often focused on emerging properties <sup>43</sup> rather than on  
17 the building blocks of the networks, that is species and interactions. Contrary  
18 to the often-argued point that coevolution should explain the local structure  
19 of interactions <sup>44</sup>, our result suggests that given the high variance in local in-  
20 teractions, coupled with the lack of relationship between coevolution and in-  
21 teraction frequency, local network structure is more likely to affect coevolution  
22 than the other way around.

## References

1. Eklof, A., Helmus, M. R., Moore, M., Allesina, S. & Eklöf, A. *et al.* Relevance of evolutionary history for food web structure. *Proc. R. Soc. B Biol. Sci.* **279**, 1588–1596 (2011).
2. Nuismer, S. L., Jordano, P. & Bascompte, J. *et al.* Coevolution and the architecture of mutualistic networks. *Evolution* **67**, 338–354 (2013).
3. Jordano, P., Bascompte, J. & Olesen, J. M. *et al.* Invariant properties in coevolutionary networks of plant-animal interactions. *Ecol. Lett.* **6**, 69–81 (2003).
4. Stouffer, D. B., Camacho, J., Guimera, R., Ng, C. A. & Amaral, L. A. N. *et al.* Quantitative patterns in the structure of model and empirical food webs. *Ecology* **86**, 1301–1311 (2005).
5. Stouffer, D. B., Sales-Pardo, M., Sirer, M. I. & Bascompte, J. *et al.* Evolutionary Conservation of Species' Roles in Food Webs. *Science* **335**, 1489–1492 (2012).
6. Thompson, J. N. *et al.* *The Geographic Mosaic of Coevolution*. (University Of Chicago Press, 2005).
7. Hembry, D. H., Yoder, J. B. & Goodman, K. R. *et al.* Coevolution and the Diversification of Life. *The American Naturalist* **184**, 425–438 (2014).
8. Yoder, J. B. & Nuismer, S. L. *et al.* When does coevolution promote diversification? *Am. Nat.* **176**, 802–817 (2010).
9. Paterson, S. *et al.* Antagonistic coevolution accelerates molecular evolution. *Nature* **464**, 275–278 (2010).
10. Buckling, A., Wei, Y., Massey, R. C., Brockhurst, M. A. & Hochberg, M. E. *et al.*



- 1 *al.* Antagonistic coevolution with parasites increases the cost of host deleteri-  
2 ous mutations. *Proc. R. Soc. B* **273**, 45–49 (2006).
- 3 11. Brockhurst, M. A., Buckling, A., Poullain, V. & Hochberg, M. E. *et al.* The  
4 impact of migration from parasite-free patches on antagonistic host-parasite  
5 coevolution. *Evolution* **61**, 1238–1243 (2007).
- 6 12. Nuismer, S. L., Thompson, J. N. & Gomulkiewicz, R. *et al.* Coevolution be-  
7 tween hosts and parasites with partially overlapping geographic ranges. *J. Evol.*  
8 *Biol.* **16**, 1337–1345 (2003).
- 9 13. Benkman, C. W., Parchman, T. L., Favis, A. & Siepielski, A. M. *et al.* Recip-  
10 rocal selection causes a coevolutionary arms race between crossbills and lodge-  
11 pole pine. *Am. Nat.* **162**, 182–194 (2003).
- 12 14. Havens, K. *et al.* Scale and structure in natural food webs. *Science* **257**,  
13 1107–1109 (1992).
- 14 15. Bascompte, J. *et al.* Disentangling the Web of Life. *Science* **325**, 416–419  
15 (2009).
- 16 16. Urban, M. C. *et al.* The evolutionary ecology of metacommunities. *Trends*  
17 *Ecol. Evol.* **23**, 311–317 (2008).
- 18 17. Proulx, S., Promislow, D. & Phillips, P. *et al.* Network thinking in ecology  
19 and evolution. *Trends Ecol. Evol.* **20**, 345–353 (2005).
- 20 18. Dunne, J. A. *et al.* in *Ecological networks: Linking structure and dynamics* (eds.  
21 Dunne, J. A. & Pascual, M.) 27–86 (Oxford University Press, 2006).
- 22 19. Stouffer, D. B., Camacho, J., Jiang, W. & Amaral, L. A. N. *et al.* Evidence for  
23 the existence of a robust pattern of prey selection in food webs. *Proc. R. Soc. B*

1 *Biol. Sci.* **274**, 1931–40 (2007).

2 20. Chamberlain, S. A. *et al.* Traits and phylogenetic history contribute to net-  
3 work structure across Canadian plant–pollinator communities. *Oecologia* 1–12  
4 (2014).

5 21. Vamosi, J. C., Armbruster, W. S. & Renner, S. S. *et al.* Evolutionary ecology  
6 of specialization: insights from phylogenetic analysis. *Proc. R. Soc. B* **281**,  
7 20142004 (2014).

8 22. Desdevises, Y., Morand, S., Jousson, O. & Legendre, P. *et al.* Coevolution  
9 between *Lamellodiscus* (Monogenea: Diplectanidae) and Sparidae (Teleostei):  
10 the study of a complex host–parasite system. *Evolution* **56**, 2459–2471 (2002).

11 23. Hafner, M. S. & Page, R. D. M. *et al.* Molecular phylogenies and host–parasite  
12 cospeciation: gophers and lice as a model system. *Philos. Trans. R. Soc. B Biol.*  
13 *Sci.* **349**, 77–83 (1995).

14 24. Hall, A. R., Scanlan, P. D. & Buckling, A. *et al.* Bacteria–Phage coevolution  
15 and the emergence of generalist pathogens. *Am. Nat.* **177**, 44–53 (2010).

16 25. Roopnarine, P. D. & Angielczyk, K. D. *et al.* The evolutionary palaeoecology  
17 of species and the tragedy of the commons. *Biol. Lett.* **8**, 147–50 (2012).

18 26. Dunne, J. a, Williams, R. J., Martinez, N. D., Wood, R. a & Erwin, D. H. *et al.*  
19 Compilation and network analyses of cambrian food webs. *PLoS Biol.* **6**, e102  
20 (2008).

21 27. Poisot, T., Stouffer, D. B. & Gravel, D. *et al.* Beyond species: why ecological  
22 interaction networks vary through space and time. *Oikos* (2014).

23 28. Devictor, V. *et al.* Differences in the climatic debts of birds and butterflies at

- 1 a continental scale. *Nature Clim. Change* **2**, 121–124 (2012).
- 2 29.Legendre, P., Desdevises, Y. & Bazin, E.*et al.* A statistical test for host-  
3 parasite coevolution. *Syst. Biol.* **51**, 217–234 (2002).
- 4 30.Fahrenholz, H. *et al.* Ectoparasiten und abstammungslehre. *Zool. Anz.* **41**,  
5 371–374 (1913).
- 6 31.Poisot, T. *et al.* in *Evolutionary Ecology of Host-Parasite Systems* (eds. Morand,  
7 S., Littlewood, D. T. & Poulin, R.) (Cambridge University Press, 2015).
- 8 32.Poisot, T., Canard, E., Mouillot, D., Mouquet, N. & Gravel, D.*et al.* The  
9 dissimilarity of species interaction networks. *Ecol. Lett.* **15**, 1353–1361 (2012).
- 10 33.Data from: Phylogenetic signal in module composition and species connec-  
11 tivity in compartmentalized host-parasite networks. (2012).
- 12 34.Balbuena, J. A., Míguez-Lozano, R. & Blasco-Costa, I.*et al.* PACo: A Novel  
13 Procrustes Application to Cophylogenetic Analysis. *PLoS ONE* **8**, e61048 (2013).
- 14 35.Krasnov, B. R. *et al.* Phylogenetic signal in module composition and species  
15 connectivity in compartmentalized host-parasite networks. *Am. Nat.* **179**, 501–  
16 11 (2012).
- 17 36.Price, P. W. *et al.* *Macroevolutionary Theory on Macroecological Patterns*. (Cam-  
18 bridge University Press, 2003).
- 19 37.Olito, C. & Fox, J. W. *et al.* Species traits and abundances predict metrics of  
20 plant–pollinator network structure, but not pairwise interactions. *Oikos* n/a–  
21 n/a (2014).
- 22 38.Mouquet, N. *et al.* Ecophylogenetics - advances and perspectives. *Biol. Rev.*  
23 *Camb. Philos. Soc.* **87**, 769–785 (2012).

- 1 39.Canard, E. F. *et al.* Empirical evaluation of neutral interactions in host-  
2 parasite networks. *Am. Nat.* **183**, 468–479 (2014).
- 3 40.Olesen, J. M. *et al.* Missing and forbidden links in mutualistic networks.  
4 *Proc. R. Soc. B* **278**, 725–732 (2011).
- 5 41.Poisot, T., Lepennetier, G., Martinez, E., Ramsayer, J. & Hochberg, M. E.*et al.*  
6 Resource availability affects the structure of a natural bacteria-bacteriophage  
7 community. *Biol. Lett.* **7**, 201–204 (2011).
- 8 42.Dupont, Y. L., Padrón, B., Olesen, J. M. & Petanidou, T.*et al.* Spatio-temporal  
9 variation in the structure of pollination networks. *Oikos* **118**, 1261–1269 (2009).
- 10 43.Blüthgen, N. *et al.* Why network analysis is often disconnected from com-  
11 munity ecology: A critique and an ecologist’s guide. *Basic and Applied Ecology*  
12 **11**, 185–195 (2010).
- 13 44.Thompson, A. R., Adam, T. C., Hultgren & Thacker, C. E.*et al.* Ecology and  
14 Evolution Affect Network Structure in an Intimate Marine Mutualism. *The*  
15 *American Naturalist* **182**, E58–E72 (2013).