

# Coevolution is detected regionally but not locally in ecological communities

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1 Coevolutionary dynamics act on both species and their interactions to drive the struc-  
2 ture of ecological communities. It remains unclear, however, how the structure of  
3 communities at larger spatial scales either influences or is influenced by local coevo-  
4 lutionary processes, and how mechanisms acting at different scales feedback into one  
5 another. Despite this, ecological networks are known to have a structure that is co-  
6 herent with evolutionary processes, which suggest that coevolution may play a role  
7 in determining their extent organisation. Here we show that even though species  
8 interaction vary substantially over a continental gradient, the coevolutionary sig-  
9 nificance of individual interactions is maintained at different scales. This occurs  
10 despite the fact that community variation at the local scale tends to weaken or re-  
11 move community-wide coevolutionary signal. We provide a new perspective on the  
12 interplay between coevolutionary theory and community ecology, by establishing  
13 the organisational scales at which the different theories have relevance: interactions  
14 are relevant locally, whereas overall community structure is relevant regionally. Al-  
15 though it has been tempting so far to understand how coevolution relates to network  
16 structure, our results suggest that the way forward is to understand how network

1 **structure may affect coevolution over space instead.**

2 Ecological interactions introduce selective pressures on the species involved – for ex-  
3 ample, lodgepole pines and red crossbills phenologies respond spatially to the presence  
4 of squirrels <sup>1</sup>, and palm species undergo changes in seed morphology in response to  
5 the extinction of disperser birds <sup>??</sup>. When taxonomically diverse species are considered  
6 at once, groups of interacting species are delineated by evolutionary boundaries <sup>2</sup>, in-  
7 variant structures in the distribution of interactions appear <sup>3</sup>, and conservatism of both  
8 the distribution of community modules <sup>4</sup> and the role of species occupy within them <sup>5</sup>  
9 becomes evident. Although the evolutionary dynamics in interacting species pairs has  
10 been well described <sup>6,7</sup>, attempts to understand how these cascade up to generate the  
11 tremendous species diversity of both species and interactions characteristic of empirical  
12 communities have been inconclusive <sup>8</sup>.

13 In multi-species systems that typically span a large taxonomic range, coevolution is often  
14 measured as the matching between the phylogenies of two sets of interacting organisms  
15 <sup>9,10</sup>. This build on the century-old ideas that extant species interact in a way similar to  
16 the way their ancestors did <sup>11</sup>. “Coevolved” systems should (i) have similar phyloge-  
17 netic trees and (ii) species at matching positions in either trees should interact. It is not  
18 clear, however, how this idea relates to dynamics occurring at smaller scales <sup>12</sup>: many  
19 ecological and evolutionary processes that occur locally are expected to blur the phylo-  
20 genetic signal. The spatial scales at which the different mechanisms involved are mostly  
21 incommensurable: coevolution is expressed within patches connected by gene-flow <sup>13,14</sup>,  
22 whereas the species diversity of complex networks is typically observed at spatial scales  
23 matching the species distribution <sup>15,16</sup>.

24 Species interaction networks have a structure which is in part driven by evolutionary

1 mechanisms, both micro <sup>3,17</sup> and macro <sup>2,18</sup>. Yet it has recently been demonstrated that  
 2 ecological interactions display important turnover over time and space <sup>19</sup>: the structure  
 3 of networks made of the same species is expected to change from one location to the  
 4 other, under the effect of local environmental contingencies, spatial mis-match in species  
 5 phenologies, variations in population abundances, and chance events <sup>20</sup>. As a conse-  
 6 quence, *locally*, the evolutionary signal on network structure is expected to be buried  
 7 under much ecological noise, and the effect of coevolution can only be inferred *region-*  
 8 *ally* – to the point where we must now ask if deep evolutionary history matters at all at  
 9 the scale where the structure of ecological networks is relevant to ecological properties.  
 10 We use data on ectoparasites of rodents from Western to Eastern Europe <sup>21</sup> to test the  
 11 following four hypotheses. First, local (observed) networks do not show evidence of  
 12 coevolution, whereas the continental-scale (henceforth regional) system does. Second,  
 13 the spatial variation of species interactions is independent from the variation in phyloge-  
 14 netic diversity. Third, interactions are distributed spatially in a way that is independent  
 15 from their evolutionary history. Finally, the contribution of interactions to coevolution  
 16 is similar at the local and regional scale.  
 17 At the regional scale, coevolutionary signal is extremely strong ( $p \leq 10^{-4}$ ), as estab-  
 18 lished by previous analysis of this system <sup>22</sup>. Most local networks, on the other hand,  
 19 show very little evidence of phylogenetic congruence (Fig. 1). Out of 51 local networks,  
 20 35 show no signal of coevolution, 11 show coevolution when using the regional interac-  
 21 tions, and 12 show coevolution using the local interactions (see *Supp. Mat. 1* for network-  
 22 level significance values). This suggests that macro-evolutionary processes (such as co-  
 23 diversification) have consequences at the macro-ecological level <sup>23</sup>, but may not be de-  
 24 tected at finer spatial scales due to a stronger effect of ecological processes locally.

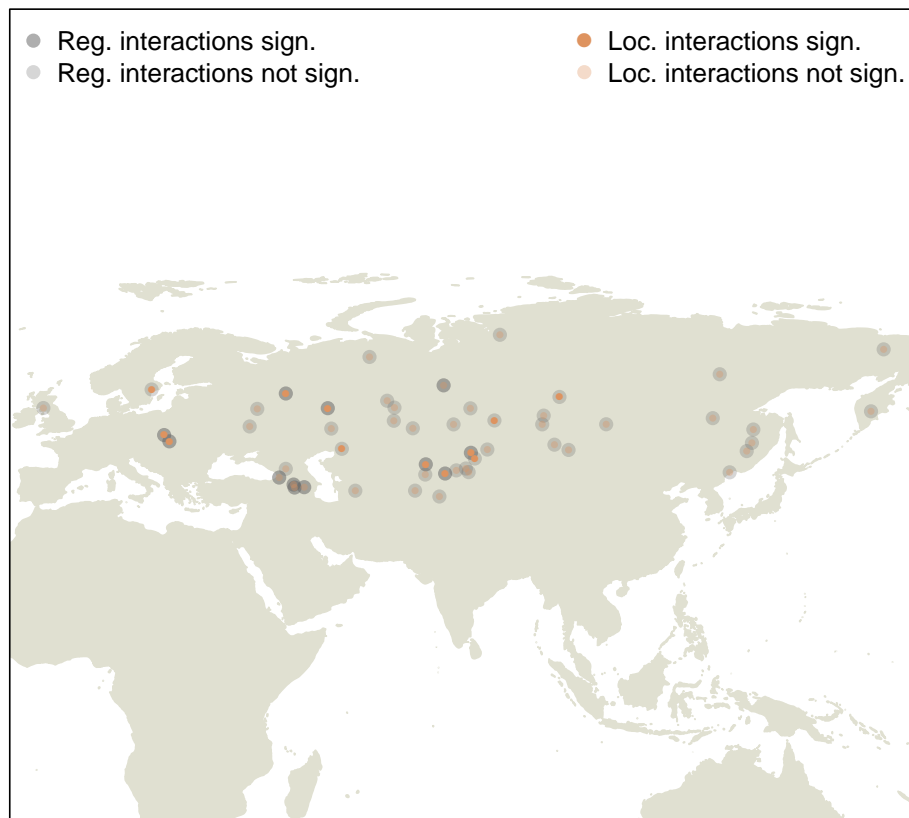


Figure 1: figure1

1 This of course implies that the variation of species interactions is not tied to the phy-  
2 logenetic relatedness of species across space. Both hosts and parasites show a distance  
3 decay of phylogenetic similarity (Fig. 2A), which we also observe for the *total* network  
4 dissimilarity (*i.e.* species and interaction variation, Fig. 2B). However when the effect  
5 of species variation is removed, the similarity of interactions shows no correlation to  
6 either spatial distance (Fig. 2C) or host or parasite phylogenetic dissimilarity (Fig. 2D).  
7 These result show that although evolutionary history ties into species distribution (be-  
8 cause communities close in space tend to have related hosts and parasites), it is a poor  
9 predictor of the way these species will interact.

10 Ecological interactions vary only insofar that there are some locations in which they *do*  
11 *not* happen – yet some interactions happen more consistently than others. The literature  
12 on host-parasite interaction usually assumes that some interactions are frequent because  
13 they reflect a significant past history of coevolution<sup>24,25</sup>. Should it be the case, the cor-  
14 relation between how frequently an interaction is (the number of times it is observed,  
15 divided by the number of time the two species co-occurred) and the importance of this  
16 interaction for coevolution (at the continental scale) is expected to be significant and  
17 positive. We find that it is neither (Fig. 3). The fact that an interaction is commonly  
18 observed does not reflect past co-evolution, but is most likely explained by local ecolog-  
19 ical factors: example mechanisms would be co-distribution of species in environments  
20 in which they can interact<sup>26</sup>, positive covariance of traits and environmental features,  
21 or random selection of partners by species with a wide range of possible interactions<sup>27</sup>.

22 We finally evaluate whether individual interactions contribute equally to coevolution-  
23 ary signal in the locals and continental network. An interaction between two species  
24 at matching positions in the tree should contribute positively to coevolution, regardless

1 of the overall score of the community. We find that it is indeed the case: interactions  
2 contributing strongly to coevolutionary signal at the continental scale *also* contribute  
3 strongly at the local scale (Fig. 4). This is a key result, as it establishes that although co-  
4 evolution does not leave an imprint on local networks, it is still detectable in *interactions*.  
5 This is in line with recent results that established that, although networks are composed  
6 of interactions, both objects seem to have uncoupled behaviors <sup>28</sup>.

7 Our results, that (i) local networks show no signal of coevolution and (ii) the strength  
8 of coevolution between two species does not predict how frequently they interact, fall  
9 when in line with recent conclusions about the spatial dynamics of species interactions.  
10 Although species interactions vary according to ecological mechanisms <sup>20</sup>, and although  
11 the identity of species in a network varies, the overall network *structure* remains constant  
12 over time <sup>29</sup>. This can suggest higher-order constraints on structure, or replacement of  
13 species by functionally equivalents from the regional pool. These result show that our  
14 current understanding of coevolution in multi-species interactions does not scale well  
15 to ecological questions – although phylogenetic structure and interaction show a strong  
16 agreement at the continental scale, community structure remains largely driven by eco-  
17 logical constraints. Ecological networks analysis has often focused on emerging proper-  
18 ties <sup>30</sup> rather than on the building blocks of the networks, that is species and interactions.  
19 Contrary to the often-argued point that coevolution should explain the local structure  
20 of interactions <sup>31</sup>, our result suggests that given the high variance in local interactions,  
21 coupled with the lack of relationship between coevolution and interaction frequency,  
22 local network structure is more likely to affect coevolution than the other way around.

## 1 **Methods**

2 We use data on observations of interactions between 121 species of rodents and 205  
3 species of parasitic fleas in 51 localities in Europe <sup>21</sup>. Individual interactions are aggre-  
4 gated to yield species interaction networks. All 51 networks (one per locality) are aggre-  
5 gated in a regional metanetwork <sup>19</sup>. The phylogenetic tree for hosts and parasites were  
6 rendered ultrametric.

7 The matching between host and parasite phylogenies knowing the species interactions  
8 is measured using the *PACO* method <sup>32</sup>: *PACO* measures both the network-level con-  
9 gruence (*i.e.* is the network coevolved) and the interaction-level signal (*i.e.* what is the  
10 contribution of each interaction to the overall coevolution signal). For each local net-  
11 work, we measure the strength of coevolution using (i) only local observations and (ii)  
12 all possible interactions between local species (as known from the regional aggregation  
13 of all local networks). This allows us to separate the effect of species sorting (regional  
14 interactions) and interaction sorting (local interactions).

15 Phylogenetic distance between two localities is measured for hosts and parasites using  
16 PCD <sup>33</sup>: this measure accounts for the dissimilarity of species, corrected for the phylo-  
17 genetic distance between all species in the dataset.

## 18 **References**

19 1. Benkman, C. W., Parchman, T. L., Favis, A. & Siepielski, A. M. *et al.* Reciprocal selection  
20 causes a coevolutionary arms race between crossbills and lodgepole pine. *Am. Nat.* **162**,  
21 182–194 (2003).

- 1 2.Eklof, A., Helmus, M. R., Moore, M., Allesina, S. & Eklöf, A.*et al.* Relevance of evolu-  
2 tionary history for food web structure. *Proc. R. Soc. B Biol. Sci.* **279**, 1588–1596 (2011).
- 3 3.Jordano, P., Bascompte, J. & Olesen, J. M.*et al.* Invariant properties in coevolutionary  
4 networks of plant-animal interactions. *Ecol. Lett.* **6**, 69–81 (2003).
- 5 4.Stouffer, D. B., Camacho, J., Jiang, W. & Amaral, L. A. N.*et al.* Evidence for the existence  
6 of a robust pattern of prey selection in food webs. *Proc. R. Soc. B Biol. Sci.* **274**, 1931–40  
7 (2007).
- 8 5.Stouffer, D. B., Sales-Pardo, M., Sirer, M. I. & Bascompte, J.*et al.* Evolutionary Conser-  
9 vation of Species' Roles in Food Webs. *Science* **335**, 1489–1492 (2012).
- 10 6.Thompson, J. N. *et al.* *The Geographic Mosaic of Coevolution*. (University Of Chicago  
11 Press, 2005).
- 12 7.Gandon, S., Buckling, A., Decaestecker, E. & Day, T.*et al.* Host-parasite coevolution  
13 and patterns of adaptation across time and space. *J. Evol. Biol.* **21**, 1861–1866 (2008).
- 14 8.Hembry, D. H., Yoder, J. B. & Goodman, K. R.*et al.* Coevolution and the Diversification  
15 of Life. *The American Naturalist* **184**, 425–438 (2014).
- 16 9.Desdevises, Y., Morand, S., Jousson, O. & Legendre, P.*et al.* Coevolution between  
17 *Lamellodiscus* (Monogenea: Diplectanidae) and Sparidae (Teleostei): the study of a  
18 complex host-parasite system. *Evolution* **56**, 2459–2471 (2002).
- 19 10.Legendre, P., Desdevises, Y. & Bazin, E.*et al.* A statistical test for host-parasite coevo-  
20 lution. *Syst. Biol.* **51**, 217–234 (2002).
- 21 11.Fahrenholz, H. *et al.* Ectoparasiten und abstammungslehre. *Zool. Anz.* **41**, 371–374  
22 (1913).



- 1 12. Poisot, T. *et al.* in *Evolutionary Ecology of Host-Parasite Systems* (eds. Morand, S.,  
2 Littlewood, D. T. & Poulin, R.) (Cambridge University Press, 2015).
- 3 13. Brockhurst, M. A., Buckling, A., Poullain, V. & Hochberg, M. E. *et al.* The impact of  
4 migration from parasite-free patches on antagonistic host-parasite coevolution. *Evolu-*  
5 *tion* **61**, 1238–1243 (2007).
- 6 14. Nuismer, S. L., Thompson, J. N. & Gomulkiewicz, R. *et al.* Coevolution between hosts  
7 and parasites with partially overlapping geographic ranges. *J. Evol. Biol.* **16**, 1337–1345  
8 (2003).
- 9 15. Havens, K. *et al.* Scale and structure in natural food webs. *Science* **257**, 1107–1109  
10 (1992).
- 11 16. Bascompte, J. *et al.* Disentangling the Web of Life. *Science* **325**, 416–419 (2009).
- 12 17. Hall, A. R., Scanlan, P. D. & Buckling, A. *et al.* Bacteria-Phage coevolution and the  
13 emergence of generalist pathogens. *Am. Nat.* **177**, 44–53 (2010).
- 14 18. Dunne, J. a, Williams, R. J., Martinez, N. D., Wood, R. a & Erwin, D. H. *et al.* Compi-  
15 lation and network analyses of cambrian food webs. *PLoS Biol.* **6**, e102 (2008).
- 16 19. Poisot, T., Canard, E., Mouillot, D., Mouquet, N. & Gravel, D. *et al.* The dissimilarity  
17 of species interaction networks. *Ecol. Lett.* **15**, 1353–1361 (2012).
- 18 20. Poisot, T., Stouffer, D. B. & Gravel, D. *et al.* Beyond species: why ecological interaction  
19 networks vary through space and time. *Oikos* (2014).
- 20 21. Data from: Phylogenetic signal in module composition and species connectivity in  
21 compartmentalized host-parasite networks. (2012).
- 22 22. Krasnov, B. R. *et al.* Phylogenetic signal in module composition and species connec-  
23 tivity in compartmentalized host-parasite networks. *Am. Nat.* **179**, 501–11 (2012).

- 1 23.Price, P. W. *et al. Macroevolutionary Theory on Macroecological Patterns.* (Cambridge  
2 University Press, 2003).
- 3 24.Combes, C. *et al. Parasitism - The Ecology and Evolution of Intimate Interactions.*  
4 (University Of Chicago Press, 2001).
- 5 25.*Biogeography of host-parasite interactions.* (Oxford University Press, 2010).
- 6 26.Gravel, D., Massol, F., Canard, E., Mouillot, D. & Mouquet, N.*et al.* Trophic theory of  
7 island biogeography. *Ecol. Lett.* **14**, 1010–1016 (2011).
- 8 27.Poisot, T., Stanko, M., Miklisová, D. & Morand, S.*et al.* Facultative and obligate para-  
9 site communities exhibit different network properties. *Parasitology FirstView*, 1–6 (2013).
- 10 28.Olito, C. & Fox, J. W. *et al.* Species traits and abundances predict metrics of plant-  
11 pollinator network structure, but not pairwise interactions. *Oikos* n/a–n/a (2014).
- 12 29.Dupont, Y. L., Padrón, B., Olesen, J. M. & Petanidou, T.*et al.* Spatio-temporal varia-  
13 tion in the structure of pollination networks. *Oikos* **118**, 1261–1269 (2009).
- 14 30.Blüthgen, N. *et al.* Why network analysis is often disconnected from community  
15 ecology: A critique and an ecologist's guide. *Basic and Applied Ecology* **11**, 185–195 (2010).
- 16 31.Thompson, A. R., Adam, T. C., Hultgren & Thacker, C. E.*et al.* Ecology and Evolution  
17 Affect Network Structure in an Intimate Marine Mutualism. *The American Naturalist*  
18 **182**, E58–E72 (2013).
- 19 32.Balbuena, J. A., Míguez-Lozano, R. & Blasco-Costa, I.*et al.* PACo: A Novel Procrustes  
20 Application to Cophylogenetic Analysis. *PLoS ONE* **8**, e61048 (2013).
- 21 33.Ives, A. R. & Helmus, M. R. *et al.* Phylogenetic Metrics of Community Similarity. *Am.*  
22 *Nat.* **176**, E128–E142 (2010).