

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

1 suggest that the way forward is to understand how network structure may affect
2 coevolution over space instead.

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

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

1 Species interaction networks have a structure which is in part driven by evolutionary
2 mechanisms, both micro ^{3,17} and macro ^{2,18}. Yet it has recently been demonstrated
3 that ecological interactions display important turnover over time and space ¹⁹: the
4 structure of networks made of the same species is expected to change from one lo-
5 cation to the other, under the effect of local environmental contingencies, spatial
6 mis-match in species phenologies, variations in population abundances, and chance
7 events ²⁰. As a consequence, *locally*, the evolutionary signal on network structure is
8 expected to be buried under much ecological noise, and the effect of coevolution can
9 only be inferred *regionally* – to the point where we must now ask if deep evolution-
10 ary history matters at all at the scale where the structure of ecological networks is
11 relevant to ecological properties.

12 We use data on ectoparasites of rodents from Western to Eastern Europe ²¹ to test the
13 following four hypotheses. First, local (observed) networks do not show evidence of
14 coevolution, whereas the continental-scale (henceforth regional) system does. Sec-
15 ond, the spatial variation of species interactions is independent from the variation in
16 phylogenetic diversity. Third, interactions are distributed spatially in a way that is in-
17 dependent from their evolutionary history. Finally, the contribution of interactions
18 to coevolution is similar at the local and regional scale.

19 At the regional scale, coevolutionary signal is extremely strong ($p \leq 10^{-4}$), as es-
20 tablished by previous analysis of this system ²². Most local networks, on the other
21 hand, show very little evidence of phylogenetic congruence (Fig. 1). Out of 51 local
22 networks, 35 show no signal of coevolution, 11 show coevolution when using the
23 regional interactions, and 12 show coevolution using the local interactions (see *Supp.*
24 *Mat. 1* for network-level significance values). **Figure?**

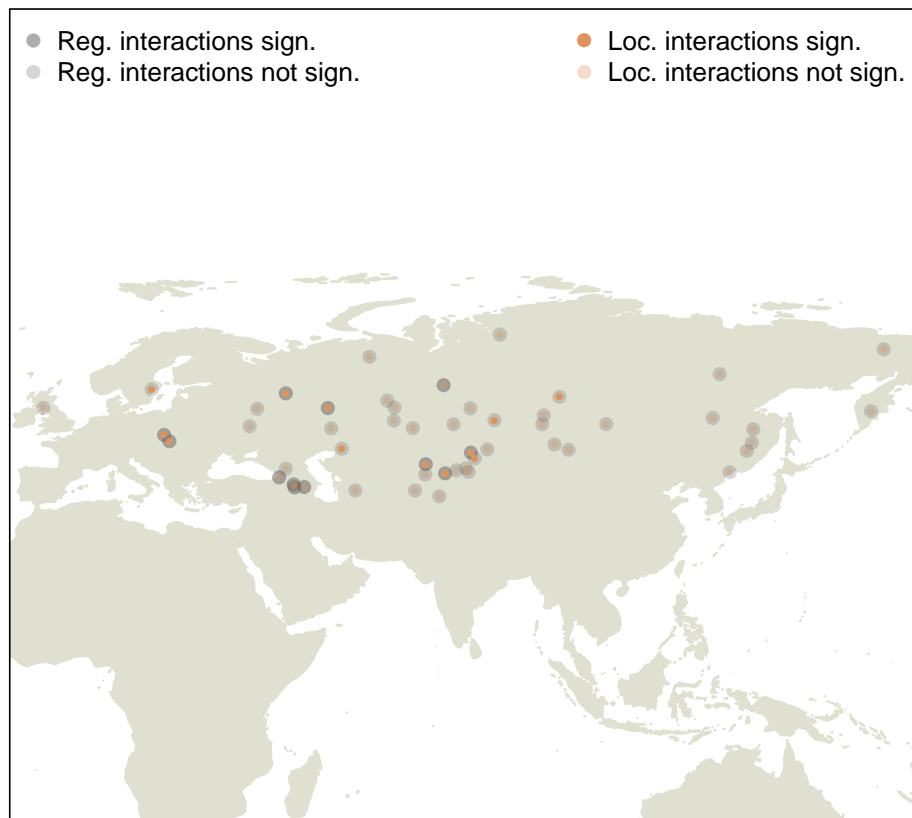


Figure 1: figure1

1 This suggests that macro-evolutionary processes (such as co-diversification) have con-
 2 sequences at the macro-ecological level ²³, but may not be detected at finer spatial
 3 scales due to a stronger effect of ecological processes locally. *PACO* permits the anal-
 4 ysis of *how strongly* each interaction contribute to coevolution, in a way that is as
 5 independent as possible from other interactions. As interactions vary only insofar
 6 that there are some locations in which they *do not* happen, we expect that the over-
 7 all contribution of interactions will be the same in the local and regional networks.
 8 For the 5 networks that show evidences of coevolution accounting both for species
 9 and interactions sorting, we measured the contribution of each interaction locally,
 10 and compared it to its contribution to the regional network. Results are presented
 11 in **FIG. one-sentence summary**. This is a key result, as it establishes that although
 12 coevolution does not leave an imprint on local networks, it is still detectable in *in-*
 13 *teractions*. This is in line with recent results that established that, although networks
 14 are composed of interactions, both objects seem to have uncoupled behaviors ²⁴.
 15 Species interactions vary in a way that is independent from species distribution ¹⁹.
 16 One possible explanation is that species that have a strong (coevolutionary) rela-
 17 tionship would either co-distribute more, or interact more frequently when they
 18 co-occur. Should it be true, we would expect that *coevolved species pairs*, or in other
 19 words, species involved in an interaction contributing strongly to the community-
 20 wide coevolution, should be interacting frequently ²⁵. This would result in a positive
 21 association between the frequency of the interaction (the number of observations
 22 of a particular interaction divided by the number of observations of the tow species
 23 together), and its overall importance for coevolution (here measured in the *regional*
 24 network). As we report in **FIGURE**, we do not find this relationship – how strongly
 25 an interaction contributes to overall coevolution does not predict how frequently it

1 will be realized when the two species are put together.

2 Our results, that (i) local networks show no signal of coevolution and (ii) the strength
3 of coevolution between two species does not predict how frequently they interact,
4 fall when in line with recent conclusions about the spatial dynamics of species inter-
5 actions. Species interactions vary according to ecological mechanisms²⁰: local popu-
6 lation abundance²⁶, local mis-matches of phenologies²⁷, local micro-environmental
7 conditions²⁸. And even though network composition varies, the overall network
8 *structure* remains constant over time²⁹, suggesting either (i) higher-order constraints
9 or (ii) replacement of species by functionally equivalents from the regional pool.
10 These result show that our current understanding of coevolution in multi-species in-
11 teractions does not scale well to ecological questions – although phylogenetic struc-
12 ture and interaction show a strong agreement at the regional scale, the structure of
13 local communities remains largely driven by ecological constraints. The analysis
14 of ecological networks has often focused on emerging properties³⁰ rather than on
15 the building blocks of the networks, that is species and interactions. Contrary to
16 the often-argued point that coevolution should explain the local structure of interac-
17 tions³¹, our result suggests that given the high variance in local interactions, coupled
18 with the lack of relationship between coevolution and interaction frequency, local
19 network structure is more likely to affect coevolution than the other way around.

20 **Methods**

21 We use data on observations of interactions between 121 species of rodents and 205
22 species of parasitic fleas in 51 localities in Europe²¹. Individual interactions are

1 aggregated to yield species interaction networks. All 51 networks (one per locality)
2 are aggregated in a regional metanetwork ¹⁹. The phylogenetic tree for hosts and
3 parasites were rendered ultrametric.

4 The matching between host and parasite phylogenies knowing the species interac-
5 tions is measured using the *PACO* method ³²: *PACO* measures both the network-level
6 congruence (*i.e.* is the network coevolved) and the interaction-level signal (*i.e.* what
7 is the contribution of each interaction to the overall coevolution signal). For each lo-
8 cal network, we measure the strength of coevolution using (i) only local observations
9 and (ii) all possible interactions between local species (as known from the regional
10 aggregation of all local networks). This allows us to separate the effect of species
11 sorting (regional interactions) and interaction sorting (local interactions).

12 Phylogenetic distance between two localities is measured for hosts and parasites us-
13 ing PCD ³³: this measure accounts for the dissimilarity of species, corrected for the
14 phylogenetic distance between all species in the dataset.

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