

Coevolutionary acts more on interactions than it does on community structure

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1 Coevolutionary dynamics are known act on both species and their in-
2 teractions in ways that drive the structure of ecological communities. It
3 remains unclear, however, how the structure of communities at larger
4 spatial scales either influences or is influenced by local coevolutionary
5 processes, and how mechanisms acting at these different scales feed-
6 back onto one another. Here we show that, though species interac-
7 tions vary substantially over a continental gradient, the coevolution-
8 ary significance of individual interactions is maintained across different
9 scales. Notably, this also occurs despite the fact that observed commu-
10 nity variation at the local scale frequently tends to weaken or remove
11 community-wide coevolutionary signal. When considered in terms of
12 the interplay between coevolutionary theory and community ecology,
13 our results demonstrate that individual interactions are show a con-
14 sistent signature of past coevolution, even when weaved in community
15 that do not.

16 Ecological interactions often exert important selective pressures on the species

involved; for example, lodgepole pines and red crossbills phenologies respond spatially to the presence of squirrels¹ and palm species undergo changes in seed morphology in response to the extinction of bird dispersing their seeds². In addition, most of these critical interactions are long-standing from a macro-evolutionary point of view³. Given that interactions are distributed in similar ways across communities, at both the large⁵ or small⁶ scale, it can be argued that much ecological structure is the end result of evolutionary or coevolutionary dynamics between species^{???}. Unfortunately, while the coevolutionary dynamic of pairs of interacting species has been well described at macro⁷ and micro⁸ evolutionary timescales, most attempts to understand how they cascade up to the levels of diversity of both species and interactions found within empirical communities have been inconclusive⁹. Moreover, because coevolutionary dynamics are often presented as a key driving force behind ecological structure across both time and space^{10,11}, it is crucial to understand the scale at which they are relevant.

Historically, the evidence for coevolution in taxonomically diverse communities is quantified as the matching between the phylogenies of two sets of interacting organisms¹². This notion builds on the century-old idea that extant species interact in a way similar to the way their ancestors did¹³. More explicitly, it is thought that communities that have assembled by successive divergence events should display phylogenetic congruence, that is (i) have similar phylogenetic trees and (ii) species at matching positions in the trees should tend to interact^{???,14}. It is not clear, however, how well this idea holds when confronted with dynamics occurring at smaller scales. Indeed, many ecological and evolutionary processes that occur locally are expected to blur the coevolutionary signal¹⁵. One possible explanation is that interactions can display substantial turnover at ecologically

1 relevant temporal and spatial scales ¹⁶: the same two species can interact in dif-
2 ferent ways under the effect of local environmental contingencies, spatial mismatch
3 in species phenologies, variations in population abundances, and chance events ¹⁷.
4 This hints that the impact of deep evolutionary history on community structure
5 can be weakened by the action of ecological mechanisms at the local scale. Yet
6 nothing in the above predicts that the coevolutionary signal within individual
7 interactions should vary across scales.

8 Only through the analysis of high-quality data can answers to the above questions
9 be reached. We study a dataset of interactions between rodents and their ectopar-
10 asites from Western to Eastern Europe ¹⁸. This dataset is uniquely suited for this
11 task as it represents a paradigmatic system in which species-species interactions
12 are thought to be driven by macro-evolution and co-speciation events ^{19,20}, and
13 coevolutionary signal is indeed significant at the continental level ²¹ ($p \leq 10^{-4}$;
14 Methods Summary). Importantly, it also provides considerable spatial replication
15 and variability ^{22,23} at a scale large enough to capture macro- ecological processes
16 (Methods Summary).

17 As host-macroparasites interactions are hypothesized to be both ecologically con-
18 strained and evolutionary conserved ²⁴, the phylogenetic congruence observed at
19 the continental level provides represents the baseline for expectations in local
20 communities. On the other hand, if ecological mechanisms reduce coevolution-
21 ary signal, we should detect coevolution at the continental scale but not locally.
22 Noting that variation of interactions can decrease congruence, we analyse the lo-
23 cal data at two different levels to test these hypotheses (Methods Summary); we
24 first use *regional* interaction data, which accounts for different species composi-

tion across sites, then the *local* interaction data, which also accounts for variation in the interactions between these species. Out of 51 local networks, 35 show no signal of coevolution, 11 show significant coevolutionary signal when using the regional interactions, and 12 show significant coevolutionary signal using the local interactions (see *Supp. Mat. 1* for network-level significance values). These results would appear to support the idea that macro-evolutionary processes such as co-diversification can have consequences at the macro-ecological level²⁵ but may not in fact be detectable at finer spatial scales.

The fact that we observed a weaker signal of coevolution at the local level implies that species at matching positions in their phylogenetic trees do not always interact. One possible explanation is that the variation of species interactions vary, over space, in a different ways than the identity of species^{???}. In this system, communities farther apart contain different species (*Suppl. Mat. 2*), but, once the phylogenetic relatedness between species is accounted for, there is actually no relationship between spatial distance and species dissimilarity (Fig. 2A). While distant networks are more dissimilar, the way shared species interact within them is independent of spatial distance (Fig. 2B). The same trend exists for networks dissimilarity as a function of (cumulative) phylogenetic dissimilarity of hosts and parasites (Fig. 2C). These results point to the fact that interactions do not vary in a way that is driven by evolutionary mechanisms or history.

Interactions also ultimately differ in how frequently they vary when the species involved co-occur^{???,26,27}. Once more, the literature on host-parasite interactions usually assumes that the reason why some interactions are more frequent is because they reflect a significant past history of coevolution^{24,28}. If this were

1 true, we should observe a significant, positive correlation between the probability
2 of observing an interaction and the importance of that interaction for coevolu-
3 tion at the continental scale. Surprisingly, we find that neither is true here since
4 interactions that are important for coevolution are not more conserved (Fig. 3).
5 Nonetheless, interactions that *are* observed at the local scale should retain their
6 signal of contribution to coevolution, because they involve species at matching po-
7 sitions in the phylogenetic trees. Indeed, we find that interactions that contribute
8 strongly to coevolutionary signal at the continental scale *also* show a significant
9 tendency to contribute strongly at the local scale (Fig. 4). Remarkably, this result
10 implies that the remnants of coevolution are still locally detectable in individual
11 *interactions* even though it does not leave its imprint on most local networks.

12 Overall, the results of our analyses demonstrate that there is a sizeable gap be-
13 tween our current understanding of coevolution as the basis of multi-species in-
14 teractions and its applicability to ecological questions. Local networks show little
15 to no signal of coevolution and, the strength of coevolution between two species
16 does not predict how frequently they interact. In opposition to the frequent as-
17 sumption that phylogenetic structure is a key driver of community structure^{29,30},
18 our data reveal that at ecologically relevant spatial scales, this impact is actually
19 minimal. Yet, individual interactions are able to retain their coevolutionary signal
20 even when the community they are woven into is not. But these discrepancies do
21 actually provide a clear roadmap about how this gap between our appreciation of
22 the role of coevolution, and its empirically measurable outcomes, is to be bridged
23 by future research: our results suggest that local network structure is far more
24 likely to affect coevolution than it is to be driven by it; this implies that net-

1 work structure is the *mechanism* by which coevolution proceeds, rather than the
2 imprint it leaves on ecological communities.

3 **Methods Summary**

4 We study data on observations of interactions between 121 species of rodents and
5 205 species of parasitic fleas in 51 locations across Europe ¹⁸ to build 51 species-
6 species interaction networks. Interactions were measured by combing rodents for
7 fleas, a method that gives high quality data as it has a high power of detection. To
8 account for differential sampling effort and across site variations in abundance, we
9 only study the networks' incidence matrices (presence and absence of interactions).

10 In our study, we define three scales for the network data and analysis— conti-
11 nental, regional, and local. The *continental* scale is the aggregated “metanetwork”
12 which includes all potential interactions between co-occurring species ¹⁶ (*i.e.*, all
13 species and all their interactions across the 51 networks). Within each site, the
14 *regional* scale is given by the list of observed species and all their possible interac-
15 tions. Hence the regional networks are always a perfect subset of the continental
16 network. The *local* scale includes only the interactions that were actually ob-
17 served in the field at a given site. Therefore, the local and regional networks
18 include the same species, but the local network has only a subset (or, at most, an
19 exact match) of the interactions in the regional network.

20 We quantified the coevolutionary signal in terms of the degree of matching be-
21 tween host and parasite phylogenies given knowledge of species interactions using
22 the *PACO* method ³¹, which is robust to variations in number of species. *PACO*

1 provides measures of both the network-level congruence (*i.e.*, is the network co-
2 evolved?) and the interaction-level signal (*i.e.*, what is the contribution of each
3 interaction to the overall coevolutionary signal?). We measured the phylogenetic
4 dissimilarity between two sites for hosts and parasites using PCD³², a measure
5 that accounts for the dissimilarity of species, corrected for the phylogenetic dis-
6 tance between all species in the dataset. Since it is a requirement of the methods
7 we use here, the phylogenetic trees for hosts and parasites were rendered ultra-
8 metric (*i.e.*, all species are at the same distance from the root).
9 We used the network β -diversity approach¹⁶ to measure the dissimilarity of in-
10 teractions across sites. It does amazing things (though Tim came up with it so
11 maybe this is universally implicit).

12 References

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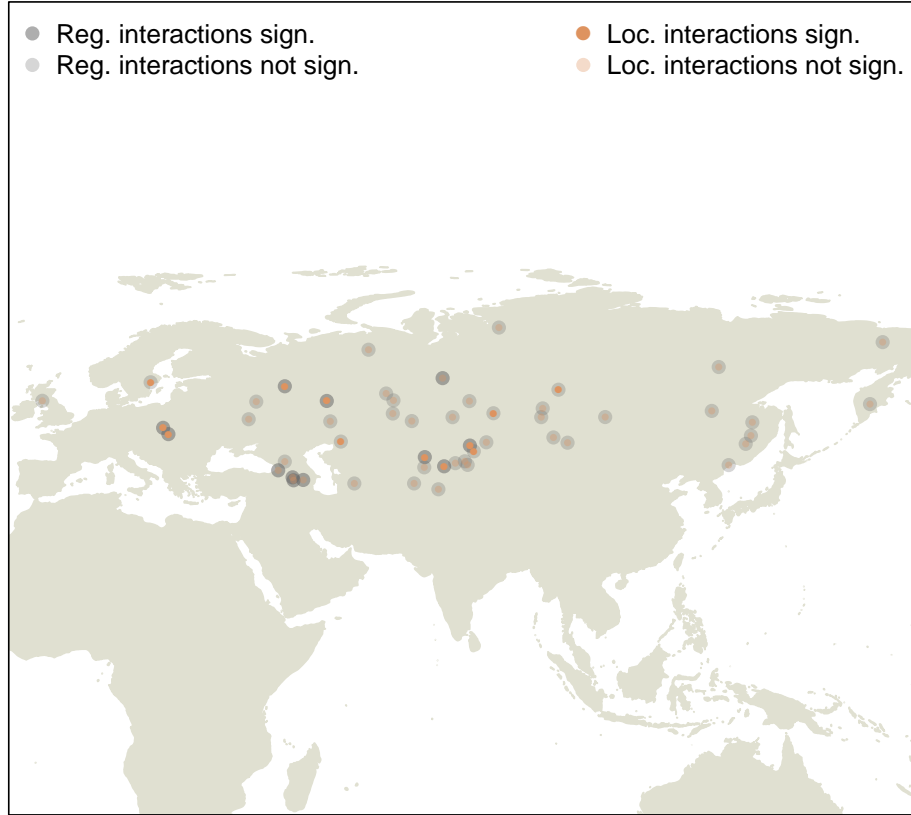


Figure 1: Spatial pattern of coevolutionary signal across the 51 sites. For each location, we indicate whether or nor the structure of regional and local interaction networks is consistent with the pattern of phylogenetic congruence. The color of the circle corresponds to regionally significant or nonsignificant (foo and bar, respectively) while the symbol within corresponds to locally significant or nonsignificant (Zoroaster’s barsom and varza, respectively).

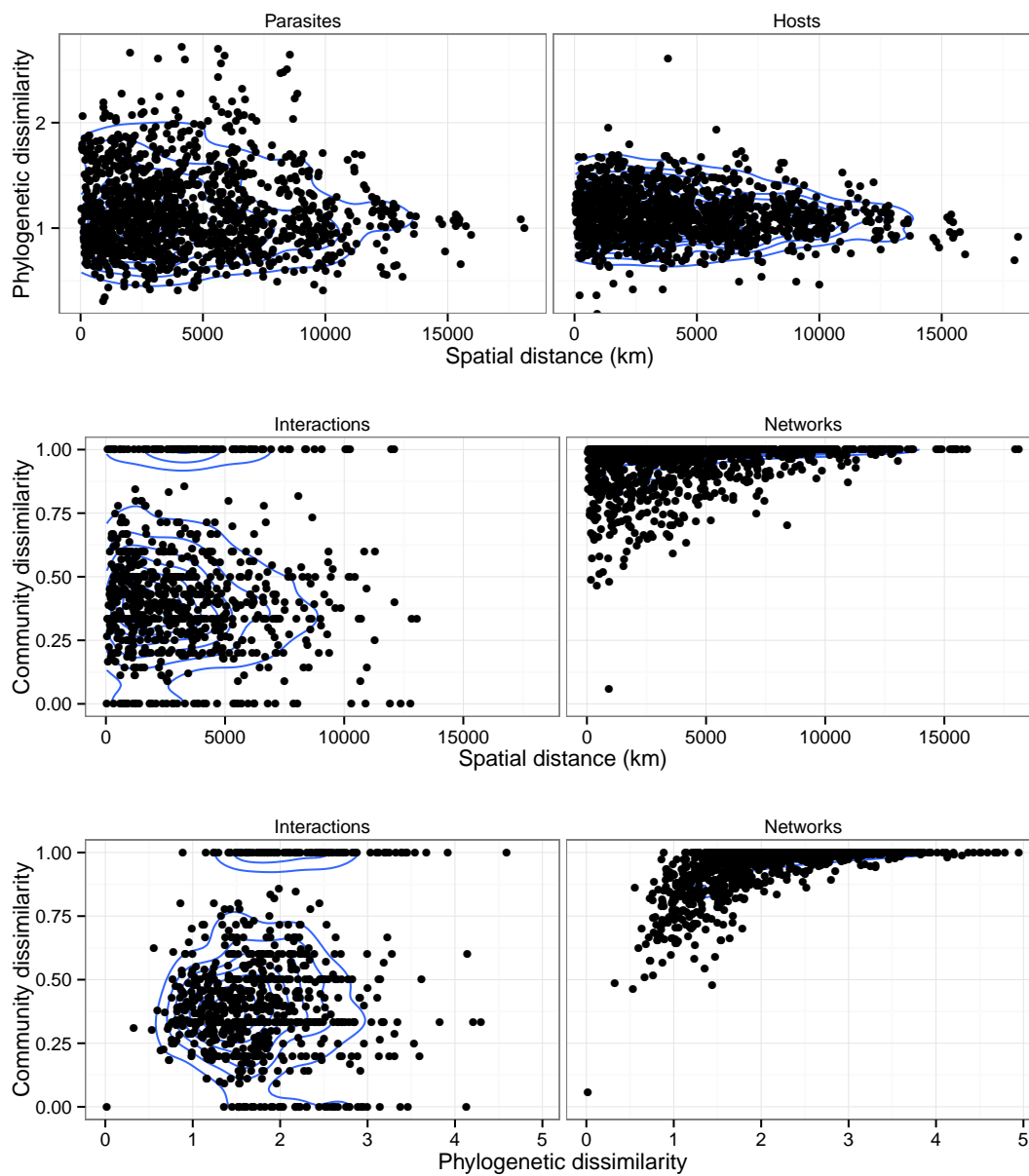


Figure 2: Relationships between spatial distance, phylogenetic dissimilarity, and the dissimilarity of interactions.

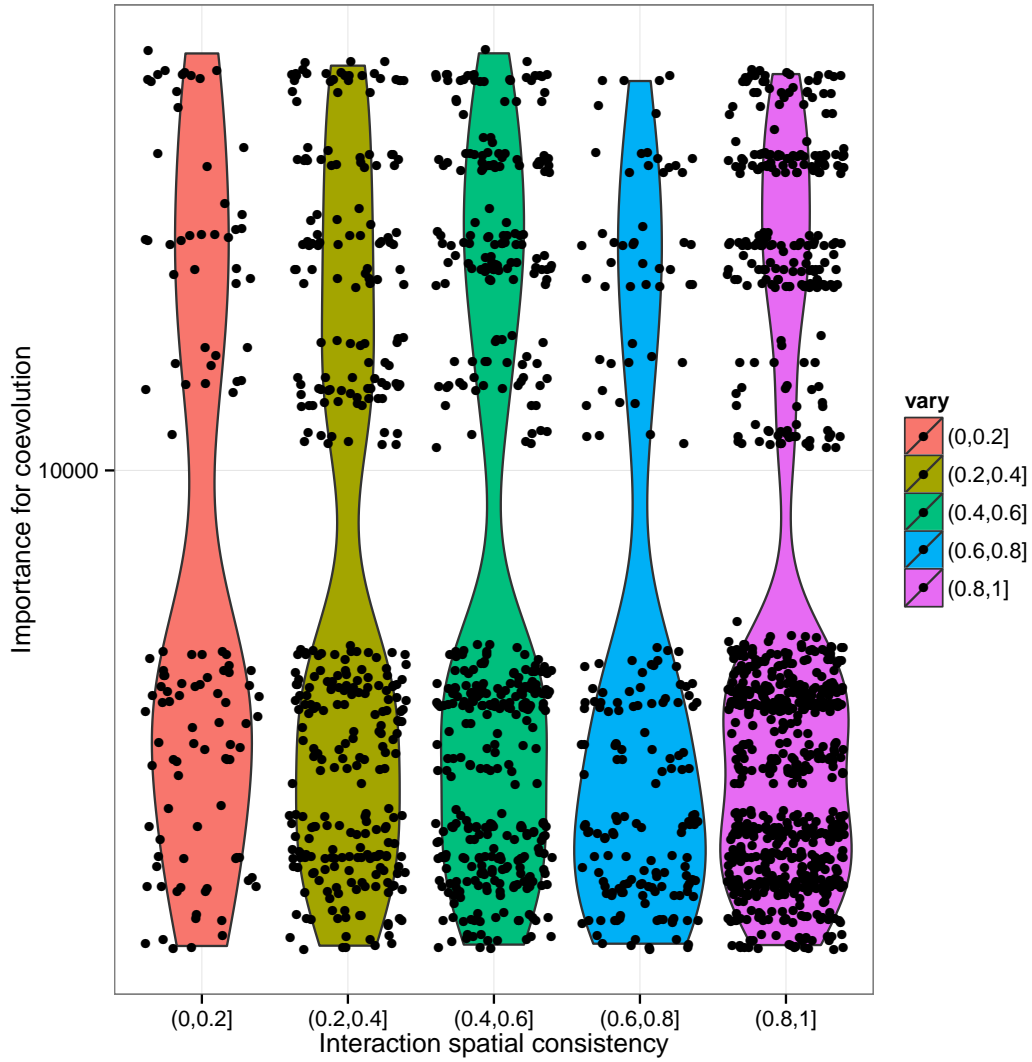


Figure 3: Lack of a relationship between the spatial consistency of an interaction and its importance for coevolution in the continental network. Spatial consistency is defined as the probability of observing an interaction between two species given that they were observed to co-occur.

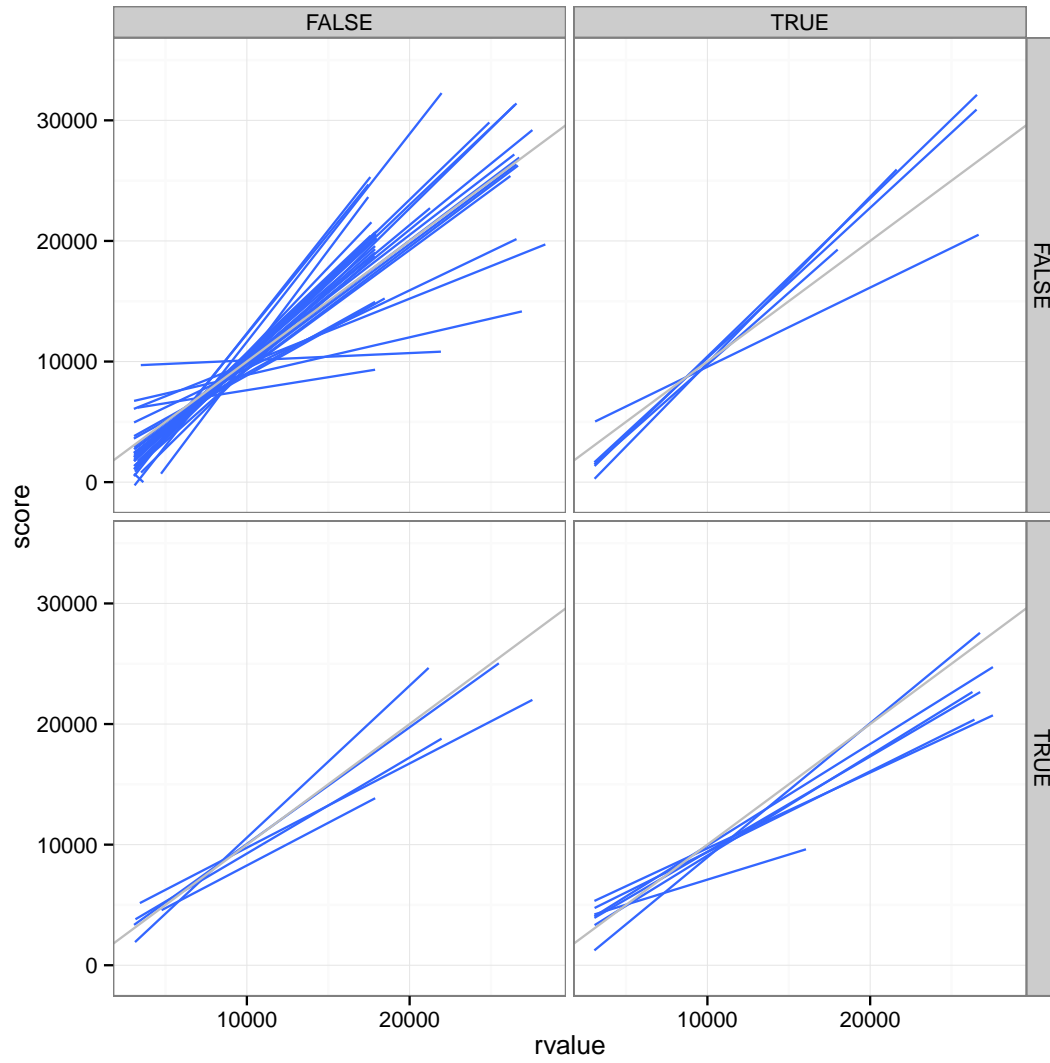


Figure 4: Relationship between continental and local contribution to coevolution (*temp.*).

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