

Coevolution leaves a stronger imprint on interactions than on community structure

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

15 Ecological interactions often exert important selective pressures on the species
16 involved. For example, the phenologies of lodgepole pines and red crossbills re-

1 spond spatially to the presence of squirrels ¹ and palm species undergo changes
2 in seed morphology in response to the extinction of bird dispersing their seeds
3 ². Given that interactions are distributed in similar ways across communities, at
4 both the large ³ or small ⁴ scale, it can be argued that much ecological structure
5 is the end result of evolutionary or coevolutionary dynamics between species ⁵.
6 Unfortunately, while the coevolutionary dynamic of pairs of interacting species
7 has been well described at macro ⁷ and micro ⁸ evolutionary timescales, most
8 attempts to understand how they cascade up to the levels of diversity of both
9 species and interactions found within empirical communities have been inconclu-
10 sive ⁹. Moreover, because coevolutionary dynamics are often presented as a key
11 driving force behind ecological structure across both time and space ¹⁰, it is crucial
12 to determine the scale at which they are both relevant and quantifiable.

13 Historically, the evidence for coevolution in taxonomically diverse communities
14 is quantified as the degree of matching between the phylogenies of two sets of
15 interacting organisms ¹¹. This notion builds on the century-old idea that extant
16 species interact in a way similar to the way their ancestors did ¹². Yet it is consid-
17 erably more restrictive than just phylogenetic conservation of species' interactions
18 ¹³, as it accounts for higher-order constraints. More explicitly, it is thought that
19 communities that have assembled by successive divergence events should display
20 phylogenetic congruence, that is (i) have similar phylogenetic trees and (ii) have
21 species at matching positions in the trees that tend to interact ^{???,14}. On the
22 other hand, many ecological and evolutionary processes that occur locally are
23 expected to blur community-wide coevolutionary signal ¹⁵. One possible explana-
24 tion is that interactions can display substantial turnover at ecologically relevant
25 temporal and spatial scales ¹⁶: the same two species can interact in different ways

1 under the effect of local environmental contingencies, spatial mismatch in species
2 phenologies, variations in population abundances, and chance events ¹⁷. It is un-
3 clear, however, whether these mechanisms influence how the coevolutionary signal
4 within individual interactions should vary across spatial scales.

5 To answer these questions, we study a dataset of interactions between rodents
6 and their ectoparasites from Western to Eastern Europe ¹⁸ (Methods Summary).
7 This dataset is uniquely suited for this task as it represents a paradigmatic system
8 in which species-species interactions are thought to be driven by macro-evolution
9 and co-speciation events ¹⁹, and coevolutionary signal is indeed significant at the
10 continental level ²⁰ ($p \leq 10^{-4}$; Methods Summary). Importantly, it also provides
11 spatial replication and variability ²¹ at a scale large enough to capture macro-
12 ecological processes.

13 As host-macroparasites interactions are hypothesized to be both ecologically con-
14 strained and evolutionary conserved ²², the phylogenetic congruence observed at
15 the continental level provides the baseline for expectations in local communities.
16 Of course, if ecological mechanisms reduce coevolutionary signal, we should de-
17 tect coevolution at the continental scale but not locally. Noting that variation
18 of interactions can decrease congruence, we analyse the local data at two differ-
19 ent levels to test these hypotheses; we first use *regional* interaction data, which
20 accounts for different species composition across sites, then the *local* interaction
21 data, which also accounts for variation in the interactions between observed these
22 species (Methods Summary). Out of 51 local networks, 35 show no signal of
23 coevolution, 11 show significant coevolutionary signal when using the regional
24 interactions, and 12 show significant coevolutionary signal using the local inter-

1 actions (see *Supp. Mat. 1* for network-level significance values). These results
2 would appear to support the idea that macro-evolutionary processes such as co-
3 diversification can have consequences at the macro-ecological level ²³ but may not
4 in fact be detectable at finer spatial scales.

5 This is particularly apparent when comparing the distribution of network-level
6 coevolutionary signal at the local and regional scales, relative to the continental
7 scale (Fig. 2A). Yet this system-level difference says little about how individual
8 interactions, on which most of the coevolutionary mechanisms purportedly act ²⁴,
9 behaves. We show that regardless of the scale at which the system is observed,
10 the distribution of the contribution of individual interactions to coevolution is
11 conserved (Fig. 2B). This allows to understand why networks differ from the
12 continental-level expectation: networks with interactions that are important for
13 coevolution at the continental scale have more coevolutionary signal at the local
14 and regional scale alike (Fig. 2C). This result shows that network-level property
15 emerge from the properties of their interactions: because interactions differ in their
16 total contribution to coevolution, their distribution across different networks will
17 drive differences in overall coevolutionary signal.

18 Interactions also ultimately differ in how frequently they vary when the species
19 involved co-occur ^{???,25}. Once more, the literature on host-parasite interactions
20 usually assumes that the reason why some interactions are more frequent is be-
21 cause they reflect a significant past history of coevolution ²⁶. If this were true,
22 we should observe a significant, positive correlation between the probability of
23 observing an interaction and the importance of that interaction for coevolution
24 at the continental scale (Methods Summary). Surprisingly, we find that neither

1 is true here since interactions that are important for coevolution are not more
2 conserved (Fig. 3).

3 Nonetheless, interactions that *are* observed at the local scale should retain their
4 signal of contribution to coevolution because they involve species at matching po-
5 sitions in the phylogenetic trees. Indeed, we find that interactions that contribute
6 strongly to coevolutionary signal at the continental scale *also* show a significant
7 tendency to contribute strongly at the local scale (Fig. 4). Remarkably, this result
8 implies that the remnants of coevolution are still locally detectable in *individual*
9 *interactions* even though it does not leave its imprint on most local networks.

10 Overall, the results of our analyses demonstrate that there is a sizeable gap be-
11 tween our current understanding of coevolution as the basis of multi-species in-
12 teractions and its applicability to ecological questions. Local networks show little
13 to no signal of coevolution and the strength of coevolution between two species
14 is a surprisingly poor predictor of how frequently they interact. In contrast to
15 the frequent assumption that phylogenetic structure is a key driver of community
16 structure^{27,28}, these data reveal that this impact is actually minimal at ecolog-
17 ically relevant spatial scales. Despite all the above, individual interactions are
18 able to maintain their coevolutionary signal even when the community they are
19 woven into does not. Thinking more broadly, these discrepancies provide a clear
20 roadmap for bridging the aforementioned gap between our appreciation of the role
21 of coevolution and its empirically measurable outcomes. Network structure is the
22 most parsimonious *mechanism* by which coevolution proceeds, not the imprint
23 coevolution leaves on ecological communities.

1 Methods Summary

2 We use data on observations of interactions between 121 species of rodents and
3 205 species of parasitic fleas in 51 locations across Europe ¹⁸ to build 51 species-
4 species interaction networks. Interactions were measured by combing rodents for
5 fleas, a method that gives high quality data as it has a high power of detection. To
6 account for differential sampling effort and across site variations in abundance, we
7 only study the networks' incidence matrices (presence and absence of interactions).

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

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 ²⁹, which is robust to variations in number of species. *PACO*
23 provides measures of both the network-level congruence (*i.e.*, is the network co-
24 evolved?) and the interaction-level signal (*i.e.*, what is the contribution of each

1 interaction to the overall coevolutionary signal?). We measured the phylogenetic
2 dissimilarity between two sites for hosts and parasites using PCD³⁰, a measure
3 that accounts for the dissimilarity of species, corrected for the phylogenetic dis-
4 tance between all species in the dataset. Since it is a requirement of the methods
5 we use here, the phylogenetic trees for hosts and parasites were rendered ultra-
6 metric (i.e., all species are at the same distance from the root).

7 References

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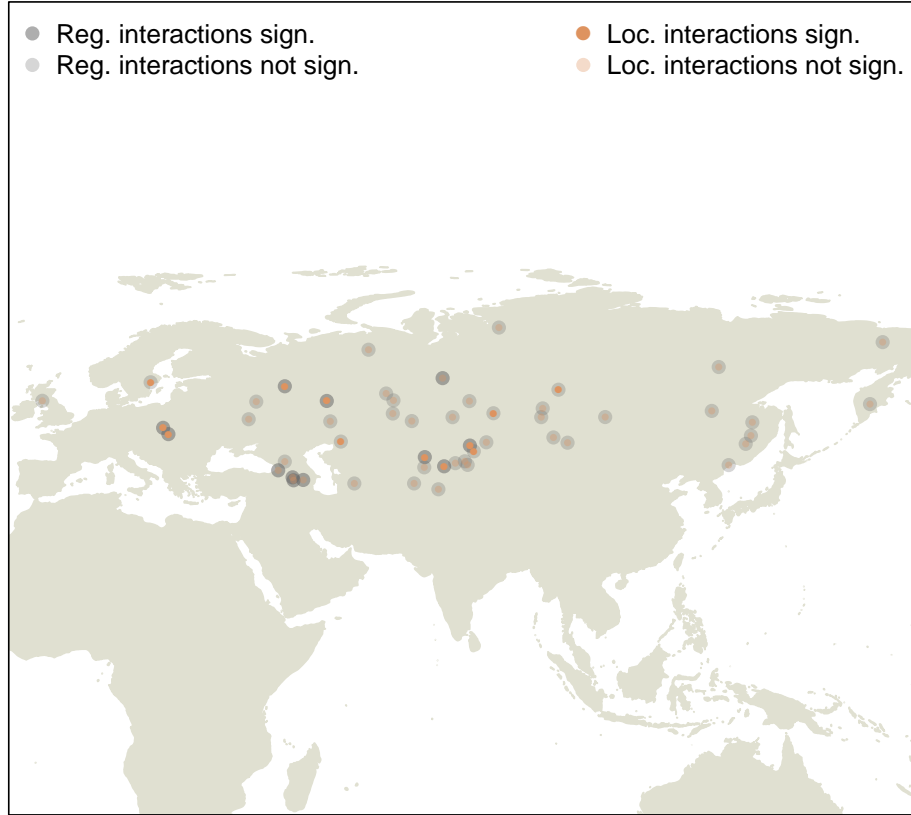


Figure 1: Spatial distribution of coevolutionary signal across the 51 sites. For each location, we indicate whether or nor the structure of regional and local interaction networks is consistent with phylogenetic congruence. The color of the circle corresponds to regionally significant or nonsignificant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

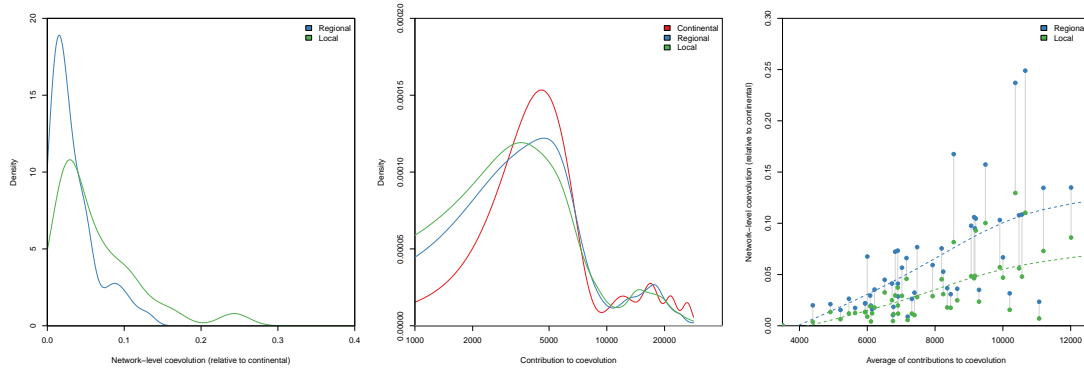


Figure 2: Distribution of coevolutionary signal at the network and interaction level. **A** Networks at the local and regional scale show less coevolutionary signal than the network at the continental scale. **B** Interactions in the local, regional, and continental scale have equal contributions to coevolution. **C** Networks that have lower coevolutionary signal are made of interactions that contribute little to coevolution at the continental scale.

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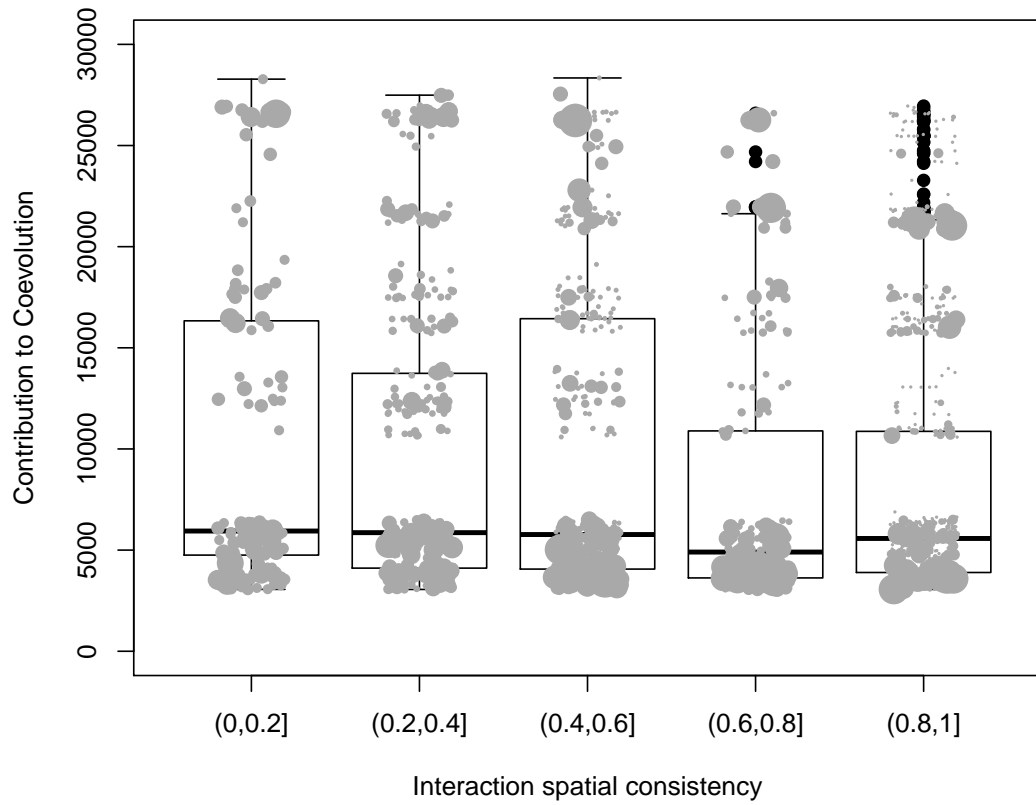


Figure 3: Lack of a relationship between the spatial consistency of an interaction and its importance for coevolution in the continental network. Spatial consistency is defined as the probability of observing an interaction between two species given that they were observed to co-occur.

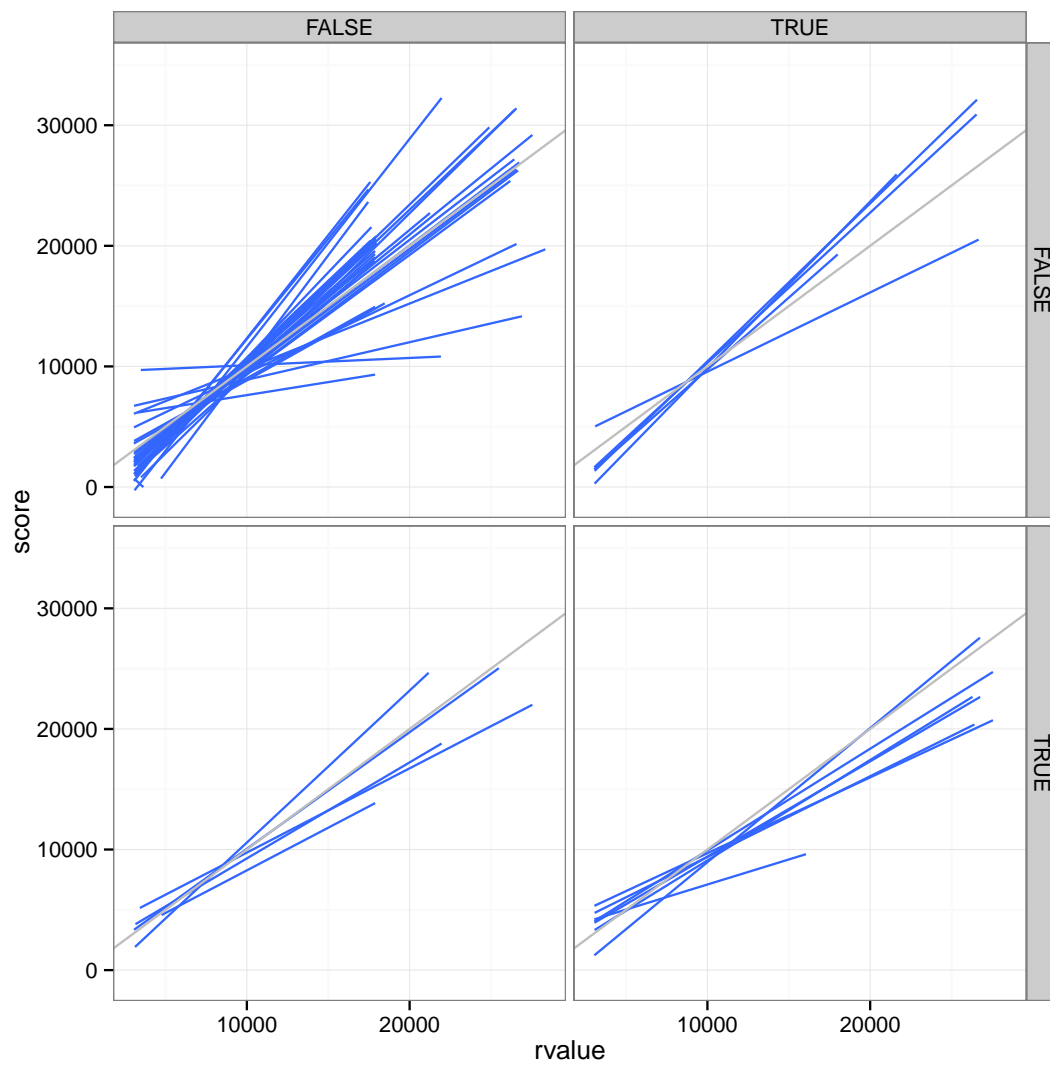


Figure 4: Relationship between continental and local contribution to coevolution. Each line corresponds to a location.

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