Coevolution acts on interactions but not on 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**

5   **one another. Most of these feedbacks are mediated by the structure of ecological in-**

6   **teractions, *i.e.* how they are distributed within communities. Here we show that,**

7   **though species interactions vary substantially over a continental gradient, the co-**

8   **evolutionary significance of individual interactions is maintained across different**

9   **scales. Intriguingly, this also occurs despite the fact that community variation at**

10 **the local scale tends to weaken or remove community-wide coevolutionary signal.**

11 **When considered in terms of the interplay between coevolutionary theory and com-**

12 **munity ecology, our results demonstrate that individual interactions are locally rel-**

13 **evant whereas the emerging structure of these interactions across many species only**

14 **becomes relevant at regional scales.**

15 Ecological interactions exert selective pressures on the species involved; for example,

16 lodgepole pines and red crossbills phenologies respond spatially to the presence of squir-

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rels [1] and palm species undergo changes in seed morphology in response to the extinc-
tion of bird dispersing their seeds [2]. Most of these interactions are long-standing from
a macroevolutionary point of view [3], explaining why interactions are distributed simi-
larly across communities, either at the large [4] or small [5] scale. Although the evolutionary
dynamics of interacting species pairs has been well described [6], attempts to understand
how these cascade up to generate the tremendous species diversity of both species and
interactions characteristic of empirical communities have been inconclusive [7].

Historically, coevolution in taxonomically diverse communities is quantified as the match-
ing between the phylogenies of two sets of interacting organisms [8]. This notion builds
on the century-old idea that extant species interact in a way similar to the way their an-
cestors did [9]. More explicitly, communities that assembled through coevolution should
(i) have similar phylogenetic trees and (ii) species at matching positions in either trees
should interact. It is not clear, however, how this idea stands when confronted to dy-
namics occurring at smaller scales: indeed, many ecological and evolutionary processes
that occur locally are expected to blur the phylogenetic signal [10]. One possible reason is
the recently demonstrated fact that interactions display important turnover, at temporal
and spatial scales relevant to ecological dynamics [11]: the same two species can interact in
different ways under the effect of local environmental contingencies, spatial mis-match
in species phenologies, variations in population abundances, and chance events [12]. As a
consequence, it is important to assess whether deep evolutionary history matters at all at
the scale where the structure of ecological networks is relevant to ecological properties.

In order to better understand the interplay between coevolutionary theory and commu-
nity ecology, we study data a dataset of rodent ectoparasites from Western to Eastern
Europe [13]. These data show high turnover of both species and their interactions over

¹ time, and have well resolved phylogenetic trees to support a fine analysis of coevolution.

² ... to test the following four hypotheses. First, local (observed) networks do not show ev-

³ idence of coevolution, whereas the continental-scale (henceforth regional) system does.

⁴ Second, the spatial variation of species interactions is independent from the variation

⁵ in phylogenetic diversity. Third, interactions are distributed spatially in a way that is in-

⁶ dependent from their evolutionary history. Finally, the contribution of interactions to

⁷ coevolution is similar at the local and regional scale.

⁸ If ecological mechanisms do reduce evolutionary signal, we expect to detect coevolu-

⁹ tion at the continental scale, but not locally. In line with this hypothesis, coevolution is

¹⁰ strong at the continental level [14] ($p \leq 10^{-4}$) but most local networks show very little evi-

¹¹ dence of phylogenetic congruence (Fig. 1). Out of 51 local networks, 35 show no signal

¹² of coevolution, 11 show coevolution when using the regional interactions, and 12 show

¹³ coevolution using the local interactions (see *Supp. Mat. 1* for network-level significance

¹⁴ values). This suggests that macro-evolutionary processes such as co-diversification have

¹⁵ consequences at the macro-ecological level [15], but may not in fact be detectable at fine

¹⁶ spatial scales.

¹⁷ That there is no signal of coevolution implies that species at matching positions in the

¹⁸ tree do not necessarily interact, which can happen if the variation of species interactions

¹⁹ is not tied to the phylogenetic relatedness of species across space. In this system, the

²⁰ phylogenetic dissimilarity of both hosts and parasites increases with distance (Fig. 2A),

²¹ and we observe the same for the joint variation of species and interactions (Fig. 2B). In

²² contrast, when we control for the effect of species variation, we find that the similarity of

²³ interactions is independent of both spatial distance (Fig. 2C) and host or parasite phylo-

²⁴ genetic dissimilarity (Fig. 2D). Therefore, while evolutionary history is tightly linked to
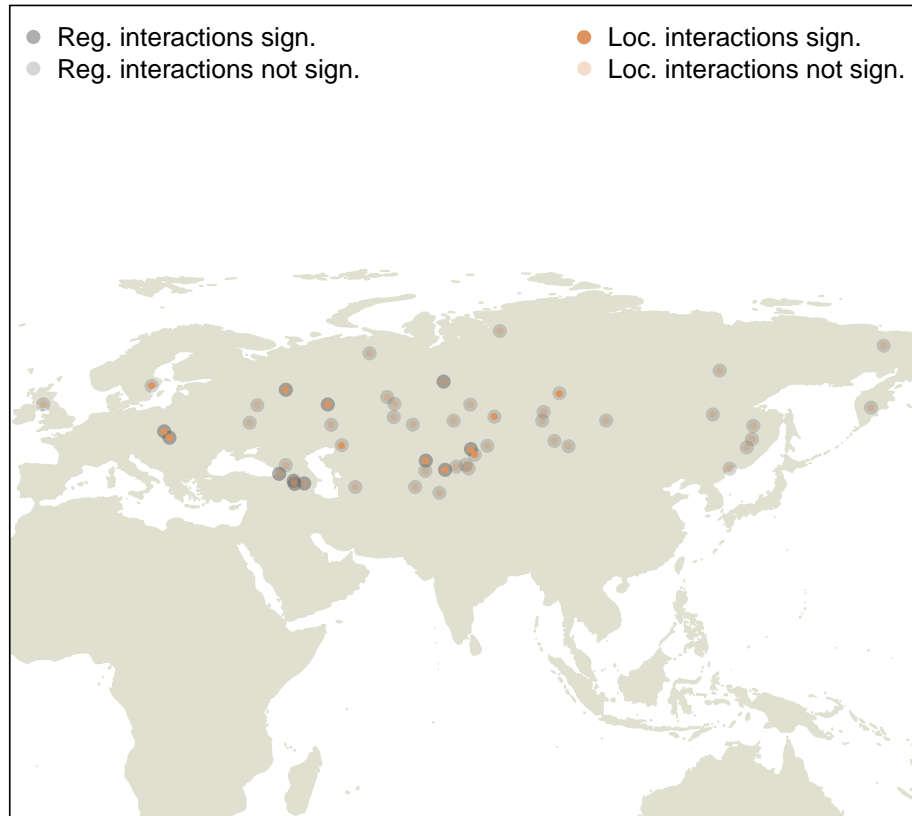
Figure 1: (A) Conceptual representation of the sampling level. (B) Spatial distribution of the 51 sampled sites, with significance of the regional and local interaction networks color-coded.

species distribution—since communities close to each other tend to have related hosts and parasites—these results show that it is also rather poor predictor of the way in which these species ultimately interact.

Interactions also ultimately differ in how frequently they vary when the species involved are co-occurring [16]. The literature on host-parasite interactions usually assumes that some interactions are more frequent because they reflect a significant past history of coevolution [17,18]. Should this be the case, the correlation between the probability of observing an interaction and the importance of that interaction for coevolution at the continental scale should be positive and significant. Surprisingly, we find that neither is true here (Fig. 3). Interactions that are important to coevolution are not more conserved.

Nonetheless, interactions that persisted at the local scale should retain their signal of contribution to coevolution, because they involve species at matching positions in the phylogenetic trees. We find that interactions that contribute strongly to coevolutionary signal at the continental scale *also* contribute strongly at the local scale (Fig. 4). Remarkably, this result implies that coevolution is still detectable in individual *interactions* even though it does not leave its imprint on most local networks.

Overall, the results of our analyses demonstrate that our current understanding of coevolution as the basis of multi-species interactions scales rather poorly to ecological questions. Although phylogenetic structure and interactions are largely congruent at the continental scale, community structure is primarily driven by ecological, and not evolutionary, constraints. This conclusion is supported by our observations that (i) local networks show no signal of coevolution and (ii) the strength of coevolution between two species does not predict how frequently they interact. Yet, individual interactions retained their coevolutionary signal whereas the community they are weaved into did
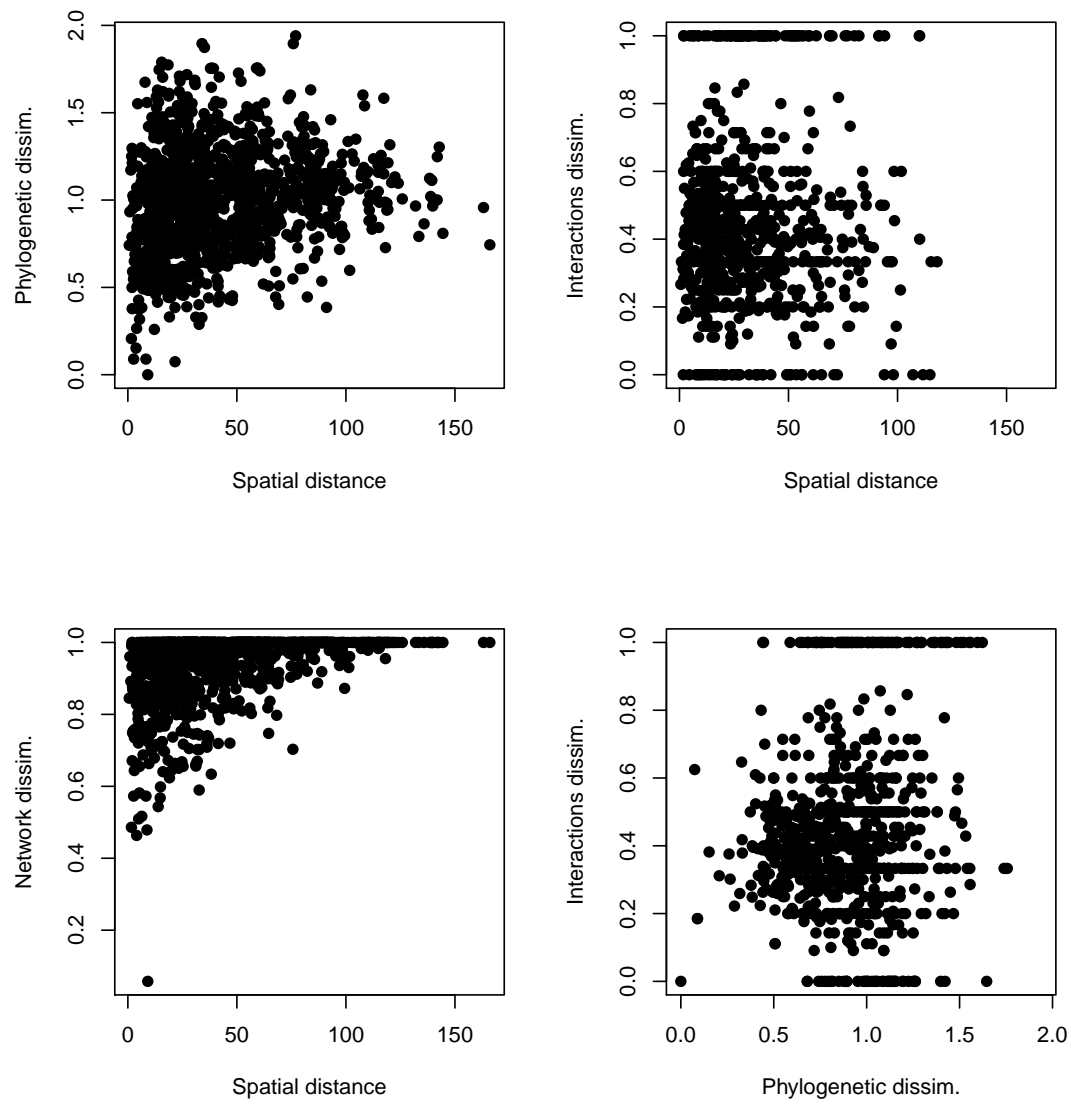
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Figure 2: Relationships between spatial distance, phylogenetic dissimilarity, and the dissimilarity of interactions at the local and regional scales. (*temp.*)
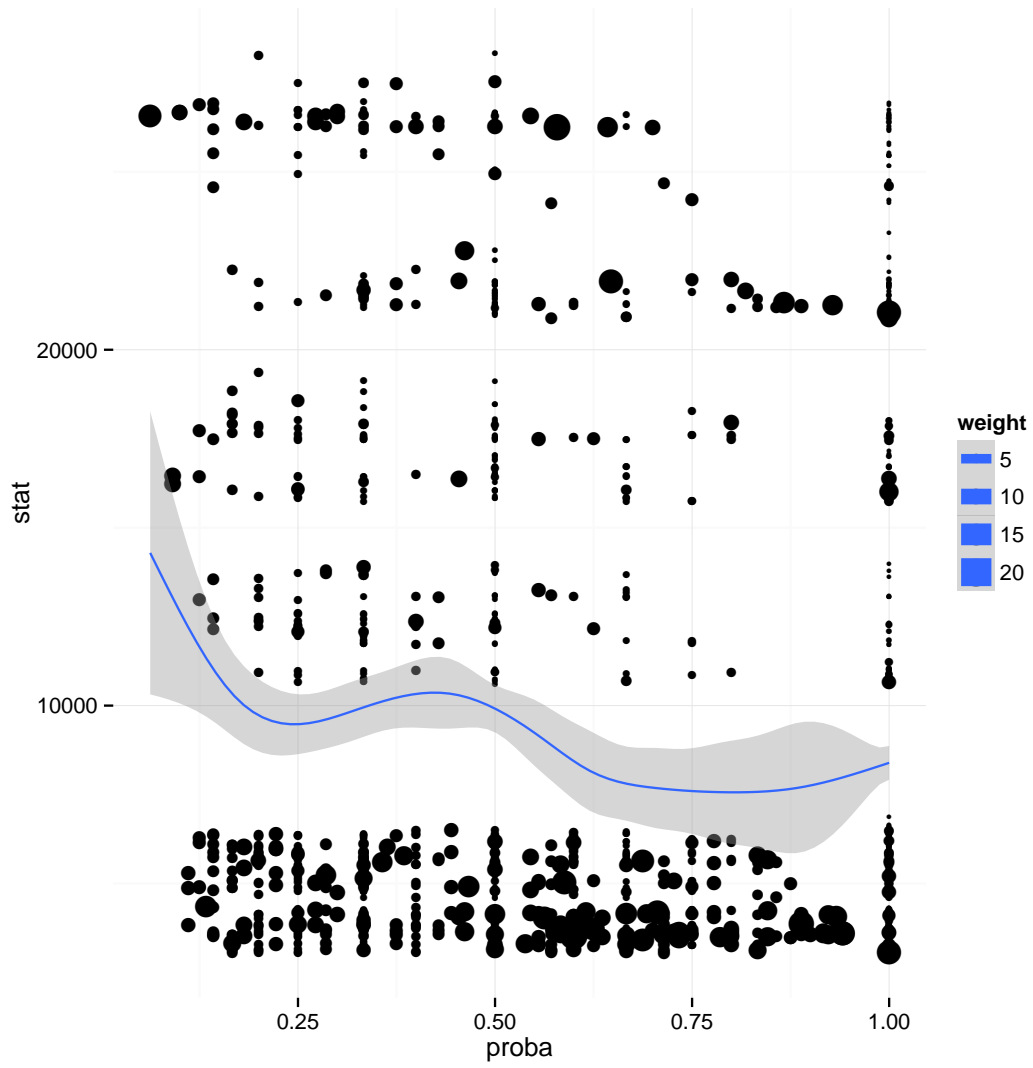
Figure 3: Lack of relationship between the probability of observing an interaction, and its contribution to coevolution in the continental network. Each interaction is weighted by the number of times the two species involved have been observed together. (*temp.*)
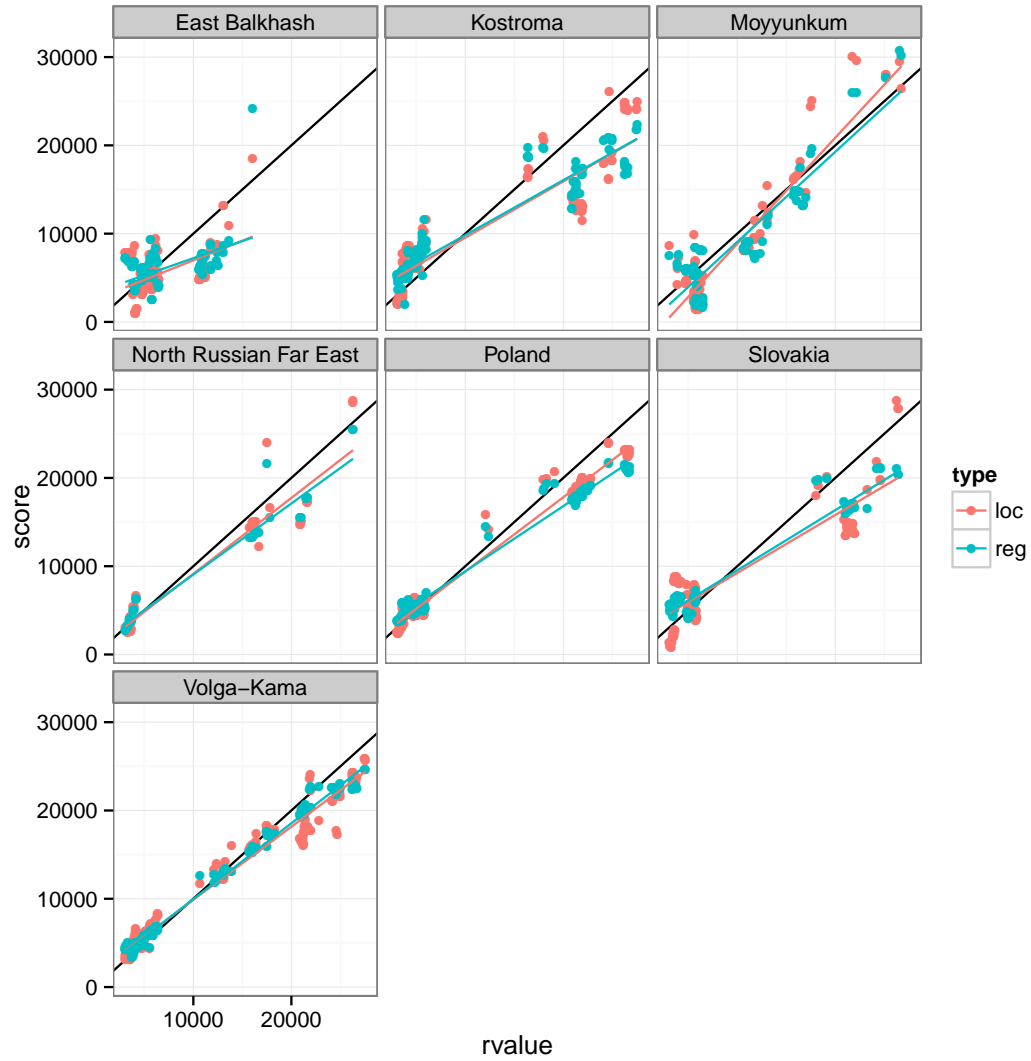
Figure 4: Relationship between continental and regional contribution to coevolution (*temp.*).

¹ not. Above all else and contrary to the oft-repeated point that coevolution should explain

² the local structure of interactions [19], our results suggest that local network structure is

³ far more likely to affect coevolution than the other way around.

Methods

Data – We study data on observations of interactions between 121 species of rodents and

205 species of parasitic fleas in 51 locations across Europe [13] to build 51 species-species

interaction networks. Interactions were measured within a 50 km radius around each

point reported in Fig. 1, by combing rodents for fleas. This method gives high quality

data, are it has a very high power to detect even rare interactions. To account for differ-

ential sampling effort, we converted all of the quantitative data in binary one, so that our

networks describe the presence and absence of interactions. We also aggregated these

51 networks in order to describe the continental "metanetwork" that therefore includes

all potential interactions between co-occurring species [11]. We define threes scales in the

data. The *continental* scale is the aggregated metanetwork, *i.e.* all species and all their

interactions. Within each site, the *regional* scale is the list of observed species, and all

their possible interactions. The regional networks is a perfect subset of the metanetwork;

the *local* scale is the interactions that were actually observed in the field at a given site.

Local and regional scales have the same species, but local has only a subset (or at most

an exact match) of the interactions in the regional level.

Community phylogenetics – The phylogenetic trees for hosts and parasites, published

alongside the original network data, were rendered ultrametric. We quantified the de-

gree of matching between host and parasite phylogenies given knowledge of species in-

teractions using the *PACO* method [20]. *PACO* provides measures of both the network-level congruence (*i.e.*, is the network coevolved?) and the interaction-level signal (*i.e.*, what is the contribution of each interaction to the overall coevolutionary signal?). For each local network, we measure the strength of coevolution using (i) local observations only and (ii) all possible interactions between locally co-occurring species (based on the interactions found in the regional metanetwork). Testing both of these networks allows us to separate the effect of species sorting (regional) and interaction sorting (local). We quantified the phylogenetic dissimilarity between two sites for hosts and parasites using PCD [21]: this measure accounts for the dissimilarity of species, corrected for the phylogenetic distance between all species in the dataset.

Interactions dissimilarity – We used the network β-diversity approach [11] to measure the dissimilarity of interactions across sites. We specifically measured the dissimilarity of the *regional* and *local* networks. We built a probabilistic model of the occurrence of each interaction based on the following rule: the probability that an interaction is observed is the number of times it is observed across all sites, divided by the number of sites in which the two species co-occur.

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