

# Coevolutionary structure is observable in interactions, not in communities

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1 Coevolutionary dynamics act on both species and their interactions  
2 to drive the structure of ecological communities. It remains unclear,  
3 however, how the structure of communities at larger spatial scales ei-  
4 ther influences or is influenced by local coevolutionary processes, and  
5 how mechanisms acting at different scales feedback into one another.  
6 The structure of ecological interactions determine how these feedbacks  
7 are distributed among species of a community. Here we show that,  
8 though species interactions vary substantially over a continental gradi-  
9 ent, the coevolutionary significance of individual interactions is main-  
10 tained across different scales. Notably, this also occurs despite the fact  
11 that community variation at the local scale tends to weaken or remove  
12 community-wide coevolutionary signal. When considered in terms of  
13 the interplay between coevolutionary theory and community ecology,  
14 our results demonstrate that individual interactions are locally rele-  
15 vant whereas the emerging structure of these interactions across many  
16 species only becomes relevant at regional scales.

1 Ecological interactions exert selective pressures on the species involved; for ex-  
2 ample, lodgepole pines and red crossbills phenologies respond spatially to the  
3 presence of squirrels <sup>1</sup> and palm species undergo changes in seed morphology in  
4 response to the extinction of bird dispersing their seeds <sup>2</sup>. Most of these interac-  
5 tions are long-standing from a macroevolutionary point of view <sup>3</sup>, explaining why  
6 the way that interactions are distributed is so similar across communities, either  
7 at the large <sup>4</sup> or small <sup>5</sup> scale. This suggests that large and small scale structure  
8 results from evolutionary dynamics of species. Although the evolutionary dynam-  
9 ics of interacting species pairs has been well described <sup>6</sup>, attempts to understand  
10 how these cascade up to generate the tremendous diversity of both species and  
11 interactions found within empirical communities have been inconclusive <sup>7</sup>.

12 Historically, coevolution in taxonomically diverse communities is quantified as the  
13 matching between the phylogenies of two sets of interacting organisms <sup>8</sup>. This no-  
14 tion builds on the century-old idea that extant species interact in a way similar  
15 to the way their ancestors did <sup>9</sup>. More explicitly, it is thought that communities  
16 that assembled through coevolution should (i) have similar phylogenetic trees and  
17 (ii) species at matching positions in either trees should interact. It is not clear,  
18 however, how this idea holds when confronted with dynamics occurring at smaller  
19 scales: indeed, many ecological and evolutionary processes that occur locally are  
20 expected to blur the phylogenetic signal <sup>10</sup>. One possible reason is that inter-  
21 actions can display substantial turnover, at ecologically relevant temporal and  
22 spatial scales <sup>11</sup>: the same two species can interact in different ways under the ef-  
23 fect of local environmental contingencies, spatial mismatch in species phenologies,  
24 variations in population abundances, and chance events <sup>12</sup>. This suggests that the  
25 impact of deep evolutionary history on community structure can be lessened by

1 the action of ecological mechanisms at the local scale. To adress this question, we  
2 study a dataset of rodent and their ectoparasites from Western to Eastern Europe  
3 <sup>13</sup>. This dataset is uniquely suited for this task, as it offers an unprecedented  
4 spatial replication at a scale large enough to capture macro-ecological processes.  
5 In addition, host-macroparasite associations are expected to be driven by macro-  
6 evolution and co-speciation events. This dataset also exhibits spatial variation in  
7 interactions across different localities.

8 If ecological mechanisms do reduce evolutionary signal, we should detect coevolu-  
9 tion at the continental scale but not locally. Phylogenetic congruence is strong at  
10 the continental level <sup>14</sup> ( $p \leq 10^{-4}$ ), which offers the baseline for the expected level  
11 of congruence in local communities. Because variation of interactions can decrease  
12 congruence, we analyse the local data at two different levels (see methods): using  
13 the *regional* interaction data, which accounts for species sorting only, and the *local*  
14 interaction data, which corresponds to the actual observations (species and inter-  
15 actions sorting). Out of 51 local networks, 35 show no signal of coevolution, 11  
16 show coevolution when using the regional interactions, and 12 show coevolution  
17 using the local interactions (see *Supp. Mat. 1* for network-level significance val-  
18 ues). This suggests that macro-evolutionary processes such as co-diversification  
19 have consequences at the macro-ecological level <sup>15</sup>, but may not in fact be de-  
20 tectable at fine spatial scales.

21 The fact that the signal of coevolution is lessened at the local level implies that  
22 species at matching positions in their phylogenetic trees do not always interact.  
23 One possible explanation is that the variation of species interactions is not related  
24 to the species phylogenetic relatedness across different communities. In this sys-

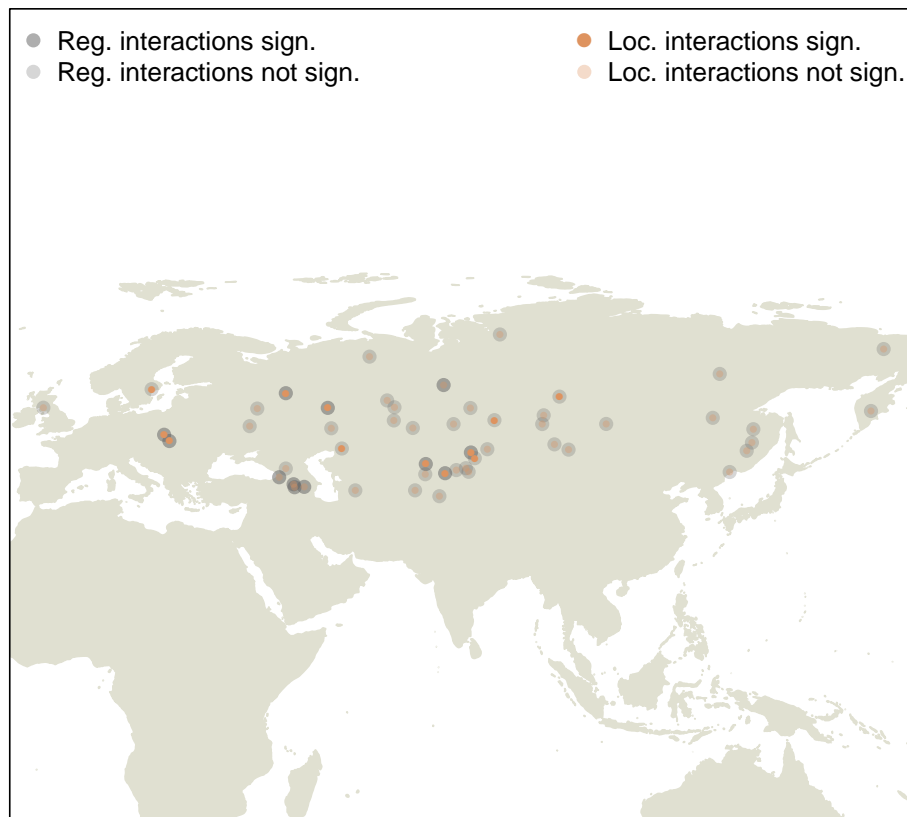


Figure 1: Spatial distribution of the 51 sampled sites, with significance of the regional and local interaction networks color-coded.

1 tem, communities farther apart had different species (*Suppl. Mat. 2*), but once  
2 the phylogenetic relatedness between species is accounted for, there is no rela-  
3 tionship between spatial distance and species dissimilarity (Fig. 2A). This is not  
4 surprising, given that species from this dataset are phylogenetically related, and  
5 widespread across the spatial extent. While distant networks are more dissimi-  
6 lar, the way shared species interact within them is independent of spatial distance  
7 (Fig. 2B). The same trend exists for community dissimilarity as a function of  
8 (cumulative) phylogenetic dissimilarity of hosts and parasites (Fig. 2C). These  
9 results point to the fact that interactions do not vary in a way that is driven by  
10 evolutionary mechanisms or history.

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

19 Nonetheless, interactions that are observed at the local scale should retain their  
20 signal of contribution to coevolution, because they involve species at matching po-  
21 sitions in the phylogenetic trees. Indeed, we find that interactions that contribute  
22 strongly to coevolutionary signal at the continental scale *also* contribute strongly  
23 at the local scale (Fig. 4). Remarkably, this result implies that coevolution is still  
24 detectable in individual *interactions* even though it does not leave its imprint on

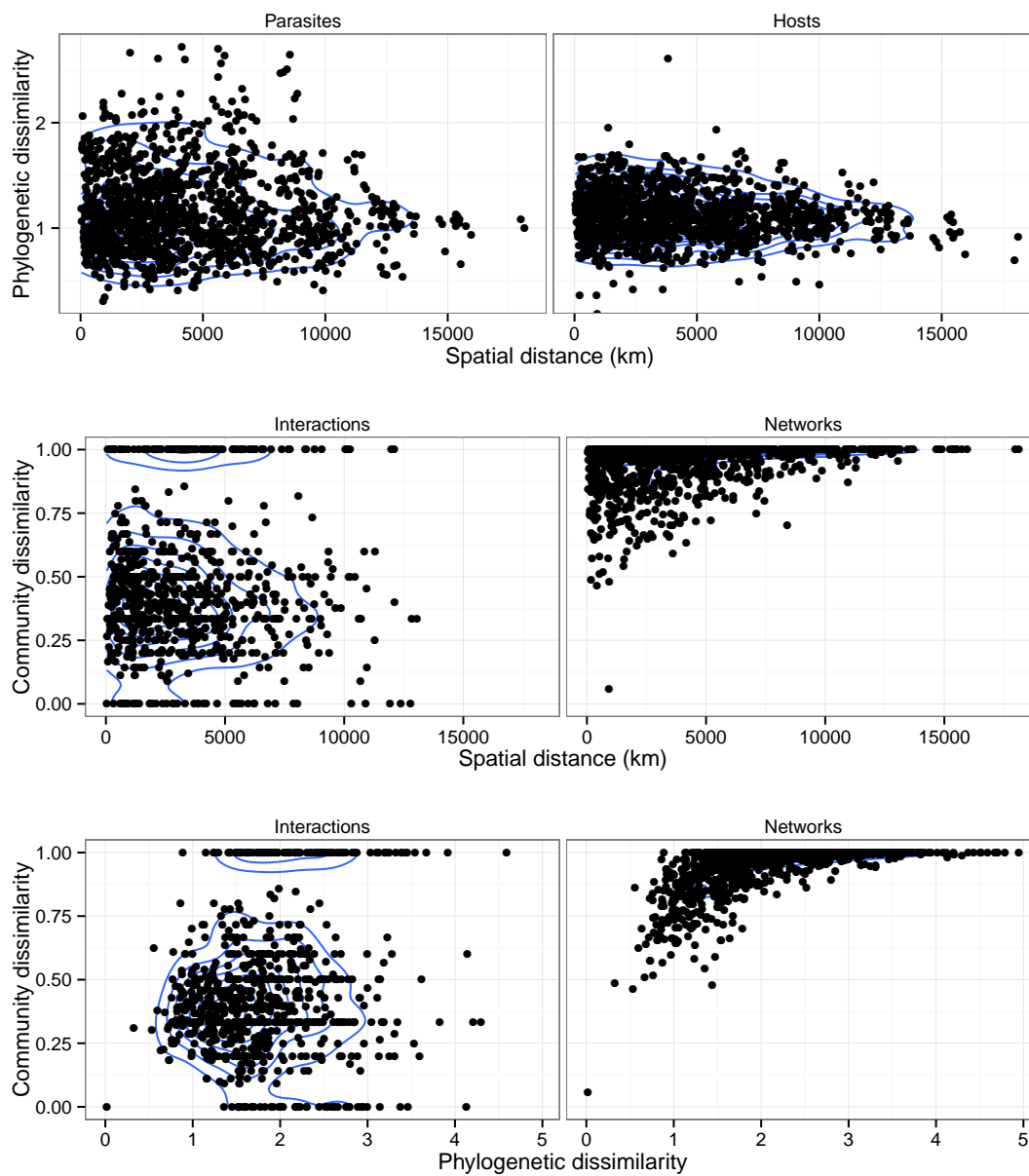


Figure 2: Relationships between spatial distance, phylogenetic dissimilarity, and the dissimilarity of interactions.

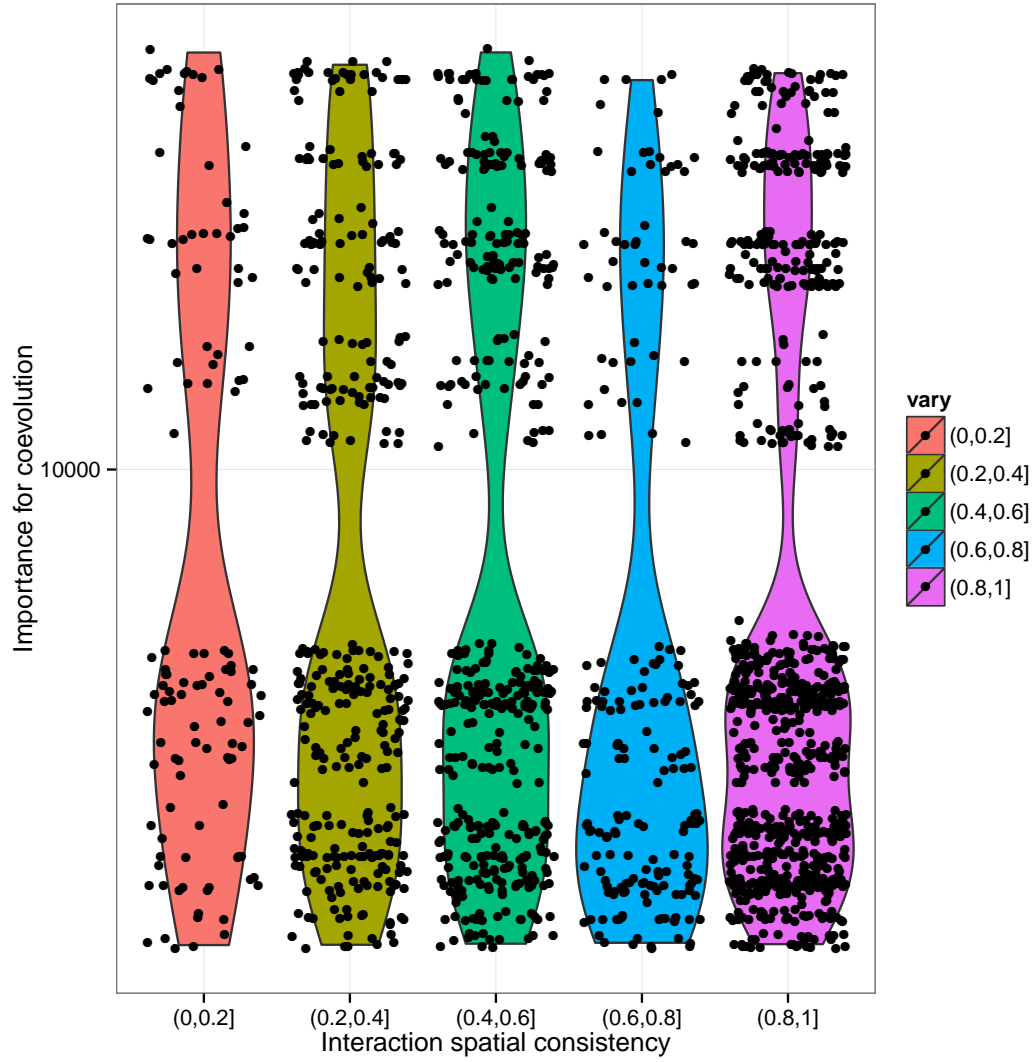


Figure 3: Lack of relationship between the probability of observing an interaction, and its contribution to coevolution in the continental network. Each interaction is weighted by the number of times the two species involved have been observed together. (*temp.*)

1 most local networks.

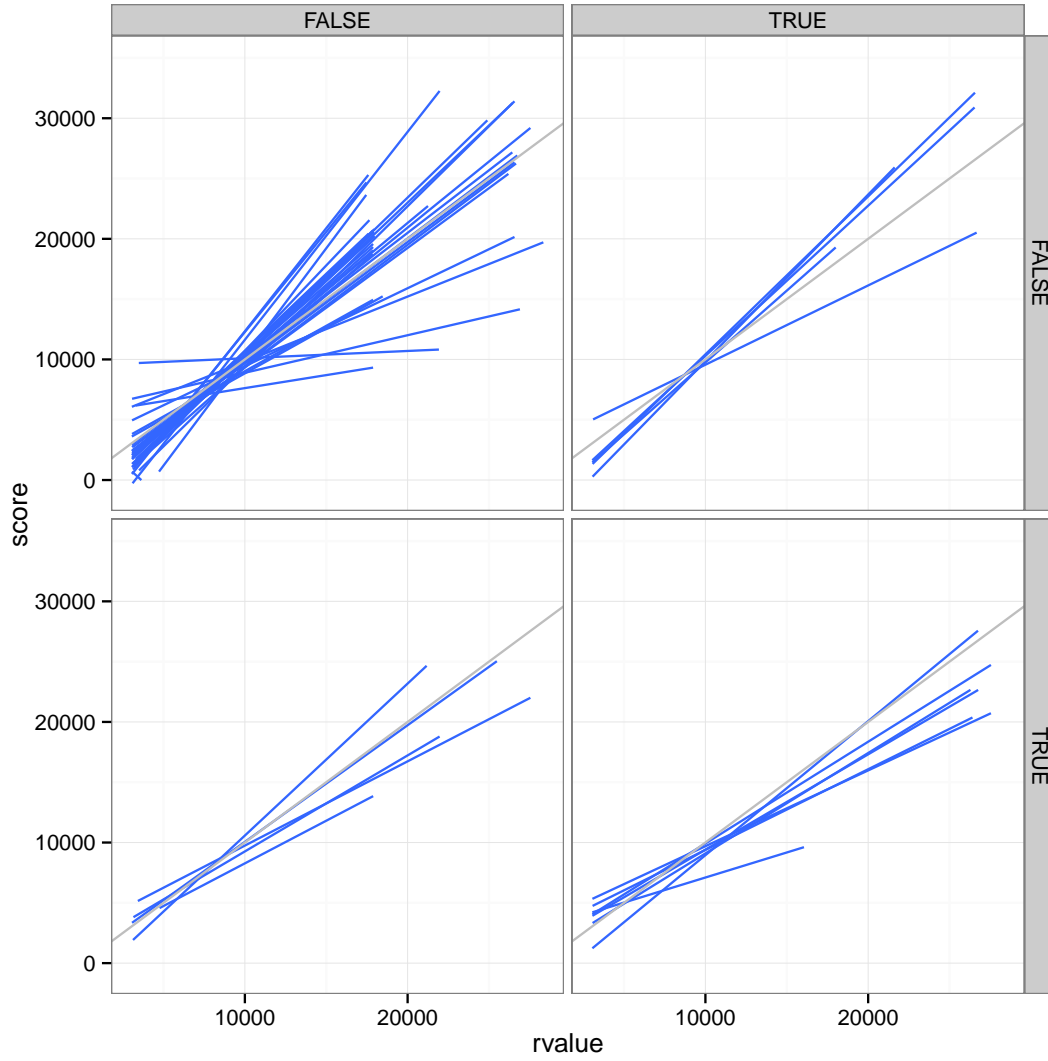


Figure 4: Relationship between continental and regional contribution to coevolution (*temp.*).

2 Overall, the results of our analyses demonstrate that our current understanding  
 3 of coevolution as the basis of multi-species interactions scales rather poorly to  
 4 ecological questions. Although phylogenetic structure and interactions are largely  
 5 congruent at the continental scale, community structure is primarily driven by



1 ecological, and not evolutionary, constraints. This conclusion is supported by  
2 our observations that (i) local networks show no signal of coevolution and (ii)  
3 the strength of coevolution between two species does not predict how frequently  
4 they interact. Yet, individual interactions retained their coevolutionary signal  
5 whereas the community they are weaved into did not. This results calls to our  
6 attention the fact that, even though the community structure might not be driven  
7 entirely by evolutionary constraints, a subset of interactions are indicative of past  
8 coevolution. Above all else and contrary to the oft-repeated point that coevolution  
9 should explain the local structure of interactions <sup>18</sup>, our results suggest that local  
10 network structure is far more likely to affect coevolution than the other way  
11 around.

## 12 **Methods**

13 **Data** — We study data on observations of interactions between 121 species of  
14 rodents and 205 species of parasitic fleas in 51 locations across Europe <sup>13</sup> to build  
15 51 species-species interaction networks. Interactions were measured by combing  
16 rodents for fleas; this method gives high quality data, as it has a high power of  
17 detection. To account for differential sampling effort and across site variations  
18 in abundance, we only consider the networks incidence matrices (presence and  
19 absence of interactions). We aggregated these 51 networks in order to describe  
20 the continental “metanetwork” that therefore includes all potential interactions  
21 between co-occurring species <sup>11</sup>. We define three scales in the network data.  
22 The *continental* scale is the aggregated metanetwork, *i.e.*, all species and all their  
23 interactions. Within each site, the *regional* scale is the list of observed species,

1 and all their possible interactions. Note that the regional networks are always a  
2 perfect subset of the metanetwork. The *local* scale is the interactions that were  
3 actually observed in the field at a given site. Therefore, the local and regional  
4 networks have the same species, but the local network has only a subset (or, at  
5 most, an exact match) of the interactions at the regional level.

6 **Community phylogenetics** – The phylogenetic trees for hosts and parasites,  
7 published alongside the original network data, were rendered ultrametric (all  
8 species are at the same distances from the root; this is a requirement of the  
9 methods used). We quantified the degree of matching between host and para-  
10 site phylogenies given knowledge of species interactions using the *PACO* method  
11 <sup>19</sup>, which is robust to variations in number of species. *PACO* provides measures  
12 of both the network-level congruence (*i.e.*, is the network coevolved?) and the  
13 interaction-level signal (*i.e.*, what is the contribution of each interaction to the  
14 overall coevolutionary signal?). For each site, we measure the strength of coevo-  
15 lution twice, using the local and regional networks. Testing both allows us to  
16 separate the effect of species sorting (regional) and interaction sorting (local). We  
17 quantified the phylogenetic dissimilarity between two sites for hosts and parasites  
18 using PCD <sup>20</sup>: this measure accounts for the dissimilarity of species, corrected for  
19 the phylogenetic distance between all species in the dataset.

20 **Interactions dissimilarity** – We used the network  $\beta$ -diversity approach <sup>11</sup> to  
21 measure the dissimilarity of interactions across sites. As with the strength of  
22 coevolution, we measured the dissimilarity of the *local* and *regional* networks. We  
23 measured the spatial consistency of an interaction as the number of times it is  
24 observed across all sites, divided by the number of sites in which the two species

1 co-occur.

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3 dinates of sites, and Juan Antonio Balbuena for discussions about the *PACo*  
4 method.

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