Coevolution acts on interactions but not on communities

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Coevolutionary dynamics act on both species and their interactions to drive the structure of ecological communities. It remains unclear, however, how the structure of communities at larger spatial scales either influences or is influenced by local coevolutionary processes, and how mechanisms acting at different scales feedback into one another. Most of these feedbacks are mediated by the structure of ecological interactions, *i.e.* how they are distributed within communities. Here we show that, though species interactions vary substantially over a continental gradient, the coevolutionary significance of individual interactions is maintained across different scales. Intriguingly, this also occurs despite the fact that community variation at the local scale tends to weaken or remove community-wide coevolutionary signal. When considered in terms of the interplay between coevolutionary theory and community ecology, our results demonstrate that individual interactions are locally relevant whereas the emerging structure of these interactions across many species only becomes relevant at regional scales.

Ecological interactions exert selective pressures on the species involved; for example, lodgepole pines and red crossbills phenologies respond spatially to the presence of squirrels [1] and palm species undergo changes in seed morphology in response to the extinction 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 similarly 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 matching 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 ancestors 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 dynamics 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 community ecology, we study data a dataset of rodent ectoparasites from Western to Eastern Europe [13]. . . . to test the following four hypotheses. First, local (observed) networks do not show evidence of coevolution, whereas the continental-scale (henceforth regional) system does. Second, the spatial variation of species interactions is independent from the variation in phylogenetic diversity. Third, interactions are distributed spatially in a way that is independent from their evolutionary history. Finally, the contribution of interactions to coevolution is similar at the local and regional scale.

Consistent with previous studies of this system [14], we found that coevolutionary signal at the regional scale is extremely strong ($p \leq 10^{-4}$), as established by previous analysis of this system [14]. Most local networks, on the other hand, show very little evidence of phylogenetic congruence (Fig. 1). Out of 51 local networks, 35 show no signal of coevolution, 11 show coevolution when using the regional interactions, and 12 show coevolution using the local interactions (see *Supp. Mat. 1* for network-level significance values). This suggests that macro-evolutionary processes such as co-diversification have consequences at the macro-ecological level [15], but may not in fact be detectable at finer spatial scales due to a stronger local effect of ecological processes.

This implies that the variation of species interactions is not tied to the phylogenetic relatedness of species across space. In this system, the phylogenetic similarity of both hosts and parasites decays with increasing distance (Fig. 2A), and we observe the same for the *total* network dissimilarity (*i.e.* species and interaction variation, Fig. 2B). In contrast, when we control for the effect of species variation, we find that the similarity of interactions is independent of both spatial distance (Fig. 2C) and host or parasite phylogenetic dissimilarity (Fig. 2D). Therefore, while evolutionary history is tightly linked to 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.

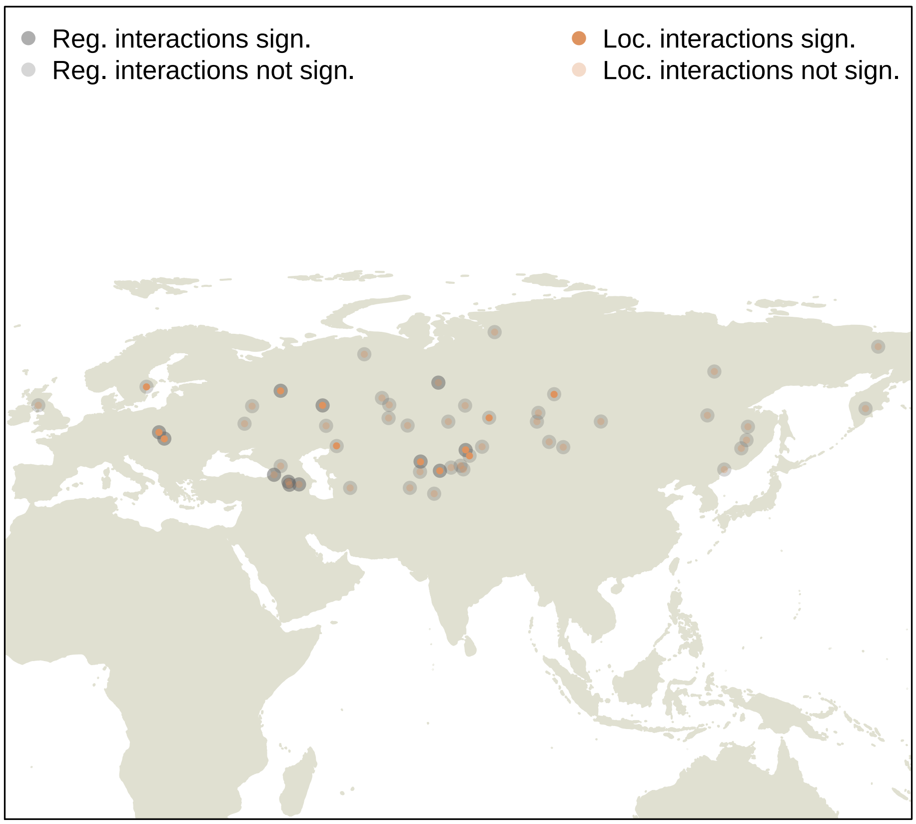

Figure 1: figure1

Ecological interactions vary only insofar that there are some locations in which they *do not* happen – yet some interactions happen more consistently than others. The literature on host-parasite interactions usually assumes that some interactions are more frequent because they reflect a significant past history of coevolution [16,17]. 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). The fact that an interaction is commonly observed does not reflect past co-evolution, but is most likely explained by local ecological factors: example mechanisms would be co-distribution of species in environments in which they can interact [18], positive covariance of traits and environmental features, or random selection of partners by species with a wide range of possible interactions [19].

We finally evaluate whether individual interactions contribute equally to coevolutionary signal in the locals and continental network. An interaction between two species at matching positions in the two phylogenetic trees should contribute positively to coevolution, regardless of the overall score of the community. We find that this is indeed the case: 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. This is in line with recent results that established that, although networks are composed of interactions, both objects seem to have uncoupled behaviors [20].

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. Above all else and contrary to the oft-repeated point that coevolution should explain the local structure of interactions [21], our results suggest that local network structure is far more likely to affect coevolution than the other way around.

Methods

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. We also aggregated thse 51 networks in order to describe the regional "metanetwork" that therefore includes all potential interactions between co-occurring species [11]. The phylogenetic trese for hosts and parasites were rendered ultrametric.

We quantified the degree of matching between host and parasite phylogenies given knowledge of species interactions using the *PACO* method [22]. *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-occuring 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 interactions) and interaction sorting (local interactions).

We quantified the phylogenetic distance between two locations for hosts and parasites using PCD [23]: this measure accounts for the dissimilarity of species, corrected for the phylogenetic distance between all species in the dataset.

Acknowledgments

Bah!

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