Coevolution is detected regionally but not locally in ecological 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. Despite this, ecological networks are known to have a structure that is coherent with evolutionary processes, which suggest that coevolution may play a role in determining their extent organisation. Here we show that even though species interaction vary substantially over a continental gradient, the coevolutionary significance of individual interactions is maintained at different scales. This occurs despite the fact that community variation at the local scale tends to weaken or remove community-wide coevolutionary signal. We provide a new perspective on the interplay between coevolutionary theory and community ecology, by establishing the organisational scales at which the different theories have relevance: interactions are relevant locally, whereas overall community structure is relevant regionally. Although it has been tempting so far to understand how coevolution relates to network structure, our results

suggest that the way forward is to understand how network structure may affect coevolution over space instead.

Ecological interactions introduce 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 disperser birds [???]. When taxonomically diverse species are considered at once, groups of interacting species are delineated by evolutionary boundaries [2], invariant structures in the distribution of interactions appear [3], and conservatism of both the distribution of community modules [4] and the role of species occupy within them [5] becomes evident. Although the evolutionary dynamics in interacting species pairs has been well described [6,7], 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 [8].

In multi-species systems that typically span a large taxonomic range, coevolution is often measured as the matching between the phylogenies of two sets of interacting organisms [9,10]. This build on the century-old ideas that extant species interact in a way similar to the way their ancestors did [11]. "Coevolved" systems 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 relates to dynamics occurring at smaller scales [12]: many ecological and evolutionary processes that occur locally are expected to blur the phylogenetic signal. The spatial scales at which the different mechanisms involved are mostly incommensurable: coevolution is expressed within patches connected by gene-flow [13,14], whereas the species diversity of complex networks is typically observed at spatial scales matching the species distribution [15,16].

Species interaction networks have a structure which is in part driven by evolutionary mechanisms, both micro [3,17] and macro [2,18]. Yet it has recently been demonstrated that ecological interactions display important turnover over time and space [19]: the structure of networks made of the same species is expected to change from one location to the other, under the effect of local environmental contingencies, spatial mis-match in species phenologies, variations in population abundances, and chance events [20]. As a consequence, *locally*, the evolutionary signal on network structure is expected to be buried under much ecological noise, and the effect of coevolution can only be inferred *regionally* – to the point where we must now ask if deep evolutionary history matters at all at the scale where the structure of ecological networks is relevant to ecological properties.

We use data on ectoparasites of rodents from Western to Eastern Europe [21] 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.

At the regional scale, coevolutionary signal is extremely strong ($p \leq 10^{-4}$), as established by previous analysis of this system [22]. 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 [23], but may not be detected at finer spatial scales due to a stronger effect of ecological processes locally.

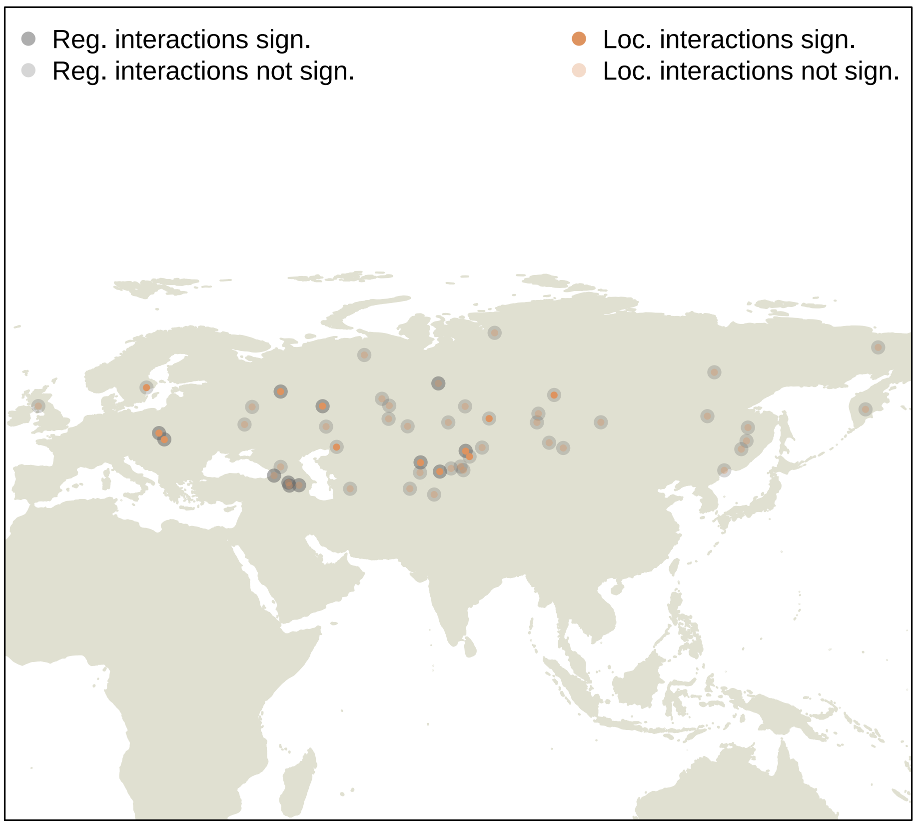

Figure 1: figure1

This of course implies that the variation of species interactions is not tied to the phylogenetic relatedness of species across space. Both hosts and parasites show a distance decay of phylogenetic similarity (Fig. 2A), which we also observe for the *total* network dissimilarity (*i.e.* species and interaction variation, Fig. 2B). However when the effect of species variation is removed, the similarity of interactions shows no correlation to either spatial distance (Fig. 2C) or host or parasite phylogenetic dissimilarity (Fig. 2D). These result show that although evolutionary history ties into species distribution (because communities close in space tend to have related hosts and parasites), it is a poor predictor of the way these species will interact.

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 interaction usually assumes that some interactions are frequent because they reflect a significant past history of coevolution [24,25]. Should it be the case, the correlation between how frequently an interaction is (the number of times it is observed, divided by the number of time the two species co-occurred) and the importance of this interaction for coevolution (at the continental scale) is expected to be significant and positive. We find that it is neither (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 [26], positive covariance of traits and environmental features, or random selection of partners by species with a wide range of possible interactions [27].

we expect that the overall contribution of interactions will be the same in the local and regional networks. For the 5 networks that show evidences of coevolution accounting both for species and interactions sorting, we measured the contribution of each interaction locally, and compared it to its contribution to the regional network. Results are presented in **FIG. one-sentence summary**. This is a key result, as it establishes that although coevolution does not leave an imprint on local networks, it is still detectable in *interactions*. This is in line with recent results that established that, although networks are composed of interactions, both objects seem to have uncoupled behaviors [28].

Species interactions vary in a way that is independent from species distribution [19]. One possible explanation is that species that have a strong (coevolutionary) relationship would either co-distribute more, or interact more frequently when they co-occur. Should it be true, we would expect that *coevolved species pairs*, or in other words, species involved in an interaction contributing strongly to the community-wide coevolution, should be interacting frequently [29]. This would result in a positive association between the frequency of the interaction (the number of observations of a particular interaction divided by the number of observations of the tow species together), and its overall importance for coevolution (here measured in the *regional* network). As we report in **FIGURE**, we do not find this relationship – how strongly an interaction contributes to overall coevolution does not predict how frequently it will be realized when the two species are put together.

Our results, 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, fall when in line with recent conclusions about the spatial dynamics of species interactions. Species interactions vary according to ecological mechanisms [20]: local population abundance [30], local mis-matches of phenologies [31], local micro-environmental conditions [32]. And even though network composition varies, the overall network *structure* remains constant over time [33], suggesting either (i) higher-order constraints or (ii) replacement of species by functionally equivalents from the regional pool.

These result show that our current understanding of coevolution in multi-species interactions does not scale well to ecological questions – although phylogenetic structure and interaction show a strong agreement at the regional scale, the structure of local communities remains largely driven by ecological constraints. The analysis of ecological networks has often focused on emerging properties [34] rather than on the building blocks of the networks, that is species and interactions. Contrary to the often-argued point that coevolution should explain the local structure of interactions [35], our result suggests that given the high variance in local interactions, coupled with the lack of relationship between coevolution and interaction frequency, local network structure is more likely to affect coevolution than the other way around.

Methods

We use data on observations of interactions between 121 species of rodents and 205 species of parasitic fleas in 51 localities in Europe [21]. Individual interactions are aggregated to yield species interaction networks. All 51 networks (one per locality) are aggregated in a regional metanetwork [19]. The phylogenetic tree for hosts and parasites were rendered ultrametric.

The matching between host and parasite phylogenies knowing the species interactions is measured using the *PACO* method [36]: *PACO* measures 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 coevolution signal). For each local network, we measure the strength of coevolution using (i) only local observations and (ii) all possible interactions between local species (as known from the regional aggregation of all local networks). This allows us to separate the effect of species sorting (regional interactions) and interaction sorting (local interactions).

Phylogenetic distance between two localities is measured for hosts and parasites using PCD [37]: this measure accounts for the dissimilarity of species, corrected for the phylogenetic distance between all species in the dataset.

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