Coevolution is detected regionally but not locally in ecological communities

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Coevolutionary dynamics acting on both species and their interactions are a key driving force behind the structure of ecological communities. The Geographic Mosaic Theory of Coevolution (GMTC) provides a spatial perspective to these dynamics by proposing the existence of feedbacks between local and regional scales. It remains unclear, however, how the structure of communities at larger spatial scales either influences or is influenced by local coevolutionary processes. Despite this, ecological networks are known to have an ecological structure, which suggest that coevolution may play a role in their evolutionary dynamics. Here we show that the coevolutionary significance of individual interactions is maintained when moving between the local and regional scale. Importantly, this occurs despite the fact that community variation at the local scale tends to weaken or remove community-wide coevolutionary signal. This apparent mismatch between our interaction-level and community-level results strongly suggests that interactions provide the correct scale to study coevolution at small spatial scales while communities are the relevant scale only at larger spatial extents. We provide a new perspective on the interplay between coevolu-

tionary theory and community ecology, by establishing the organisational scales at which the different theories have relevance. 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. At large organisational scales, this results in taxonomic boundaries delineating groups of interacting species [1], invariant structures in some ecological communities [2], and conservatism of both the distribution of community modules [4] and the role of species occupy within them [5]. Although the evolutionary dynamics for a pair of interacting species has been well described [6], attempts to understand how these mechanisms cascade up to generate species diversity observed in large ecological networks have been inconclusive [7,8], despite the well known effect of antagonistic coevolution on genomic diversification [9,10]. The scales at which these diversities happen are hard to reconcile: coevolution is expressed within patches connected by gene-flow [11–13], whereas the species diversity of complex networks is typically observed at spatial scales matching the species distribution [14,15]. Because these scales differ by orders of magnitude, one must question the relevance of previous calls to scale the theory on coevolution up to multi-species systems covering large spatial extents [16].

Network-based approaches [17,18], on the other hand, were designed to study and describe species-rich systems. Previous empirical findings revealed the impact of evolutionary dynamics on overall network structure in food webs [1,19], pollination networks [20,21], and host-parasite networks [22,23]. Both micro [3,24] and macro [25,26] evolutionary dynamics have been measured or modelled in species-rich communities, but there is no understanding of how, or even of whether, local/micro-evolutionary and regional/macro-evolutionary feedback into one another. Another layer of complexity is that ecological networks are known to vary in their structure over time and space [27]: the same two species will not interact in a consistent way locally, either because of local environmental contingencies, by chance, or because their phenologies do not positively covary in space [28]. 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*.

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 [22,29]. This build on the century-old ideas that extant species interact in a way similar to the way their ancestors did [30]. "Coevolved" systems should (i) have approximately 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 [31]: many ecological and evolutionary processes that occur locally, or over small spatial scales, can disturb this expected structure. Notably, it has been shown that species interactions are not consistent through space [27,32]. Local loss of both interactions and species from the regional pool is most likely to result in observed communities that do not appear to have been shaped by coevolution.

We use data on ectoparasites of rodents from Western to Eastern Europe [33] to test the following four hypotheses. First, local species assemblages do not show evidence of coevolution even though the system has a whole does. Second, interaction-level coevolutionary signal is conserved. Third, interaction-level coevolutionary signal does not predict the spatial consistency of interactions. We do so by coupling two novel methods: the *PACO* algorithm for detection of phylogenetic congruence [34], and a general framework for the variation of ecological networks [32].

Local observations on the 51 localities (*Supp. Mat. 1*) are aggregated into a regional metanetwork [32], and the two phylogenetic trees have been rendered ultrametric (see Suppl. Methods). We use *PACO* [34] to measure the congruence between trees knowing the interactions. *PACO* yields a network-level significance value for the likelihood that hosts and parasites have coevolved. 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). At the regional scale, coevolutionary signal is extremely strong ($p \leq 10^{-4}$), as established by previous analysis of this system [35]. Most local networks, on the other hand, show very little evidence of phylogenetic congruence. 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). **Figure?**.

This suggests that macro-evolutionary processes (such as co-diversification) have consequences at the macro-ecological level [36], but may not be detected at finer spatial scales due to a stronger effect of ecological processes locally. *PACO* permits the analysis of *how strongly* each interaction contribute to coevolution, in a way that is as independent as possible from other interactions. As interactions vary only insofar that there are some locations in which they *do not* happen, we expect that the overall contribution of interactions will be the same in the local and regional networks.

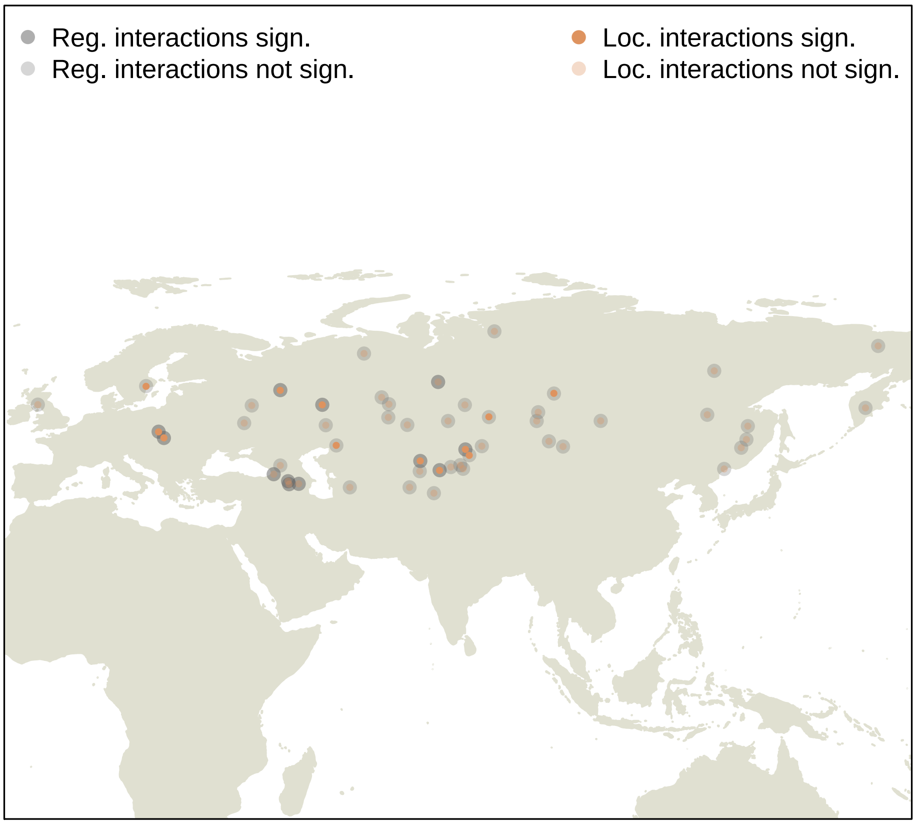

Figure 1: figure1

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 [37].

Species interactions vary in a way that is independent from species distribution [32]. 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 [38]. 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 [27]: local population abundance [39], local mis-matches of phenologies [40], local micro-environmental conditions [41]. And even though network composition varies, the overall network *structure* remains constant over time [42], 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 [43] 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 [44], 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.

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