Coevolution leaves a stronger imprint on interactions than on community structure

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Abstract: Coevolutionary dynamics act on both species and their interactions in ways that shape ecological communities. It remains unclear, however, how the structure of communities at larger spatial scales influences or is influenced by local coevolutionary processes, and how mechanisms acting at these different scales feedback onto one another. Here we show that, although species interactions vary substantially over a continental gradient, the coevolutionary significance of individual interactions is maintained across different scales. Notably, this occurs despite the fact that observed community variation at the local scale frequently tends to weaken or remove community-wide coevolutionary signal. When considered in terms of the interplay between community ecology and coevolutionary theory, our results demonstrate that individual interactions are capable and likely to show a consistent signature of past coevolution even when woven into communities that do not.

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Ecological interactions often exert important selective pressures on the species involved. For example, the phenologies of lodgepole pines and red crossbills respond spatially to the presence of squirrels (Benkman et al. 2003). Palm species undergo changes in seed morphology in response to the extinction of bird dispersing their seeds (Galetti et al. 2013). tp Darwin's predicted species? . In addition, interactions, and the emergent structures they define, are distributed in similar ways across communities at both large or small scales (Jordano, Bascompte, and Olesen 2003). Together, these observations suggest that much ecological structure could be the end result of (co)evolutionary dynamics between species (Eklof et al. 2011; Stouffer et al. 2012). Unfortunately, although the coevolutionary dynamics of pairs of interacting species have been well described at macro (Van Valen 1973) and micro (Gandon et al. 2008) evolutionary timescales, most attempts to understand how they cascade up to the levels of diversity of both species and interactions found within empirical communities have been inconclusive (Hembry, Yoder, and Goodman 2014). Moreover, coevolutionary dynamics are often presented as a key driving force behind ecological structure across both time and space (Thompson 1994; Thompson 2005); it is therefore crucial to determine the scale at which they are both relevant and quantifiable.

Historically, the evidence for coevolution in taxonomically diverse communities is quantified as the degree of matching between the phylogenies of two sets of interacting organisms (Legendre, Desdevises, and Bazin 2002). This notion builds on the century-old idea that extant species interact in a way similar to the way their ancestors did (Fahrenholz 1913). Note that testing these assumptions is related to, but markedly more restrictive than, testing for phylogenetic conservatism of species' interactions (Rezende et al. 2007; Eklof et al. 2011). This is because of additional, higher-order constraints related to the shape of both trees at all depths (Cavender-Bares et al. 2009; Mouquet et al. 2012): ancestral constraints create high phylogenetic inertia which carries forward to extant taxa (Vale and Little 2010; Desdevises et al. 2003; Diniz-Filho and Bini 2008). For this reason, although several systems have been described that exhibit matching phylogenetic structure, many deviate from this assumption for a variety of factors (see Poisot 2015 for a review). Detecting matching phylogenies for interacting clades nonetheless indicates that their coevolutionary history is long standing and is therefore suggestive that their extant ecological structure is an outcome of ancestral constraints.

The considerations outlined above can be expressed as quantitative predictions. Communities that have assembled by successive divergence events due to coevolution should display phylogenetic congruence, that is (i) have similar phylogenetic trees and (ii) have species at matching positions in the trees that tend to interact (Page 2003). Of course, this matching can be imperfect, as some interactions display substantial variability at ecologically relevant temporal and spatial scales (Poisot et al. 2012; Olito and Fox 2014; Carstensen et al. 2014; Trøjelsgaard et al. 2015), and the same two species can interact in different ways under the effect of local environmental contingencies, spatial mismatch in species phenologies, variations in population abundances, and chance events (Poisot, Stouffer, and Gravel 2015). Variability of interactions, however, does not predict (i) how the signal of pairwise interactions is kept or lost at the scale of the whole community nor (ii) whether or not this variability is related to changes in the amount of coevolutionary signal that can be detected locally.

In this manuscript, we analyze a large dataset of over 300 species of mamallian hosts and their ectoparasites, sampled throughout Eurasia, for which phylogenetic relationships are known. Using a Procrustean approach to quantify the strength of coevolutionary signal (Balbuena, Míguez-Lozano, and Blasco-Costa 2013), we show that locally sampled communities rarely show strong evidence of coevolution despite the fact that the overall system does at the continental scale. We then provide evidence to support the claim that the amount of coevoluationary signal within a local community is predictable based on the importance of interactions for coevolutions in the *regional* network. We finally show that the contribution of these interactions to coevolution is invariant across scales, and is unrelated to their tendency to vary across space. These results suggest that the key unit at which coevolution ought to be studied is the interaction rather than the complex networks they form, and this is true even at large taxonomical and spatial scales.

1 Methods

1.1 Data source and pre-treatment

We use data on observations of interactions between 121 species of rodents and 205 species of parasitic fleas in 51 locations across Europe (B. R. Krasnov, Fortuna, Mouillot, Khokhlova, Shenbrot, Poulin, et al. 2012) to build 51 species-species interaction networks. Interactions were measured by combing rodents for fleas, a method that gives high quality data as it has a high power of detection. Previous analyses revealed that this dataset shows significant coevolutionary signal at the continental level (B. R. Krasnov, Fortuna, Mouillot, Khokhlova, Shenbrot, and Poulin 2012). Importantly, it also provides spatial replication and variability (Canard et al. 2014) at a scale large enough to capture macro-ecological processes. This dataset is uniquely suited for our analysis, as it represents a thorough spatial and taxonomic sampling of a paradigmatic system in which interspecific interactions are thought to be driven by macro-evolution and co-speciation events (Combes 2001; Verneau, Du Preez, and Badets 2009);

The original dataset gives quantitative interaction strengths (expressed as an averaged number of parasites per species per host). Quantitative interactions strength, in this system, were shown to be affected to a very high degree by local variations in abundance across sampling locations (Canard et al. 2014), and it therefore seems unlikely that they reflect macro-ecological processes. To account for differential sampling effort (which cannot readily be quantified) and across site variations in abundance (which do not pertain to macro-evolutionary proccesses), we only study the networks' bipartite incidence matrices (presence and absence of infection of hosts by the parasites).

1.2 Spatial scales and interaction spatial consistency

Noting that variation of interactions across locations (which can be caused by local ecological mechanisms, as opposed to reflecting evolutionary dynamics) can decrease congruence, we analyze the data at three different levels: the continental level dataset (the aggregated "metanetwork" which includes all documented interactions between species from the regional species pool, Poisot et al. (2012)), and two location-level scales, henceforth *regional* and *local*.

First, we use *regional* interaction data; this accounts for different species composition across sites, specifically by testing whether sampling from the regional species pool affects coevolutionary signal. Within each site, the regional scale is given by the subset of the metanetwork formed by the locally present species (properly speaking, the induced subgraph of the metanetwork induced from the nodes of the local network). Hence the regional networks are always a perfect subset of the continental network, and do not reflect whether species were actually observed to interact locally or not, but whether they *can* interact at all.

Second, we use the *local* interaction data; this, in addition to encompassing the above, also accounts for variation in the interactions between observed species. By contrast to the regional scale, the local scale includes only the interactions that were actually observed in the field at a given site. Therefore, the local and regional networks always include the same species, but the local network has only a subset (or, at most, an exact match) of the interactions in the regional network.

Note that although they are reported as 0 (*i.e.* having no interactions), we actually have no information about species pairs that have never co-occured; this is a common, but hard to correct, feature of spatially replicated datasets in which species occurrence vary (**???**). We finally define the spatial consistency of every interaction as the number of sites in which the two species involved co-occur, or simply

$$S_{ij} = \frac{L_{ij}}{C_{ij}}, \tag{1}$$

the spatial consistency of an interaction C_{ij} between species i and j is measured by dividing the number of locations in which both are present (L_{ij}) and the number of locations in which they interact (L_{ij}). Because $L_{ij} \in [0, C_{ij}]$, this measure takes values in $[0, 1]$. Larger values reflect high spatial consistency. Note that, because of the co-occurence issue mentioned above, this measure is only defined for species that have been observed to *co-occur* at least once.

1.3 Quantifying coevolutionary signal

We quantify the strength of coevolutionary signal in terms of the degree of matching between host and parasite phylogenies, given knowledge of species interactions (at varying spatial scales). We do so using the *PACo* method (Balbuena, Míguez-Lozano, and Blasco-Costa 2013), which is robust to variations in both number of species and interactions. *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?). Importantly, and by contrast to previous methods such as *ParaFit* (Legendre, Desdevises, and Bazin 2002), *PACo* measures the contribution of every interaction to the network-level signal in a meaningful way even though the network shows no significant coevolutionary signal. As required by *PACo*, the phylogenetic trees for hosts and parasites were rendered ultrametric (*i.e.*, all species are at the same distance from the root).

2 Results and discussion

2.1 Local and regional scale networks show no coevolutionary signal

As host-macroparasite interactions are hypothesized to be ecologically constrained, as a result of their being evolutionary conserved (Combes 2001), the congruence observed at the continental level sets the baseline for what would be expected in local communities. Of course, if ecological mechanisms reduce coevolutionary signal, we should detect coevolution at the continental scale but not locally. Out of 51 sites, 35 show no signal of coevolution at all, 11 show significant coevolutionary signal when using the regional interactions, and 12 show significant coevolutionary signal using the local interactions (see *Supp. Mat. 1* for network-level significance values; Figure 1). These results support the idea that macro-evolutionary processes, such as co-diversification, can have consequences at the macro-ecological level but may not in fact be detectable at finer spatial scales.

2.2 Coevolutionary signal is predicted by the contribution of interactions

On the other hand, system-level differences say little about the behavior of individual interactions. Despite the fact most coevolutionary mechanisms act at the interaction level (Thompson 1999), most *measures* of it are expressed at the community level. We observe here that networks with interactions that are important for coevolution at the continental scale indeed have more coevolutionary signal at the local and regional scales alike (Fig. 2A). Intriguingly, we also find that the distribution of individual interactions' contributions to coevolution is strongly conserved, regardless of the scale at which the interactions are quantified (Fig. 2B). Because interactions differ in their total contribution to coevolution, this implies that their distribution across networks (*i.e.* whether the local network is a sampling of strongly contributing, or weakly contributing, interactions) is what actually drives differences in overall coevolutionary signal. Network-level coevolutionary signal emerges directly from the properties of interactions and is not a property of the network itself.

2.3 Interactions contributing to coevolution are not more spatially consistent

tp Add more references on int. variab.

Beyond their contribution to coevolution, interactions also ultimately differ in how frequently they vary when the species involved co-occur (Olito and Fox 2014). Once more, the literature on host-parasite interactions usually assumes that the reason why some interactions are more frequent is because they reflect a significant past history of coevolution (Morand and Krasnov 2010); the ecological constraints emerge from the evolutionary conservatism. If this were true, we should observe a significant, positive correlation between the probability of observing an interaction and the importance of that interaction for coevolution at the continental scale. Surprisingly, we find that neither is true here since interactions that are important for coevolution are not more spatially consistent (Fig. 3). This implies that the spatial consistency of an interaction do not reflect its evolutionary past, but rather (extant) ecological processes **REF**.

2.4 The contribution of interactions to coevolution is consistent across scales

Ultimately, coevolutionary signal varies across scale because of the simultaneous variation of species' interactions *and* communities' phylogenetic tree structure. In a system characterised by substantial turnover, we would expect the contribution of each separate interaction to differ across scales as well. Instead, we observe here that interactions that contribute strongly to coevolutionary signal at the continental scale *also* show a significant tendency to contribute strongly at the local ($p < 0.05$ for positive correlations in 48 out of 51 networks) and regional (in 47 out of 51 networks), and this observation is independent of network-wide coevolutionary signal (Fig. 4). Remarkably, this result implies that the remnants of coevolution are still locally detectable in *individual interactions* even though coevolution regularly fails to leave its imprint on most local networks.

3 Discussion

Overall, the results of our analyses demonstrate that there is a sizeable gap between our current understanding of coevolution as the basis of multi-species interactions and its applicability to ecological questions. Local networks show little to no signal of coevolution and the strength of coevolution between two species is a surprisingly poor predictor of how frequently they interact. In contrast to the frequent assumption that phylogenetic structure is a key driver of community structure (Cavender-Bares et al. 2009), these data reveal that this impact is actually minimal at ecologically relevant spatial scales. Despite all the above, individual interactions are able to maintain their coevolutionary signal even when the community they are woven into does not. Thinking more broadly, these discrepancies provide a clear roadmap for bridging the aforementioned gap between our appreciation of the role of coevolution and its empirically measurable outcomes. Network structure is the most parsimonious *mechanism* by which coevolution proceeds, not the imprint coevolution leaves on ecological communities.

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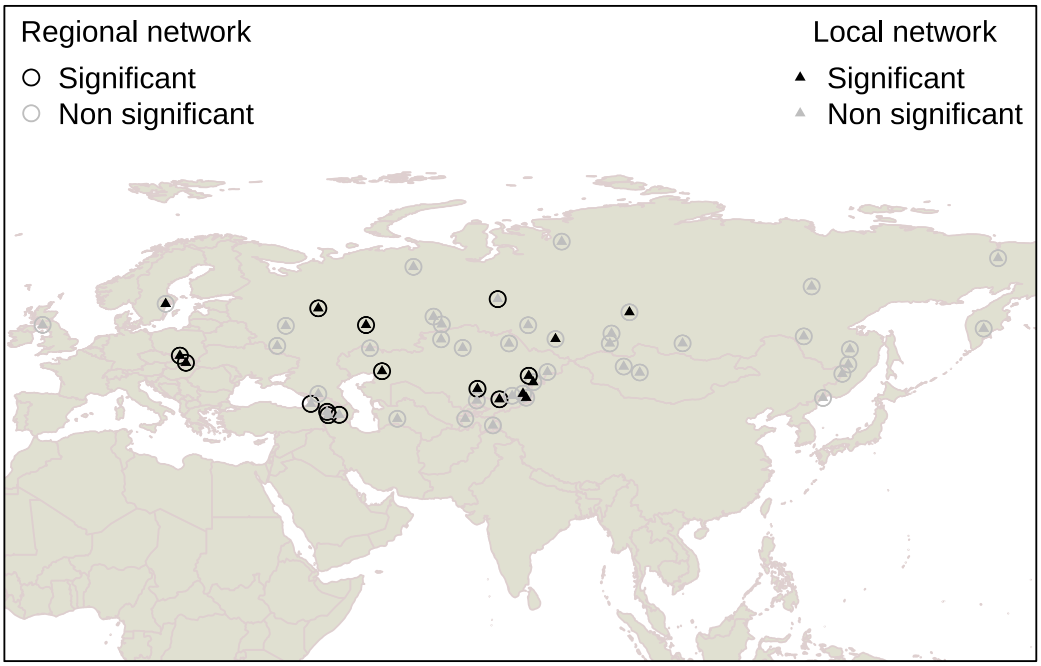

Figure 1: Spatial distribution of coevolutionary signal across the 51 sites. For each location, we indicate whether or not the structure of regional and local interaction networks is consistent with phylogenetic congruence. The colour of the circle corresponds to regionally significant or non-significant (black and grey, respectively) while the colour of the symbol within corresponds to locally significant or non-significant (black and grey, respectively).

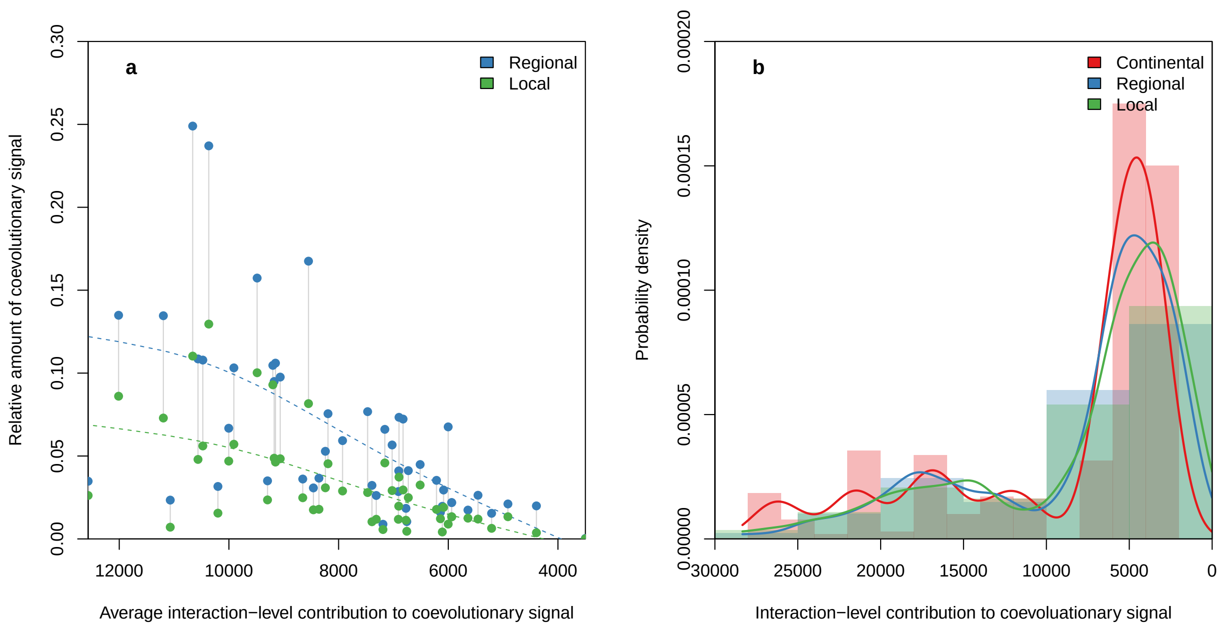

Figure 2: Distribution of coevolutionary signal at the network and interaction levels. **a**, Networks that have lower coevolutionary signal at the local or regional level are composed of interactions that on average contribute little to coevolution at the continental scale. Dashed lines are a cubic smoothing spline, and the two levels of the same networks are linked by solid grey lines. **b**, Overall, interactions observed at the local, regional, and continental scale have roughly equivalent contributions to coevolutionary signal. Probability density was smoothed using a Gaussian kernel density estimator. Raw probability densities are shown as semi-transparent bars.

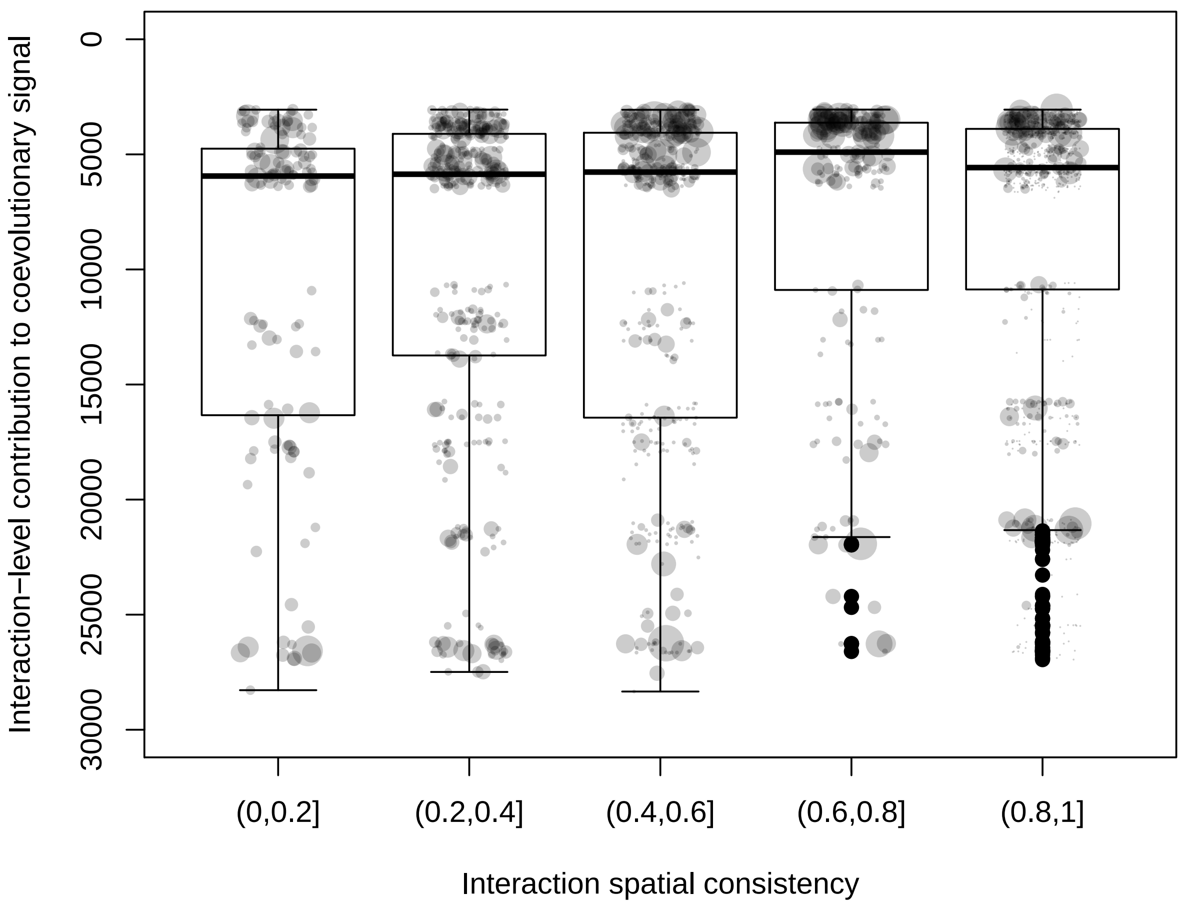

Figure 3: Spatial consistency of an interaction and its contribution to coevolutionary signal. Spatial consistency is defined as the probability of observing an interaction between two species given that they were observed to co-occur. Although statistically significant, there was no biologically meaningful relationship between spatial consistency and an interaction's importance for coevolution in the continental network ($R^2 \approx 0.01$, $\rho = -0.1$, $p \leq 10^{-5}$).

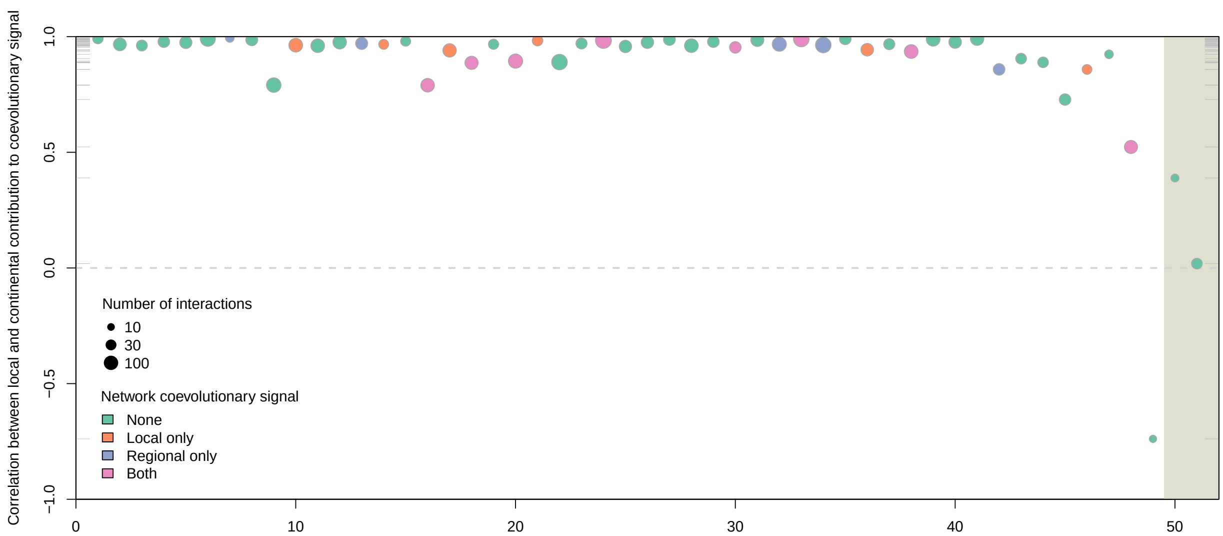

Figure 4: The contribution to coevolutionary signal of the interaction between two species is maintained across scales. For every site, we show the Pearson's correlation between interaction-level coevolutionary signal in the continental network and the same in the local network. The size of each point is proportional to the size of the network, and all correlations are significant at $\alpha = 0.05$ except in the grey shaded area.