Coevolution leaves a stronger imprint on interactions than on community structure

Timothée Poisot (1,2,3) and Daniel B. Stouffer (1)

(1) School of Biological Sciences, University of Canterbury, Christchurch, New Zealand; (2) Département des Sciences Biologiques, Université de Montréal, Montréal, Canada; (3) Québec Centre for Biodiversity Sciences, Montréal, Canada

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 either 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.

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 [@benk03a] and palm species undergo changes in seed morphology in response to the extinction of bird dispersing their seeds [@gale13]. Given that interactions are distributed in similar ways across communities, at both the large or small scale [@jord03], it can be argued that much ecological structure is the end result of evolutionary or coevolutionary dynamics between species [@eklo11;@stou12]. Unfortunately, while the coevolutionary dynamic of pairs of interacting species has been well described at macro [@van73] and micro [@gand08] 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 [@hemb14]. Moreover, because coevolutionary dynamics are often presented as a key driving force behind ecological structure across both time

and space [@thom05], it is 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 [@lege02]. This notion builds on the century-old idea that extant species interact in a way similar to the way their ancestors did [@fahr13], but it is considerably more restrictive than just phylogenetic conservation of species' interactions [@reze07;@eklo11] because it additional higher-order constraints. More explicitly, 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 [@page03]. On the other hand, many ecological and evolutionary processes that occur locally are expected to blur community-wide coevolutionary signal [@pois15]. One possible explanation is that interactions can display substantial turnover at ecologically relevant temporal and spatial scales [@pois12c]: 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 [@pois14]. It is unclear, however, whether these mechanisms influence how the coevolutionary signal within individual interactions should vary across spatial scales.

To answer these questions, we study a dataset of interactions between rodents and their ectoparasites from 51 sites across Western to Eastern Europe [@kras12b] (Methods Summary). This dataset is uniquely suited for this task as it represents a paradigmatic system in which species-species interactions are thought to be driven by macro-evolution and co-speciation events [@vern09], and coevolutionary signal is indeed significant at the continental level [@kras12a] ($p \leq 10^{-4}$; Methods). Importantly, it also provides spatial replication and variability at a scale large enough to capture macro-ecological processes.

As host-macroparasite interactions are hypothesized to be both ecologically constrained and evolutionary conserved [@comb01], 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. Noting that variation of interactions can decrease congruence, we analyse the data at two different levels to test these hypotheses: first, we use *regional* interaction data— which accounts for different species composition across sites–and second, we use the *local* interaction data—which also accounts for variation in the interactions between observed these species (Methods Summary). Out of 51 sites, 35 show no signal of coevolution, 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).

These results would appear to 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. On the other hand, system-level differences say little about the behaviour of individual interactions, despite the fact most coevolutionary mechanisms act at the interaction level [@thom99]. As might be expected, 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 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.

Beyond their contribution to coevolution, interactions also ultimately differ in how frequently they vary when the species involved co-occur [@olit14]. 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 [@mora10]. 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 (Methods Summary). Surprisingly, we find that neither is true here since interactions that are important for coevolution are not more conserved (Fig. 3).

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.

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 [@cave09], 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

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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.

Methods

We use data on observations of interactions between 121 species of rodents and 205 species of parasitic fleas in 51 locations across Europe [@kras12b] 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. To account for differential sampling effort and across site variations in abundance, we only study the networks' incidence matrices (presence and absence of interactions).

In our study, we define threes scales for the network data and analysis— continental, regional, and local. The continental scale is the aggregated "metanetwork" which includes all potential interactions between co-occurring species [@pois12c] (*i.e.*, all species and all their interactions across the 51 networks). Within each site, the regional scale is given by the list of observed species and all their possible interactions. Hence the regional networks are always a perfect subset of the continental network. 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. The spatial consistency of every individual interaction is measured as the number of sites in which the two species involved co-occur.

We quantified the coevolutionary signal in terms of the degree of matching between host and parasite phylogenies given knowledge of species interactions using the *PACO* method [@balb13], which is robust to variations in number of species. *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?). We measured the phylogenetic dissimilarity between two sites for hosts and parasites using PCD [@ives10], a measure that accounts for the dissimilarity of species, corrected for the phylogenetic distance between all species in the dataset. Since it is a requirement of the methods we use here, the phylogenetic trees for hosts and parasites were rendered ultrametric (i.e., all species are at the same distance from the root).
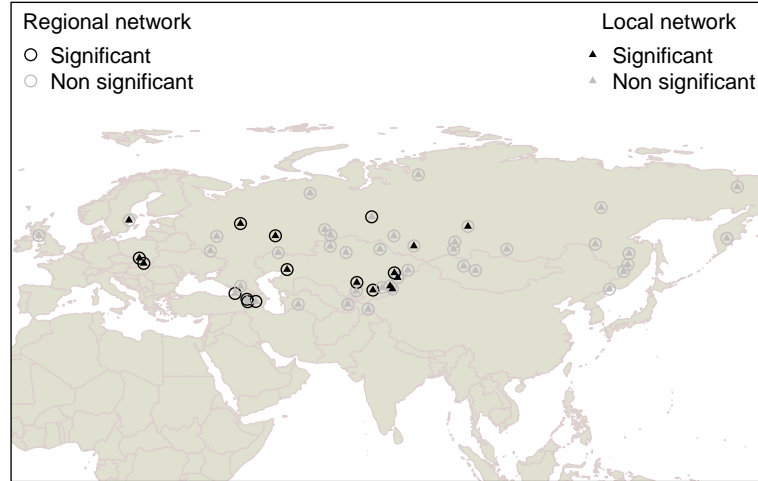
Figures

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).
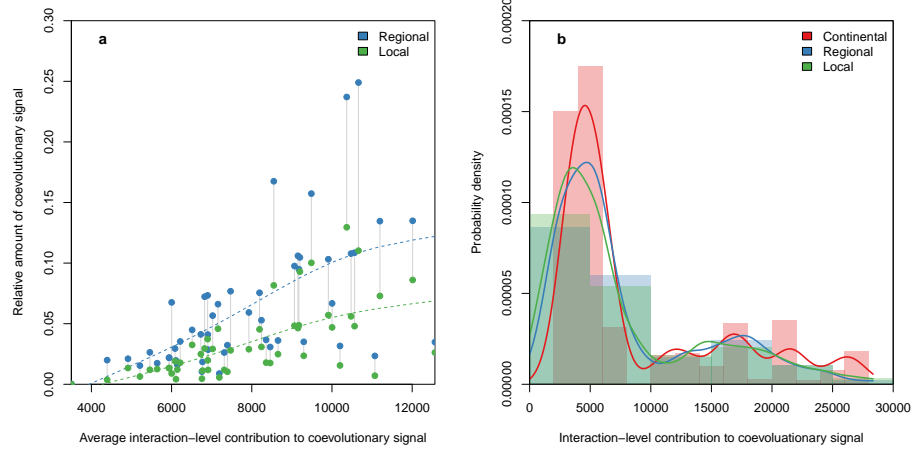
Figure 2: Distribution of coevolutionary signal at the network and interaction levels. **a**, Networks that have lower coevolutionary signal at the local or regional level are composed of interactions that on average contribute little to coevolution at the continental scale. Dashed lines are the cubic smoothing spline; 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 equal contributions to coevolutionary signal. Probability density was smoothed using a Gaussian kernel density estimator. Raw probability densities are shown as semi-transparent bars.
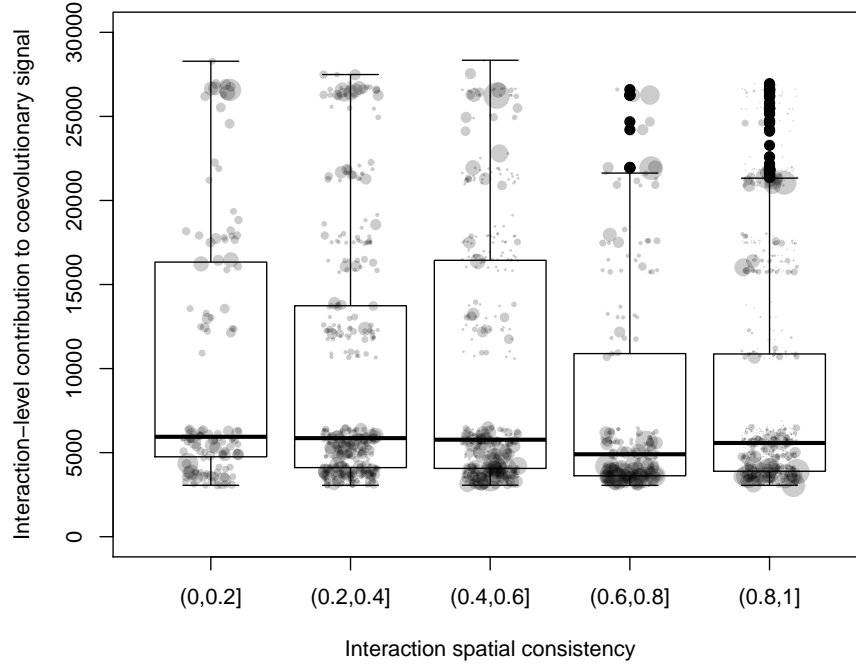
Figure 3: Spatial consistency of an interaction and its contribution to coevolutionary signal. Spatial consistency is defined as the probability of observing an interaction between two species given that they were observed to co-occur. Although statistically significant, there was no biologically meaningful relationship between spatial consistency and an interaction's importance for coevolution in the continental network ($R^2 \approx 0.01$, $\rho = -0.1$, $p \leq 10^{-5}$).
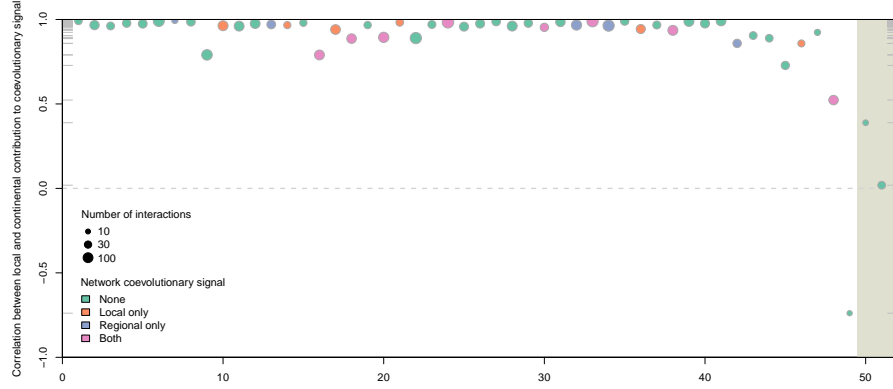
Figure 4: The contribution to coevolutionary signal of the interaction between two species is maintained across scales. For every site, we show the Pearson's correlation between interaction-level coevolutionary signal in the continental network and the same in the local network. The size of each point is proportional to the size of the network, and all correlations are significant at $\alpha = 0.05$ except in the grey shaded area.

References