Should we build a macro-scale theory for coevolution? Nope.

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1 Coevolutionary dynamics acting on both species and their interactions

2 are a key driving force behind the structure of ecological communi-

3 ties. The Geographic Mosaic Theory of Coevolution (GMTC) provides

4 a spatial perspective to these dynamics by proposing the existence of

5 feedbacks between local and regional scales. It remains unclear, how-

6 ever, how the structure of communities at larger spatial scales either in-

7 fluences or is influenced by local coevolutionary processes. Despite this,

8 ecological networks are known to have an ecological structure, which

9 suggest that coevolution may play a role in their evolutionary dynamics.

10 Here we show that the coevolutionary significance of individual interac-

11 tions is maintained when moving between the local and regional scale.

12 Importantly, this occurs despite the fact that community variation at

13 the local scale tends to weaken or remove community-wide coevolution-

14 ary signal. This apparent mismatch between our interaction-level and

15 community-level results strongly suggests that interactions provide the

16 correct scale to study coevolution at small spatial scales while commu-

17 nities are the relevant scale only at larger spatial extents. 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. 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 [???], attempts to understand how these mechanisms cascade up to generate species diversity observed in large ecological networks have been unconclusive [6,7], despite the well known effect of antagonistic coevolution on genomic diversification [8,9]. The scales at which these diversities happen are hard to reconcile: coevolution is expressed within patches connected by gene-flow [10–12], whereas the species diversity of complex networks is typically observed at spatial scales matching the species distribution [13,14]. 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 [???].

Network-based approaches [15,16], 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 [1,17], pollina-

tion networks [18,19], and host-parasite networks [20,21]. Both micro [3,22] and macro [23,24] 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 [25]: 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 [26]. As a consequence, *locally*, the evolutionary signal on network structure is expected to be burried 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 [20,27]. This build on the century-old ideas that extant species interact in a way similar to the way their ancestors did [28]. "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 [29]: 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 [25,30]. 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 [31] 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 co-evolutionary 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 [32], and a general framework for the variation of ecological networks [30].

Local observations on the 51 localities (*Supp. Mat. 1*) are aggregated into a regional metanetwork [30]. The two phylogenetic trees have been rendered ultra-metric. We use *PACO* [32] to measure the congruence between trees knowing the matrix of interaction. *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 [33]. 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 [34], but may not be detected at finer spatial scales due to a stronger effect of ecological processes locally. *PACO* per-
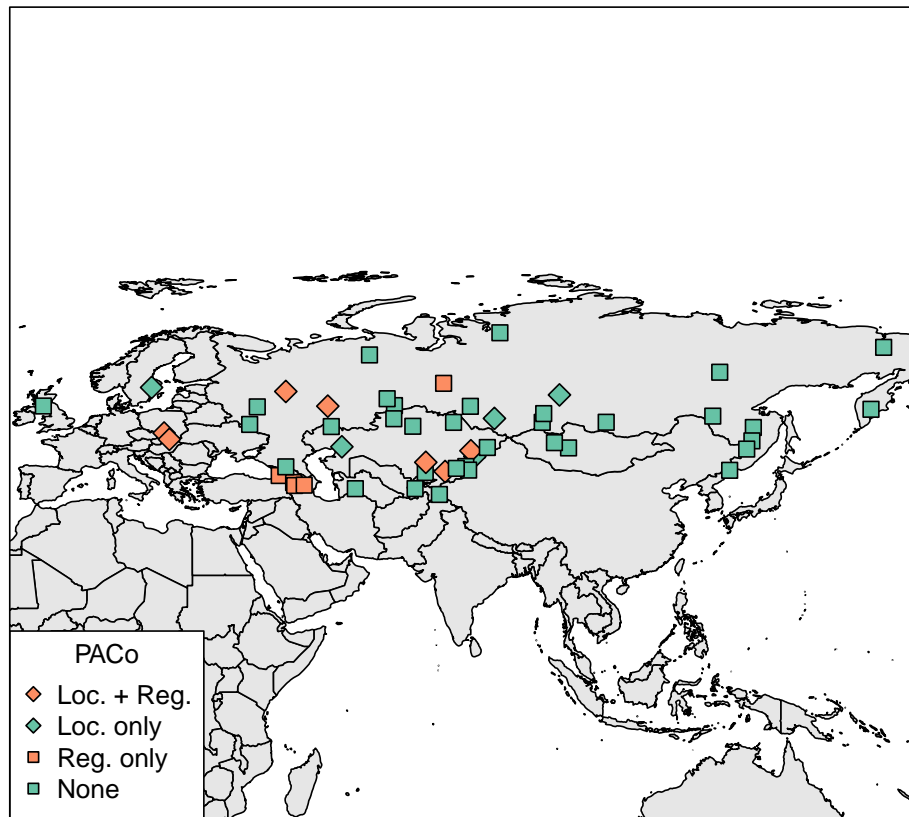
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Figure 1: figure1

mits 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. 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 [35].

Point 2 – Interactions respond locally to micro-processes

- Review of mechanisms involved in interactions locally: neutrality and trait-based mechanisms

- Key refs: Oikos paper, Canard, Olesen, Combes

- These mechanism can only *filter* from a pool of regional interactions

- Key refs: Biol Lett paper, Olito & Fox, Lounnas, . . .

- Key points: i) even though they will change the network-level signal, contribution of interactions should not vary locally vs. regionally ii) this is the

1 expectation because (a) past knowledge about motifs/evolution and (b) in-

2 teractions are the unit in which selection takes place, not networks

3 • Illustration: distribution of the significance in each interaction locally (mea-
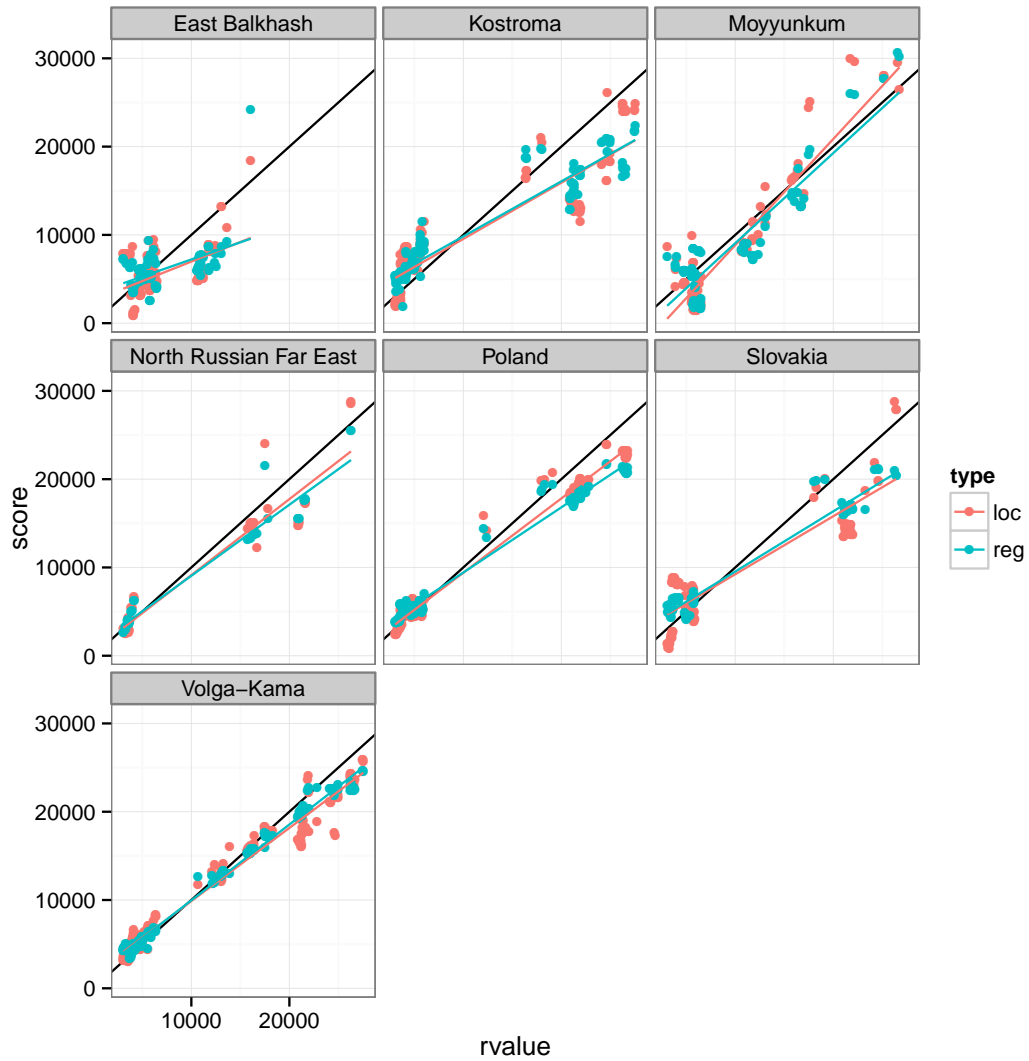
4 sured vs. metaweb) vs. in the regional network.

Figure 2: figure2

Point 3 – The spatial replication of networks is imperfect

- Ecological processes = sorting of interactions + species

- Key refs: Ecol Lett -div

- Key points: observation of interactions result from filtering through two processes, and not clear they are related to past coevolution = we expect a loss of signal locally

- Illustration: jacknife score vs. observed/possible : there is no relationship between how important an interaction is (coevo) and how frequent it will be. suggests that ecological >> evolutionary drivers of local network structure

- This is caused by local ecological processes, but also influences local evolutionary dynamics
- Key refs: Gomulkiewicz, Hochberg, Benkman, Siepilski
- Key points: i) Opportunity to integrate more network theory to understand between-sites differences ii) Even though coevo theory recognized variation in effects, very little attention to variation in presence/absence of int and its implications

Conclusions

- Need to bridge ecological networks with co-evolution (understand the impact of ecology vs. evolution in the local observations)
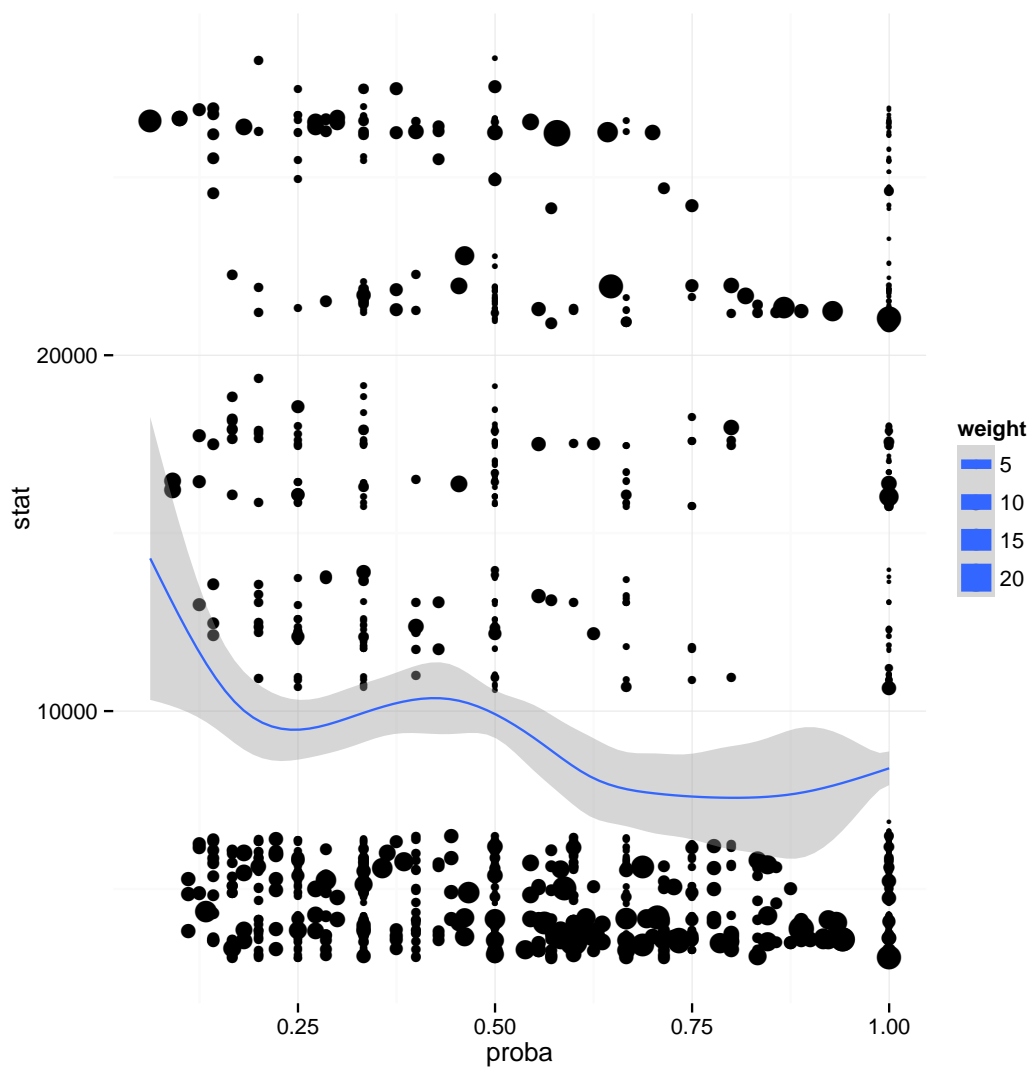
Figure 3: figure3

- Main advance: coevolutionary dynamics are important at the continental/regional scale, much less at the local scale

- Focus on datasets that are spatially replicated, with as good as possible phylogenies. Ref Buckley, Hearkel.

- Currently local variability is not accounted for by statistical methods, need to do a better job. See Desdevises chapter on ParaFit 2.0.

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