

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

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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 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.

Introduction

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 inconclusive ^{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 ^{???,??,??}, whereas the species diversity of complex networks is typically observed at spatial scales matching the species distribution ^{???,10}. 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 ^{???,??}, 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 ^{???,??,??}, pollination networks ^{???,??}, and host-parasite networks ^{???,??,??}. Both micro ^{???,??,??} and macro ^{???,??} 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 ^{???}: 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 ^{???}. 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*.

We use data on ectoparasites of rodents from Western to Eastern Europe ¹¹. The local observations on 51 localities are aggregated into a regional metanetwork ¹². The two phylogenetic trees have been rendered ultrametric. We use *PACO* ¹³ 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). **Explain – species sorting vs interaction sorting.** More informations about the networks are given in *Suppl. Mat. 1*. At the regional scale, coevolutionary signal is extremely strong ($p \leq 10^{-4}$), as shown by previous studies ¹⁴. 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. XX* for associated tests). **Figure?**.

This suggests that macro-evolutionary processes (such as co-diversification) have

consequences at the macro-ecological level ¹⁵, but may not be detected at finer spatial scales due to a stronger effect of ecological processes locally. **Transition into hyp 2.**

Point 1 – Strong hypothesis that macro-evolutionary processes have macro-ecological consequences

- We expect a matching between the scales of eco/evo mechanisms
- Key refs: Reference 15 mostly, also Reference 16
- Key points: acquisition/loss of interactions is viewed as acquisition of character in cladistics, macro-evo event
- Interactions well predicted by species traits that evolve slowly (body size in food webs)
- Show how this influenced the methodological toolkit (virtually all assumptions derive from Farenholz's rule)
- Illustration: PACo or ParaFit score in the metaweb vs. distributions of the local webs
- Key references: Desdevises papers on *Lamellodiscus*, Swafford papers on mites, Chamberlain et al 2014 *Oecologia*

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 expectation because (a) past knowledge about motifs/evolution and (b) interactions are the unit in which selection takes place, not networks
- Illustration: distribution of the significance in each interaction locally (measured vs. metaweb) vs. in the regional network.

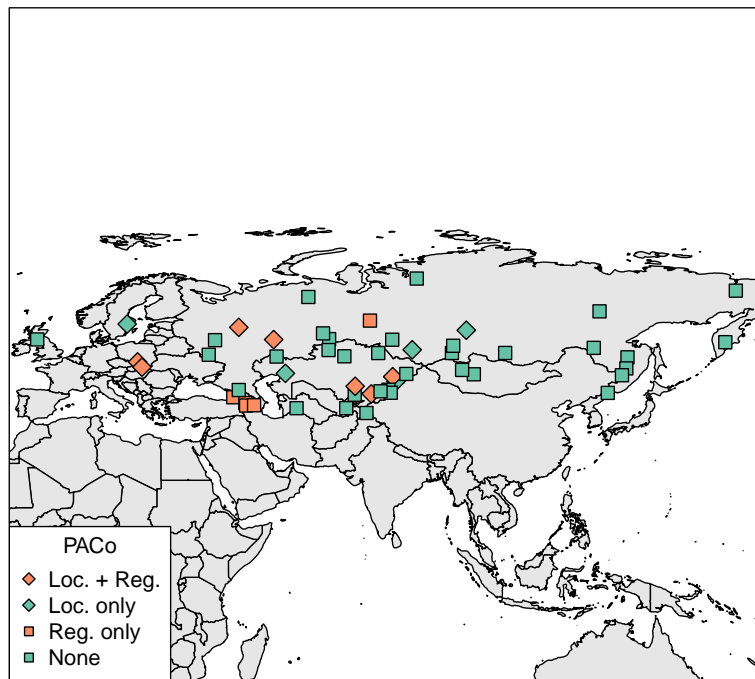


Figure 1: figure1

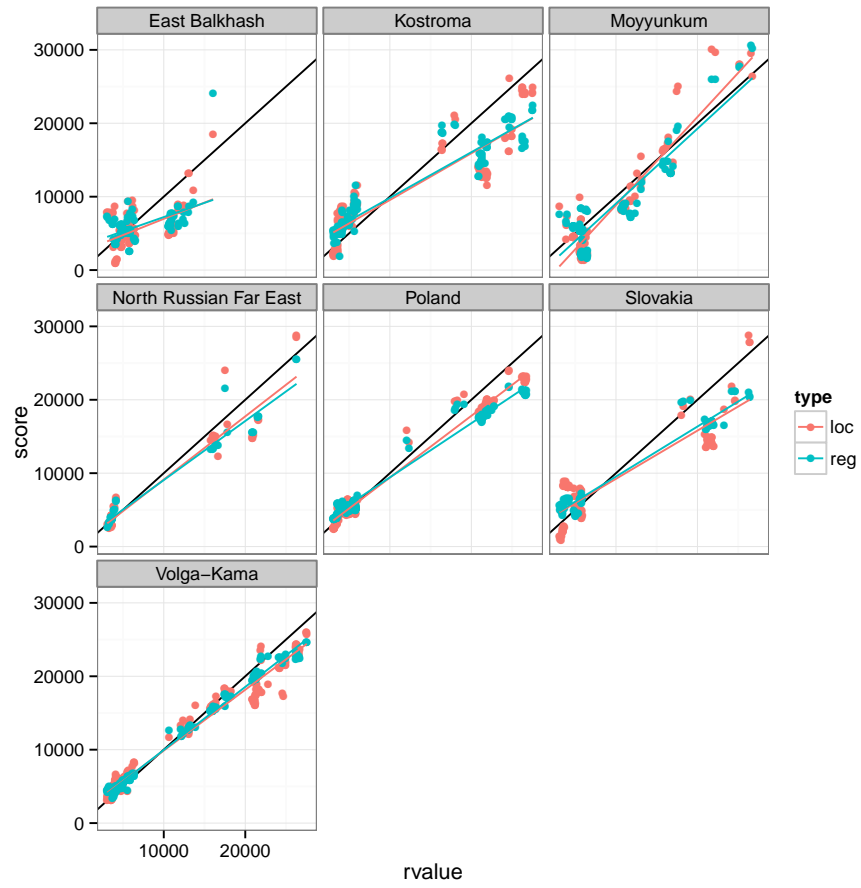


Figure 2: figure2

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

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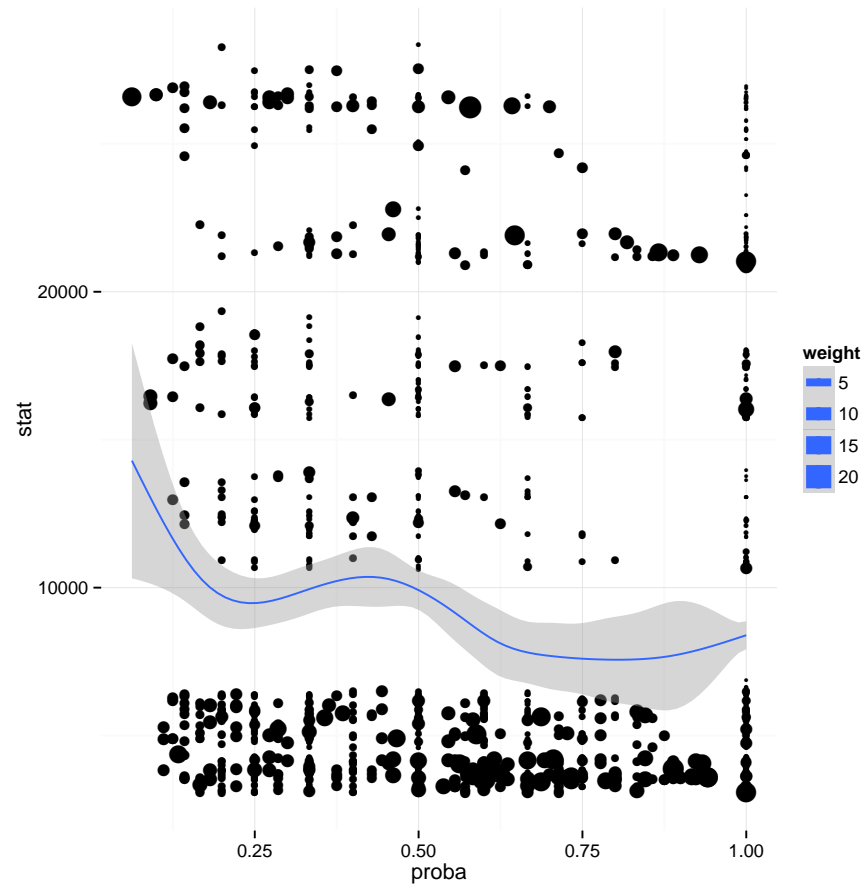


Figure 3: figure3

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