

# 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 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.

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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?**. That interactions, and the emergent structures they define, are distributed in similar ways across communities, at both large or small scale (Jordano, Bascompte, and Olesen 2003), suggest that much ecological structure is 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 has 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 this assumptions is related to, but markedly more restrictive than, testing for phylogenetic conservatism of species' interactions (Rezende et al. 2007; Eklof et al. 2011) 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 have a high phylogenetic inertia, which carries over 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 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). Yet this matching can be imperfect, as interactions do 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): 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). This, however, does not predicts (i) how the signal of pairwise interactions is kept, or lost, at the scale of the whole community, and (ii) whether the variability of interactions relates the changes in the amount of coevolutionary signal that can be detected locally.

**tp This whole paragraph is new** 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 the question of coevolutionary signal (Balbuena, Míguez-Lozano, and Blasco-Costa 2013), we show that althout the overall system (at the continental scale) displays evidences of coevolution, locally sampled communities do not. We present evidences to support the claim that the amount of coevolutionary signal within a local community is a simple sampling effect of interactions with different contributions to overall coevolution. We finally show that the contribution of these interactions 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, even at large taxonomical and spatial scales, is the interaction rather than the complex networks they form.

# 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. To account for differential sampling effort and across site variations in abundance, we only study the networks' incidence matrices (presence and absence of interactions). 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 paradigmatic system in which species-species interactions are thought to be driven by macro-evolution and co-speciation events (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. For this reason, we transform all quantitative matrices into bipartite incidence matrices, in which 1 represents the presence of an interaction, and 0 its absence.

## 1.2 Spatial scales and interaction spatial consistency

We define three scales for the network data and their subsequent analysis—continental, regional, and local. The continental scale is the aggregated “metanetwork” which includes all documented interactions between species from the regional species pool (Poisot et al. 2012). Note that although they are reported as 0, we actually have no information about species pairs that have never co-occurred.

Within each site, the regional scale is given by the subset of metanetwork formed by the locally present species. 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. By contrast, 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.

We define the spatial consistency of every interaction as the number of sites in which the two species involved co-occur. Note that, because of the co-occurrence issue mentioned above, this measure is only defined for species that have been observed to *interact* at least once.

## 1.3 Measure of 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. We do so using the *PACo* method (Balbuena, Míguez-Lozano, and Blasco-Costa 2013), which is robust to variations in 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, Desdevices, and Bazin 2002), *PACo* allows measuring the contribution of

every interaction to the network-level signal 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

### 2.1 Local and regional scale networks show no coevolutionary signal

As host-macroparasite interactions are hypothesized to be both ecologically constrained and 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. 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; Figure 1).

### 2.2 Coevolutionary signal is predicted by the contribution of interactions

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 (Thompson

1999). 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.

### 2.3 Interactions contributing to coevolution are not more spatially consistent

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). 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).

### 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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## References

- Balbuena, Juan Antonio, Raúl Míguez-Lozano, and Isabel Blasco-Costa. 2013. "PACo: A Novel Procrustes Application to Cophylogenetic Analysis." *PLoS ONE* 8 (4): e61048.
- Benkman, Craig W., Thomas L. Parchman, Amanda Favis, and Adam M. Siepielski. 2003. "Reciprocal Selection Causes a Coevolutionary Arms Race Between Crossbills and Lodgepole Pine." *Am. Nat.* 162 (2): 182–94.
- Canard, E. F., N. Mouquet, D. Mouillot, M. Stanko, D. Miklisova, and D. Gravel. 2014. "Empirical Evaluation of Neutral Interactions in Host-Parasite Networks." *The American Naturalist* 183 (4): 468–79.
- Carstensen, Daniel W., Malena Sabatino, Kristian Trøjelsgaard, and Leonor Patricia C. Morellato. 2014. "Beta Diversity of Plant-Pollinator Networks and the Spatial Turnover of Pairwise Interactions." *PLoS ONE* 9 (11): e112903.
- Cavender-Bares, Jeannine, Kenneth H. Kozak, Paul V. A. Fine, and Steven W. Kembel. 2009. "The Merging of Community Ecology and Phylogenetic Biology." *Ecol. Lett.* 12 (7): 693–715.
- Combes, Claude. 2001. *Parasitism - The Ecology and Evolution of Intimate Interactions*. University Of Chicago Press.
- Desdevises, Yves, Pierre Legendre, Lamia Azouzi, and Serge Morand. 2003. "Quantifying Phylogenetically Structured Environmental Variation." *Evolution* 57 (11): 2647–52.
- Diniz-Filho, José Alexandre Felizola, and Luis Mauricio Bini. 2008. "Macroecology, Global Change and the Shadow of Forgotten Ancestors." *Glob. Ecol. Biogeogr.* 17 (1): 11–17.
- Eklof, Anna, Matthew R. Helmus, M. Moore, Stefano Allesina, and Anna Eklöf. 2011. "Relevance of Evolutionary History for Food Web Structure." *Proc. R. Soc. B Biol. Sci.* 279 (November 2011):

202 1588–96.

203 Fahrenholz, H. 1913. “Ectoparasiten Und Abstammungslehre.” *Zool. Anz.* 41: 371–74.

204 Galetti, Mauro, Roger Guevara, Marina C. Côrtes, Rodrigo Fadini, Sandro Von Matter, Abraão  
 205 B. Leite, Fábio Labecca, et al. 2013. “Functional Extinction of Birds Drives Rapid Evolutionary  
 206 Changes in Seed Size.” *Science* 340 (6136): 1086–90.

207 Gandon, Sylvain, Angus Buckling, Ellen Decaestecker, and Troy Day. 2008. “Host-Parasite Co-  
 208 evolution and Patterns of Adaptation Across Time and Space.” *J. Evol. Biol.* 21 (6): 1861–66.

209 Hembry, David H., Jeremy B. Yoder, and Kari Roesch Goodman. 2014. “Coevolution and the  
 210 Diversification of Life.” *The American Naturalist* 184 (4): 425–38.

211 Jordano, Pedro, Jordi Bascompte, and Jens M Olesen. 2003. “Invariant Properties in Coevolution-  
 212 ary Networks of Plant-Animal Interactions.” *Ecol. Lett.* 6 (1): 69–81.

213 Krasnov, Boris R., Miguel A. Fortuna, David Mouillot, Irina S. Khokhlova, Georgy I. Shenbrot,  
 214 and Robert Poulin. 2012. “Phylogenetic Signal in Module Composition and Species Connectivity  
 215 in Compartmentalized Host-Parasite Networks.” *The American Naturalist* 179 (4): 501–11.

216 Krasnov, Boris R., Miguel A. Fortuna, David Mouillot, Irina S. Khokhlova, Georgy I. Shenbrot,  
 217 Robert Poulin, and Boris R. Krasnov. 2012. “Data from: Phylogenetic Signal in Module Composi-  
 218 tion and Species Connectivity in Compartmentalized Host-Parasite Networks.”

219 Legendre, Pierre, Yves Desdevises, and Eric Bazin. 2002. “A Statistical Test for Host-Parasite  
 220 Coevolution.” *Syst. Biol.* 51 (2): 217–34.

221 Morand, Serge, and Boris Krasnov, eds. 2010. *Biogeography of Host-Parasite Interactions*. Ox-  
 222 ford: Oxford University Press.

223 Mouquet, Nicolas, Vincent Devictor, Christine N. Meynard, Francois Munoz, Louis-Félix Bersier,

- 224 Jérôme Chave, Pierre Couteron, et al. 2012. “Ecophylogenetics: Advances and Perspectives.” *Biol.*  
225 *Rev.* 87 (4): 769–85.
- 226 Olito, Colin, and Jeremy W. Fox. 2014. “Species Traits and Abundances Predict Metrics of Plant-  
227 pollinator Network Structure, but Not Pairwise Interactions.” *Oikos*, n/a–/a.
- 228 Page, Roderick D M. 2003. *Tangled Trees: Phylogeny, Cospeciation, and Coevolution*. University  
229 of Chicago Press.
- 230 Poisot, Timothée. 2015. “When Is Cophylogeny Evidence of Coevolution?” In *Evolutionary Ecol-*  
231 *ogy of Host-Parasite Systems*, edited by Serge Morand, D T Littlewood, and Robert Poulin. Cam-  
232 bridge University Press.
- 233 Poisot, Timothée, Elsa Canard, David Mouillot, Nicolas Mouquet, and Dominique Gravel. 2012.  
234 “The Dissimilarity of Species Interaction Networks.” *Ecol Lett* 15 (12): 1353–61.
- 235 Poisot, Timothée, Daniel B. Stouffer, and Dominique Gravel. 2015. “Beyond Species: Why Eco-  
236 logical Interaction Networks Vary Through Space and Time.” *Oikos* 124 (3): 243–51.
- 237 Rezende, Enrico L, Jessica E Lavabre, Paulo R Guimarães, Pedro Jordano, and Jordi Bascompte.  
238 2007. “Non-Random Coextinctions in Phylogenetically Structured Mutualistic Networks.” *Nature*  
239 448 (7156): 925–8.
- 240 Stouffer, Daniel B., Marta Sales-Pardo, M. Irmak Sirer, and Jordi Bascompte. 2012. “Evolutionary  
241 Conservation of Species’ Roles in Food Webs.” *Science* 335 (6075): 1489–92.
- 242 Thompson, John N. 1994. *The Coevolutionary Process*. Chicago: University of Chicago Press.
- 243 ———. 1999. “The Raw Material for Coevolution.” *Oikos* 84 (1): 5–16.
- 244 ———. 2005. *The Geographic Mosaic of Coevolution*. University Of Chicago Press.
- 245 Trøjelsgaard, Kristian, Pedro Jordano, Daniel W. Carstensen, and Jens M. Olesen. 2015. “Geo-

246 graphical Variation in Mutualistic Networks: Similarity, Turnover and Partner Fidelity.” *Proc. R.*  
247 *Soc. B* 282 (1802): 20142925.

248 Vale, Pedro F, and Tom J Little. 2010. “CRISPR-Mediated Phage Resistance and the Ghost of  
249 Coevolution Past.” *Proc. R. Soc. B Biol. Sci.*, no. March.

250 Van Valen, Leigh. 1973. “A New Evolutionary Law.” *Evol. Theory* 1 (1): 1–30.

251 Verneau, Olivier, Louis Du Preez, and Mathieu Badets. 2009. “Lessons from Parasitic Flatworms  
252 About Evolution and Historical Biogeography of Their Vertebrate Hosts.” *C. R. Biol.* 332 (2):  
253 149–58.

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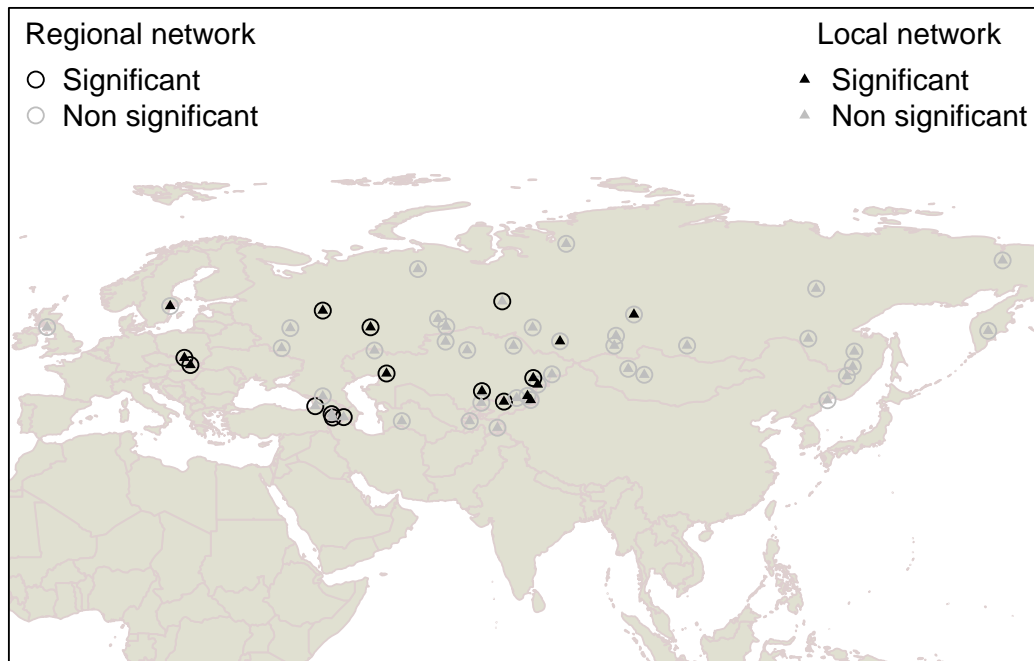


Figure 1: Spatial distribution of coevolutionary signal across the 51 sites. For each location, we indicate whether or not the structure of regional and local interaction networks is consistent with phylogenetic congruence. The colour of the circle corresponds to regionally significant or non-significant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

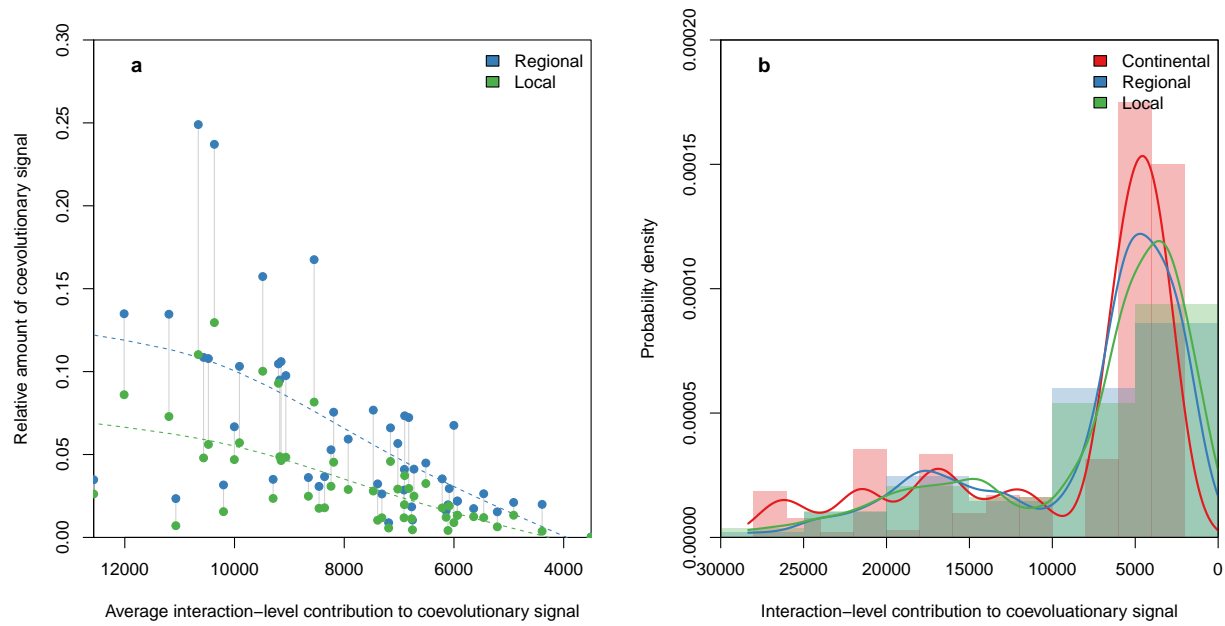


Figure 2: Distribution of coevolutionary signal at the network and interaction levels. **a**, Networks that have lower coevolutionary signal at the local or regional level are composed of interactions that on average contribute little to coevolution at the continental scale. Dashed lines are the cubic 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.

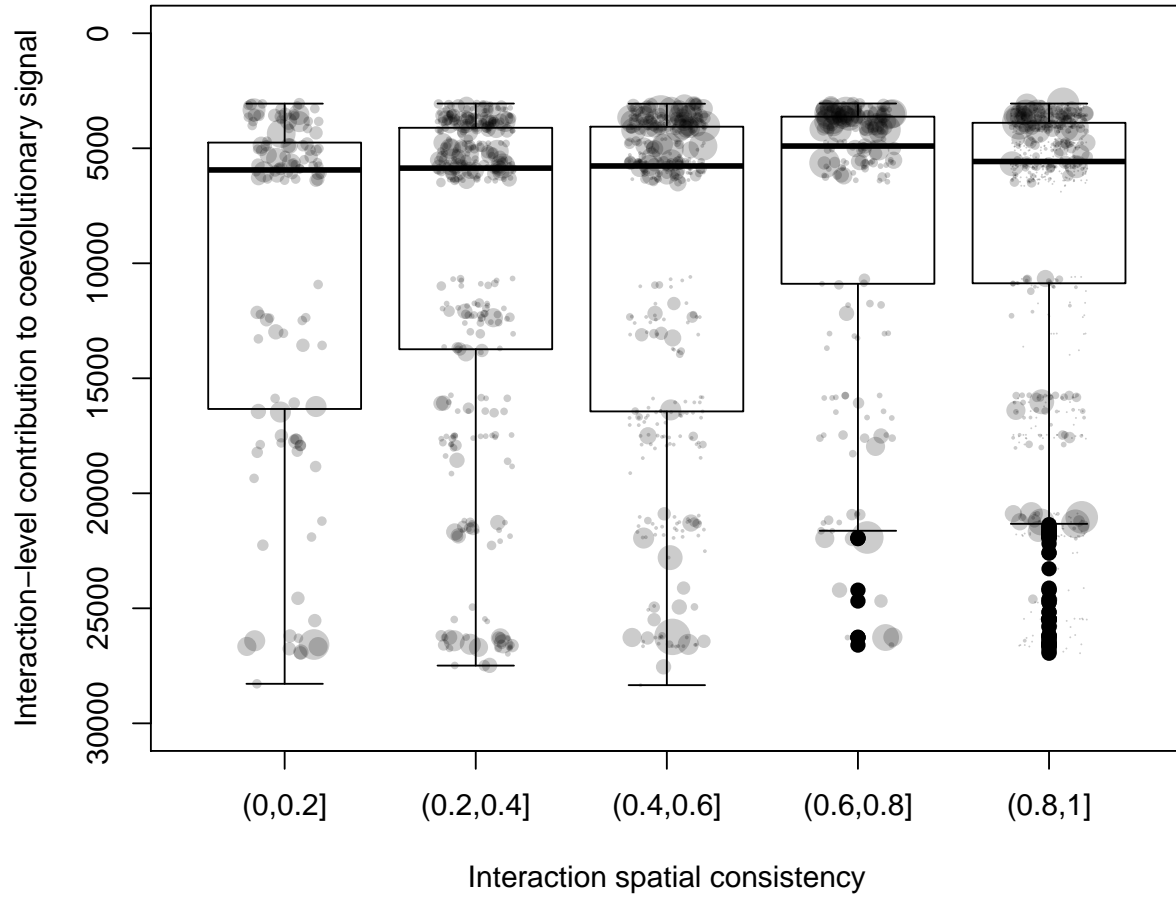


Figure 3: Spatial consistency of an interaction and its contribution to coevolutionary signal. Spatial consistency is defined as the probability of observing an interaction between two species given that they were observed to co-occur. Although statistically significant, there was no biologically meaningful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



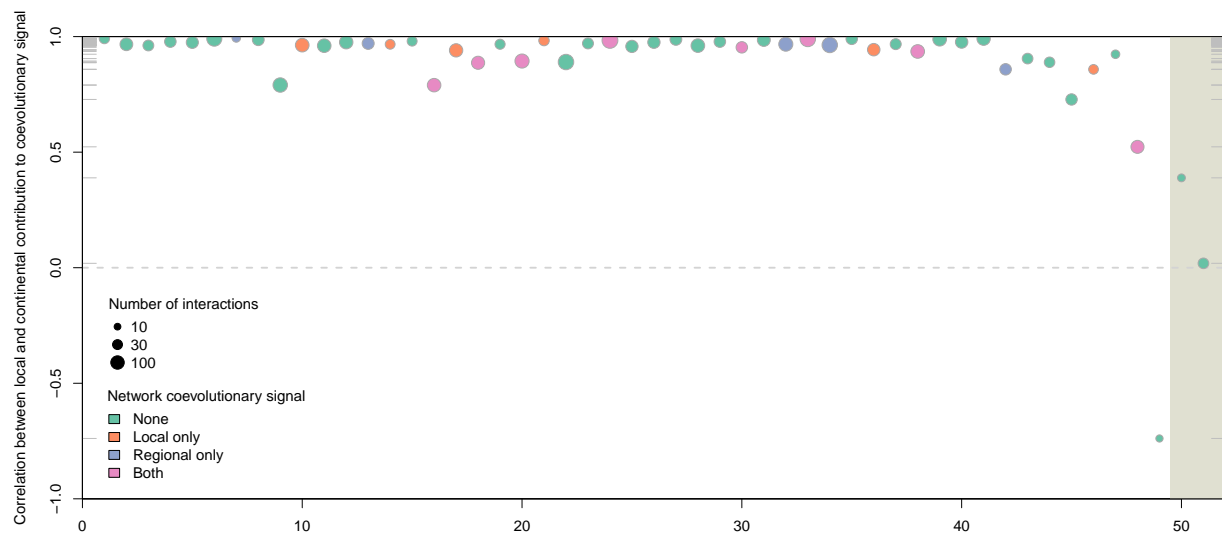


Figure 4: The contribution to coevolutionary signal of the interaction between two species is maintained across scales. For every site, we show the Pearson’s correlation between interaction-level coevolutionary signal in the continental network and the same in the local network. The size of each point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