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Interactions retain the co-phylogenetic matching that communities lost

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Both species and their interactions are affected by changes that occur at evolutionary time-scales, and shape both ecological communities and their phylogenetic structure. But because extent ecological community structure is contingent upon random chance, environmental filters, and local effects, it is unclear how much ecological signal local communities should retain. Here we show that, in a host–parasite system where species interactions vary substantially over a continental gradient, the ecological 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 phylogenetic signal. When considered in terms of the interplay between community ecology and coevolutionary theory, our results demonstrate that individual interactions are capable and indeed likely to show a consistent signature of past evolutionary history even when woven into communities that do not.

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Keywords species interactions host-parasites phylogenetic congruence

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). Likewise, palm species undergo changes in seed morphology in response to the extinction of bird dispersing their seeds (Galetti et al. 2013). Interactions can be lost, too, when phenologies of the species involved shift (Rafferty et al. 2015). Interactions are, in fact, so important that the existence of a species has been inferred by the fact that another species bore traits that matched no other known species: Kritsky (1991) relates the discovery of the moth *Xanthopan morganii*, with a proboscis famously over a foot long, which Darwin predicted would exist based on the phenology of local plant *Angraecum sesquipedale*. In addition, interactions, and the emergent structures they define, are distributed in similar ways across communities at both large or small scales (Jordano et al. 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 evolutionary dynamics of pairs of interacting species have been well described at macro-evolutionary (Van Valen 1973) and micro-evolutionary (Gandon et al. 2008) 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 et al. 2014).

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Historically, the evidence for shared evolutionary history in taxonomically diverse communities relied on the quantification of the degree of matching between the phylogenies of two sets of interacting organisms, accounting for the distributions of interactions across the phylogeny (Legendre et al. 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; Guimarães Jr et al. 2011; Nuismer et al. 2013). 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 (Desdevises et al. 2003; Diniz-Filho & Bini 2008; Vale & Little 2010). Consequently, many of the systems that have been described as exhibiting matching phylogenetic structure ultimately deviate from this last constraint, for a variety of factors. Nonetheless, detecting matching phylogenies for interacting clades indicates that their shared evolutionary history is long standing and is therefore suggestive that their extant ecological structure is an outcome of ancestral constraints and/or co-adaptation (Nuismer & Harmon 2014).

It is important to note further that discovering matching phylogenies do not mean that coevolutionary dynamics *sensu e.g* Thompson (1999) took place at any time. In fact, coevolution is not expected to necessarily result in matching phylogenies, nor are matching phylogenies only produced through coevolution (Poisot 2015). It follows that community-level measures of phylogenetic signal, while they *do* quantify how closely interactions are a product of phylogeny, do not allow to draw conclusions on coevolution. Nevertheless, *interaction*-level measures are useful, in that, when expressed as the contribution of interactions to the overall signal, allow to *compare* the importance of interactions across replicated communities. Communities from the same regional pool vary because (i) the local species pool is at best a subset of the regional species pool and (ii) the local interactions are at best a subset of the interactions in the regional community (Poisot et al. 2015). This implies that (i) the phylogenetic signal in the regional pool will be different from the signal in the local communities, and (ii) the phylogenetic signal across local communities will differ. Species sampling and variability of interactions, however, does no predict (i) how the phylogenetic 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 phylogenetic 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 mathcing between host and parasite trees (Balbuena et al. 2013), we show that locally sampled communities rarely show strong matching despite the fact that the overall system does at the continental scale. We then provide evidence to support the conclusion that the amount of phylogenetic matching within a local community is predictable based on the importance of interactions in the *regional* network. We finally show that the contribution of these interactions to phylogenetic matching is invariant across scales, and is unrelated to their tendency to vary across space. The lack of co-phylogenetic structure in local communities suggest that, while interactions are undeniably important for community assembly, they might be less so than abiotic factors.

METHODS

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 (Krasnov et al. 2012b) 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 co-phylogenetic matching at the continental level (Krasnov et al. 2012a). 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 et al. 2009);

The original dataset gives quantitative interaction strengths (expressed as an averaged number of parasites per species per host). In this system, quantitative interaction strengths 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. Therefore, to account for differential sampling effort—which cannot readily be quantified—and across site variations in abundance—which do not pertain to macro-evolutionary processes—we only study the networks' bipartite incidence matrices (that is, presence and absence of infection of hosts by the parasites).

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 which we will refer to as continental, regional, and local. Notably, the continental level summarizes the complete dataset whereas both the regional and local levels are location-specific scales.

The first, *continental* interaction data consists of the aggregated "metanetwork" which includes all documented interactions between species from the regional species pool (Poisot et al. 2012).

The second, *regional* interaction data accounts for differ-

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ent species composition across sites, specifically by testing whether sampling from the regional species pool affects co-phylogenetic matching. 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. This *regional* network is a baseline estimate derived from interactions within the species pool, and measures the effect of species sampling on co-phylogenetic matching.

The third, *local* interaction data also accounts for variation in the interactions between observed species, in addition to encompassing the above. In 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.

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 S_{ij} between species i and j is measured by dividing the number of locations in which both are present (C_{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 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 varies (Morales-Castilla et al. 2015). Therefore, the values of S_{ij} can only be defined for species that have been observed to *co-occur* at least once.

Quantifying co-phylogenetic matching We quantify the strength of co-phylogenetic matching in terms of the degree of matching between host and parasite phylogenies, given knowledge of extant species interactions (at varying spatial scales). We do so using the *PACo* method (Balbuena et al. 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 there phylogenetic signal in the species interactions across the entire network?) and the interaction-level signal (*i.e.*, what is the contribution of each interaction to the overall signal?). Strong values of the latter metric reflect *low* contributions to co-phylogenetic matching – interactions that contribute strongly to phylogenetic congruence have low *PACo* values. Importantly, and in contrast to previous methods such as *ParaFit* (Legendre et al. 2002), *PACo* also can be used to meaningfully quantify the contribution of every interaction to the network-level signal even in cases where the entire network shows no significant phylogenetic 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).

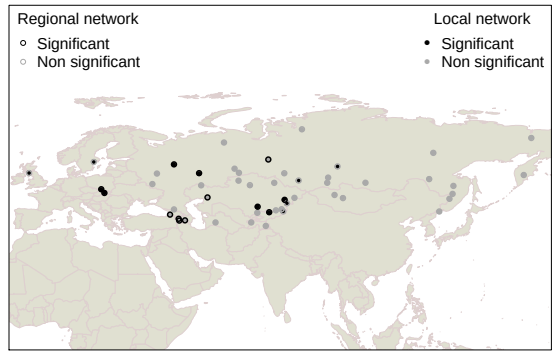

Figure 1 Spatial distribution of co-phylogenetic matching across the 51 sites. For each location, we indicate whether or not the structure of regional and local interaction networks is consistent with phylogenetic congruence. The colour of the circle corresponds to regionally significant or non-significant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

RESULTS AND DISCUSSION

Splitting the datasets at the continental, regional, and local levels delineates clear quantitative predictions. Should community assembly favor the co-occurence of evolutionarily linked species pairs, we expect that regional networks will have a high degree of phylogenetic matching compared with the continental one. In the contrary, a relatively lower phylogenetic matching would be indicative of a weaker selection for the co-occurence of evolutionarily tied species pairs. At the local scale, if interactions between species at matching phylogenetic positions are conserved, we would expect both a similar or higher level of phylogenetic matching between the local and the regional scale, and a positive relationship between the frequency of interaction and its overall importance for phylogenetic matching. In the contrary, if local assembly proceeds largely independently from the co-evolutionary history, the relative level of phylogenetic matching in local networks should be the same as in the regional networks through a sampling effect, but the frequency of interactions should bear no relationship to their importance in overall matching.

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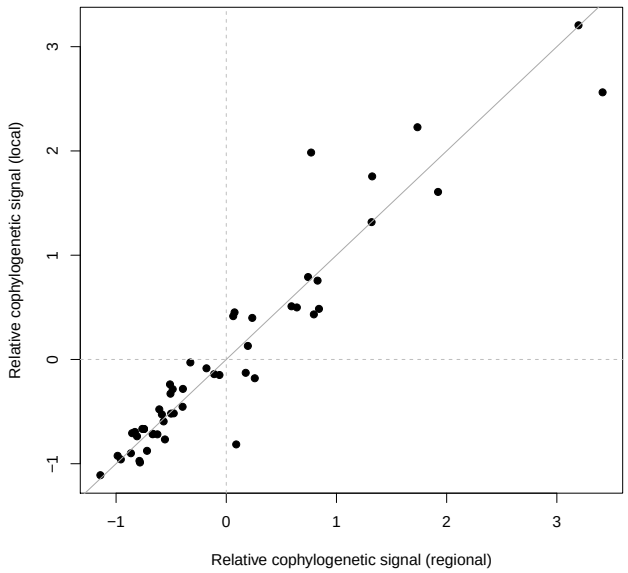

Figure 2 The regional and local networks have the same relative amount of co-phylogenetic matching. The values presented are the z-scores of the PACo statistic for the entire network, with the 1:1 relationship added.

Local and regional scale networks show no co-phylogenetic matching 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 co-phylogenetic matching, we should detect this signal at the continental scale but not locally. Out of 51 sites, 35 show no signal of co-phylogenetic matching at all, 11 show significant co-phylogenetic matching when using the regional interactions, and 12 show significant co-phylogenetic matching 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.

Local and regional scale networks have the same relative co-phylogenetic matching In Figure 2, we relate the relative (z-score transformed) degree of phylogenetic matching in the local and regional communities. The relationship between the two is linear (95% confidence interval for the correlation coefficient $0.914 - -0.971$). This fits with the hypothesis of local networks being assembled by a random sampling from regional networks: if the presence of selection to maintain pairs of species at matching positions in the phylogenies, the local networks should have a higher degree of phylogenetic matching (through the filtering acting against species pairs at dissimilar positions).

Co-phylogenetic matching 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 co-phylogenetic matching at the continental scale are also important for co-phylogenetic matching at the local and regional scales as well (Fig. 2A). Intriguingly, we also find that the distribution of individual interactions' contributions to co-phylogenetic matching is strongly conserved, regardless of the scale at which the interactions are quantified (Fig. 2B). Because interactions differ in their total contribution to co-phylogenetic matching, this implies that their distribution across networks (*i.e.* whether the local network contains a sample of strongly contributing, or weakly contributing, interactions) is what actually drives differences in overall co-phylogenetic matching. As such, network-level co-phylogenetic matching emerges directly from the properties of interactions and is not a property of the network itself.

Interactions contributing to co-phylogenetic matching are marginally more spatially consistent Beyond their contribution to co-phylogenetic matching, interactions also ultimately differ in how frequently they vary when the species involved co-occur (Carstensen et al. 2014; Olito & Fox 2015; Trøjelsgaard et al. 2015). This can happen, for example, when one of the partner is able to forage for optimal resources (Betts et al. 2015). Once more, the literature on host-parasite interactions assumes that the reason why some interactions are more frequent is because they reflect a significant past history of co-evolution (Guimaraes et al. 2007; 2010); that is, the ecological constraints emerge from the evolutionary conservatism. Using a weighted Pearson's correlation between the interaction frequency, interaction contribution to co-phylogenetic matching, and the number of observations of each interaction as the weight, we observe that this is marginally true ($\rho \approx -0.11$. $t \approx -5.09$ with weights; $\rho \approx -0.10$, $t \approx -4.6$ without; both significant at $\alpha = 0.05$). Results are presented in Fig. 3. Recall that the *negative* correlation here arises from the fact that high interaction-level values in PACo means *low* contribution to co-phylogenetic signal. Nevertheless, this result ought to be tempered by the fact that the R^2 of both regressions is close to 0.01. Consequently, the association between spatial consistency and contribution to co-phylogenetic signal, while statistically significant, explains so little variance of either quantities that it is likely of negligible biological importance. This implies that the spatial consistency of an interaction does not reflect its evolutionary past, but rather (possibly) extant ecological processes.

The contribution of interactions to co-phylogenetic matching is consistent across scales Ultimately, co-phylogenetic matching 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

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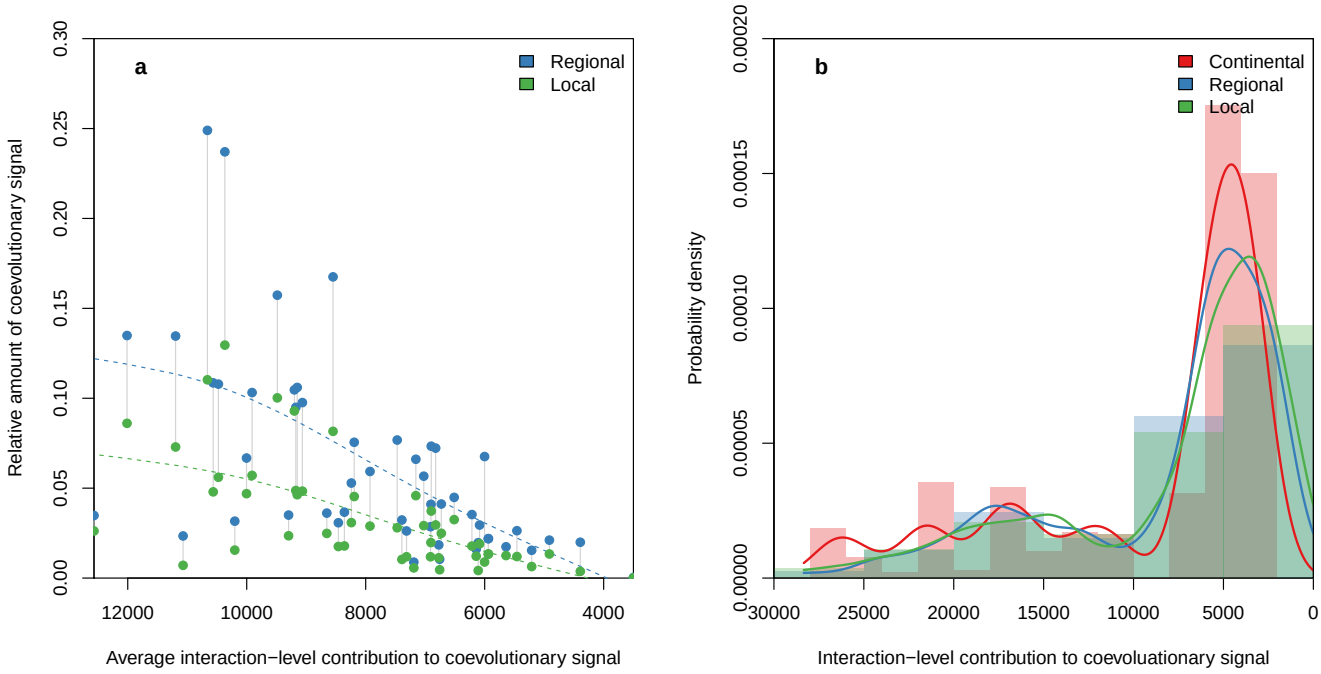

Figure 3 Distribution of co-phylogenetic matching at the network and interaction levels. **a**, Networks that have lower co-phylogenetic matching at the local or regional level are composed of interactions that on average contribute little to co-phylogenetic matching at the continental scale. co-phylogenetic matching is presented relatively to the continental level co-phylogenetic matching. 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 co-phylogenetic matching. Probability density was smoothed using a Gaussian kernel density estimator. Raw probability densities are shown as semi-transparent bars.

separate interaction to differ across scales as well. Instead, we observe here that interactions that contribute strongly to co-phylogenetic matching 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 co-phylogenetic matching Figure 5. Remarkably, this result implies that the remnants of co-phylogenetic inertia are still locally detectable in *individual interactions* even though shared evolutionary history regularly fails to leave its imprint on most local networks.

CONCLUSIONS

Overall, the results of our analyses demonstrate that there is a sizeable gap between our current understanding of host-parasite co-evolution as the basis of multi-species interactions, its phylogenetic consequences, and their applicability to ecological questions. Our results suggest that, while the continental-scale system might show a strong signal of past co-evolution (which was also reported, through different analyses, by other studies of this system), the quasi-entirety of this signal is lost when species and their interactions are filtered to assemble local communities. That there is no further loss of signal from the regional to the local scale strongly suggests that the loss of signal from the continental to regional scale is due to species sampling, that proceeds independantly of the evolutionary history of species pairs. It would seem that local species pools are driven more by the interaction between abiotic conditions and species tolerance, than they are by potential species interactions.

Local networks show little to no signal of co-phylogenetic matching, and the strength of co-phylogenetic matching that can be ascribed to the interactions 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. And yet, despite all the above, individual interactions are somehow able to maintain their co-phylogenetic matching even when the community they are woven into does not. Thinking more broadly, these discrepancies provide a clear roadmap for bridging the 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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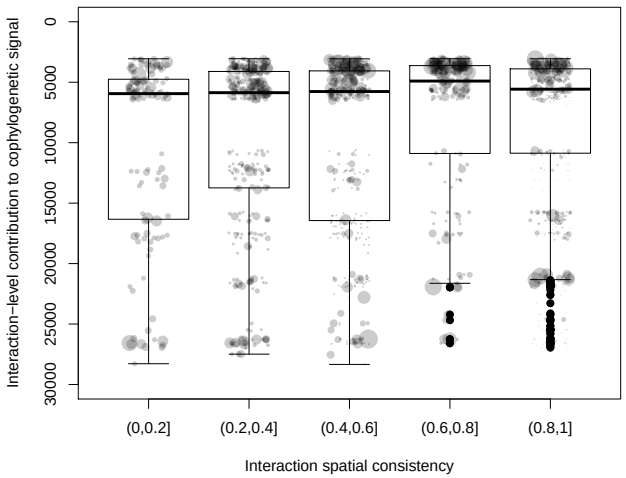

Figure 4 Spatial consistency of an interaction and its contribution to co-phylogenetic matching. Note that because *PACo* gives low scores to interactions with a strong contribution to co-phylogenetic matching, the y axis is reversed. Spatial consistency is defined as the probability of observing an 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 co-phylogenetic matching in the continental network ($R^2 \approx 0.01$, $\rho = -0.1$, $p \leq 10^{-5}$).

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REFERENCES

Balbuena et al. (2013). PACo: A novel procrustes application to cophylogenetic analysis. *PLoS ONE.* 8:e61048.

Benkman et al. (2003). Reciprocal selection causes a coevolutionary arms race between crossbills and lodgepole pine. *Am Nat.* 162:182–94.

Betts et al. (2015). Pollinator recognition by a keystone tropical plant. *Proceedings of the National Academy of Sciences of the United States of America.* 112:3433–8.

Canard et al. (2014). Empirical evaluation of neutral interactions in host-parasite networks. *The American Naturalist.* 183:468–79.

Carstensen et al. (2014). Beta diversity of plant-pollinator networks and the spatial turnover of pairwise interactions. *PLoS ONE.* 9:e112903.

Cavender-Bares et al. (2009). The merging of community ecology and phylogenetic biology. *Ecol Lett.* 12:693–715.

Combes. (2001). Parasitism - the ecology and evolution of intimate interactions. University Of Chicago Press;

Desdevises et al. (2003). Quantifying phylogenetically structured environmental variation. *Evolution.* 57:2647–52.

Diniz-Filho & Bini. (2008). Macroecology, global change and the shadow of forgotten ancestors. *Glob Ecol Biogeogr.* 17:11–7.

Eklof et al. (2011). Relevance of evolutionary history for food web structure. *Proc R Soc B Biol Sci.* 279:1588–96.

Fahrenholz. (1913). Ectoparasiten und abstammungslehre. *Zool Anz.* 41:371–4.

Galetti et al. (2013). Functional extinction of birds drives rapid evolutionary changes in seed size. *Science.* 340:1086–90.

Gandon et al. (2008). Host-parasite coevolution and patterns of adaptation across time and space. *J Evol Biol.* 21:1861–6.

Guimarães Jr et al. (2011). Evolution and coevolution in mutualistic networks. *Ecol Lett.* 14:877–85.

Guimaraes et al. (2007). Interaction intimacy affects structure and coevolutionary dynamics in mutualistic networks. *Curr Biol.* 17:1797–803.

Hembry et al. (2014). Coevolution and the diversification of life. *The American Naturalist.* 184:425–38.

Jordano et al. (2003). Invariant properties in coevolutionary networks of plant-animal interactions. *Ecol Lett.* 6:69–81.

Krasnov et al. (2012a). Phylogenetic signal in module composition and species connectivity in compartmentalized host-parasite networks. *The American Naturalist.* 179:501–11.

Krasnov et al. (2012b). Data from: Phylogenetic signal in module composition and species connectivity in compartmentalized host-parasite networks.

Kritsky. (1991). Darwin's madagascan hawk moth prediction. *American Entomologist.* Oxford University Press (OUP); 37:206–10.

Legendre et al. (2002). A statistical test for host-parasite coevolution. *Syst Biol.* 51:217–34.

Morales-Castilla et al. (2015). Inferring biotic interactions

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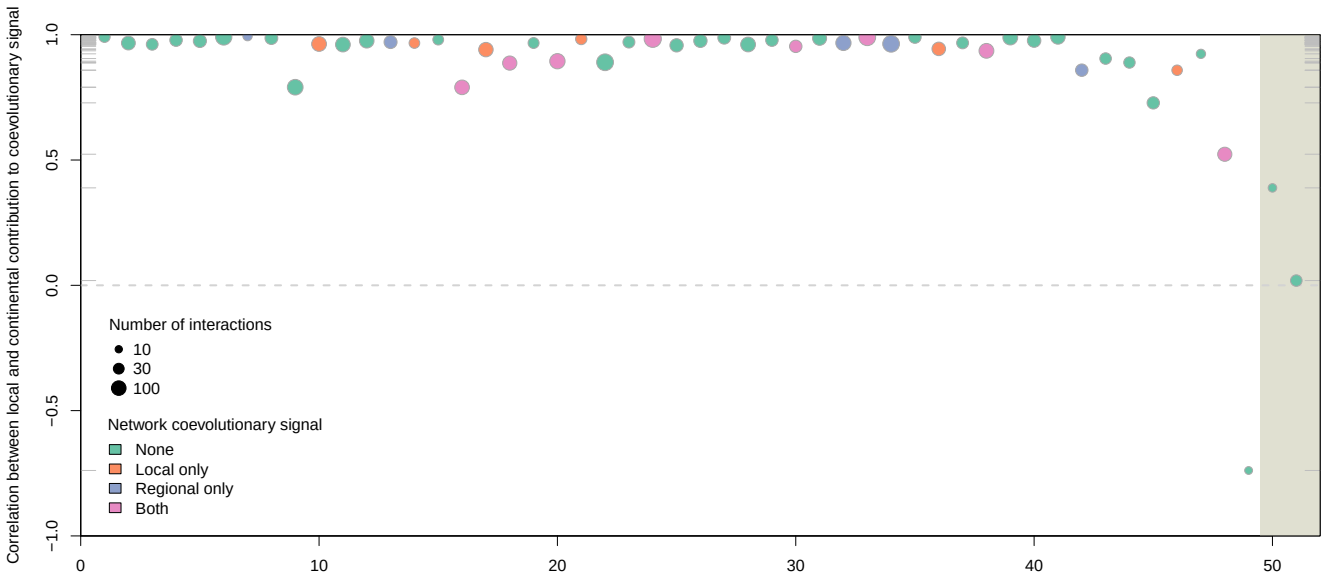

Figure 5 The contribution to co-phylogenetic matching of the interaction between two species is maintained across scales. For every site, we show the Pearson's correlation between interaction-level co-phylogenetic matching in the continental network and the same in the local network. The size of each point is proportional to the size of the network, and all correlations are significant at $\alpha = 0.05$ except in the grey shaded area.

from proxies. *Trends in Ecology & Evolution.* Elsevier BV;

Mouquet et al. (2012). Ecophylogenetics: Advances and perspectives. *Biol Rev.* 87:769–85.

Nuismer & Harmon. (2014). Predicting rates of interspecific interaction from phylogenetic trees. *Ecol Lett.*:n/a–a.

Nuismer et al. (2013). Coevolution and the architecture of mutualistic networks. *Evolution.* 67:338–54.

Olito & Fox. (2015). Species traits and abundances predict metrics of plantpollinator network structure, but not pairwise interactions. *Oikos.* 124:428–36.

Poisot. (2015). 23 when is co-phylogeny evidence of coevolution? *Parasite Diversity and Diversification: Evolutionary Ecology Meets Phylogenetics.* Cambridge University Press;420.

Poisot et al. (2012). The dissimilarity of species interaction networks. *Ecol Lett.* 15:1353–61.

Poisot et al. (2015). Beyond species: Why ecological interaction networks vary through space and time. *Oikos.* 124:243–51.

Rafferty et al. (2015). Phenological shifts and the fate of mutualisms. *Oikos.* Wiley Online Library; 124:14–21.

Rezende et al. (2007). Non-random coextinctions in phylogenetically structured mutualistic networks. *Nature.* 448:925–8.

Stouffer et al. (2012). Evolutionary conservation of species' roles in food webs. *Science.* 335:1489–92.

Thompson. (1999). The raw material for coevolution. *Oikos.* 84:5–16.

Trøjelsgaard et al. (2015). Geographical variation in mutualistic networks: Similarity, turnover and partner fidelity. *Proc R Soc B.* 282:20142925.

Vale & Little. (2010). CRISPR-mediated phage resistance and the ghost of coevolution past. *Proc R Soc B Biol Sci.*

Van Valen. (1973). A new evolutionary law. *Evol Theory.* 1:1–30.

Verneau et al. (2009). Lessons from parasitic flatworms about evolution and historical biogeography of their vertebrate hosts. *C R Biol.* 332:149–58.

(2010). Biogreography of host-parasite interactions. Morand, Krasnov, eds. Oxford: Oxford University Press;