Beta and phylogenetic diversities tell complementary stories about ecological networks biogeography

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Abstract: The beta-diversity of interactions between communities does not necessarily correspond to the differences related to their species composition because interactions show greater variability than species co-occurrence. Additionally, the structure of species interaction networks can itself vary over spatial gradients, thereby adding constraints on the dissimilarity of communities in space. We used published data on the parasitism interaction between Soricomorpha and Rodentia in 51 regions of the Palearctic to investigate how beta-diversity of networks and phylogenetic diversity are related. The networks could be separated in groups based on the metrics that best described the differences between them, and these groups were also geographically structured. We also found that each network beta-diversity index relates in a particular way with phylogenetically community dissimilarity, reinforcing that some of these indexes have a strong phylogenetic component. Our results clarify important aspects of the biogeography of hosts and parasites communities in Eurasia, while suggesting that networks beta-diversity and phylogenetic dissimilarity interact with the environment in different ways.

Introduction

Ecological networks are complex units that incorporate many aspects of the biodiversity multidimensional fabric, such as species identity, interactions, and shared coevolutionary history. Because of that, investigating the biodiversity and the biogeography of communities through species interactions can be highly informative. A local network carries biogeographical and historical characteristics of the regional pool of species and interactions, given that it is a subset of a regional metaweb (Holt 2002). However, some of these characteristics (such as the phylogenetic signal of interactions (Desdevises et al. 2015; Boris R. Krasnov, Morand, and Poulin 2015)) can be lost or modified in different ways due to the environmental filtering that occurs in the community formation process, resulting in a non-correlative variation of ecological networks components (Poisot and Stouffer 2018; Poisot et al. 2016).

The differences between ecological interactions, in turn, are more prone to variability and are always equal or greater than the differences in species composition, and, therefore, are more informative than the number of species or functional diversity alone (Poisot et al. 2017). This is because ecological interactions are conditional to characteristics of the occurrence of two or more given species. For instance, the probability of interaction may be modified by environmental changes that affect the metabolic rate of organisms (Rall et al. 2012), by changes in their habitats (Tylianakis and Morris 2017) or by community's phylogenetic structure (Coelho, Rodrigues, and Rangel 2017) – which, in turn, varies with the abundance and specialization of species involved (Canard et al. 2014; Tylianakis and Morris 2017). Additionally, environmental conditions also have direct effects over the reproductive success of species, changing their populational parameters (such as birth and death rates). In this sense, environmental gradients can change the frequency of interactions through direct influence on species' characteristics and population abundance, which, on the other hand, are also affected by interactions (Poisot et al. 2017). For example, pathogens can develop adaptations that protect them from the immune system of their hosts (an example of the effect of an interaction over species' characteristics), or a predator can elevate the death rate of its prey population, therefore altering its abundance (an example of the effect of an interaction over populations' characteristics). Other examples are the effect of the environment on the production of secondary metabolites that exert selective pressure on the organisms that interact with certain plants (Muola et al. 2010), how the geographical variation of functional characteristics generates changes in the interaction network and in species composition (König, Wiklund, and Ehrlén 2014; CHA et al. 2015), as well as the substitution of species along environmental gradients, variation in reproductive success and in the trophic network, or, yet, how the population density regulated by the environment can change the sign of an interaction (Bruder et al. 2017; Doxford, Ooi, and Freckleton 2013; Kaplan and Eubanks 2005). The differences between communities related to interactions may be, but not necessarily are, correspondent to those related to their species composition (Poisot, Stouffer, and Gravel 2014).

As well as several other biodiversity metrics, the indexes that measure characteristics of ecological networks can also respond to environmental gradients in space and time (Baiser et al. 2019; Gravel et al. 2019). For example, the speed of climate change can reduce modularity (how much a network is partitioned into nuclei of closely connected species) and increase nestedness (how much specialist species interact with a subset of species with which generalists interact) in pollination networks (Dalsgaard et al. 2013). One of these indexes that carries important historical information is the phylogenetic diversity, measured as the sum of the lengths of the phylogeny branches that include all the species that interact in a community. Dispersion and speciation events are the main factors that affect the phylogenetic diversity of a network of ecological interactions (Coelho, Rodrigues, and Rangel 2017; Sebastián-González et al. 2015; Trøjelsgaard and Olesen 2013). Moreover, phylogenetic diversity is very sensitive to addition of species and may indicate, for example, the extent of impacts caused by an invasive species in a community (Davies and Buckley 2011). Therefore, beta diversity (the difference in the composition of communities) and the phylogenetic diversity of interaction networks are related, and both can respond to environmental variation in different ways. For example, by acting as an "environmental filter," the environment can affect the substitution of species by selecting their functional characteristics, and these, in turn, can limit the impacts of environmental conditions in substituting interactions (Carnicer, Jordano, and Melián 2009), suggesting that functional diversity also plays an important role in the stability of ecological networks. Investigating the relationship between these characteristics can help us understand why ecological networks vary in space.

Interaction networks between parasites and hosts have great potential to be used as study systems in the geographic variation of interactions, especially those involving ectoparasites. Because of the particular type of association between parasites and hosts, the dissimilarity of these interactions networks reflect not only the environmental differences, but also the replacement of the host species (Eriksson et al. 2019; Boris R. Krasnov et al. 2005; Poulin and Krasnov 2010). Nonetheless, the association between parasites and hosts is often the result of the evolutionary history of the groups, and this history can result in a non-neutral contribution of these species to the beta diversity of these communities (Poisot et al. 2012). Based on a parasite-host system distributed over a vast biogeographic region, we identified similar numerical and geographical associations between the phylogenetic diversity and the dissimilarity of species composition and interactions of ecological networks. This result adds to our previous understanding of biodiversity distribution and help us tell a more complete story on the biogeography of ecological communities.

Methods

We used the Hadfield et al. (2014) data on the parasitism interaction between Soricomorpha and Rodentia in 51 regions of the Palearctic to investigate how beta-diversity of networks and phylogenetic diversity are related. This publication gathers occurrence records of 536,000 mammal individuals of 121 species, 1,692,000 individuals from 206 flea species that occurred in those mammals, and the interactions between them (Hadfield et al. 2013). Original data is available at Data Dryad (`http://dx.doi.org/10.5061/dryad.jf3tj`) and interaction data is available at `mangal` database (`http://mangal.io`).

The authors also used molecular and morphological traits of species to retrieve the phylogenetic relationships between species. We used the resulting trees to measure the phylogenetic community dissimilarity (PCD) of both hosts and parasites metacommunities using the function `pcd` of the package `phyr`, in R (Li et al. 2020; R Core Team 2018). To do that, we discarded sites with no correspondents taxa in the phylogenetic trees. The output of the `pcd` function can be divided in compositional (PCDc) and phylogenetic (PCDp) aspects of beta-diversity, which were summarized through a Principal Component Analysis (PCA) and grouped by their own *k-means* for both parasites and hosts.

Because of particular characteristics such as communities' species composition and relationship with local environment, the differences in ecological networks can be due to species turnover, links established by shared species or a combination of both. In this sense, networks beta-diversity indexes are composed by their characteristics on species composition and interactions both on local and regional networks (Poisot et al. 2012). Here we assessed three indexes that summarize these information in different ways:

1. βs: this index corresponds to the differences on species composition between networks. A high βs means solely a high species turnover (Koleff, Gaston, and Lennon 2003).
2. βos: this index represents the differences on interactions between shared species. It is the component of networks dissimilarity only related to interactions, not species identity (Canard et al. 2014).
3. βwn: this summarizes the global differences between all networks in a metaweb, calculated as $\beta_w n = \beta_o s + \beta_s t$. It has two components: the difference in interactions between shared species (βos) and the difference in interactions due to species turnover βst. Therefore, βos can not assume values higher than βwn (Canard et al. 2014).

These measures were calculated using the `EcologicalNetworks.jl` and `Mangal.jl` modules in Julia (Poisot et al. 2020; Poisot, Banville, and Dansereau 2020; Bezanson et al. 2017) and summarized with the `KGL11` function, which calculates the Sørensen index of beta-diversity (Koleff, Gaston, and Lennon 2003). βs was the only metric calculated separately for hosts and parasites because it represents their taxonomic diversities. The dissimilarity matrices resulting from this analysis represented, therefore, the differences between networks considering each of the indexes described above. In order to use these matrices on the following analyses as a single variable, we performed a PCA on each matrix and selected the first component of each. A subsequent PCA and *k-means* analysis on a combined matrix of these variables allowed us to investigate how they co-vary among networks.

Results & Discussion

Communities can be grouped according to network beta-diversity.

The beta-diversity indexes described the dissimilarity of local networks in different ways across the metacommunity. In our case these differences were very prominent, making it possible to group communities by their interactions dissimilarity decomposition.

The first two axes of the Principal Component Analysis performed on the network beta-diversity indexes, which explain 95.5% of the variation of the data, separates the 50 networks (those with corresponding species in the phylogenetic trees) in those that have more similar βs, βos and βwn values (fig. 1). This separation is more explicit between βs and βwn, and more diffuse for βos, which is aligned to the assumption that βs and βwn are only indirectly related, while βos have a more proximate relationship both with βwn and βs. The fact that the networks grouped by βs values are so different from those grouped by βwn may suggest that the turnover of species in the first group causes loss of links through loss of co-occurrence, while in the former group this turnover is translated into new connections. The βos group, however, would be composed by communities that change less in species composition, but more in ecological interactions.

Because βs and the species composition of the phylogenetic community dissimilarity (PCDc) can be interpreted in the same way, a Principal Component Analysis of PCDc would provide a closer look to the βs metric. Our results suggest that, from a species composition point of view, parasites communities are much more similar across the metaweb than hosts, that can be more easily described in three main groups (fig. 1 D and fig. 1 E, respectively). The diversity of fleas can be much more uniform in space because it is common that a single host interacts with more than one species of parasites. In this particular case, only a few fleas communities have a distinguished species composition and can be grouped together.

On the other hand, the three groups of the phylogenetic component of PCD (PCDp) for both hosts and parasites are distinct: the diffuse group that appears in parasites' PCDc does not repeat on PCDp. Additionally, both clades are arranged similarly in the Principal Components space, with groups 2 and 3 being more alike than group 1. This may be a reflex of the biogeographic history of communities, where one group is ancestral to the other two.

Each beta-diversity index relates in a particular way with phylogenetically community dissimilarity (PCD).

As expected, βs and PCDc are proxies for each other both for hosts and parasites, while PCDc is inversely correlated with βwn (fig. 2). Communities with a high βs value are very different from those around them, and the change in species composition could also represent a shift in the links inside these networks either because new species will probably explore different ranges of ecological niche or because the loss of species would also represent a loss of interaction. These changes in links inside networks are represented by βos, and its relationship with both PCDc and PCDp is highly variable (fig. 3 and fig. 5).

Because any change in species composition highly affects phylogenetic diversity, βs is also positively correlated with PCDp (fig. 3). Communities with high values for any of those metrics are located in regions with expected higher biodiversity (fig. 4 and fig. 5), and this may indicate that the biogeographical history of these communities are more related to migration than diversification of local lineages (Davies and Buckley 2011). Therefore, networks with

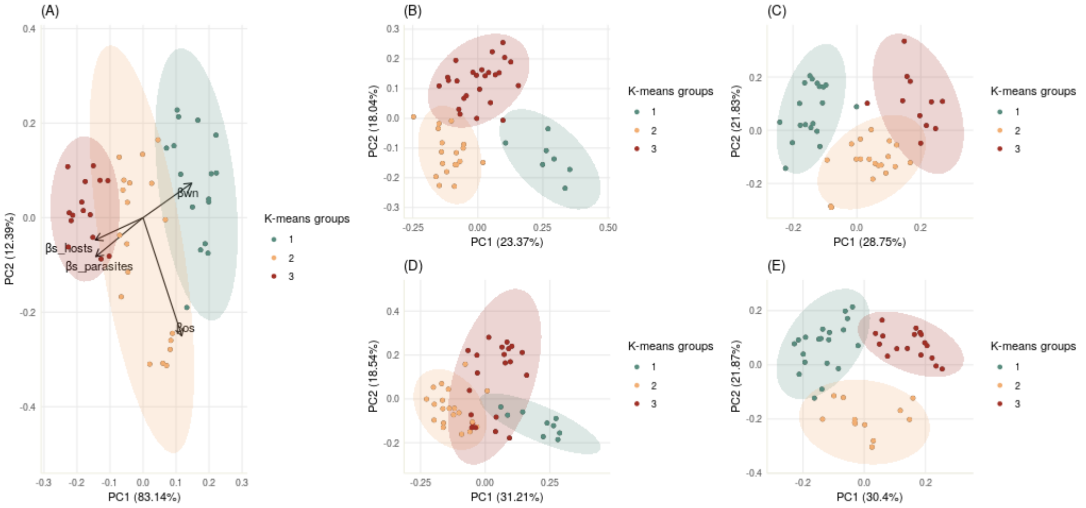


Figure 1: Principal Component Analysis of networks beta-diversity metrics and projection of local networks. For the dataset used here, networks are clearly described by three dimensions of beta-diversity: while βs captures part of the variation that is complementary to that captured by βwn, βos describes a completly different dimension of the data. (A) PCA of networks beta-diversity metrics βs, βwn and βos; PCA of the phylogenetic component of PCD (PCDp) for fleas (B) and rodents (C); PCA of the compositional component of PCD (PCDc) for fleas (D) and rodents (E).

high PCDp also represent communities with lower ecological redundancy and higher functional diversity because it indicates that the species turnover is happening between species phylogenetically distant.

On the other hand, networks that are better represented by βwn - i.e., those which differences between them are significantly smaller than the differences in relation to the metaweb - are also phylogenetically similar, varying always inside a limited range of small dissimilarity (both with PCDc and PCDp). Because these communities also have low values of βs, indicating less frequent species turnover, this dissimilarity is due to different links between shared species. This result may reflect two possible scenarios:
1. In similar communities with low phylogenetic diversity (shorter branch lengths) the turnover of species could be adding very ecologically similar lineages, which leads to different interactions to prevent local extinction through competition.
2. In similar communities with high phylogenetic diversity (longer branch lengths) the species turnover may have been a result of invasion and migration, which may lead to opportunistic interactions.

This is also illustrated in fig. 2 and fig. 3 on scatterplots of βos vs. PCD: networks that differ little in phylogenies have a broader range of values of βos, while highly phylogenetically distinct newtorks only have very low values of βos - meaning that, for communities with high values of PCD, the few species that are shared interact in the same way. Additionally, because those same communities also have low values of βwn (i.e., they are very similar to the overall metaweb) and high values of βs (i.e., high species turnover), the interactions are probably being conserved also when species are replaced, like when two species that are phylogenetically distant replace each other in the same ecological function.

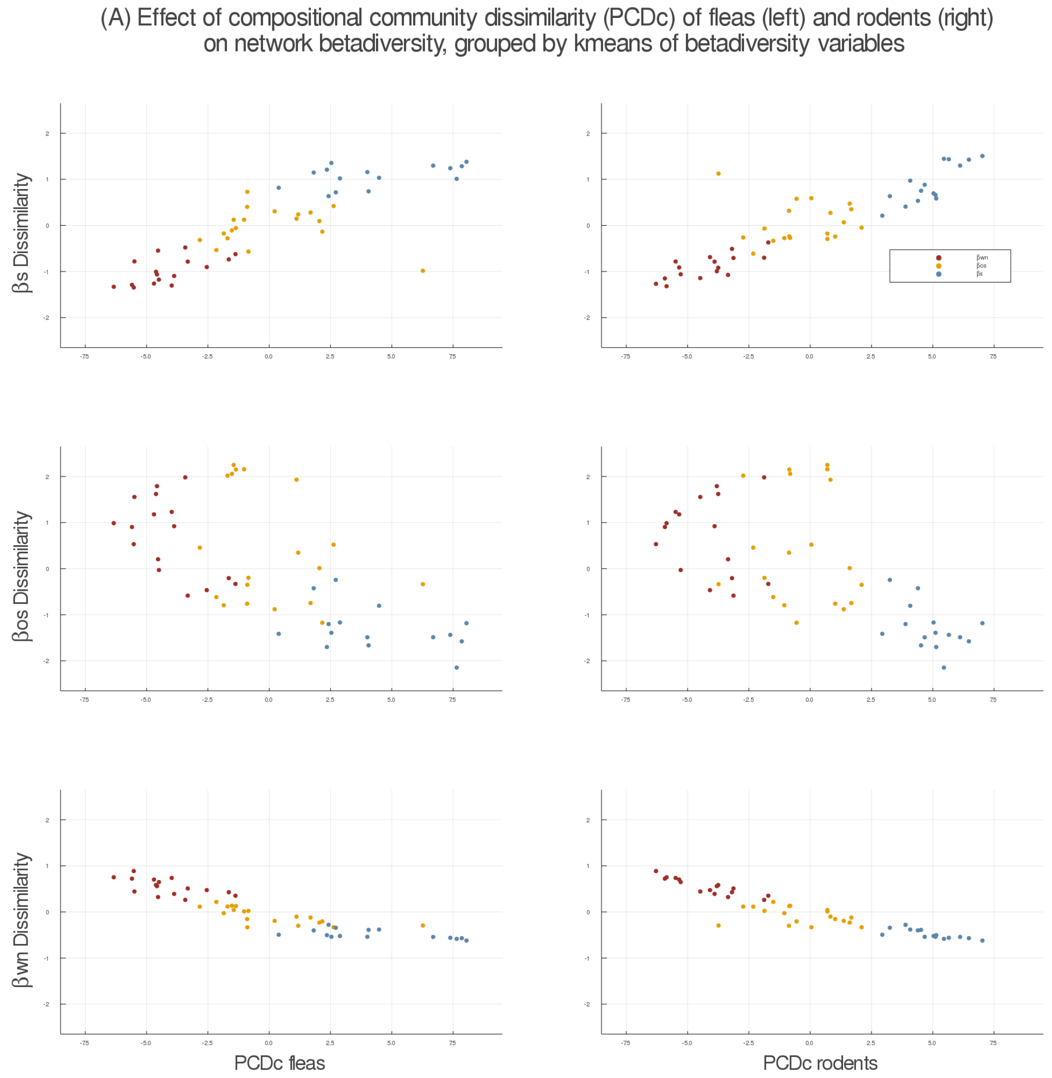


Figure 2: Effects of the compositional element of phylogenetic diversity dissimilarity on network beta-diversity for both parasites (left) and hosts (right). The colours correspond to the groups described on fig. 1. Networks with higher values of PCDc are taxonomically more distinct and therefore have higher values of βs and lower values of βos because they do not share many species.

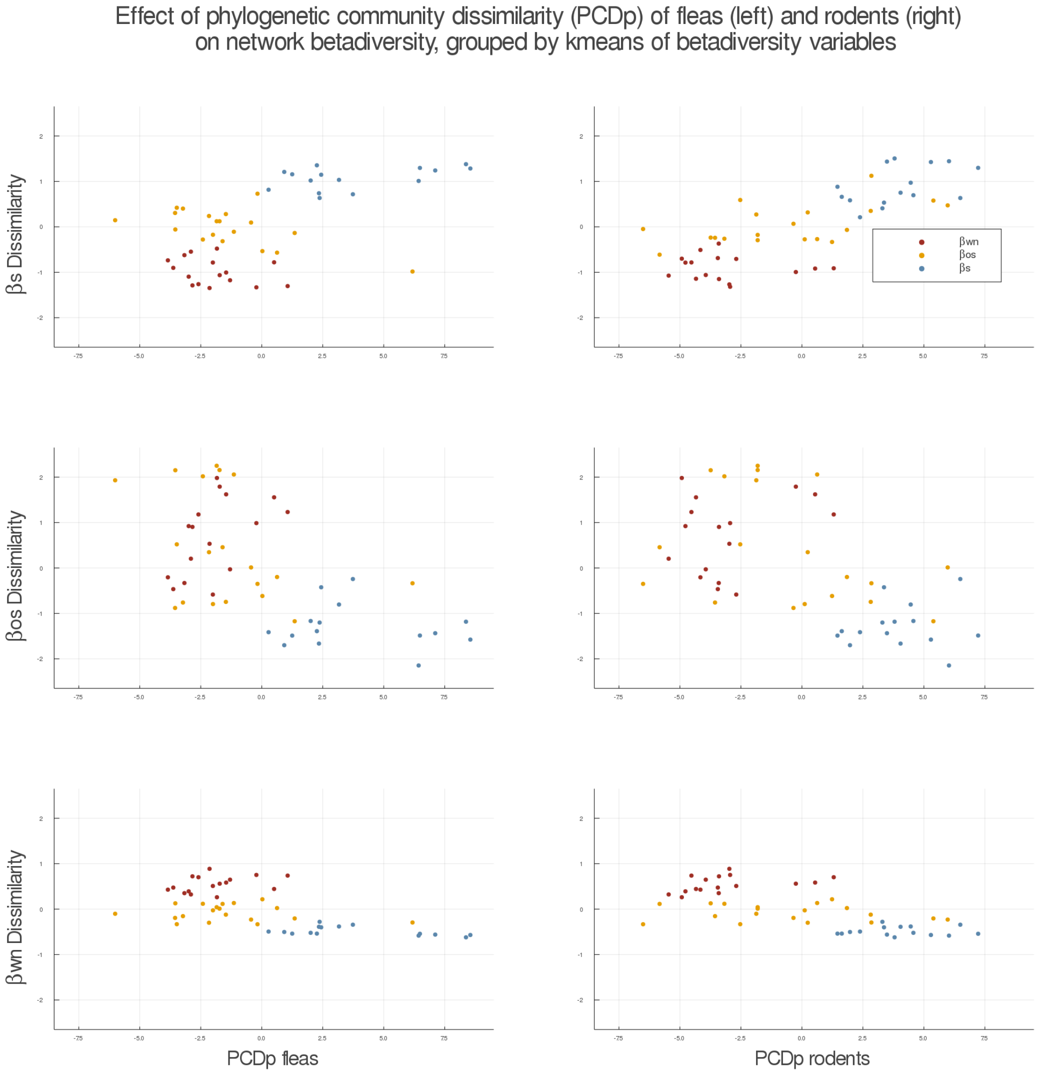


Figure 3: Effects of the phylogenetic component of the phylogenetic diversity dissimilarity on network beta-diversity for both parasites (left) and hosts (right). The colours correspond to the groups described on fig. 1. Networks with higher values of PCDp are phylogenetically more distinct, and therefore have lower values of βos (because they do not share many species). Networks better represented by βwn and βos are less distinguished on this aspect, but usually have lower values of PCDp.

The separation of communities by components of beta-diversity was also observed geographically

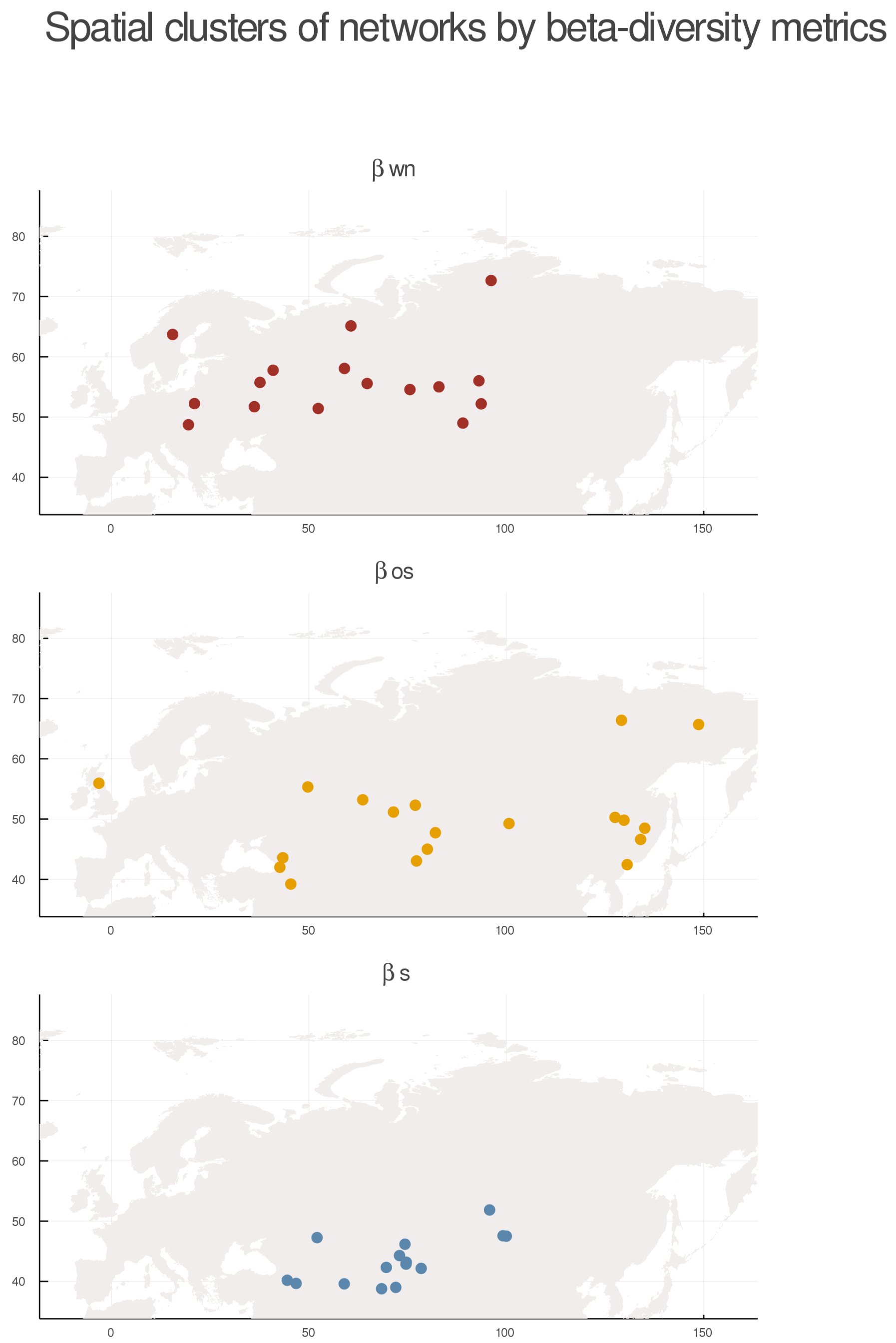
There is a gradual transition between networks that were better described by turnover of species, clustered in central south Eurasia, to those more unique compared to the metaweb, spread in the north (fig. 4). The regional species pool is expected to be more diverse towards the tropics, and therefore local networks have a higher chance to have different species composition, which results in a strong contribution of βs for networks beta-diversity. Because of the high diversity, species are functionally "packed," and although some species could have more generalist interactions, they would rarely do so, in order to avoid competition. Heading north, species turnover would be less frequent due to a decrease in regional species richness, and now networks have more shared species. They start to "unpack" and establish interactions with other remaining species, and therefore the βos component of beta-diversity explains better why networks are different. The third group of networks, characterized by a high value of βwn, is also composed by phylogenetically similar communities (as seen in fig. 3). Because the species richness is even lower, any change in composition can have a high impact on interactions. Therefore, the βos component is still very important, but now differences in interactions due to species turnover contribute much more to networks' beta-diversity.

The phylogenetic community dissimilarity of networks was also geographically grouped, and in the region where βs was more important, there was a very distinguished group for both fleas' and rodents' phylogenetic dissimilarity (fig. 5). The two other groups are differently arranged in space: PCDc groups have a similar latitudinal distribution, but different longitudinal ranges, while PCDp groups are the opposite. This distribution of phylogenetic groups highlight the uniqueness of the southern-central set of communities, which suggests historical isolation of species. Additionally, the purely phylogenetic component of PCD reinforces the geographic distribution of beta-diversity metrics as seen in fig. 4, with one group largely spread in the north - occupying a diverse range of environments - and two other groups restricted to latitudes under 60° (fig. 5).

Conclusion

The conspicuous association - both numerical and geographical - between the evolutive history of species and networks' beta-diversity properties clarifies important aspects of the biogeography of hosts and parasites communities in Eurasia. For example, the longitudinal PCDc clusters separation roughly coincide with the presence of the Ural Mountains. From this point of view, considering the longitudinal spread of PCDp, the history of both hosts and parasites seems to have a clear path of migration and diversification from south-central Eurasia towards the north. This history is also sustained by the metaweb beta-diversity metrics: with a distinguished βs group at the south of the Ural Mountains suggesting higher species richness and common origin, followed towards north by gradual changes in interactions and composition, they sum up to the information unveiled by PCDp to describe a very likely biogeographic history.

By describing how the phylogenetic differences between networks vary in the same way within groups, this result seems to reinforce previous findings that there is no co-phylogenetic matching between regional and local networks (Poisot and Stouffer 2018). If networks co-varied in continental scale in the same way they co-vary in local scale, our analyses would not detect the groups illustrated in fig. 5.


Spatial clusters of networks by beta-diversity metrics

β wn

β os

β s

Figure 4: Spatial distribution of beta-diversity metrics. The groups detected in fig. 1 are also geographically distinguished

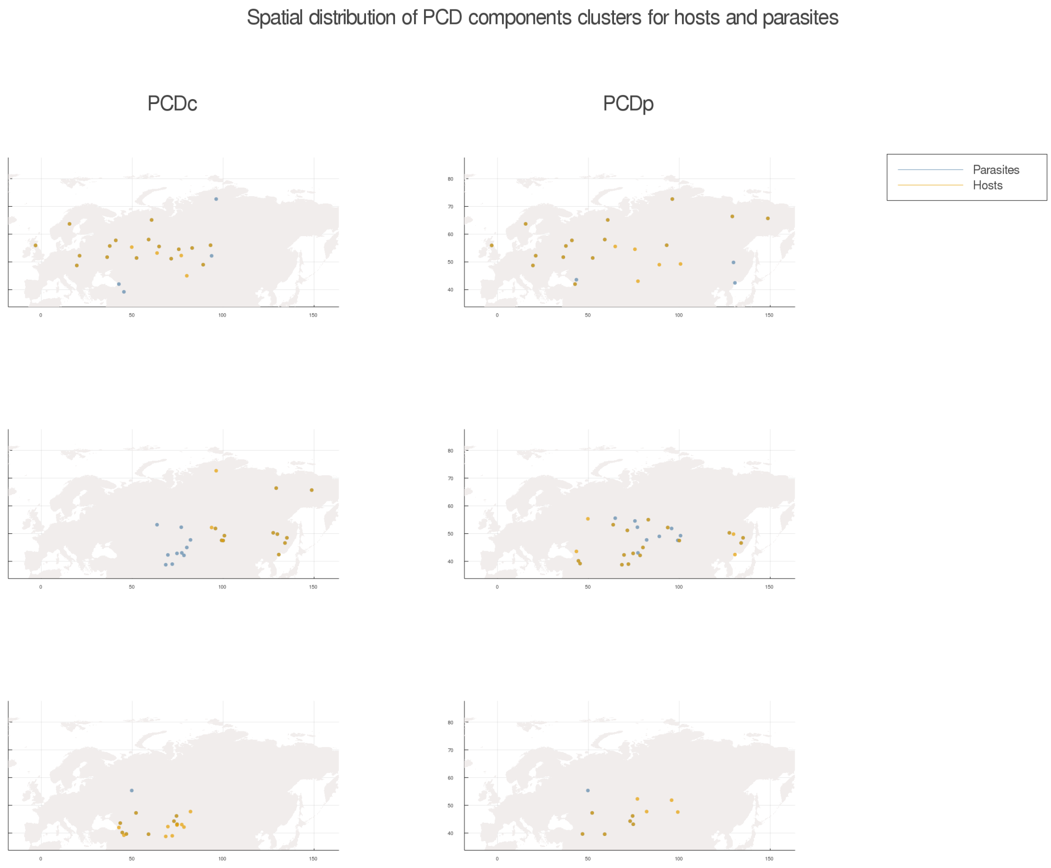


Figure 5: Spatial distribution of PCD components. Again, a distinct PCDc cluster (as seen on the third map of the left column) matches the cluster for which βs metric is more important.

Finally, this paper highlights how beta-diversity and phylogenetic dissimilarity are related to each other, and sheds light on the possibility that they interact with the environment in different ways. While βs seems to be connected to environmental uniqueness and geographical barriers, βos and βwn better reflect migration processes and evolutive trajectories. As stated at the beginning of this text, ecological networks are valuable, multidimensional lenses through which we can investigate biodiversity and its history. Although we did not account for properties such as phenology and natural history aspects of species, we did find that small scale processes such as species interactions can be integrated in large scale investigations and can have a stamp in macroecological processes.

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