

Beta and phylogenetic diversities tell complementary stories about ecological networks biogeography

Research Article

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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 fleas and small mammals 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 threads of the fabric of biodiversity, namely species identity, interactions and shared coevolutionary history. Investigating the structure and the biogeography of communities through species interactions can therefore be highly informative. Local networks carry a record of both biogeographical and historical features of the regional pool of species and interactions, as they are subsets of a regional metaweb (Holt, 2002), and so result from the fact that species both co-occur and interact. However, some of these characteristics can be lost over time, in response to local ecological pressure or random change. This is notably true of the co-phylogenetic signal of interactions (Desdevises *et al.*, 2015; Krasnov *et al.*, 2015), which can be eroded by environmental filtering during community assembly. This would result in a non-correlative variation of ecological networks components (Poisot *et al.*, 2016; Poisot and Stouffer, 2018).

Dissimilarity of species interactions is always equal to, or greater than, the differences in species composition, because there cannot be an interaction without the presence of both partners. Therefore, interactions can be more informative than the species richness or functional diversity alone (Poisot *et al.*, 2017). 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 *et al.*, 2017) – which, in turn, varies with the abundance and specialization of species involved (Canard *et al.*, 2014; Tylianakis and Morris, 2017), but is not captured by looking solely at species composition.

Environmental conditions also have direct effects over species fitness. 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.*, 2014). For example, the environment can affect 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 *et al.*, 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 (Kaplan and Eubanks, 2005; Doxford *et al.*, 2013; Bruder *et al.*, 2017).

Due to all independent factors that can determine their occurrence, the differences between communities related to interactions may be, but not necessarily are, correspondent to those related to their species composition (Poisot *et al.*, 2014), and therefore the indexes that measure characteristics of ecological networks can also respond to environmental gradients in space and time (Dalsgaard *et al.*, 2013; Baiser *et al.*, 2019; Gravel *et al.*, 2019). 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

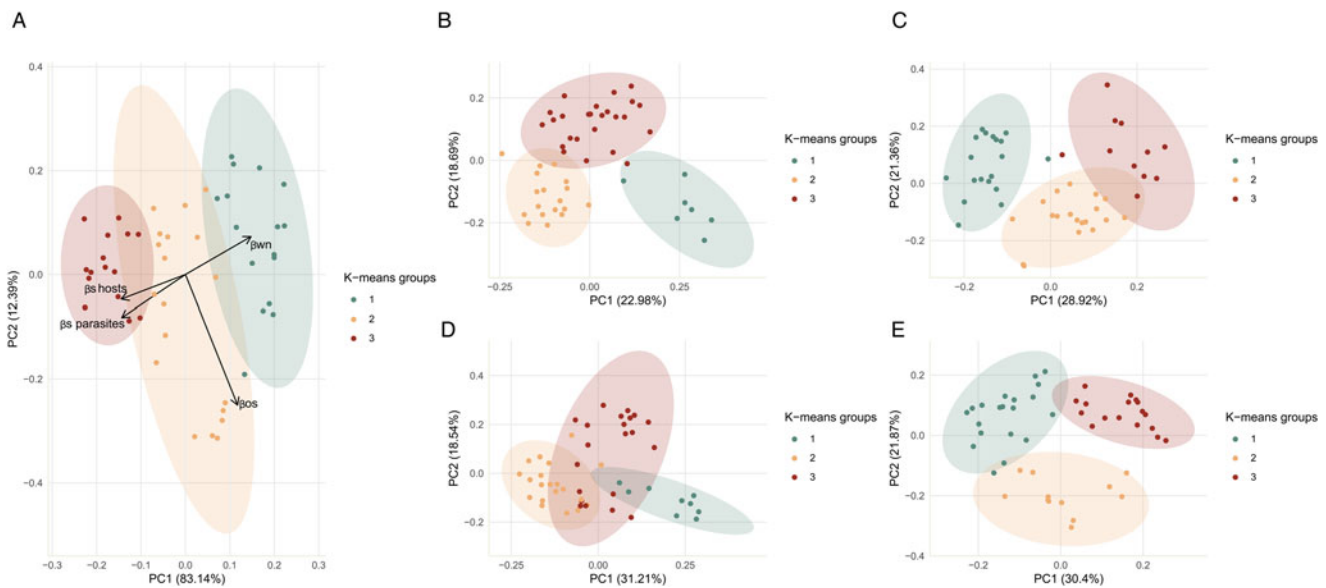


Fig. 1. Principal component analysis of networks beta-diversity metrics and projection of local networks. For the dataset used here, networks are described by three dimensions of beta-diversity: while β_s captures part of the variation that is complementary to that captured by β_{wn} , β_{os} describes a completely different dimension of the data. (A) PCA of networks beta-diversity metrics β_s , β_{wn} and β_{os} ; PCA of the phylogenetic component of PCD (PCDp) for parasites (B) and hosts (C); PCA of the compositional component of PCD (PCDc) for parasites (D) and hosts (E).

community. Dispersion and speciation events are the main factors that affect the phylogenetic diversity of a network of ecological interactions (Trojelsgaard and Olesen, 2013; Sebastián-González *et al.*, 2015; Coelho *et al.*, 2017). 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.

Based on a parasite–host system distributed over a vast biogeographic region (Eurasia), we identified similar numerical and geographical clusters 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 helps us tell a more complete story on the biogeography of ecological communities. Specifically, we have found that local networks are characterized by beta-diversity metrics in different ways across the metaweb, and these metrics co-vary with networks' phylogenetic diversity. Specifically, we have found that local networks are characterized by beta-diversity metrics in different ways across the metaweb, and these metrics co-vary with networks' phylogenetic diversity.

Methods

We used the Hadfield *et al.* (2014) data on the parasitism interaction between fleas and small mammals (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 (R Core Team, 2019; Li *et al.*, 2020). To do that, we discarded sites with no correspondents taxa in the phylogenetic trees. The output of the *pcd* function can be divided into compositional (i.e. the shared species between communities, PCDc) and phylogenetic (i.e. evolutionary relationships among species, 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. The *k-value* for all clustering analyses was defined as 3 by the Elbow method.

Due to intrinsic 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 this information in different ways:

- (1) β_s : this index corresponds to the differences on species composition between networks. A high β_s means solely a high species turnover (Koleff *et al.*, 2003).
- (2) β_{os} : 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) β_{wn} : this summarizes the global differences between all networks in a metaweb, calculated as $\beta_{wn} = \beta_{os} + \beta_{st}$. It has two components: the difference in interactions between shared species (β_{os}) and the difference in interactions due to species turnover (β_{st}). Therefore, β_{os} cannot assume values higher than β_{wn} (Canard *et al.*, 2014).

These measures were calculated using the *EcologicalNetworks.jl* and *Mangal.jl* modules in Julia (Bezanson *et al.*, 2017; Poisot *et al.*, 2020a, 2020b) and summarized with the KGL11 function,

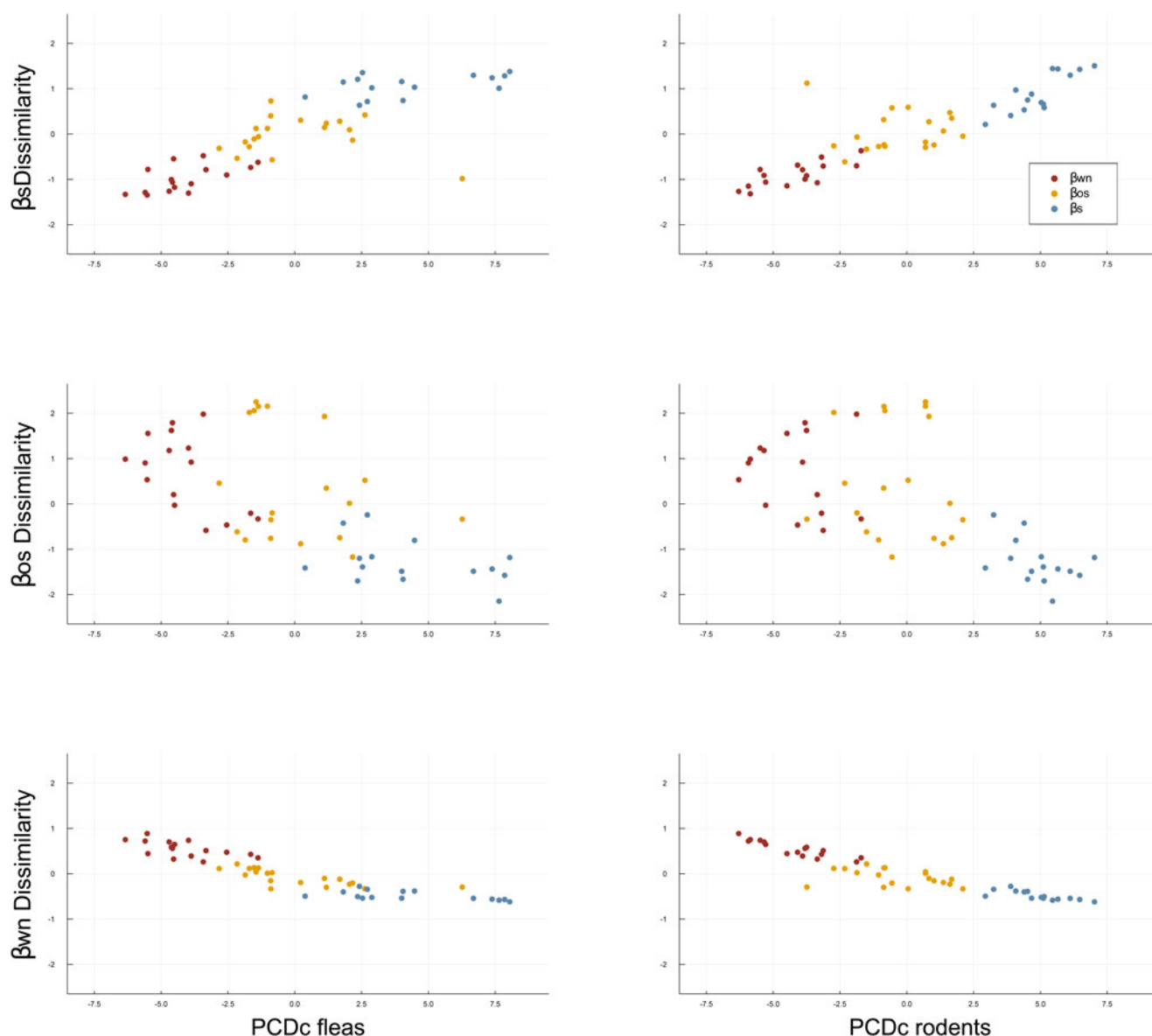


Fig. 2. Effects of the compositional element of phylogenetic diversity dissimilarity on network beta-diversity for both parasites (left) and hosts (right). The colours correspond to the groups described in Fig. 1. Networks with higher values of PCDc are taxonomically more distinct and therefore have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

which calculates the Sørensen index of beta-diversity (Koleff *et al.*, 2003). β_s 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 component that best described the variation of the data. A subsequent PCA and *k-means* analysis (which) on a combined matrix of these variables allowed us to investigate how they co-vary among networks.

Results and 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 PCA 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 β_s , β_{os} and β_{wn} values (Fig. 1). This separation is more explicit between β_s and β_{wn} , and more diffuse for β_{os} , which is aligned to the assumption that β_s and β_{wn} are only indirectly related, while β_{os} have a more proximate relationship both with β_{wn} and β_s . The fact that the networks grouped by β_s values are so different from those grouped by β_{wn} 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 β_{os} group, however, would be composed by communities that change less in species composition, but more in ecological interactions.

As β_s and the species composition of the phylogenetic community dissimilarity (PCDc) can be interpreted in the same way, a

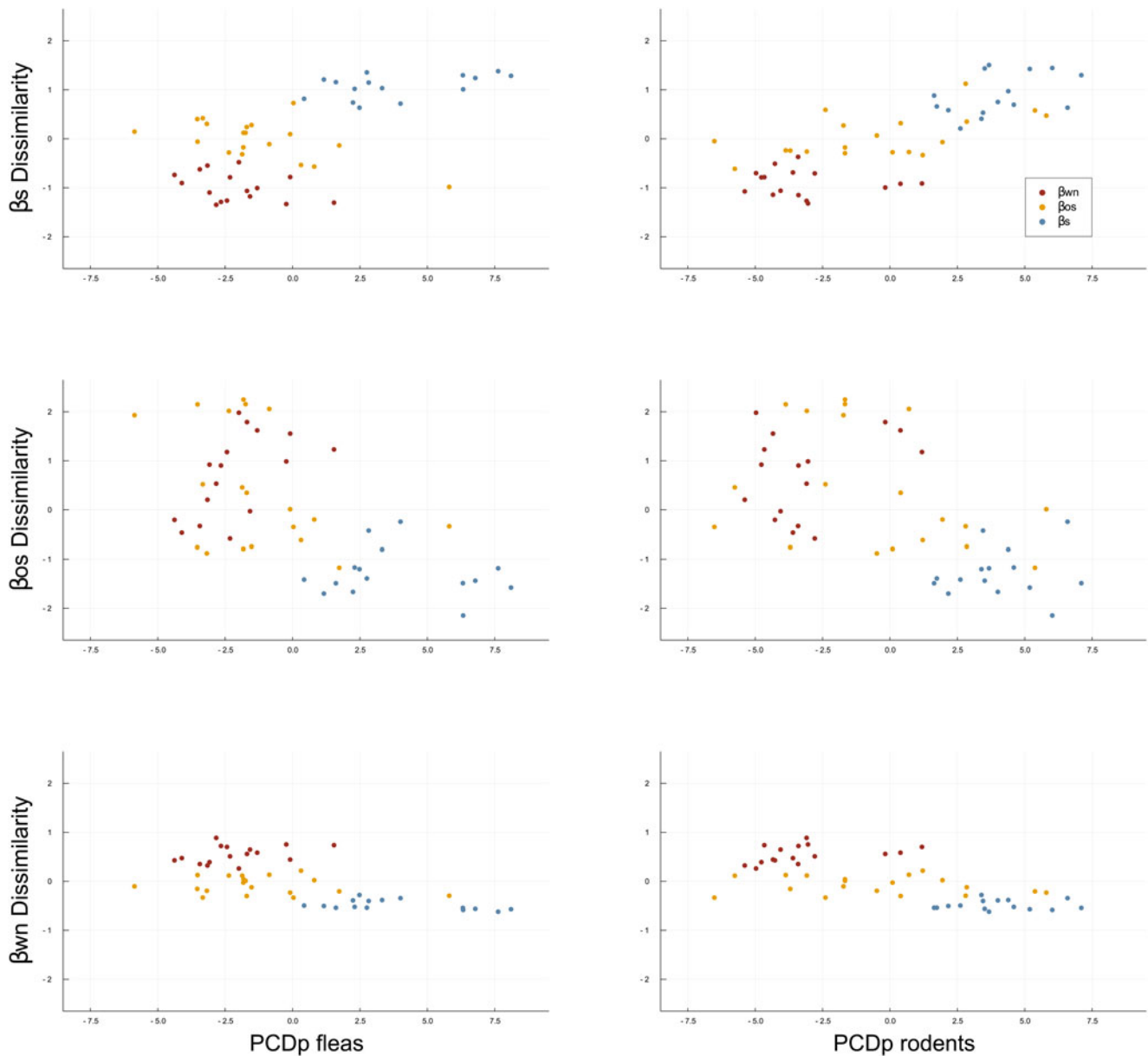


Fig. 3. Effects of the phylogenetic component of the phylogenetic diversity dissimilarity on network beta-diversity for both parasites (left) and hosts (right). The colours correspond to the groups described in Fig. 1. Networks with higher values of PCDp are phylogenetically more distinct, and therefore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

PCA of PCDc would provide a closer look to the β_s metric. Our results suggest that, from a species composition point of view, parasites communities are much more similar across the metaweb than hosts, which can be more easily described in three main groups (Fig. 1D and 1E, 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 flea 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, β_s and PCDc are proxies for each other both for hosts and parasites, while PCDc is inversely correlated with β_{wn} (Fig. 2). Communities with a high β_s 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 β_{os} , and its relationship with both PCDc and PCDp is highly variable (Figs 2 and 3).

As any change in species composition highly affects phylogenetic diversity, β_s 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 (Figs 5 and 4), and

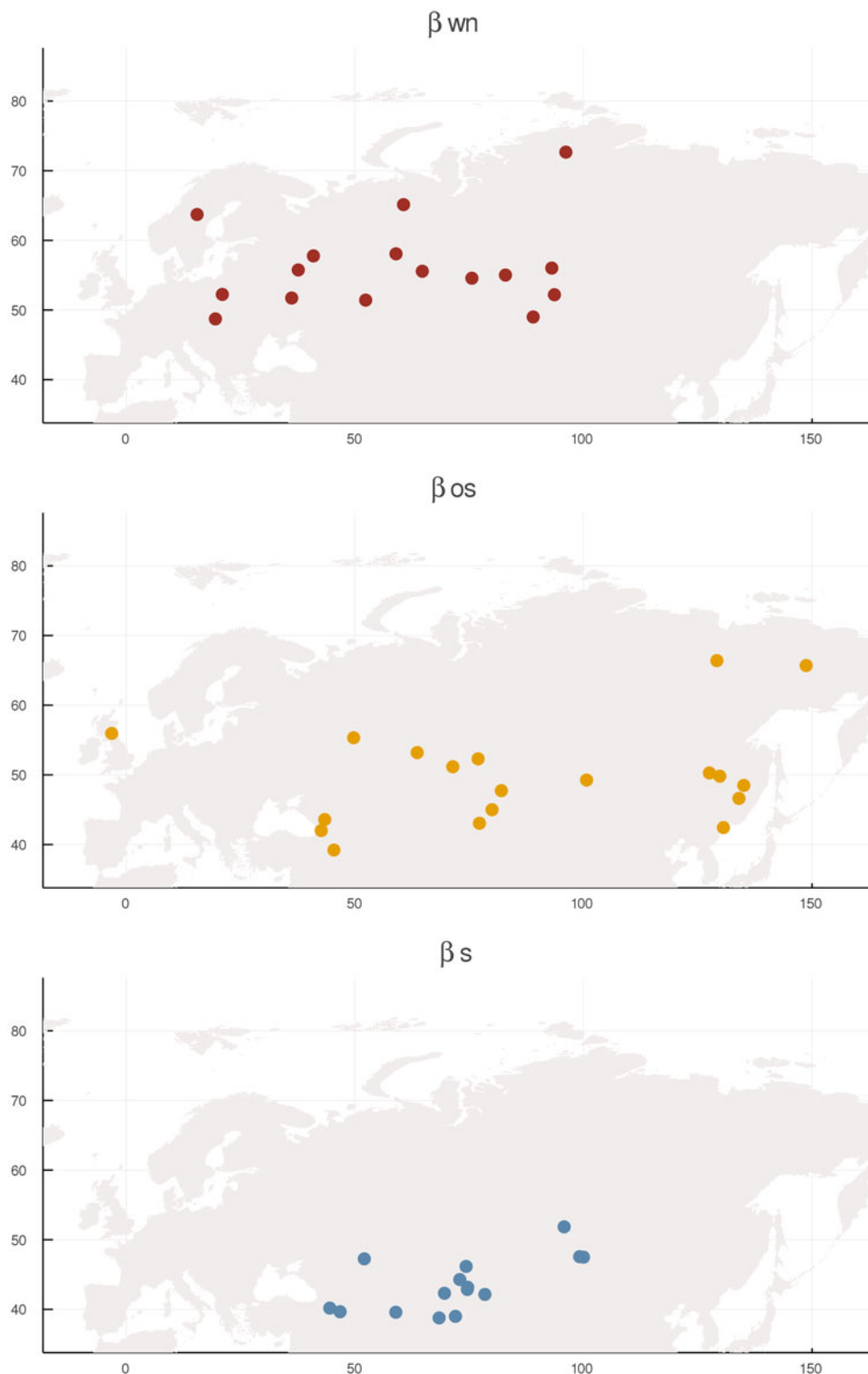


Fig. 4. Spatial distribution of PCD components for both hosts and parasites: the compositional component on the left and the phylogenetic component on the right. On the margins of each map there is a density plot to better visualize where networks are concentrated. Again, a distinct PCD cluster (as seen on the third row of maps) matches the cluster for which β_s metric is more important (as in Fig. 5). For the PCDC component, there is a longitudinal separation, while for the PCDP component this separation is latitudinal (first and second rows of maps), which suggests different processes acting over different aspects of networks composition.

this may indicate that the biogeographical history of these communities is more related to migration than diversification of local lineages (Davies and Buckley, 2011). Therefore, networks with 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 β_{wn} – 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). As these communities also have low values of β_s , indicating less frequent species turnover, this dissimilarity is due to different links

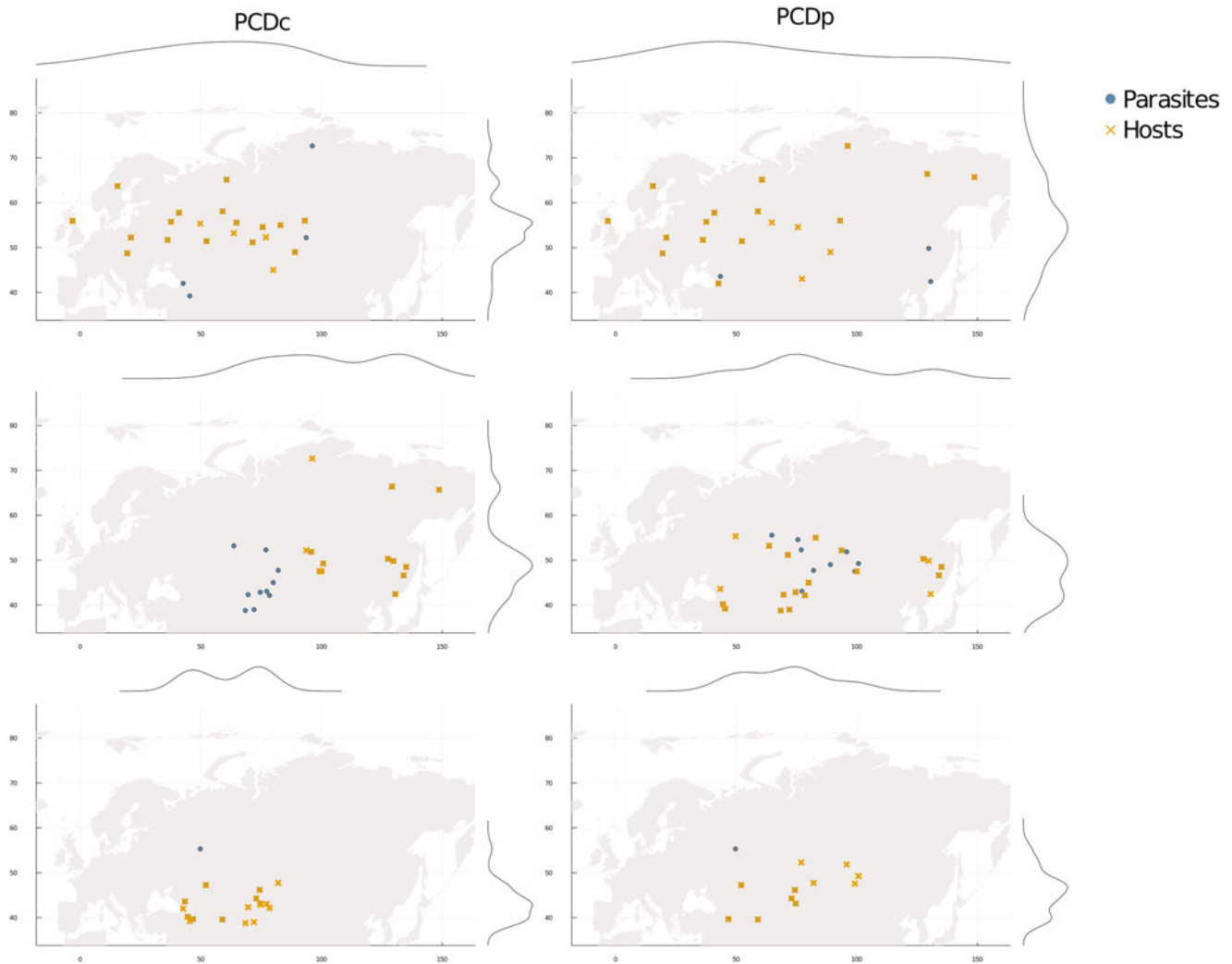


Fig. 5. Spatial distribution of beta-diversity metrics. The groups illustrated in Fig. 1 are also geographically distinguished. Networks that are better represented by β_s are aggregated in the centre-south of the continent, characterizing a region with a high species turnover rate. Networks which dissimilarities are due to links turnover between shared species enclose most of communities' variability, as we can also see in Figs 1–3. Finally, networks represented by β_{wn} occupy a geographical range even more at north, with a small superposition with the geographical range of those represented by β_{os} .

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 Figs 2 and 3 on scatterplots of β_{os} vs PCD: networks that differ little in phylogenies have a broader range of values of β_{os} , while highly phylogenetically distinct networks only have very low values of β_{os} – 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 β_{wn} (i.e. they are very similar to the overall metaweb) and high values of β_s (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.

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. 5). 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 β_s for networks beta-diversity. Due to 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 β_{os} component of beta-diversity explains better why networks are different. The third group of networks, characterized by a high value of β_{wn} , is also composed by phylogenetically similar communities (as seen in Fig. 3). As the species richness is even lower, any

change in composition can have a high impact on interactions. Therefore, the β_{os} component is still very important, but now differences in interactions due to species turnover contribute much more to networks' beta-diversity.

The PCD of networks was also geographically grouped, and in the region where β_s was more important, there was a very distinguished group for both fleas' and mammals' phylogenetic dissimilarity (Fig. 4). 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 highlights 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. 5, with one group largely spread in the north – occupying a diverse range of environments – and two other groups restricted to latitudes under 60° (Fig. 4).

Conclusion

The conspicuous association – both numerical and geographical – between the evolutionary history of species and networks' beta-diversity properties clarifies key aspects of the biogeography of hosts and parasites communities in Eurasia. For example, the longitudinal PCDc clusters separation roughly coincides 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 follow a 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 distinctive β_s 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. 4.

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 β_s seems to be connected to environmental uniqueness and geographical barriers, β_{os} and β_{wn} better reflect migration processes and evolutionary 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.

Interaction networks between parasites and hosts have great potential to be used as study systems in the geographic variation of interactions (Proulx *et al.*, 2005; Poulin, 2010). Due to 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 (Krasnov *et al.*, 2005; Poulin and Krasnov, 2010; Eriksson *et al.*, 2019). Nevertheless, 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. The

underlying logic of our approach pertains to a wide diversity of systems; not only do rodents act as reservoirs for zoonotic diseases, Albery *et al.* (2020) show that understanding the global-scale structure of host–virus interactions *requires* a joint understanding of the geographical and evolutionary mechanisms involved in shaping them. We argue that when the data are available, there is even more information to be gained by looking at the way interactions vary.

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Author contribution. GH and TP designed the study and wrote the article. GH performed statistical analysis.

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Conflicts of interest. The authors declare there are no conflicts of interest.

Ethical standards. Not applicable.

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