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Hosts, parasites, and their interactions respond to different climatic variables

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Aim: Although there is a vast body of literature on the causes of variation in species composition in ecological communities, less effort has been invested in understanding how interactions between these species vary. Since interactions are crucial to the structure and functioning of ecological communities, we need to develop a better understanding of their spatial dynamics. Here, we apply novel numerical tools to data on species interactions, and reveal that they vary more, and in response to different climate variables, than species do. Location: Eurasia. Methods: We used a measure of Locality Contribution to Beta-Diversity to evaluate the compositional uniqueness of 51 host–parasite communities across Eurasia, using publicly available data. We measured uniqueness based on the species composition, and based on potential and realized biotic interactions. Results: We show that interactions vary more, over space, than species do. In particular, we show that interactions respond to some climatic variables that have no effect on species distribution or dissimilarity. Main conclusions: Species interactions provide far more resolution than species occurrences alone, while still retaining all information about species occurrences. We suggest that they be put front and center in analyses of communities, especially in a biogeographic context.

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Keywords beta-diversity species interaction networks climatic niches species distribution models

Ecological communities are made of species and their interactions. Understanding how community structure changes requires to address the variability of both these components. One way to investigate the variability of ecological communities is through the use of spatially replicated systems: by observing the presence/absence of species originating from the same regional pool at different localities and documenting their interactions, it is possible to *compare* these communities to gain insights about why and how ecological communities vary. Information about both species and their interactions can be efficiently represent using ecological networks, and the recent years saw the developments of approaches to quantify the variation of ecological networks (Poisot et al. 2012). In parallel, advances in the quantification of β-diversity allows the identification of *hotspots* of variation, *i.e.* localities that through their unique composition, have a high contribution to the overall β-diversity (Legendre & De Cáceres 2013; Legendre 2014; Legendre & Gauthier 2014). In this manuscript, we bring these

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families of approaches together, by describing the variation of community structure across space, and identifying the mechanisms and environmental variables responsible for this variation.

Understanding species within their communities, and by extension communities themselves, can be done through a quantification of the species' Grinnellian and Eltonian niches (Devictor et al. 2010). To summarize, species contribute to community structure first by being present within the community (which assumes that the local environmental conditions are amenable to their persistence), and second by fulfilling a *functional role* within this community, which is in part defined by the way they interact with other species (Coux et al. 2016). Community therefore differ it two complementary ways: first, because they harbour different species; second because whichever species they share might interact in different ways (Poisot et al. 2014b). This dissimilarity of both species composition and species interactions, over space and time, has raised increasing empirical attention in recent years (Carstensen et al. 2014; Maruyama et al. 2014; Vizentin-Bugoni et al. 2014; Olito & Fox 2015; Trojelsgaard et al. 2015). Although the drivers of species distributions have been well elucidated in the past decades, there is virtually no knowledge (nor hypotheses) regarding how species interactions should be distributed in space. Most of the earliest datasets on ecological interactions replicated across space (*e.g.* Havens 1992) assume that interactions are constant: two species will always interact if they are found in the same location, environment, etc. Because empirical data contradict this assumption, there is an urgent need to revise our understanding of how community structure should be defined at both the local and global scale. Specifically, we need to do so in a way that accounts simultaneously for the variability of species occurrences, and for the variability of species interactions.

Building on the framework put forth by Poisot et al. (2014b), it is possible to develop quantitative hypotheses regarding the variation of species presence, interactions, and the relationship between them. The key point is that an interaction between any pair of species is only possible when the two species of this pair co-occur. Therefore, the dissimilarity of interactions is greater or exactly equal to the dissimilarity of species composition; it cannot be smaller if the two dissimilarities are measured from the same community data. There are two important consequences to this fact. First, overall, species composition across multiple localities should be *less dissimilar* than interactions. Second, interaction dissimilarity will display a *finer picture* of how communities differ, because the distribution of interactions is intrinsically more variable than that of species: even when two species are found together, they *may* not interact locally. Most importantly, species are *nested* within interactions (at least from a purely mathematical standpoint, whereby nodes/species are embedded into edges/interactions) – therefore, describing interactions is a more informative way of depicting community structure, which not only includes but actually supersedes the usual approach of communities-as-lists-of-species.

This study is the first demonstration of the fact that species interactions, in a biogeographic perspective, are more informative than species distributions to describe the variation of community structure and its response to climatic variables. In particular, we show that (i) species interactions are more diversified, and allow the identification of more sites with unique contribution to β-diversity, than species only; and (ii), species interactions react to climatic variables of their own, in addition to capturing most of the climatic variables acting on species distributions. We discuss these results in the light of our current definition of ecological communities, and highlight ways of refining this definition in order to make more accurate and realistic predictions about community structure.

MATERIALS AND METHODS

We will measure how species composition and species interactions in host–parasite communities vary across environmental gradients. Specifically, we will use novel methods to quantify the compositional uniqueness of localities based on different definitions of community structure, then identify the climatic variables involved in driving the dissimilarity between localities. An interactive document allowing to reproduce all analyses (including downloading all data) is available as supplementary information (Appendix S2 in supporting information).

Species interaction data Species interactions data were taken from Hadfield et al. (2013). They describe species interactions between rodents and ecto-parasites at 51 locations throughout Eurasia. This system is species-rich, and likely originates from successive co-speciation events within pairs of interacting species (Krasnov et al. 2012; Hadfield et al. 2014). The data were downloaded from the *mangal* database [Poisot et al. (2014a); `http://mangal.io/data/dataset/4/`]. The communities (where "community" is defined as the species and interactions detected at one location) have between 3 and 27 (median 11) hosts, 7 and 40 (median 19) parasites, and 12 and 226 (median 63) interactions between them. Out of 326 species, 94 were observed only once, and 43 were observed at more than 10 locations.

For every location, we define two levels of analysis. First, the *realized* interactions; this corresponds to interactions that where reported to occur within individual locations in the original data. Second, the *potential* interactions; this corresponds to the interactions that *could* happen given the information contained in the entire dataset. For example, if parasite $\boldsymbol{P}_j$ and host $\boldsymbol{H}_k$ do not interact locally, but interact in at least one other location, there will be an interaction between them in the *potential* interaction network. These two levels correspond to the effect of sampling of species only (*potential interactions*; interactions are assumed not to vary), and of interactions between sampled species (*realized interactions*; interactions can vary) with regard to a regional pool (Poisot et al. 2012). For a given location, the *realized* and *potential* interaction networks have an equal number of species, and the *realized* network has as many or fewer interactions than the *potential* one. The extent to

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which the *realized* and *potential* interactions differ is measured using β'_{OS} (Poisot et al. 2012). β'_{OS} is measured by comparing the number of interactions in the *realized* and *potential* networks, and therefore works as a measure of the strength of local interaction sorting. Values close to 0 mean that all *potential* interactions are *realized* (weak interaction filtering), whereas values close to unity indicate that most potential interactions are lost (strong interaction filtering).

This distinction between realized and potential interactions, as we detail below, is of the utmost importance. Drivers of the variability of interactions exist at different scales, ranging from the distribution of functional traits (Olesen et al. 2011) that are likely expressed at macro-ecological scales, to neutral and random-chance events (Canard et al. 2014) that are applied at the micro-ecological scale. In short, potential interactions are more likely to reflect the evolutionary history of the species pairs, while the realized interactions are more likely to reflect how this species pairs reacts to a set of local environmental condition. From a species distribution point of view, potential interactions offer the possibility to look at the co-distribution of interacting pairs of species – any signal on the spatial distribution of potential interactions is highly suggestive of the fact that species that interact distribute non-randomly.

Climatic variables data We downloaded the 19 *BioCLIM* data (Hijmans et al. 2005) at a geographic resolution of 5 arc minutes. The data for each location were then extracted using the GPS coordinates of the sampling location. Since the precise extent that was sampled around each location is unknown, we deemed more conservative to use a coarser spatial resolution to capture the general environmental conditions around each site.

Quantification of species and interactions variation We use the approach put forth by Legendre & De Cáceres (2013) – the overall β-diversity between sites of a spatially replicated sampling is measured as the variance of a community data matrix $\mathbf{Y}$, and noted $\beta_{\mathbf{Y}}$. $\mathbf{Y}$ is a binary matrix with locations as rows, and items on which to measure the dissimilarity in columns. These matrices are defined such that $Y(l, i)$, that is the value at row l and column i of matrix $\mathbf{Y}$, is 1 if item i is found at location l, and 0 otherwise. For site-species matrices, the row sums give the richness at the locations, and the column sums give the number of occurrences of the species. We define four community data matrices. $\mathbf{H}$ has host species in columns; $\mathbf{P}$ has parasite species in columns. These first two matrices will generate a baseline estimate for the dissimilarity of localities based on species composition. Finally, we also define $\mathbf{R}$, with *realized* interactions in columns, and $\mathbf{Q}$ with *potential* interactions in columns. This approach is represented in Figure 1.

The method of Legendre & De Cáceres (2013) also yields a distance matrix between localities of a community data matrix, which we note $\mathbf{D_Y}$. As per the recommendations in Legendre & Gallagher (2001), we used the Hellinger distance to measure the dissimilarity across locations for all four matrices detailed above, resulting in $\mathbf{D_H}$, $\mathbf{D_P}$, $\mathbf{D_R}$, and $\mathbf{D_Q}$. This distance has

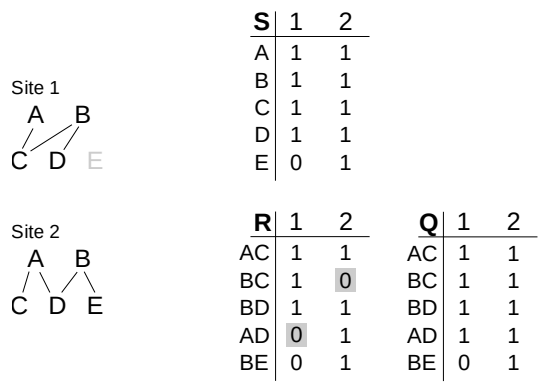

Figure 1 Illustration of the construction of the four community data matrices. Assuming two interaction networks with shared species A, B, C, and D, and unique species E in location 2, one can construct the usual community data matrix (S) where 1 denotes species presence at a location. Similarly, we build community data matrices for the interactions (R and Q). In R, a 1 denotes the existence of the interaction at a location. In Q, a 1 denotes that the interaction could potentially exist; for example, altough A and D do not interact in location 1, they do interact in location 2, and therefore the AD interaction has a 1 in matrix Q. Note that the interaction BE cannot exist in site 1, because the species E is not present here.

been shown to be appropriate for β-diversity studies (Legendre & De Cáceres 2013). This method also allows measuring the local contribution to beta-diversity (LCBD). LCBD is a quantification of how much every location (row of the $\mathbf{Y}$ matrix) contributes to the overall dissimilarity, presented as a vector $\mathbf{l_Y}$. We interpret this value as a measure of the *originality* of a location: a large contribution to beta-diversity indicates that the location has a set of species or interactions that is different from the overall species pool. The values of LCBD can be tested for statistical significance under a permutation scheme, specifically by re-distributing species or interactions across locations. This tests, in effect, the fact that the LCBD values obtained were not due to chance (specifically, the fact that the LCBD values are larger than expected from random variations in species composition). We assume that LCBDs larger than expected by chance indicate that the locality is *unique* with regard to the species or interactions found therein. We used the default threshold of $\alpha = 0.05$, with 9999 random permutations of each column of the four community data matrices.

To summarize, for each community data matrix $\mathbf{Y}$ representing hosts, parasites, potential, and realized interactions, we measure the β-diversity ($\beta_{\mathbf{Y}}$), the pairwise distance between sites ($\mathbf{D_Y}$), the extent to which each location contributes to β_Y ($\mathbf{l_Y}$), and the significance of each element $l_{\mathbf{Y}}(i)$.

Ordination and variable selection We investigated the extent to which the structure of the dissimilarity matrices ($\mathbf{D}$...)

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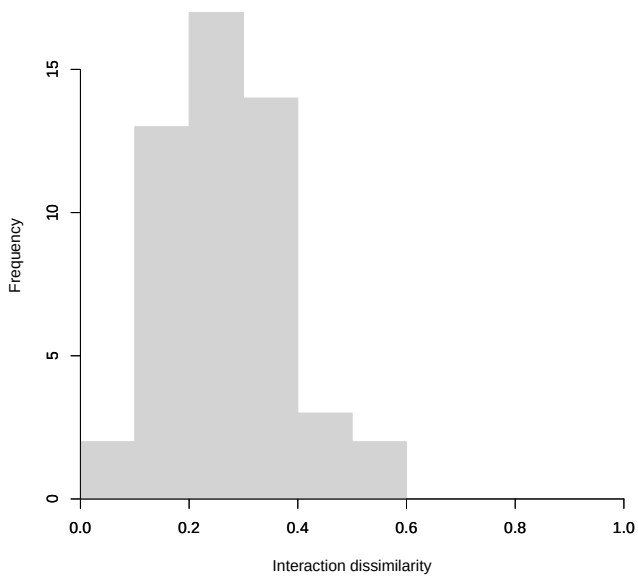

Figure 2 Distribution of β'_{OS} across the entire dataset. Local communities tend to be relatively good images of the regional interactions, as evidence by dissmilarity values going down to 0, with nevertheless some variability. The inset shows the value of β'_{OS} in space.

was driven by climatic variables using db-RDA (using the `caspcale` function of the `vegan` package for `R`; see *Appendix S1 in supporting information*; Legendre & Legendre (1998)]. The 19 *bioClim* variables were put in a matrix $\mathbf{E}$ with one location per row. To identify the most significant climatic variables, we used stepwise model building using forward variable selection over 9999 replicate runs for each matrices. This approach yields four models of the form CAP($\mathbf{D_Y} \sim \mathbf{E}$), for which we extract $\mathbf{e_Y}$, *i.e.* a vector of significant climatic variables to explain the structure of $\mathbf{D_Y}$. In each model, we also record the rank of each climatic variable; variables selected early have a stronger contribution to the structure of dissimilarity.

RESULTS

Species and interactions vary across space In Figure 2, we show that the 51 locations have interactions that are not the same found at the regional level. Specifically, the mode of the distribution of β'_{OS} is around 0.3, indicating that the filtering of interactions from the regional pool to local communities is comparable to other rodents–parasite systems (Poisot et al. 2013 reported values between 0.2 and 0.4 in a central European system). Using the Legendre & De Cáceres (2013) approach reveals that interactions vary *more* than species. Specifically, $\beta_{\mathbf{R}} \approx 0.94$, $\beta_{\mathbf{Q}} \approx 0.90$, $\beta_{\mathbf{H}} \approx 0.80$, and $\beta_{\mathbf{P}} \approx 0.79$. That the variation in $\mathbf{R}$ is larger than that in $\mathbf{Q}$ is expected, as the *realized* interactions account for one additional ecological mechanism, namely the filtering of potential interactions. These are known to react in stochastic ways to population abundances (Canard et al. 2014), and are therefore inherently more variable. That localities in this dataset exhibit different interactions, and have varying strengths of filtering from the potential to the realized interactions, raises the question of identifying which of these localities have the strongest contribution to β-diversity.

Species and interactions contribute differently to site uniqueness Using the LCBD approach, we measure the extent to which every location contributes to the beta-diversity of hosts, parasites, local, and potential interactions. These results are presented in Figure 3.

For each distance matrix, we clustered the locations using partition around the medoids, and selecting the number of medoids that gave the smallest silhouette. This yielded respectively three clusters for hosts (east; north west; south west), and two for the parasites, the local interactions, and the realized interactions (north; south). Overwhelmingly, the locations with significant contributions to beta-diversity are located in the southernmost half of the dataset, in more desertic areas (*i.e.* Turkestan, Taklamakan, and Gobi deserts). Using information on host (resp. parasites) identifies 8 (resp. 12) locations with significant contributions to beta-diversity, *i.e.* locations that have *unique* species compositions. By contrast, using local (resp. potential) interactions yields 23 (resp. 25) such locations. With six exceptions, local and potential interactions agree on which locations are unique. In the next part, we investigate how the dissimilarity of communities is driven by local climatic variables.

Beta-diversity of species and interactions is structured by the environment In Figure 4, we present the results of a db-RDA on the four beta-diversity matrices, using the *bioClim* variables as predictors (additional informations such as number of constrained axes and inertia are given in the *supp. mat.*). As in Figure 3 (and because environmental variables tend to be spatially auto-correlated), locations from the same cluster, and locations with significant contributions to beta-diversity tend to occupy the same area of the space defined by the canonical axes. This suggests that (i) clustering of communities as a function of their species or interaction composition is the result of species or interactions having the same requirements about the habitat, and (ii) locations with significant contributions to beta-diversity are unique because their local environmental conditions select unique species and interactions assemblages.

Finally, in Table 1, we present the variables that have been retained during stepwise model building. The most important variables are `bio06` (minimum temperature during the coldest month), and `bio08` and `bio10`, minimum temperatures during the wettest and coldest quarters.Some precipitation related variables were associated to hosts and interactions, but not parasites. Meanwhile, a number of variables where associated to parasites only (and, surprisingly, not to interactions). Finally, two variables (`bio04`, seasonality of temperature; `bio11`, mean temperature of warmest quarter) where associated to interactions only.

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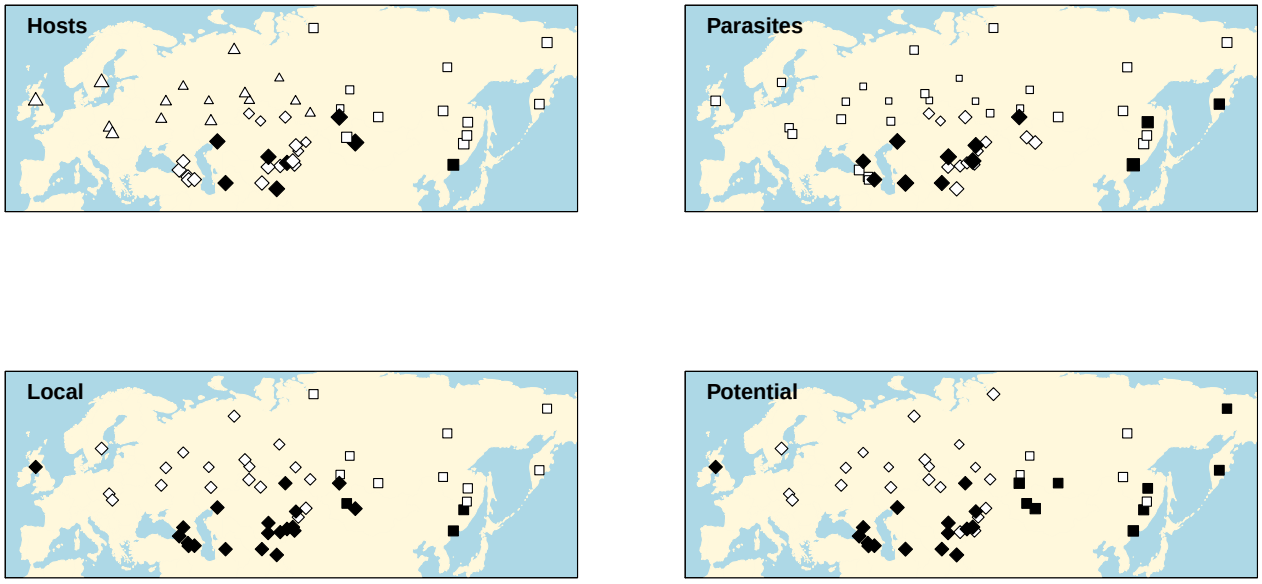

Figure 3 The beta-diversity matrices were divided in clusters (indicated by different symbols). Black-filled symbols have significant LCBD values. The size of each symbol is proportional to its LCBD value. Note that there is no correspondance between the symbols used to denote cluster identity across the four panels.

DISCUSSION

The β-diversity of interactions was higher than the β-diversity of species. Although notable, this is not a surprising result for at least two reasons. First, in any community there are many more interactions than species, and therefore interactions paint a finer picture of community structure than species do. Second, interactions are probabilistic events (Poisot et al. 2015) that can vary even if the two species involved are consistently co-occurring. Since the information in species presence/absence is by definition included in the information about species interactions, it stands to reason that we would more adequately describe community structure and variation by systematically considering species interactions. This is emphasized by the fact that measuring LCBD indices based on interactions revealed *more* (over twice as many) unique sites that measuring the LCBD of species (Figure 3). Quantifying the β-diversity of communities as based only on their species composition (i) consistently under-estimates β-diversity and (ii) consistently underestimates the uniqueness of localities in the dataset. A species-centered vision of diversity, in short, does artificially homogenize the structure of communities by missing important sources of variation.

An additional result of out study is that, although species and their interactions in this system do share a lot of their bioclimatic predictors, interactions responded to two variables that had no bearing on species composition (Table 1). We recognize that this can, in part, stem for the mismatch of scales between the observation of species interactions, and the observation of climatic variables; in itself, this is an intriguing question: what is the scale at which ecological interactions are affected by the environment? Nevertheless, our results highlight a challenge for current efforts to add biotic interactions to species distribution models (Boulangeat et al. 2012; Araújo & Rozenfeld 2013; Blois et al. 2014): from additional predictors, species interactions become objects that must first be predicted themselves based on local environmental condition. This is in addition to the fact that interactions require first and foremost the presence of both species (Gravel et al. 2011) to be realized. Nevertheless, this problem may prove less complicated based on the observation that there is little difference (besides their relative importance) in the predictors of potential and realized interactions. What this suggests is that climatic variables act on the distribution of *species pairs that can interact*, and the signal at the level of realized interactions is *inherited* from the co-distribution of potential interaction partners. Or in other words, the signal on potential interactions is a predictor of the co-occurrence of interacting species. As suggested in Poisot et al. (2014b), interactions are filtered *after* the two species involved have co-distributed – it therefore stands to reason that environmental conditions that do not affect the co-distribution of the two species can affect the realization of the interaction locally.

Taken together, the results of this study highlight two important notions. First, interactions contain intrinsically more information than species; second, interactions react to climatic

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Table 1 List of bioclim variables retained during the model selection step (also used in Figure 4). Numbers identify the rank in the forward-selected model. Variables 4 and 11 (in bold) are unique to interactions.

bioclim variable	Explanation	**H**	**P**	**R**	**Q**
06	Min temp. cold. month	1	1	1	1
08	Mean temp. of wettest quarter	2	3	2	2
10	Mean temp. of coldest quarter	5	4	6	5
13	Precipitation of wettest month	4	5	9	4
01	Annual mean temp.	3		3	3
18	Precipitation of warmest quarter	6		5	6
15	Precip. seasonality	7		4	8
19	Precipitation of coldest quarter	8		10	7
17	Precipitation of driest quater	10			9
02	Mean diurnal range		2		
05	Max temp. warm. month		6		
12	Annual precip.		8		
14	Precipitation of wettest month		7		
04	Temp. seasonality			7	10
11	Mean temp. of warmest quarter			8	11
03	Isothermality				
07	Temp. ann. range				
09	Mean temp. of driest quarter				
16	Precipitation of wettest quater				

variables in ways that seem to have no bearing on species themselves. Taken together with the fact that the information on species occurrence is by definition nested within the information on species interactions, this points to the idea that we should be extremely cautious when defining what a "community" is. In particular, we show that while describing the presence and absence of species at different locations is important, it misses a lot of information by systematically underestimating the variability *and* the uniqueness of these locations. For these reasons, we believe that the more desirable way of representing community structure is to describe, not only species, but also their interactions. Although this demands a much larger sampling effort, it is the correct approach not to neglect an entire aspect of what is community *structure*: species, not being independent entities, are organized in non-random ways through their interactions.

Supporting information
Appendix S1 – Supplementary material
Appendix S2 – Document and code source to generate the supplementary material

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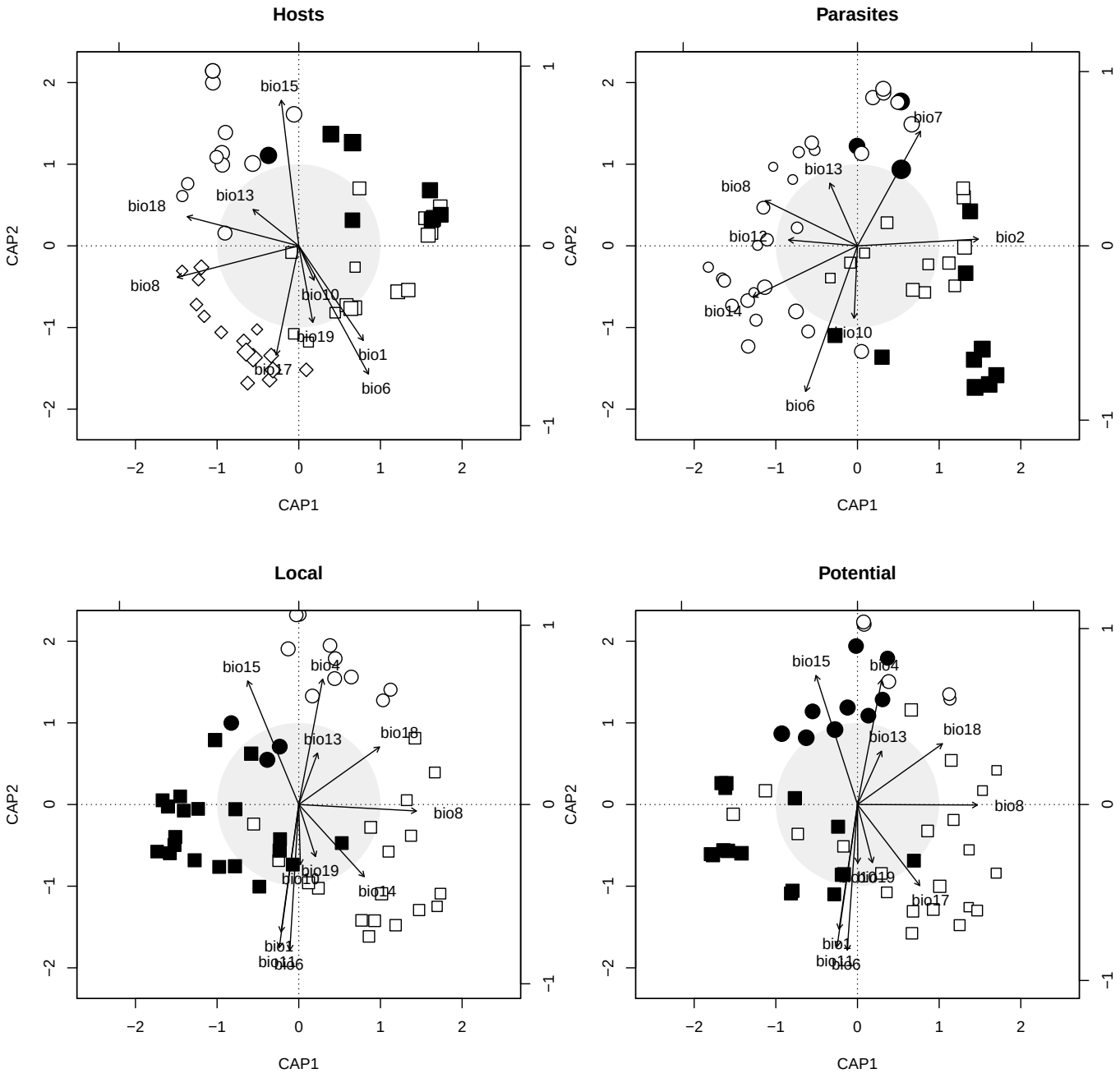

Figure 4 Ordinations of the four distance matrices, based on the scaled bioclimatic variables. Shape represents the cluster to which each location belongs, symbol size scales with LCBD, and filled symbols have significant LCBD.