

Title: Mapping planktonic communities: a network approach to assess the role of scale and centrality on their diversity and composition

Running head: Centrality as a key driver of lake communities

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Abstract

The distribution of habitats across a landscape and their centrality gradient are key elements defining the effective pathways of dispersal, and thus of metacommunity assembly. Understanding how centrality shapes diversity patterns is essential for predicting the impact of future landscape changes on diversity. While alpine lakes have been extensively studied, often considering the fluvial network as a potential landscape, small planktonic communities have frequently been overlooked as potential dispersers due to their assumed ubiquity. In this study, we investigate the diversity patterns of alpine lake planktonic communities along lake networks constructed at different scales, ranging from 6.5 to 650 km and the fluvial network. We sampled 55 lakes in the northern Alps (16S, 18S, phytoplankton and zooplankton) and calculated several diversity metrics (alpha, beta diversity and LCBD) and multivariate analysis. We then constructed several networks responding to different scales, determined their centrality gradients, and finally explored their relationship with the diversity of each planktonic group. We expected that a groups' diversity would relate differently across scales based on body size, but the outcomes were varied. Bacterioplankton and zooplankton diversity were both affected across scales higher than 100 km, whereas phytoplankton appeared completely unrelated to centrality. Nonetheless, we could observe that when significant, the relationships between diversity and centrality were shared among organisms. These findings not only underscore that planktonic organisms are influenced by landscape configurations larger than the fluvial system but also emphasise the critical role of dispersal for these groups and the scales at which it impacts metacommunity assembly.

Keywords: metacommunities, landscape, alpine lakes, dispersal, community assembly

39 **Significance statement**

40 While dispersal is widely recognized as a key driver of assembly, some groups and systems
 41 remain insufficiently explored to fully grasp the impact of landscape and dispersal on their
 42 assembly. Planktonic communities have traditionally been considered ubiquitous and detached
 43 from regional-level structure, primarily due to their small size, leading to the notion that
 44 "everything is everywhere". Additionally, alpine lake communities have traditionally been
 45 perceived as solely connected through fluvial systems. In this study, we challenge these notions
 46 by demonstrating how planktonic communities are indeed influenced by the relative positioning
 47 of lakes in the landscape, with significant impacts occurring at larger scales, spanning hundreds
 48 of kilometres. However, not all planktonic groups responded uniformly to the analysed factors,
 49 emphasizing the marked differences among groups and the diverging drivers shaping planktonic
 50 metacommunities.

51

Introduction

Metacommunity theory has contributed to a better comprehension of how the spatial arrangement of communities influences community assembly (Leibold et al. 2004, Leibold and Chase 2018, Thompson et al. 2020). The increasing recognition and quantification of spatial features has greatly advanced the field (Dale 2017, Gounand et al. 2018, Chubaty et al. 2020) since the first seminal works on metacommunity ecology (MacArthur and Wilson 1963, Hanski 1999). We are now able to quantify the scales at which the spatial arrangement plays a stronger role (Dray et al. 2006, Borcard et al. 2011), how these scales might be affected by directionality (Larsen et al. 2012, Altermatt 2013, Horváth et al. 2016), how the spatial arrangement impacts community patterns (Carrara et al. 2014, Epele et al. 2021, Borthagaray et al. 2023b) and how the relative position within a network defines diversity patterns (Economo and Keitt 2010, Altermatt et al. 2011, Henriques-Silva et al. 2019). All these approximations have been mostly focused on disentangling how space, in a broad sense, was shaping community assembly and its relative importance with respect to other variables (Peres-Neto et al. 2006, Gilbert and Bennett 2010, Bo et al. 2020, Almeida-Gomes et al. 2020). However, more detailed landscape analyses have unravelled the inherent complexity of spatial features, especially when considering the capacity of organisms to interact with, or to disperse across, a landscape (Newman 2003, Borthagaray et al. 2015a, Erős and Lowe 2019). Such organism-landscape interactions might greatly determine the scale at which spatial processes influence diversity and how species interact with one another (Ishiyama et al. 2014, Borthagaray et al. 2015b, Cunillera-Montcusí et al. 2021). Ultimately, dispersal, together with landscape structure, are the elements defining the canvas through which metacommunities assemble (Leibold and Chase 2018, Thompson et al. 2020, Borthagaray et al. 2023b).

Most previous works on aquatic metacommunity assembly have been focused on how organisms are able to actively disperse between habitats (i.e. invertebrates; (Ishiyama et al. 2014, Perez Rocha et al. 2018, Burgazzi et al. 2020), if they move shorter or longer distances within aquatic habitats (i.e. fish, molluscs; (Kappes and Haase 2012, Radinger and Wolter 2014, Herrera-Pérez et al. 2019), or disperse passively relying on different vectors, with adaptations that enables them to cross the “dry ocean” (Dodson 1992, Incagnone et al. 2015). However, the role of spatial processes in smaller microscopic organisms has received less attention until recently (Reche et al. 2005, Declerck et al. 2013, Winter et al. 2013, Jamoneau et al. 2018, Daffonchio et al. 2019, Choudoir and DeAngelis 2022). For these groups we are beginning to unfold how “everything might not be actually everywhere” (Whitfield 2005, Fontaneto et al. 2008, O’Malley 2008, Custer et al. 2022, Barbour et al. 2023).

When focusing on landscape structure, lotic systems (riverscapes) and small lentic system (pondscapes) have been mostly the grounds where studies focusing on spatial structure have been carried out in limnology (Almeida-Gomes et al. 2020, Heino et al. 2021, Hill et al. 2021). These systems often have specific dynamics that constrain dispersal of most of their inhabitants, because the strong directional component pushes organisms downstream (Seymour et al. 2015, Tonkin et al. 2018b), or its environmental features force organisms to move between habitats in order to complete their life cycles (Cunillera-Montcusí et al. 2020, Hill et al. 2021, Onandia et al. 2021), or in case of temporary lentic or lotic systems, drying mandates organisms to leave to more perennial neighbouring systems or resist drought in the soil (Martins et al. 2019, Cañedo-Argüelles et al. 2020, Florencio et al. 2020). In this sense, bigger and deeper lentic systems such as alpine lakes have remained understudied (Almeida-Gomes et al. 2020). In general, for these systems, landscape has been primarily considered as a determinant of local lake conditions linked to

catchment geo-physical characteristics (e.g. bedrock, water residence time, land use; (Füreder et al. 2006, Schindler 2009, Klaus et al. 2021). However, the spatial position of lakes in the landscape can also define the connectivity between its communities and its neighbouring aquatic habitats. Being connected through waterways and/or closer to each other should foster more similar communities due to higher probability of exchange of individuals between lakes (Leibold and Norberg 2004, Heino et al. 2015). However, while the relevance of catchment geo-physical characteristics is clearly acknowledged as a diversity driver, the role of connectivity is often debated, especially for planktonic and microscopic aquatic organisms (Leibold and Norberg 2004, Winter et al. 2013, Custer et al. 2022).

The influence that landscape position might have on organisms may largely vary depending on the scale at which the landscape is considered (Declerck et al. 2011, Chase and Knight 2013, Borthagaray et al. 2015a, Morán-Ordóñez et al. 2015). Ultimately, a landscape is defined a priori based on the objectives, metrics or sites under study (Newman 2003, Turner 2005, Turner and Gardner 2015). However, how we simplify the landscape in our analyses can affect our inference about the assembly of focal communities (Baguette and Van Dyck 2007, Newman 2019). For example, if we set the boundaries of our landscape too large or too small, we might fail to capture the spatial pattern that affects community assembly. Thus, the challenge for our analyses lies in how to define an appropriate scale to consider the landscape (Baguette et al. 2013, Borthagaray et al. 2015a, Cunillera-Montcusí et al. 2021). In the case of organisms that can be transported along long distances due to dominant winds (Cáceres and Soluk 2002, Csabai and Boda 2005, Pinceel et al. 2016) or inside/attached to other organisms such as aquatic microorganisms or small crustaceans (Vanschoenwinkel et al. 2008, Coughlan et al. 2017, Lovas-Kiss et al. 2020), the scales at which landscape features might be relevant could extend several hundreds of kilometres

(Green et al. 2002, Lovas-Kiss et al. 2019) or be only linked to the fluvial network connecting lakes if only dispersal by drift exist (Doretto et al. 2020). Hence, if we want to assess the role of landscape centrality for lake planktonic communities it is key to consider different scales granting the possibility to quantify how landscape arrangement might impact diversity patterns for these different taxonomic groups (Borthagaray et al. 2014, Cunillera-Montcusí et al. 2021).

Network theory can contribute to a better representation of landscape structures and understanding about the potential effect of different landscapes on biodiversity patterns (Urban and Keitt 2001, Dale 2017). By creating networks based on previously defined landscapes, we are able to calculate metrics that quantify the relative position of habitats in these networks, and directly test how relevant these are for biodiversity (e.g. centrality gradient; (Estrada and Bodin 2008, Economo and Keitt 2010, Horváth et al. 2019, Borthagaray et al. 2020). Furthermore, congruent patterns between different organisms and the scales at which they relate with centrality can inform us about the extent at which landscape is impacting their assembly patterns (Hill et al. 2017, Sarremejane et al. 2017, Schmera et al. 2018). Such congruence might be related with body size (Ortiz et al. 2023), that will markedly differ across planktonic groups, from bacterioplankton to zooplankton (Figure 1 H1). Smaller organisms (e.g. bacterioplankton and protists) might be related with larger scales not necessarily linked to fluvial connections whereas zooplankton might be related to smaller scales or to the fluvial network (Michels et al. 2001, Braghin et al. 2015, Chaudhary et al. 2022, Custer et al. 2022). However, even though the relationship of organisms with centrality might differ across scales, we could expect that the direction of these relationships would be preserved across organism groups (Figure 1 H2). Thus, on the one hand, we could hypothesise that communities located at more central positions would present greater species richness diversity and lower beta diversity as central communities could be easily reached by most of the regional pool

of species (Mouquet and Loreau 2003, Ai et al. 2013, Grainger and Gilbert 2016, Custer et al. 2022). On the other hand, more isolated communities would contain lower alpha diversity and higher beta diversity (Chase and Shulman 2009, Tonkin et al. 2016b, Bender et al. 2017, Custer et al. 2022). This would reflect a concomitant change in composition, with central communities being more similar among them while greater differentiation would be observed in more isolated ones, potentially affecting communities contribution to beta diversity (Legendre and De Cáceres 2013). These general patterns may foster a stronger mismatch with environment when it relates with species richness but not against composition as environmental characteristics may fail to explain the total number of species in central sites (i.e. higher due to mass effects) but may perform better in explaining community dissimilarity (i.e. higher homogeneity). At which scales centrality will drive this mismatch will shed light on the impact of landscape on these processes and the equilibria between main assembly drivers (Thompson et al. 2020, Suzuki and Economo 2021).

In this study, we explore the connection between network centrality and how diversity patterns interact with the environment in planktonic communities. Our goal is to enhance our understanding of the role that landscape structure plays in influencing the assembly of these taxonomic groups. To explore this, we obtained data from four groups of organisms ranging in size and ecological role (i.e. bacterioplankton, protists, phytoplankton and zooplankton) from 55 alpine lakes located across Austria, Germany, and Switzerland. Using the sampled lakes as reference, we constructed six networks that cover various landscape scales, considering the neighbouring lakes (ranging from 6.5 km to 650 km) as well as the fluvial network. Based on these data, we were able to relate how diversity and composition of planktonic communities were affected by the centrality gradient calculated at each scale. Across all these elements, we hypothesise that 1) large-bodied organisms (e.g. zooplankton) will relate with centrality at small scales (6.5 or 65 km) or the fluvial network

while we expect the opposite for small-bodied organisms (Figure 1-H1). Nevertheless, we also hypothesise that 2) the sign of the relationships will be shared among groups being more central lakes, the ones consisting of richer and more similar communities contrasting with isolated ones (Figure 1-H2), thus raising community mismatch with lakes environmental characteristics.

Methods

Sampling procedure in the field

The general sampling protocol is described in (Horváth et al. 2017). Briefly, we sampled 55 lakes in the perialpine area of Austria, Southern Germany and Switzerland in 2011 & 2012 (Switzerland: n = 20; EAWAG sampling, summer and autumn 2011; Austria and Germany, WasserCluster sampling, summer and autumn 2012; n = 27 and 8, respectively; see Figure 2). Coordinates for all 55 lakes can be found in Supplementary S1. Five environmental variables were recorded for each lake: water temperature (°C), chlorophyll *a* concentration (µg/l), electrical conductivity (µS/cm), lake area (hectares), and altitude (m). These variables were used as proxies of the lakes' main environmental characteristics and the level of anthropogenic influence. Sampling was carried out by a boat, with smaller lakes being sampled above their deepest points, and larger lakes at depths >15m, except for Hubertussee, where water was collected from the outlet of the lake. Water samples were collected by a tube sampler from the upper mixed layer (i.e., epilimnion), following inspection of temperature profiles which were measured prior to collecting the water samples. Phytoplankton samples were obtained following the same protocol as with zooplankton (see Horvath et al. 2017) and fixed with Lugol's iodine solution. Sampling equipment was always rinsed with lake water before collecting water samples and cleaned by dilute hypochloric acid solution in between lakes. Analytical protocols for recording and measuring standard limnological

variables are outlined in (Horváth et al. 2017). For molecular analysis 300-800 ml water samples were filtered through 0.2 µm nitrocellulose membrane filters until they were clogged. The equipment for filtration was thoroughly rinsed with water and cleaned with ethanol in between lakes to avoid contamination. Molecular filters were frozen immediately after filtration and kept stored at -20°C until further processing. Unfortunately, we could not obtain the same number of samples for each one of the targeted taxonomic groups and therefore we eventually used 52 lakes for bacterioplankton based on 16S, 47 for protists based on 18S, 50 for phytoplankton, 52 for zooplankton obtained by microscopic analyses, and 49 for zooplankton based on 18S of a total of 55 lakes (Figure 2).

Molecular analyses for 16S and 18S

DNA from the molecular filters was extracted using the MoBio PowerSoil DNA isolation kit and amplified with general primers targeting the 16S rRNA gene of bacteria (Caporaso et al. 2011) and 18S rRNA gene of eukaryotes (Hugert et al. 2014). The two-step PCR amplification was carried out according to Caporaso et al. (2011) and included sample-specific barcode combinations. Illumina MiSeq sequencing libraries were prepared at the Centre of Genomic Research in Liverpool using Nextera kits (Illumina). For 16S, overlapping forward and reverse reads were combined. For 18S only the forward direction reads, ~180 bp were used. Raw sequencing reads were quality filtered and OTU clustered (16S: 97% identity, 18S: 95% identity) using the VSEARCH pipeline (Rognes et al. 2016). OTUs were taxonomically classified using a manually curated version of the SILVA database with the CREST LCA Classifier (Lanzén et al. 2012). Through this molecular processing and classification, we obtained an OTUs and species list for bacterioplankton, protists, and zooplankton (18S zooplankton). The raw sequence data have

been submitted to the European Nucleotide Archive under project PRJEB70292 and the processed datasets are available in the online supplementary material.

Microscopic analysis of phyto- and zooplankton

A detailed outline on the microscopic analysis of zooplankton is given in Horváth et al. 2017. Overall, all crustacean zooplankton were identified to the minimum taxonomic level possible (species or species complex). Phytoplankton were quantified by inverted microscopy, following standard protocols (Utermöhl 1958, Başoğlu et al. 2017). Depending on the biomass, 20-100 ml were allowed to settle for 24-48 hours. A minimum of 500 cells were identified and counted, employing different magnifications. The raw datasets are available in the online supplementary material.

Community structure and composition

In total, we obtained five community datasets of different organism groups: bacterioplankton, protists, phytoplankton and zooplankton. For the latter, we independently considered datasets originating from morphological identification (“zooplankton”) and molecular identification (“18S zooplankton”). In all these five datasets, we used binary data on species or OTUs (presence/absence) after the exclusion of rare species (<10 sites for bacterioplankton and 18S zooplankton, <3 for protists, phytoplankton, and zooplankton). With these datasets, we analysed planktonic diversity by calculating specific community metrics (species richness, average replacement, richness difference and LCBP) and multivariate responses (dbRDA). Species richness (Rich) corresponded to the number of taxa found in each lake. Replacement and richness differences correspond to the beta diversity partitions that we averaged for each lake to obtain a unique sample value. Replacement (Repl) refers to what extent the composition of each pair of

communities corresponds to species substitutions, whereas richness difference (Rich-Diff) informs to what extent this difference can be attributed to differences in species numbers between each pair of lakes (Legendre 2014). Local contribution to beta diversity, hereafter named LCBD, was used to quantify the relevance of each lake at a regional level, providing an estimate on how unique its community is with respect to all the other lakes (Legendre and De Cáceres 2013). For average replacement, average richness difference and LCBD we used Jaccard's dissimilarity index for presence absence data from the Podani's families of indices (Borcard et al. 2011, Podani and Schmera 2011, Legendre and De Cáceres 2013). Finally, for the multivariate analysis we carried out a distance-based redundancy analysis (dbRDA) also using the Jaccard index. All these analyses were done with the *vegan* package (Oksanen et al. 2010). For the calculation of all dissimilarity metrics and multivariate analysis, we considered only the lakes that were belonging to the same network for the cases where more than one subgraph was built (i.e. 65 km, 6.5 km and fluvial scales; see next paragraph).

Landscape scales and network construction

In order to create a set of different networks representing different spatial scales, we defined a total of five different landscapes by using the geographic position of all lakes surrounding the 55 sampled lakes based on a global database (Lehner and Do 2004). These five scales represent five different landscapes capturing lake distribution surrounding the sampled lakes. We used these five landscapes to construct five networks from which to calculate centrality values. First, we calculated the maximum distance between all the sampled lakes (from Neuenburgersee to Hubertussee of around 650 km). Second, we identified all the lakes within a buffer of that distance (resulting in a total of 2406 lakes in our dataset). This landscape constituted the largest scale (hereafter referred to as 650 km). We then repeated this procedure but dividing the scale by

approximately half at each step to decrease the considered scale and the number of lakes included in each buffer. Thus, modifying the obtained potential network structure. This resulted in four landscapes with the following scales: 325 km including 771 lakes, 100 km including 185 lakes, 65 km including 127 lakes and 6.5 km including 58 lakes (Supplementary S2).

With the five landscapes, which included the 55 sampled lakes, we constructed five undirected networks (Figure 3). In these networks, each lake was considered a node and each connection an effective dispersal route. We connected these networks using the percolation distance, which is defined as the minimum linkage distance needed to connect all network nodes to at least one neighbour (Keitt 1997, Urban and Keitt 2001, Solé 2012). This distance was of 142 km for the 650 km scale, 71 km for the 325 km scale, 68 km for the 100 km scale, and of 6 and 6.9 km for the two subgraphs of the 65 and 6.5 km scales. We used the percolation distance because it allowed us to connect all nodes within one unique network while conserving the regional structure caused by the distribution of nodes in the landscape. Also, it allows consideration of all nodes when calculating centrality metrics. Thus, percolation networks represent the intermediate transition between a disconnected and a global network, where all nodes are potentially reachable but still preserve their regional structure (Borthagaray et al. 2015a). For each network we calculated closeness centrality, which represents the centrality gradient (Figure 3). Closeness centrality is the reciprocal of the average distance from the focal node to all the other network nodes, where higher values represent more central habitats in the network (Borthagaray et al. 2015a, Dale 2017). The two smaller scales (65 km and 6.5 km) consisted of two separated subgraphs and their closeness centrality values were calculated separately for each subgraph and later normalised dividing the values by each graph maximum. By including these scales in our analysis, we assumed that dispersal at these two scales was not occurring between subgraphs and maintained each subgraph

centrality gradient avoiding the effect of having different numbers of nodes. Overall, with the five landscapes, we generated five networks and hence five gradients of centrality using the percolation distances (Figure 3).

The fluvial directed network was created using the two river networks where the sampled lakes belong (the Danube and the Rhine river catchments: Figure 3F). We obtained the shapefiles from these two fluvial networks from HydroRIVERS and HydroBASINS databases (Lehner et al. 2008, Lehner and Grill 2013). Then, we transformed the shapefile into a graph where each segment intersection was considered as a node using the package *shp2graph* (Lu et al. 2018). Once the network was defined, we located the position of the sampled lakes in it. Finally, we calculated the centrality isolation gradient considering a directed network from up- to downstream (i.e., out-closeness centrality). We considered a directed network to capture the natural dendritic structure of the rivers to also account for drift dispersal through the fluvial network. The two fluvial catchments consisted of two different subgraphs as the 65 and 6.5 km scales, thus, we followed the same approach and calculated centrality values (i.e. out-closeness) separately for each subgraph and later normalised dividing the values by each subgraph maximum. As out-closeness presented a marked skewness due to the dendritic network of rivers we additionally log-transformed their values to correct this. Overall, out-closeness presented the same gradient as the values of undirected networks with lower values of out-closeness representing more isolated parts of the stream basins (i.e. headstream nodes; Figure 3) and *vice versa*. For the five undirected networks and the fluvial network calculations and representation, we used the packages *igraph* (Csárdi and Nepusz 2006) and *sna* (Butts 2023).

Centrality-isolation against community facets

We followed two different procedures for community metrics and the multivariate analysis to relate them against centrality but in both cases we excluded environmentally explained variation in order to focus on the pure effect that the centrality gradient had on diversity and composition. For each one of the community metrics (Rich, LCBD, Repl, and Rich-Diff) we first selected the most relevant environmental variables using a random forest (randomForestSRC package, (Ishwaran and Kogalur 2023)). Second, we conducted a linear model with each community metric as response variable and the selected environmental variables as explanatory variables. Third, we extracted the residuals of that linear relation retaining the unexplained part of this relationship. Finally, we used the residuals as a response variable against the centrality values of each one of the six networks using a generalized additive model (GAM; mgcv package, Wood 2017). We considered the residuals of each diversity metric as the response variable and the centrality-isolation gradient as the smooth term. Our focus on using residuals aimed to capture the discrepancies between environmental variables and the diversity patterns observed in planktonic communities, exploring their relationship with centrality measures (i.e. closeness and inverse out-closeness). In essence, any significant trends identified would indicate the pure impact of the centrality gradient on community assembly, independent of underlying gradients in environmental drivers and eliminating any potential autocorrelation between the environment and centrality.

For community composition (dbRDA; (Oksanen et al. 2010)), we first subtracted the unexplained coordinates of the first two axes of the dbRDA. Second, we fitted a GAM using the *ordisurf* function of the vegan package (Oksanen et al. 2010) into the unexplained multivariate space. Here, centrality (closeness and out-closeness) was fitted as a smooth surface using penalised splines in GAM (Wood 2003) to later predict its fitted values in a regular grid. In summary, this function plots the fitted contours with a convex hull of data points over the existing unexplained

multivariate space and calculates its significance (Oksanen et al. 2010). The two analyses considering community metrics and multivariate analysis were carried for each one of the five considered taxonomic groups (Bacterioplankton, Protists, Phytoplankton, Zooplankton and S18 Zooplankton) and considering the closeness values of each network (650 km, 325 km, 100 km, 65 km, 6.5 km and fluvial). So, overall, we conducted a total of 120 models for community structure and 30 dbRDA for community composition. From these we selected only the significant smooth terms ($p < 0.05$), which indicated that there was some significant trend between community structure or composition and the centrality.

Results

Community structure and composition

While there were major differences in the five taxonomic groups in their richness values, inherent to the two main identification pipelines (microscopic versus molecular), average LCBD values were quite similar between the groups (Table 1). Within LCBD, protists, zooplankton and S18 zooplankton presented a greater standard deviation, indicating a greater variation in uniqueness of their communities in comparison to Phytoplankton and Bacterioplankton. Average replacement and richness also showed differences between groups that overall indicated the strong variation at the regional level of each group (Table 1). Average replacement was markedly high for bacterioplankton and phytoplankton but bacterioplankton presented the lowest values of richness difference. Contrastingly, other groups had much more similar beta diversity partition values such as protists and S18 zooplankton. Tables with the specific values for each sampled lake as well as the plots representing these metrics can be found in Supplementary S3 and S4.

Landscape scales and network building

The six networks that we built presented some differences between the structure that they were capturing (Figure 3). For example, 650 km and 325 km networks represented markedly different scenarios, for 650 km the network was much denser and many links were present while for 325 km the structure was much less connected and related to the distribution of nodes through the landscape (Figure 3). On the other hand, 65 km and 6.5 km networks were more similar in terms of connections between lakes even though the first had two times the number of lakes of the other (Figure 3). Finally, the fluvial network was unique among the other networks as it was directed (i.e. each node was connected to its downstream neighbour following a head- to downstream sense). The parameters describing the six built networks can be found in Supplementary S5. For all the networks, the sampled lakes were located along the entire centrality-isolation gradient indicating that sampled lakes were representing most of the variability in closeness centrality of each network (Supplementary S6).

Centrality-isolation against community facets

- Community metrics

The GAMs conducted for each one of the five organism groups (bacterioplankton, protists, phytoplankton, zooplankton, and 18S zooplankton) using each one of the residual values from the four community metrics (Rich, Repl, RichDiff, and LCBd) as response variables and the centrality gradient from the six networks (6.5, 65, 100, 325, 650 km and fluvial) as smooth term showed differences between taxonomic groups and across scales (Figure 4). Mostly bacterioplankton, zooplankton and 18S zooplankton showed significant trend with centrality isolation gradient at some scales (650km, 320km, 100km, 65km and Fluvial) while protists only appeared related with one scale (Fluvial) and phytoplankton did not show any significant trend. From these, 18S zooplankton was the group presenting more significant trends of all the studied ones being the only

group where Richness difference and LCBD values showed some significant trends (Figure 4).

See all model results in Supplementary material S7.

From the significant trends that we observed, species richness was significant for bacterioplankton, zooplankton and 18S zooplankton (Figure 5). Richness was significant for the networks built at 100, 325, 650 km, the Fluvial and for most of the groups it presented higher residual values at more central sites (Figure 5A:H), thus pointing to a greater mismatch between environment and species richness in these locations. Only for bacterioplankton it presented a more U-shaped trend for alpha diversity with lower residuals in sites with intermediate centrality values. In contrast, for the Fluvial network these patterns were reversed with lower residuals in more downstream sites (Figure 5D & H). Replacement presented a negative trend being more central communities, the ones having lower residual values for both zooplankton and 18S zooplankton at 100 and 325 km networks (Figure 5I,J,L & M) and thus showing a better match with environmental constraints for replacement. On the other hand, bacterioplankton and protists replacement was negatively related with centrality but from the fluvial network (Figure 5K & N), being downstream sites better explained by environment. Richness difference was only related with 18S zooplankton for the fluvial network (Figure 5O), having a positive trend with higher residuals in more downstream lakes. Finally, LCBD had significant trends only for the 18S zooplankton at 100, 325, 650 km, being more central sites, the ones having lower residuals and thus having a stronger link with environment (Figure 5P:R). Overall, all the significant models explained 10-20% of deviance and had consistent patterns across scales and even across groups for the significant community structure metrics (Figure 5). In general, there was a positive association between species richness residuals and centrality, indicating a disconnection from environmental factors in central positions. Conversely, the residuals for average replacement and LCBD exhibited a negative relationship

with centrality, suggesting that in central locations, replacement and LCBD were more effectively explained by environment. Most observed trends followed a monotonous pattern, apart from bacterioplankton, which displayed distinctive U-shaped trends (Figure 5).

- *Multivariate analysis*

For the multivariate analysis we observed similar results than with community metrics, the groups presenting a significant smooth surface against centrality were basically bacterioplankton, zooplankton and 18S zooplankton (Figure 6) with protists being only significant in one case (Figure 6G). Bacterioplankton had a significant relationship across all networks (Figure 6A:F). For networks encompassing larger scales (e.g. 650km), more central sites tended to be more separated (Figure 6E & F). On the other hand, as scales decreased (e.g. 65 and 6.5km) this pattern was the inverse and more isolated lakes were the ones being in more external positions of the multivariate space (Figure 6A & B). For these smaller scales only one subgraph showed a significant relationship for composition (the lakes within Austria and Germany) for bacterioplankton, protists and zooplankton at 6.5 km scales (Figure 6A, G & H) and bacterioplankton at 65 km scales (Figure 6B). Contrastingly, 18S zooplankton appeared significantly related with 6.5 and 65km scales (Figure H & M) but only from the other group of lakes (lakes within Switzerland). For these scales, protists, zooplankton and 18S zooplankton showed more similar communities among isolated lakes. Finally, zooplankton and 18S zooplankton presented the same significance trends for 100, 325, 650 km (Figure 6I:K & O:Q). In these cases, the relationship with the centrality gradient was similar being more central sites, the ones tending to have similar composition through all the significant scales. See all dbRDA model results in Supplementary material S8.

Discussion

The impact of spatial structure on diversity patterns has been broadly discussed in the last years of ecological research (Turner and Gardner 2015, Leibold and Chase 2018, Erős and Lowe 2019, O'Connor et al. 2020). It connects directly with main assembly patterns as spatial structure defines the canvas in which metacommunities assemble and therefore, it drives diversity of species that are able to move throughout it (Vellend 2016, Thompson et al. 2020). In the current work, we highlighted the strong role that landscape structure plays as a driver of alpine lakes planktonic communities as well as the scales at which it takes place (i.e. 650, 325, 100 km and Fluvial). In these systems, landscape structure has generally been attributed to the fluvial connection between lakes (Almeida-Gomes et al. 2020). However, here, we saw that not only fluvial structure affects diversity patterns and that bacterioplankton, protists and zooplankton diversity appear also shaped at undirected network structures (i.e. 650, 325, 100, 65 and 6.5 km of distance). Furthermore, Phytoplankton did not show any relationship with centrality of these landscape structures, neither fluvial nor undirected. Such findings emphasise the complexity in quantifying spatial structures that appear relevant for diversity patterns and the strong variability that can exist between taxonomic groups (Boix et al. 2017, Tonkin et al. 2018a, Newman 2019), and they contribute to gather new insights in how, and more specifically at which scales, planktonic and microscopic organisms are being affected by centrality and thus the scales at which metacommunity processes might be taking place for them (Leibold and Chase 2018, Custer et al. 2022).

On the one hand, our hypotheses were partially refuted because we observed that organisms did not respond to different scales in relation to size (hypothesis 1, i.e. Bacterioplankton and Zooplankton appeared related through similar scales), and some groups community structure and composition was not correlated with centrality (i.e. Phytoplankton). On the other hand, when a

pattern was detected across several groups the sign of it was consistent for all of them, which implies that the captured process was having the same effect across groups. For example, alpha diversity responded in the same way against centrality for both bacterioplankton and zooplankton or replacement for bacterioplankton, protists & zooplankton (hypothesis 2). An increase in centrality was concomitantly increasing the mismatch between environment and species richness. This loss of connections might be related to the higher species richness of more central sites (Economo and Keitt 2010, Altermatt 2013, Borthagaray et al. 2020). Interestingly, composition responded the other way around (for 325 and 100 km landscapes), where more central lakes and downstream lakes replacement had a better fit with environment. Although not shared among groups, zooplankton beta diversity was related with several scales and for both, Zooplankton and 18S Zooplankton. In all these cases, more central communities were better explained in central positions both for composition and uniqueness in comparison with more isolated lakes. Such patterns respond to a stronger impact of dispersal in more central communities (e.g. mass effects archetype; (Leibold et al. 2004), which would favour the foster community homogenization and the overall match of its replacement and LCBD values with respect to the regional pool (Altermatt et al. 2011, Ai et al. 2013, Carrara et al. 2014, Tonkin et al. 2016a, Jamoneau et al. 2018). These patterns were found at similar landscape scales for both Bacterioplankton and Zooplankton, which meant that the network structure obtained between 650 and 100 km was actually capturing a landscape structure that was affecting these two groups beta diversity patterns (Economo and Keitt 2008, Chisholm et al. 2011, Dale 2017). Thus, these scales could represent the most probable level at which dispersal processes would be impacting these groups defining the effective landscape at which the exchange of individuals drives diversity patterns and metacommunity assembly (Vellend 2016, Leibold and Chase 2018, Thompson et al. 2020).

The observed responses highlight not only that smaller-bodied organism groups are affected by the centrality gradient (i.e. Bacterioplankton), but also that the assembly of these groups is affected across different regional scales (Custer et al. 2022, Barbour et al. 2023, Tytgat et al. 2023). Therefore, even for smaller microscopic taxa, broad-regional patterns might explain their regional diversity distribution (Tytgat et al. 2023), something that highlights the relevance for accounting for landscape and centrality metrics even for these groups (Whitfield 2005, Fontaneto et al. 2008, Vannette and Fukami 2017). Along the same lines, Zooplankton appeared related with the same scales as Bacterioplankton, which could point towards both groups being dispersed by the same vectors or by vectors that act at the same scales of hundreds of kilometres (Incagnone et al. 2015, Pinceel et al. 2016, Coughlan et al. 2017). It is worth noting that bacterioplankton was sampled via filtration in a size-inclusive manner, meaning that bacteria associated with larger particles such as Zooplankton bodies are also included in our analysis. Contrastingly, phytoplankton showed the total opposite pattern, not being affected by any of the tested centrality isolation gradients. Protists behaved similarly only showing relationships at the fluvial scale and at the smallest network scales. Based on our results, we should expect that these two groups would have been related to same scales than bacterioplankton and zooplankton, as they could also be transported by the same vectors (Naselli-Flores and Padisák 2016, Padisák et al. 2016). As a consequence, we assume that these organisms were potentially transported through the same corridors but their establishment failed either due to different environmental conditions (Abonyi et al. 2018, Chaparro et al. 2018), or due to stronger priority effects (Fukami 2015, Leibold and Chase 2018). Furthermore, these two groups, specially Phytoplankton, are primary producers which strongly rely on environmental conditions (e.g. available nutrients, stratification; Stomp et al. 2011, Li et al. 2019, Borics et al. 2021), which, together with the fact that we focused

on the pure spatial effect (i.e. centrality gradient across scales) might have hidden the spatial signal for these groups if both environment and centrality gradients were equally relevant or correlated (Chaparro et al. 2018, Loewen et al. 2020, Rocha et al. 2020). Nonetheless, the current findings point towards the relevance of spatial distribution for the diversity of two key planktonic groups such as bacterioplankton and zooplankton not uniquely related to the fluvial network. Such results stress the strength of spatial processes for these groups but also the scales at which this occurs (i.e. hundreds of kilometres) that should be considered if regional diversity patterns are to be preserved (Edge et al. 2017, Horváth et al. 2019, Brauer and Beheregaray 2020).

One limitation of our work is that our environmental variables are a limited simplification of the actual local environment. Our simplification of the environment and our focus on how well landscape structure (i.e. centrality) was explaining the mismatch between it and diversity patterns was marked by the few environmental variables available. Although we accounted for several environmental variables to tease apart their contribution to diversity, the number of metrics was short (i.e. water temperature, chlorophyll-a concentration, electrical conductivity, lake area, and altitude) and therefore some key environmental variables may not have been considered (e.g. nutrients, fish community). However, the five considered metrics also represent main proxies of lake state and human impact for alpine lakes (Jacquemin et al. 2019, Li et al. 2021). In a similar line, landscapes were built based on existing databases with a determined level of accuracy (Lehner and Do 2004). Although satellite identification of water bodies is improving (Pekel et al. 2016), there is still a lack of accuracy to detect small water bodies, which in turn can play an important role in determining network scale fluxes (Downing 2010, Borthagaray et al. 2023a). Furthermore, we connected our landscapes based on the percolation distance which represents a compromise between local and regional network structure. However, networks could have been built based on

different distances representing different perceptions of the landscape (Borthagaray et al. 2015a, Dale 2017, Cunillera-Montcusí et al. 2021). These networks would have corresponded to different ways to perceive each one of the different landscapes and thus, represent different centrality gradients (Borthagaray et al. 2014, Newman 2019, Savary et al. 2023). In the current work, we focused on varying the scale at which the landscape is constructed to focus on the relevance of habitat distribution at different scales in determining diversity patterns (Gilarranz 2020, Faggioni et al. 2021, Borthagaray et al. 2023b). Nevertheless, to additionally explore how different threshold distances might also impact diversity patterns constitutes an avenue to follow in the coming years to further disentangle how planktonic communities are perceiving and interacting with the landscape (Almeida-Gomes et al. 2020, Custer et al. 2022). We employed both morphological and molecular techniques to describe community structure and composition of the different organism groups, aligned with current and emerging best practice approaches to target aquatic diversity (Hillebrand et al. 1999, Deiner et al. 2015). The detection of similar patterns for the same organism group using independent methodology (e.g. zooplankton and 18S zooplankton), strengthens our observations.

In the current work we highlighted the complexity of defining a landscape that will drive diversity patterns across ecosystems at different scales. This complexity will become more evident with the greater availability of satellite information and computationally powerful tools that will allow us to process further layers of the landscape (Newman 2019, O'Connor et al. 2020, Savary et al. 2023). Therefore, the current work is an important step toward accounting for landscape structural features that shape planktonic groups in bigger lentic systems (Almeida-Gomes et al. 2020). These features are, together with abiotic and biotic interactions, key when assessing the diversity of these communities in face of global change as they have an impact on the species that

are available to assemble communities (Leibold and Chase 2018, Thompson et al. 2020). The landscape structure of Alpine lakes is also particularly threatened as alterations at the regional level on the presence of these lakes (Zhang et al. 2017), their connectivity (Monaghan et al. 2005, Robinson and Kawecka 2005) and environmental characteristics (Moser et al. 2019) is subject to global change. Thus, potentially impacting future community diversity patterns (Fuller et al. 2015, Thompson et al. 2017, Pardini et al. 2018). As a consequence, to improve the current knowledge on the relevance of landscape structure on these groups appears key to further understanding the consequences of global change on them as they constitute the basal elements of lake trophic structure. Finally, the consideration of network scale patterns for alpine lakes, moving further from lotic networks, constitutes an advance to better disentangle how these systems are impacted by landscape structure (Almeida-Gomes et al. 2020) and thus, how their metacommunities are assembled and how the layers driving diversity are acting in these threatened ecosystems (Leibold and Chase 2018, Moser et al. 2019).

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Table 1

Taxonomic group	Alpha		LCBD		Repl		RichDiff	
	Mean	sd	Mean	sd	Mean	sd	Mean	sd
16S								
Bacterioplankton	717,692	±145,776	0,019	±0,002	0,477	±0,043	0,155	±0,048
18S Protists	71,714	±7,182	0,020	±0,012	0,106	±0,050	0,101	±0,030
Phytoplankton	9,660	±5,476	0,020	±0,002	0,521	±0,103	0,359	±0,111
Zooplankton	5,904	±1,752	0,019	±0,006	0,372	±0,103	0,225	±0,110
18S Zooplankton	17,122	±5,073	0,020	±0,007	0,226	±0,078	0,252	±0,079

938

939

Figures:

Figure 1: Hypothesised trends for each taxonomic group along the six scales defined in this study for the four metrics of community (richness, replacement, richness difference and LCBBD) and multivariate analysis (dbRDA). Each scale corresponds to a network built out from all lakes found at 6.5, 65, 100, 325, 650 km and along the fluvial network of the sampled lakes from which centrality gradients were calculated (see methods). Centrality gradient is represented in the x axis of the plots ranging from isolated (yellow) until central (purple) lakes. Dark solid lines (or symbols) represent significant trends and grey dashed lines (or symbols) non-significant trends.

Figure 2: Sampled lakes locations and the number of groups that we sampled in each one of the lakes, not all groups were samples in all lakes. The smaller map highlights in black the three countries containing sampled lakes: Austria, Germany and Switzerland.

Figure 3: The five networks generated using global lakes database. From top-left to bottom-right there is 6.5 km, 65 km, 100 km, 352 km, 650 km, and fluvial respectively. Red contoured circles indicate the 55 sampled lakes. Circle fill colours indicate closeness centrality being the more purple/blue circles the ones more centrally located and green/yellow circles the ones in a more isolated position.

Figure 4: P-values for all generalised additive models considering closeness centrality as smooth term for community metrics (Rich, LCBBD, Repl, RichDiff) and for the multivariate analysis ordination surface (dbRDA). Results are represented for all the networks (6.5, 65, 100, 325, 650 km and Fluvial) and considering the five organism groups (Bacterioplankton in yellow, Protists in blue, Phytoplankton in green, Zooplankton in red, and 18S zooplankton in cyan). Larger coloured

circles indicate the models with a significant smooth term (i.e. below 0.05). Note that point location along the X axis is randomly assigned within each network.

Figure 5: Significant trends for each community metric against centrality based on generalised additive models (GAM). Plot background and top-right symbol indicate the corresponding organismal group: bacterioplankton (yellow), zooplankton (red), and 18S zooplankton (cyan). Circle colours represent centrality gradient (same as X axis) to facilitate visualisation, purple colours correspond to more central lakes and yellow colours more isolated lakes. Out of the 120 models, only the 17 significant models ($p < 0.05$) are presented here. See all model results in Supplementary material S7.

Figure 6: Significant multivariate analysis based on the generalised additive models (dbRDA with smooth surfaces). Plot background and top-right symbol indicate the corresponding taxonomic group: bacterioplankton (yellow), zooplankton (red), and 18S zooplankton (cyan). Contour lines and circle colours represent centrality gradient, purple colours correspond to more central lakes and yellow colours more isolated lakes. See all model results in Supplementary S8.

Scales

Trends across scales (H1)

6.5

65

100

325

650

Fluvial

Richness



Bacterioplankton (16S)



Protista (18S)



Phytoplankton



Zooplankton



Zooplankton (18S)

Replacement



Richness differences



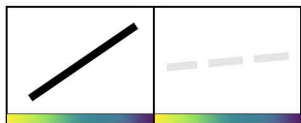
LCBD



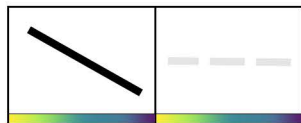
Composition



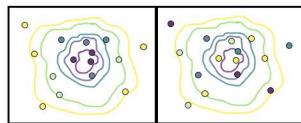
Trend direction (H2)



Isolated - Central Isolated - Central



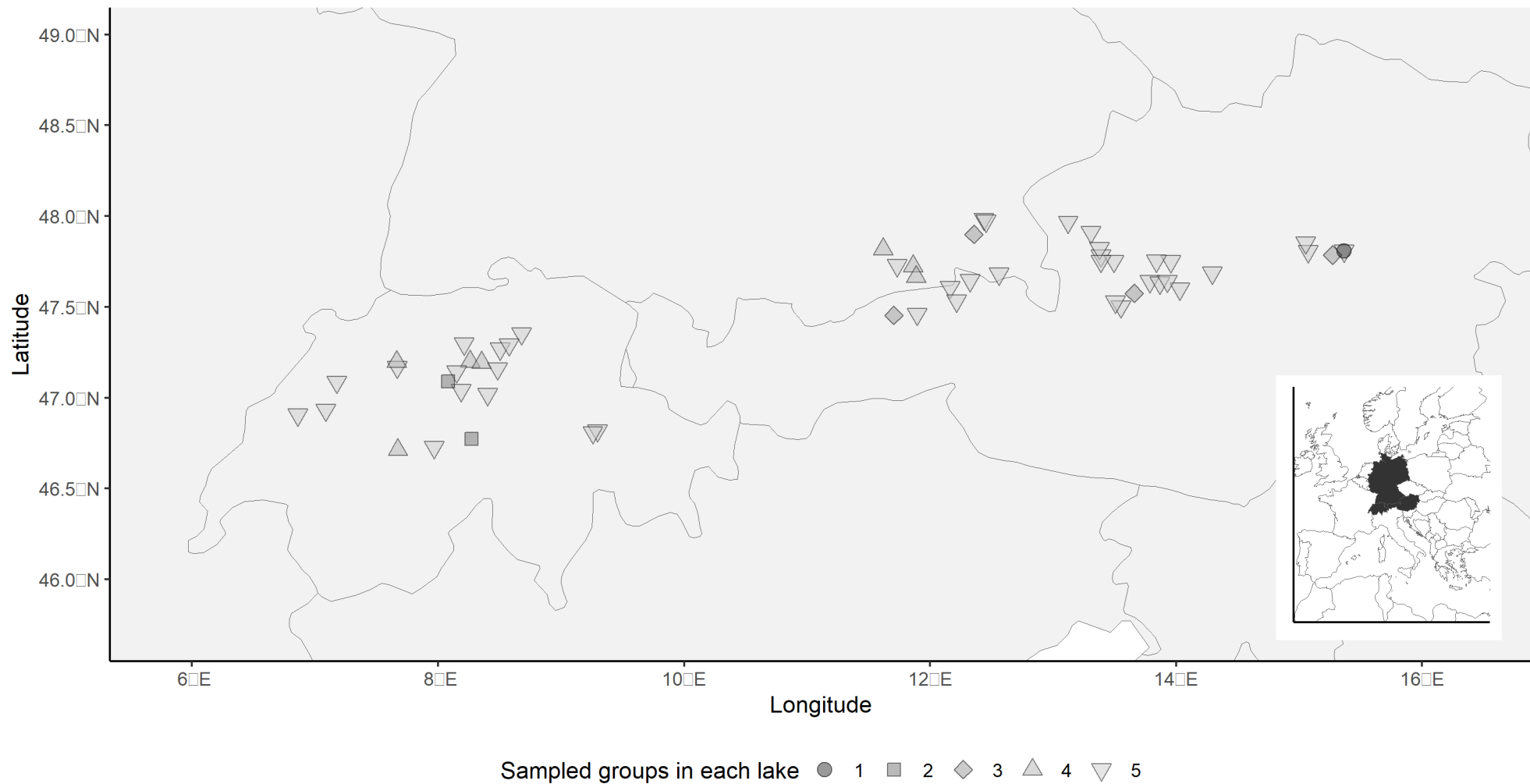
Isolated - Central Isolated - Central



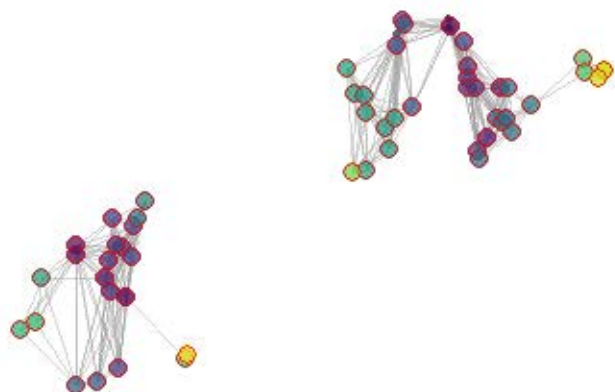
Isolated - Central



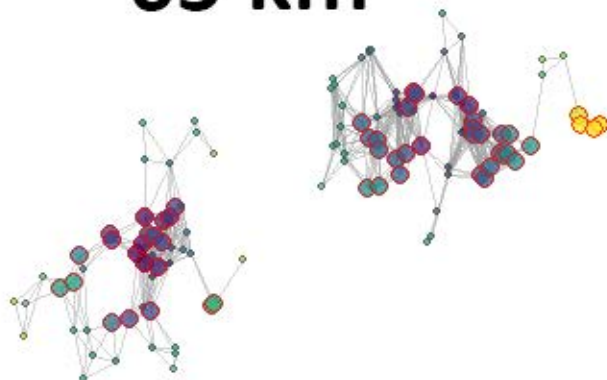
Sampled lakes



6.5 km



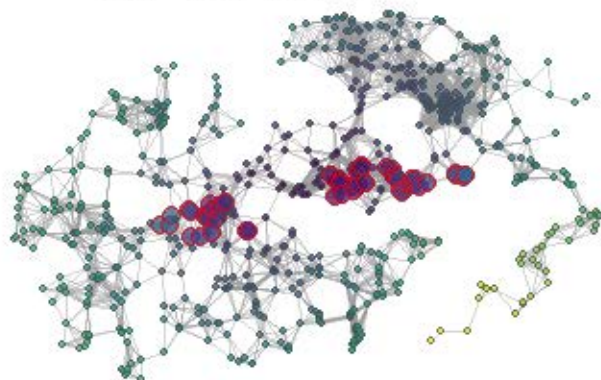
65 km



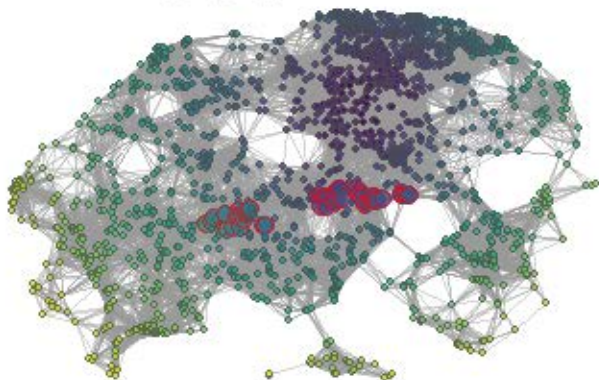
100 km



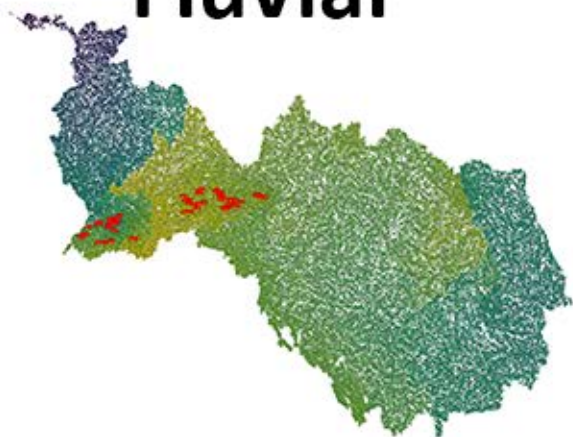
325 km



650 km

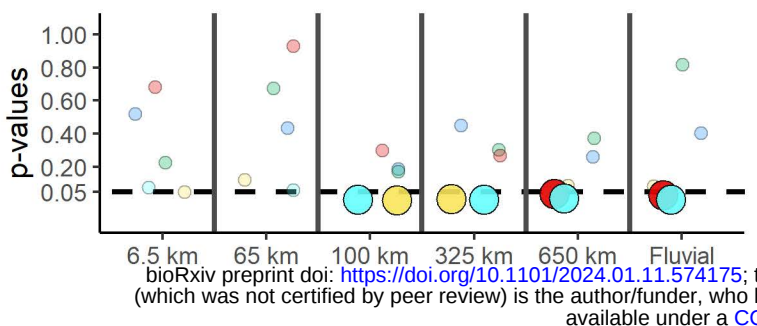


Fluvial

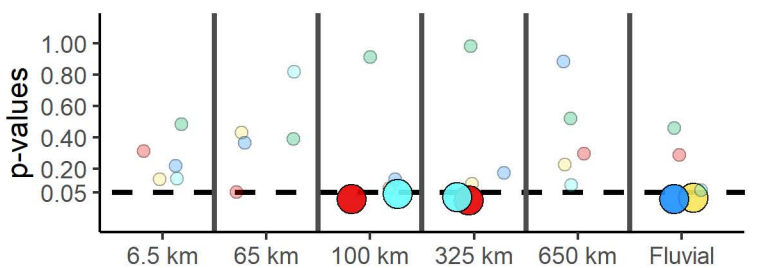


Significance values

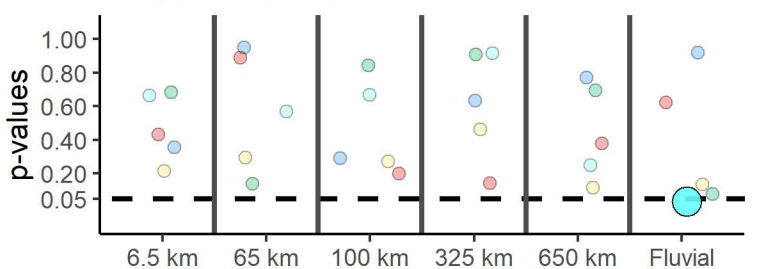
Species richness



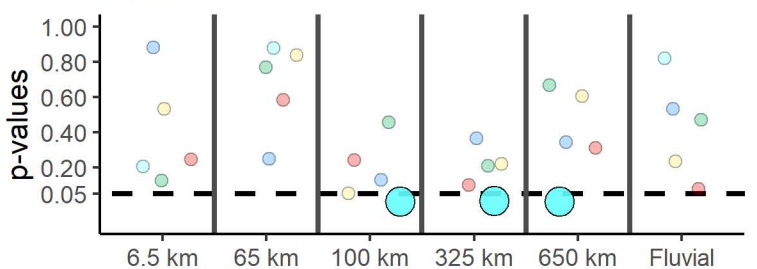
Replacement



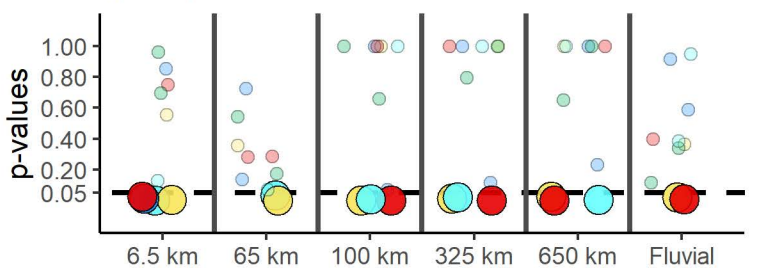
Richness difference



LCBD



dbRDA

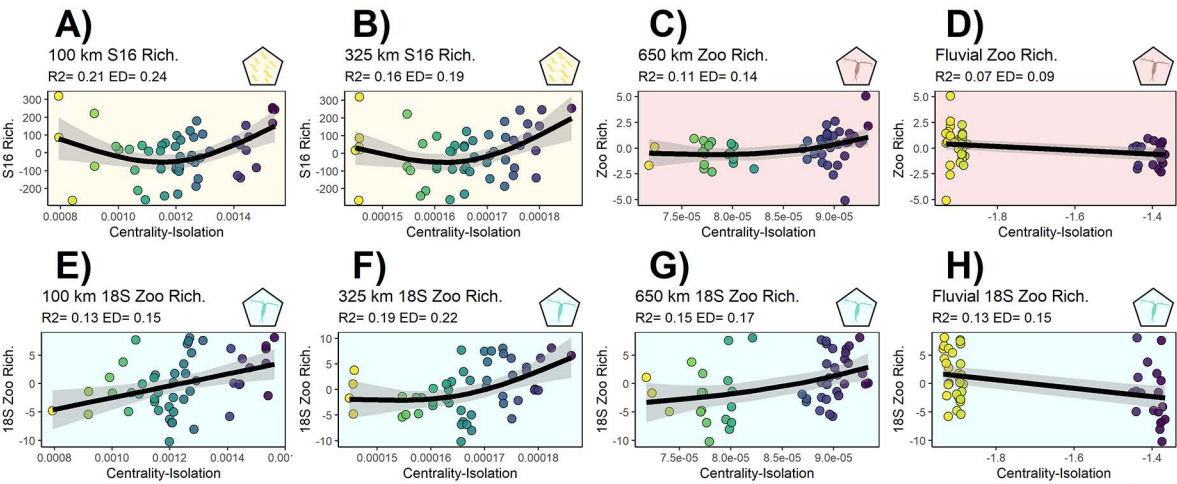


Sign  <0.05  >0.05

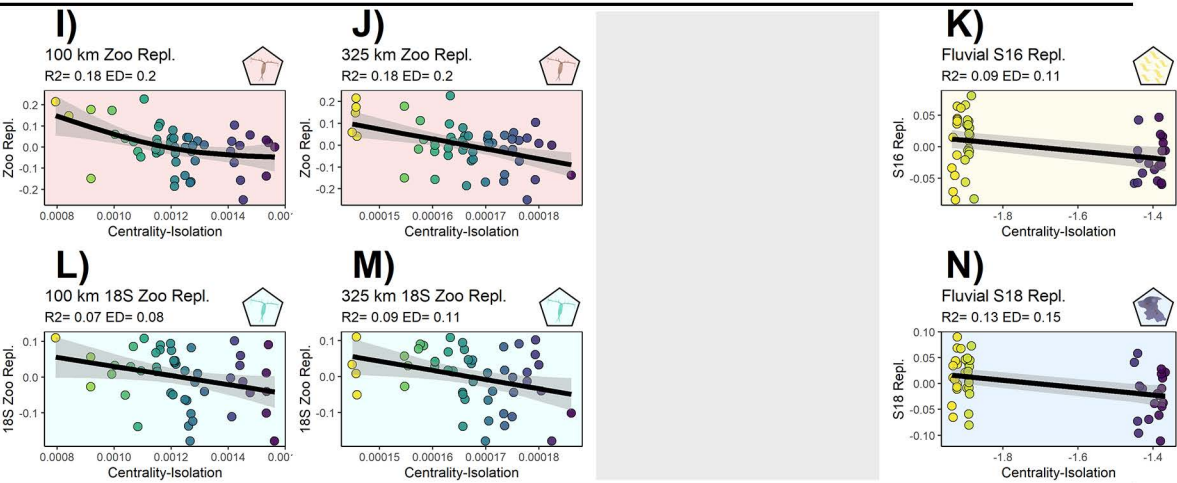
Group  S16  S18  Phy  Zoo  S18 Zoo

6.5 km 65 km 100 km 325 km 650 km Fluvial

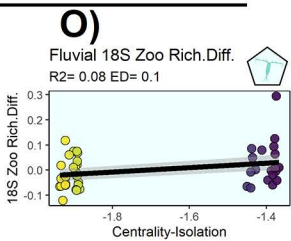
Richness



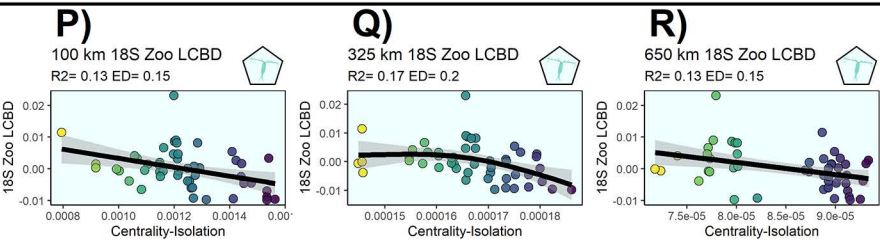
Replacement



Rich. Diff.



LCBD



6.5 km

65 km

100 km

325 km

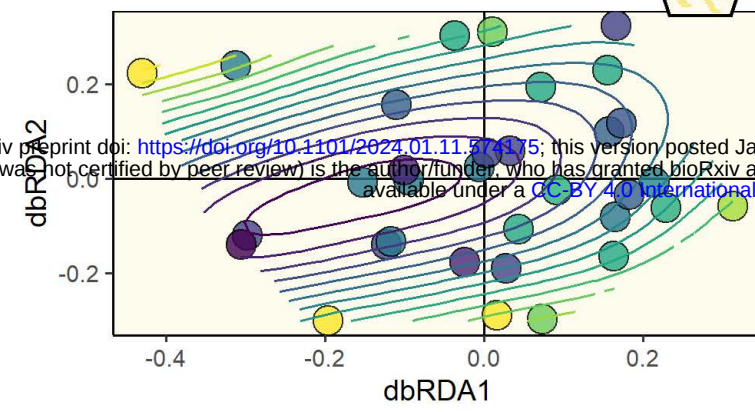
650 km

Fluvial

A)

S16 6.5 km - Austria

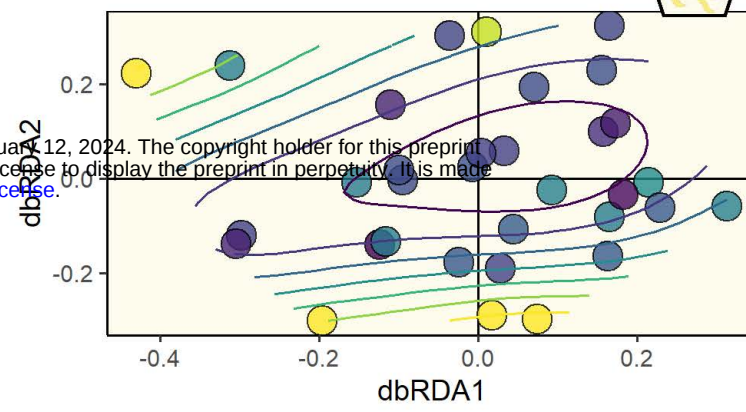
Unc. Inert.= 0.77 R2= 0.33 ED= 0.43



B)

S16 65 km - Austria

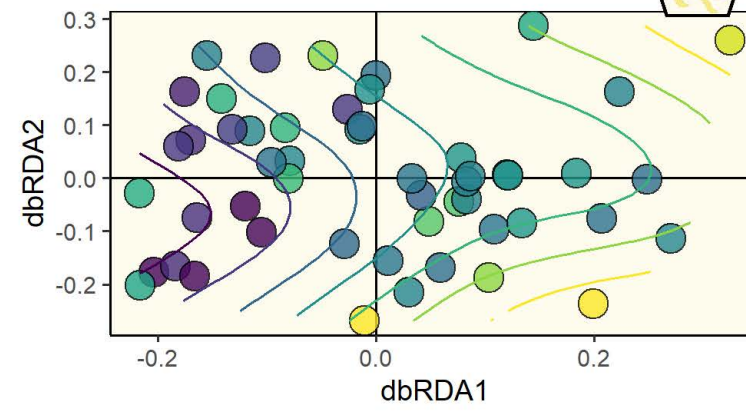
Unc. Inert.= 0.77 R2= 0.43 ED= 0.53



C)

S16 100 km

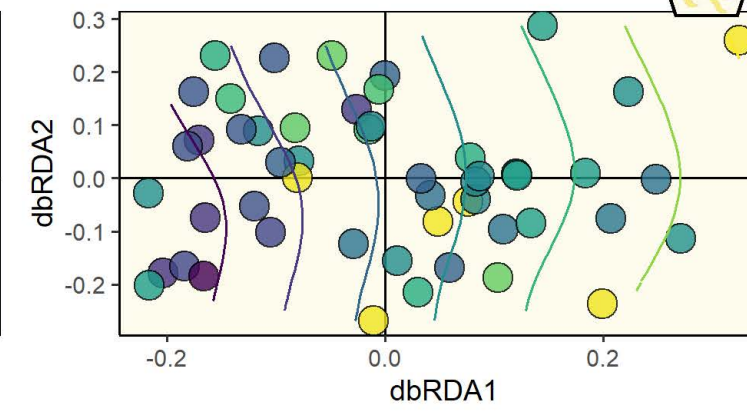
Unc. Inert.= 0.79 R2= 0.27 ED= 0.34



D)

S16 325 km

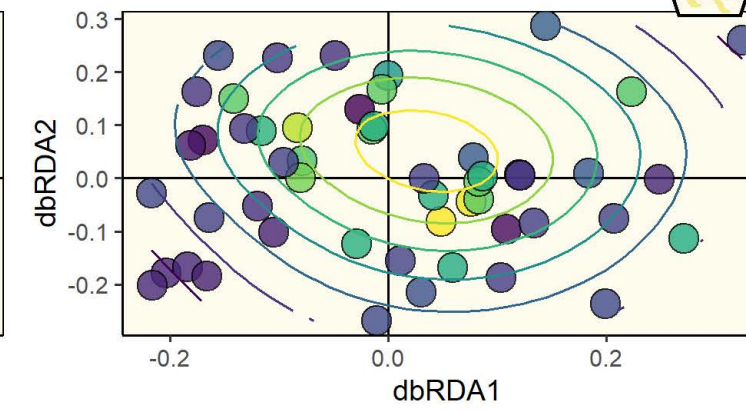
Unc. Inert.= 0.79 R2= 0.15 ED= 0.19



E)

S16 650 km

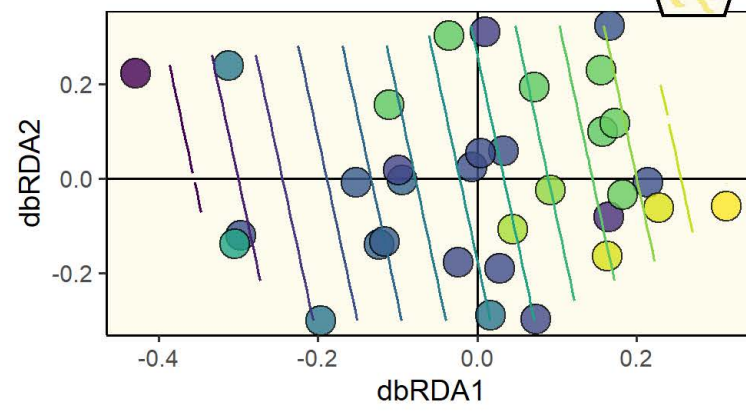
Unc. Inert.= 0.79 R2= 0.15 ED= 0.2



F)

S16 Fluvial - Austria

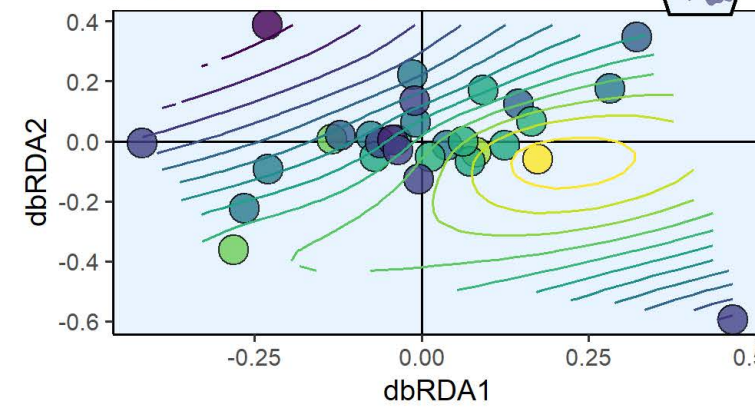
Unc. Inert.= 0.77 R2= 0.18 ED= 0.22



G)

S18 6.5 km - Austria

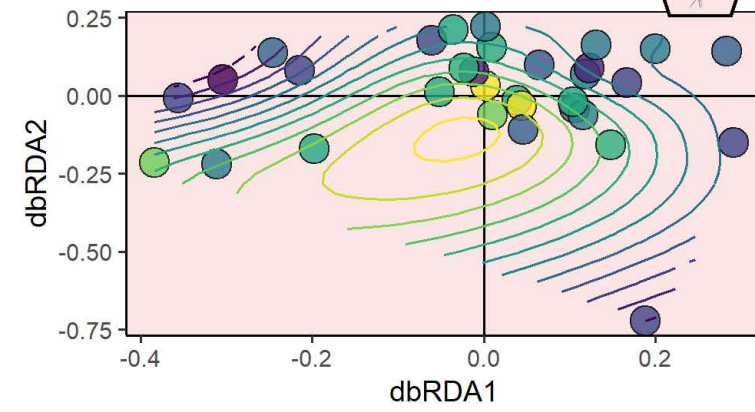
Unc. Inert.= 0.74 R2= 0.28 ED= 0.36



H)

Zoo 6.5 km - Austria

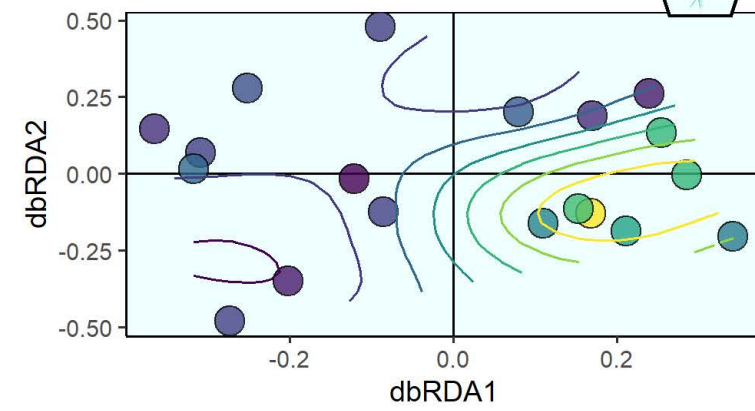
Unc. Inert.= 0.68 R2= 0.27 ED= 0.37



M)

18S Zoo 6.5 km - Switzerland

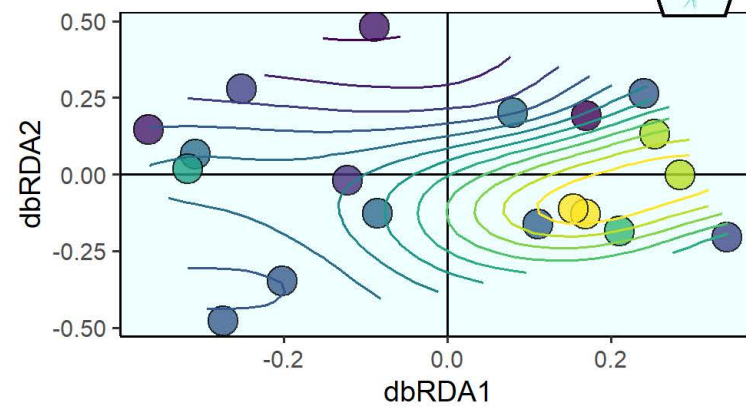
Unc. Inert.= 0.74 R2= 0.64 ED= 0.74



N)

18S Zoo 65 km - Switzerland

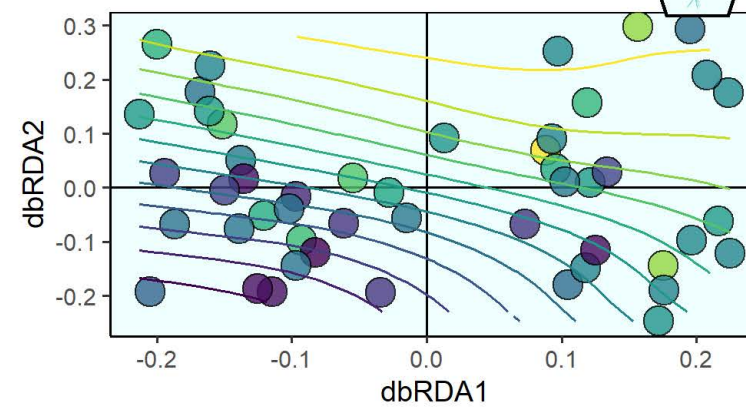
Unc. Inert.= 0.74 R2= 0.41 ED= 0.55



O)

18S Zoo 100 km

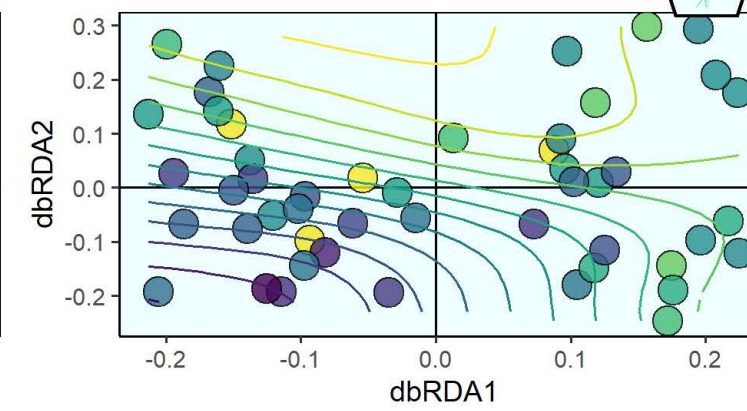
Unc. Inert.= 0.86 R2= 0.18 ED= 0.23



P)

18S Zoo 325 km

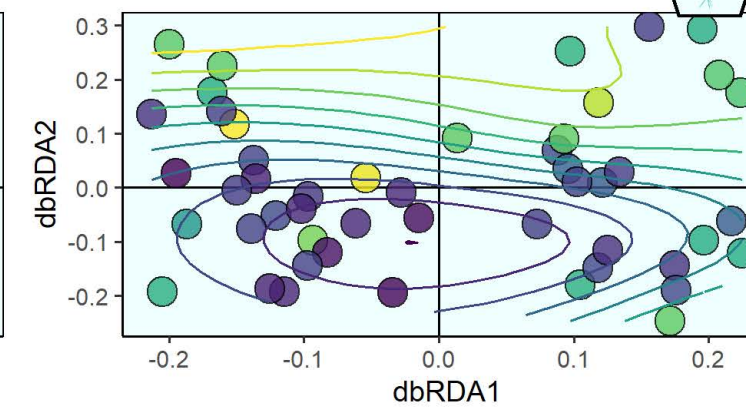
Unc. Inert.= 0.86 R2= 0.16 ED= 0.21



Q)

18S Zoo 650 km

Unc. Inert.= 0.86 R2= 0.22 ED= 0.29



Title: Mapping planktonic communities: a network approach to assess the role of scale and centrality on their diversity and composition

Authors: David Cunillera-Montcusi^{1,2,3,4,5}, Mia Bengtsson⁷, Blake Matthews⁶, Christian Preiler¹, Zsófia Horváth², Csaba F. Vad², Robert Ptacnik¹

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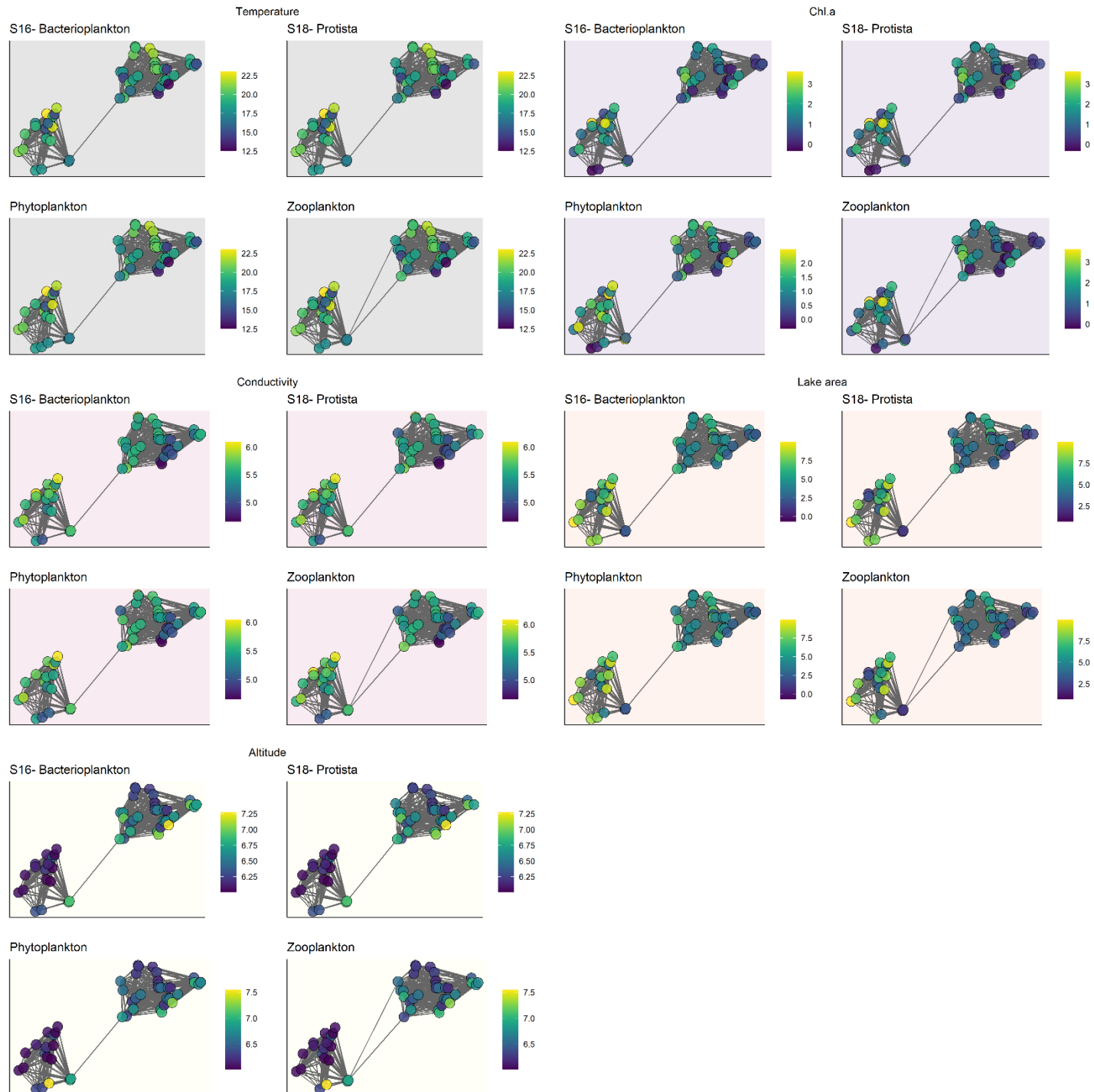
Supplementary S1: Lakes coordinates and recorded environmental variables. Not all sampled lakes were sampled for the same organism groups. Groups sampled in a respective lake are marked with an “X” and a map can be seen in Figure 2 of the main manuscript.

Lake	Longitude	Latitude	Temp	Chlorophyll.a	Conductivity	Lake_area	Altitude	16S_Bacteriopl	18S_Protista	Phytoplankton	Zooplankton	18S_Zooplankt
Achensee	11,71	47,45	16,80	0,52	224,40	680	929	X	X	-	-	X
Almsee	13,96	47,75	14,20	0,07	145,50	85	487	X	X	X	X	X
Ausseer_See	13,79	47,64	20,04	0	127,00	210	712	X	X	X	X	X
Baldeggersee	8,26	47,20	15,82	3,47	299,33	520	463	X	X	-	X	X
Bielensee	7,17	47,09	20,09	1,14	270,50	3780	429	X	X	X	X	X
Brienzersee	7,97	46,73	17,83	0	151,83	2980	564	X	X	X	X	X
Brunnsee	12,44	47,98	19,70	1,41	422,80	6	530	X	X	X	X	X
Burgschisee	7,67	47,17	19,38	1,80	307,17	21	465	X	X	X	X	X
Caumasee	9,30	46,82	16,90	0,49	295,00	10	997	X	X	X	X	X
Gleinkersee	14,29	47,69	18,80	1,74	199,00	13	804	X	X	X	X	X
Greifensee	8,68	47,35	21,90	2,30	415,33	845	435	X	X	X	X	X
Grundlsee	13,87	47,63	19,27	0,24	177,40	422	708	X	X	X	X	X
Halwilersee	8,21	47,30	23,06	0,55	306,00	1030	449	X	X	X	X	X
Hechtsee	12,16	47,61	20,10	1,84	263,83	28	542	X	X	X	X	X
Hinterer_Gosausee	13,55	47,50	13,30	0,00	105,00	31	1154	X	X	X	X	X
Hintersteiner_See	12,22	47,53	16,60	0,04	270,50	55	882	X	X	X	X	X
Hubertussee	15,37	47,81	15,20	0,52	261,50	15	820	X	X	X	X	X
Inkwilersee	7,66	47,20	17,75	3,62	419,40	10	461	X	X	-	X	X
Irrsee	13,31	47,91	21,52	1,18	248,50	355	553	X	X	X	X	X
Kirchsee	11,62	47,82	18,20	1,93	162,40	42	705	-	X	X	X	X
Klostersee	12,45	47,97	19,90	1,59	223,75	140	530	X	X	X	X	X

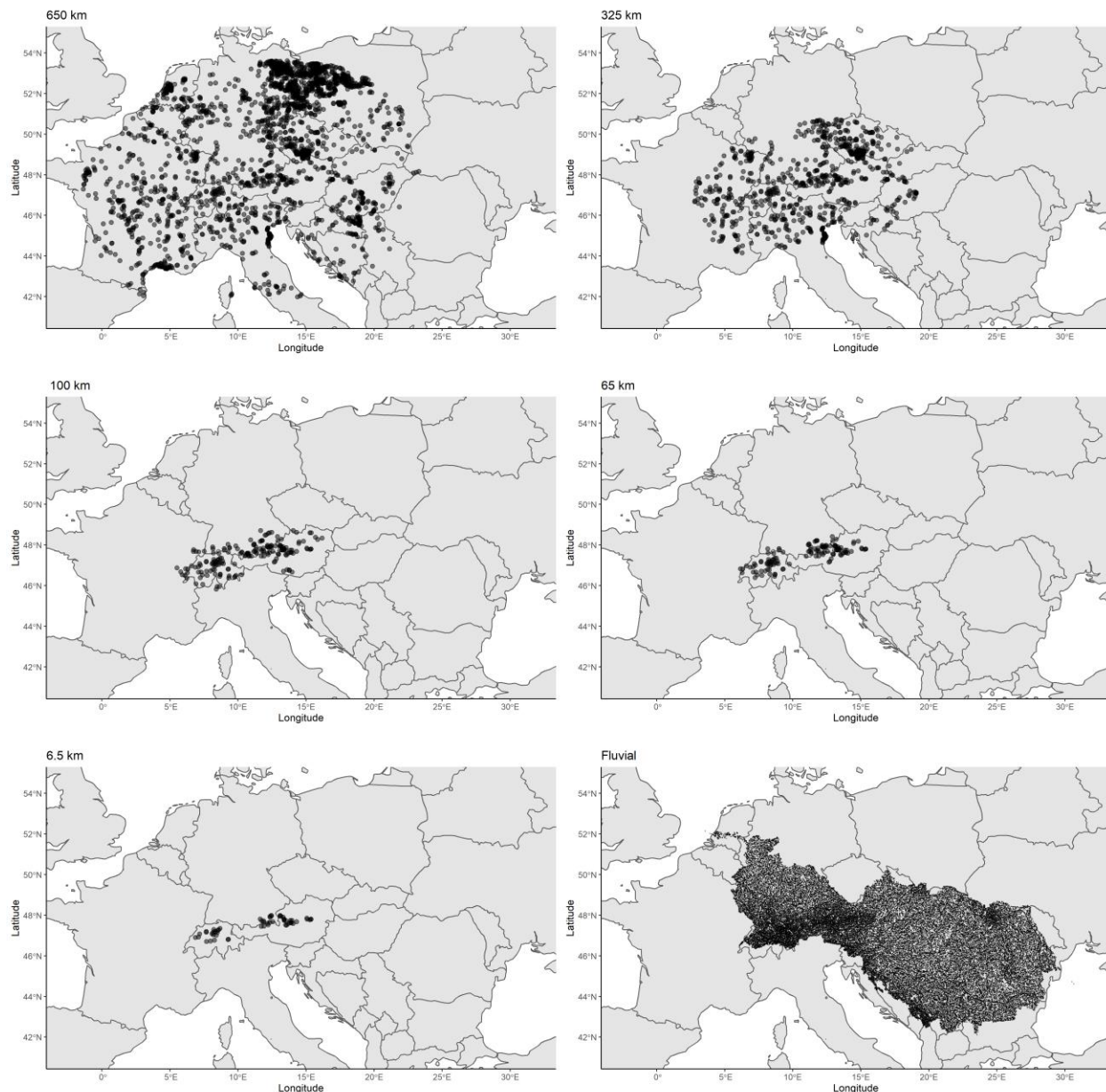
Krotensee	13,39	47,78	19,78	1,06	272,40	9	538	X	X	X	X	X
Lag_Grond	9,26	46,81	17,41	2,41	259,30	5	1016	X	X	X	X	X
Lunzer_Obersee	15,07	47,81	18,95	0,22	173,70	8	1113	X	X	X	X	X
Lunzer_Untersee	15,05	47,85	18,92	0,34	227,20	68	608	X	X	X	X	X
Mondsee	13,37	47,82	20,56	1,55	273,13	1378	481	X	X	X	X	X
Murtensee	7,09	46,93	20,73	2,35	357,67	2280	429	X	X	X	X	X
Neuenburgersee	6,86	46,91	21,10	0,82	265,00	21790	429	X	X	X	X	X
Offensee	13,84	47,75	19,05	0,02	219,50	57	649	X	X	X	X	X
Reintalersee	11,90	47,46	20,00	1,75	328,75	29	564	X	X	X	X	X
Rotsee	8,19	47,04	18,71	2,12	190,83	48	419	X	X	X	X	X
Rumensee	8,35	47,19	18,48	3,15	443,40	2	545	X	X	-	X	X
Schliersee	11,86	47,72	17,90	2,62	234,50	222	776	X	X	-	X	X
Schwarzensee Strobl	13,50	47,75	20,54	1,24	224,60	48	716	X	X	X	X	X
Sempachersee	8,15	47,14	15,31	1,49	248,00	1450	505	X	X	X	X	X
Spitzingsee	11,89	47,67	14,70	2,90	215,80	28	1084	X	X	-	X	X
Steirersee	14,03	47,60	12,50	2,33	149,50	11	1447	X	X	X	X	X
Tegernsee	11,73	47,73	17,50	0,80	286,30	890	726	X	X	X	X	X
Thunersee	7,67	46,71	18,27	- 0,34	227,50	4769	558	X	X	X	-	X
Toplitzsee	13,93	47,64	18,29	0,48	144,75	54	718	X	X	X	X	X
Tuerlersee	8,50	47,27	19,85	2,50	366,50	49	643	X	X	X	X	X
Vierwaldstaettersee	8,58	47,29	14,75	0,96	213,33	11372	406	X	X	X	X	X
Vorderer_Gosausee	13,51	47,53	16,70	0,44	127,50	52	933	X	X	X	X	X
Walchsee	12,33	47,65	18,20	1,86	263,00	95	655	X	X	X	X	X
Wallersee	13,12	47,97	22,02	1,94	285,70	610	503	X	X	X	X	X
Weitsee	12,56	47,68	18,60	1,44	256,88	64	753	X	X	X	X	X

Wolfgangsee	13,39	47,75	20,85	0,31	210,75	1284	538	X	X	X	X	X
Zuerichsee	8,40	47,02	19,75	1,50	244,50	8817	407	X	X	X	X	X
Zugersee	8,48	47,16	22,42	1,40	233,83	3841	413	X	X	X	X	X
Erlaufsee	15,27	47,79	17,10	0,45	236,33	58	835	X	-	X	X	-
Hallstaettersee	13,66	47,58	17,31	0,63	168,75	855	508	X	-	X	X	-
Langbuergner_See	12,36	47,90	20,70	1,15	244,38	104	530	X	-	X	X	-
Melchsee	8,27	46,77	17,58	1,04	164,10	54	1891	-	-	X	X	-
Soppensee	8,08	47,09	21,00	1,82	312,50	23	596	-	-	X	X	-
Seitenarm Hubertussee	15,37	47,81	14,90	0,77	254,50	1	820	-	-	X	-	-

Supplementary S1.2: Maps representing environmental variables across lakes and for each one of the groups of organisms.



Supplementary S2: List of detected lakes for each scale considered. Lakes were subtracted from Lehner, B., and P. Do. 2004. Development and validation of a global database of lakes, reservoirs and wetlands. *Journal of Hydrology* 296: 1–22. doi:10.1016/j.jhydrol.2004.03.028. Fluvial network was subtracted from on Lehner, B., K. Verdin, and A. Jarvis. 2008. New global hydrography derived from spaceborne elevation data. *Eos, Transactions, American Geophysical Union* 89: 93–94. For the fluvial network, each point corresponds to a river reach where lakes were snapped.



Supplementary S3: Community structure values for all the organisms' groups (grey rows). *Rich* corresponds to the species richness, *LCBD* to the local contribution to beta diversity, *Repl* to the average site replacement and *RichDif* to average site richness difference. Both *Repl* and *RichDif* correspond to the beta diversity partitions calculated with Jaccard dissimilarity index.

	Rich	LCBD	Repl.	RichDif.
16S Bacterioplankton				
Achensee 16S_Bacterioplankton	929	0,018	0,421	0,191
Almsee 16S_Bacterioplankton	671	0,022	0,568	0,116
Ausseer_See 16S_Bacterioplankton	570	0,019	0,465	0,166
Baldeggersee 16S_Bacterioplankton	730	0,020	0,532	0,111
Bielensee 16S_Bacterioplankton	732	0,017	0,490	0,114
Brienzersee 16S_Bacterioplankton	445	0,023	0,403	0,289
Brunnsee 16S_Bacterioplankton	585	0,022	0,520	0,152
Burgschisee 16S_Bacterioplankton	798	0,018	0,479	0,128
Caumasee 16S_Bacterioplankton	495	0,023	0,469	0,229
Erlaufsee 16S_Bacterioplankton	413	0,024	0,385	0,326
Gleinkersee 16S_Bacterioplankton	782	0,018	0,498	0,122
Greifensee 16S_Bacterioplankton	872	0,018	0,456	0,159
Grundlsee 16S_Bacterioplankton	557	0,020	0,468	0,175
Hallstaettersee 16S_Bacterioplankton	785	0,018	0,483	0,125
Halwilersee 16S_Bacterioplankton	605	0,019	0,493	0,142
Hechtsee 16S_Bacterioplankton	662	0,019	0,515	0,121
Hinterer_Gosausee 16S_Bacterioplankton	571	0,021	0,500	0,162
Hintersteiner_See 16S_Bacterioplankton	733	0,019	0,510	0,113
Hubertussee 16S_Bacterioplankton	770	0,021	0,537	0,117
Inkwilersee 16S_Bacterioplankton	588	0,023	0,552	0,147
Irrsee 16S_Bacterioplankton	700	0,018	0,502	0,114
Klostersee 16S_Bacterioplankton	748	0,019	0,515	0,113
Krotensee 16S_Bacterioplankton	798	0,018	0,483	0,129
Lag_Grond 16S_Bacterioplankton	952	0,018	0,414	0,202
Langbuerchner_See 16S_Bacterioplankton	757	0,019	0,506	0,116
Lunzer_Obersee 16S_Bacterioplankton	891	0,018	0,437	0,170
Lunzer_Untersee 16S_Bacterioplankton	599	0,019	0,485	0,146
Mondsee 16S_Bacterioplankton	679	0,019	0,508	0,117
Murtensee 16S_Bacterioplankton	787	0,018	0,481	0,125
Neuenburgersee 16S_Bacterioplankton	733	0,017	0,489	0,114
Offensee 16S_Bacterioplankton	703	0,018	0,504	0,114
Reintalersee 16S_Bacterioplankton	985	0,017	0,374	0,226
Rotsee 16S_Bacterioplankton	830	0,018	0,470	0,141
Rumensee 16S_Bacterioplankton	843	0,020	0,498	0,143

Schliersee 16S_Bacterioplankton	873	0,019	0,471	0,158
Schwarzensee_Strobl 16S_Bacterioplankton	841	0,018	0,458	0,146
Seitenarm_Hubertussee 16S_Bacterioplankton	1015	0,020	0,408	0,236
Sempachersee 16S_Bacterioplankton	497	0,022	0,449	0,229
Spitzingsee 16S_Bacterioplankton	962	0,017	0,394	0,210
Steirersee 16S_Bacterioplankton	505	0,021	0,441	0,223
Tegernsee 16S_Bacterioplankton	951	0,017	0,387	0,206
Thunersee 16S_Bacterioplankton	546	0,020	0,464	0,185
Toplitzsee 16S_Bacterioplankton	693	0,019	0,515	0,115
Tuerlersee 16S_Bacterioplankton	748	0,019	0,507	0,114
Vierwaldstaettersee 16S_Bacterioplankton	714	0,018	0,494	0,114
Vorderer_Gosausee 16S_Bacterioplankton	607	0,019	0,492	0,141
Walchsee 16S_Bacterioplankton	620	0,020	0,503	0,135
Wallersee 16S_Bacterioplankton	605	0,020	0,506	0,141
Weitsee 16S_Bacterioplankton	880	0,018	0,450	0,163
Wolfgangsee 16S_Bacterioplankton	636	0,018	0,487	0,131
Zuerichsee 16S_Bacterioplankton	708	0,017	0,490	0,114
Zugersee 16S_Bacterioplankton	621	0,019	0,493	0,135
18S Protista				
Achensee 18S_Protista	79	0,008	0,047	0,098
Almsee 18S_Protista	58	0,046	0,161	0,173
Ausseer_See 18S_Protista	68	0,024	0,134	0,088
Baldeggersee 18S_Protista	57	0,047	0,158	0,185
Bielensee 18S_Protista	82	0,004	0,000	0,125
Brienzersee 18S_Protista	70	0,023	0,141	0,079
Brunnsee 18S_Protista	58	0,045	0,156	0,174
Burgschisee 18S_Protista	74	0,016	0,112	0,073
Caumasee 18S_Protista	80	0,007	0,032	0,106
Gleinkersee 18S_Protista	72	0,019	0,125	0,074
Greifensee 18S_Protista	76	0,012	0,085	0,080
Grundlsee 18S_Protista	74	0,015	0,107	0,073
Halwilersee 18S_Protista	73	0,020	0,131	0,072
Hechtsee 18S_Protista	74	0,016	0,112	0,073
Hinterer_Gosausee 18S_Protista	68	0,024	0,138	0,088
Hintersteiner_See 18S_Protista	75	0,015	0,100	0,076
Hubertussee 18S_Protista	65	0,033	0,161	0,106
Inkwilersee 18S_Protista	67	0,026	0,142	0,093
Irrsee 18S_Protista	77	0,012	0,077	0,085
Kirchsee 18S_Protista	73	0,016	0,114	0,072
Klostersee 18S_Protista	59	0,044	0,163	0,162
Krotensee 18S_Protista	74	0,016	0,109	0,073
Lag_Grond 18S_Protista	78	0,011	0,070	0,091
Lunzer_Obersee 18S_Protista	62	0,036	0,153	0,131

Lunzer_Untersee 18S_Protista	62	0,035	0,148	0,131
Mondsee 18S_Protista	81	0,006	0,017	0,115
Murtensee 18S_Protista	77	0,012	0,080	0,085
Neuenburgersee 18S_Protista	79	0,010	0,055	0,098
Offensee 18S_Protista	76	0,013	0,088	0,080
Reintalersee 18S_Protista	70	0,025	0,152	0,078
Rotsee 18S_Protista	73	0,019	0,130	0,072
Rumensee 18S_Protista	64	0,034	0,160	0,114
Schliersee 18S_Protista	73	0,019	0,127	0,072
Schwarzensee_Strobl 18S_Protista	80	0,007	0,032	0,106
Sempachersee 18S_Protista	61	0,038	0,157	0,141
Spitzingsee 18S_Protista	73	0,017	0,119	0,072
Steirersee 18S_Protista	63	0,033	0,147	0,123
Tegernsee 18S_Protista	81	0,006	0,018	0,115
Thunersee 18S_Protista	71	0,025	0,152	0,075
Toplitzsee 18S_Protista	62	0,036	0,152	0,131
Tuerlersee 18S_Protista	82	0,004	0,000	0,125
Vierwaldstaettersee 18S_Protista	81	0,005	0,015	0,115
Vorderer_Gosausee 18S_Protista	67	0,025	0,135	0,093
Walchsee 18S_Protista	67	0,028	0,153	0,093
Wallersee 18S_Protista	70	0,022	0,135	0,079
Weitsee 18S_Protista	76	0,014	0,095	0,080
Wolfgangsee 18S_Protista	77	0,012	0,079	0,085
Zuerichsee 18S_Protista	82	0,004	0,000	0,125
Zugersee 18S_Protista	73	0,016	0,112	0,072
Phytoplankton				
Achensee Phytoplankton	3	0,023	0,449	0,488
Almsee Phytoplankton	5	0,020	0,519	0,357
Ausseer_See Phytoplankton	8	0,021	0,644	0,266
Bielensee Phytoplankton	14	0,018	0,495	0,333
Brienzersee Phytoplankton	5	0,021	0,559	0,344
Brunnsee Phytoplankton	10	0,019	0,574	0,279
Burgschisee Phytoplankton	5	0,023	0,611	0,333
Caumasee Phytoplankton	4	0,023	0,540	0,401
Erlaufsee Phytoplankton	3	0,020	0,362	0,517
Gleinkersee Phytoplankton	14	0,019	0,529	0,324
Greifensee Phytoplankton	20	0,018	0,406	0,436
Grundlsee Phytoplankton	7	0,021	0,628	0,281
Hallstaettersee Phytoplankton	1	0,022	0,162	0,769
Halwilersee Phytoplankton	13	0,018	0,537	0,310
Hechtsee Phytoplankton	16	0,018	0,481	0,361
Hinterer_Gosausee Phytoplankton	7	0,021	0,632	0,278
Hintersteiner_See Phytoplankton	8	0,019	0,571	0,280

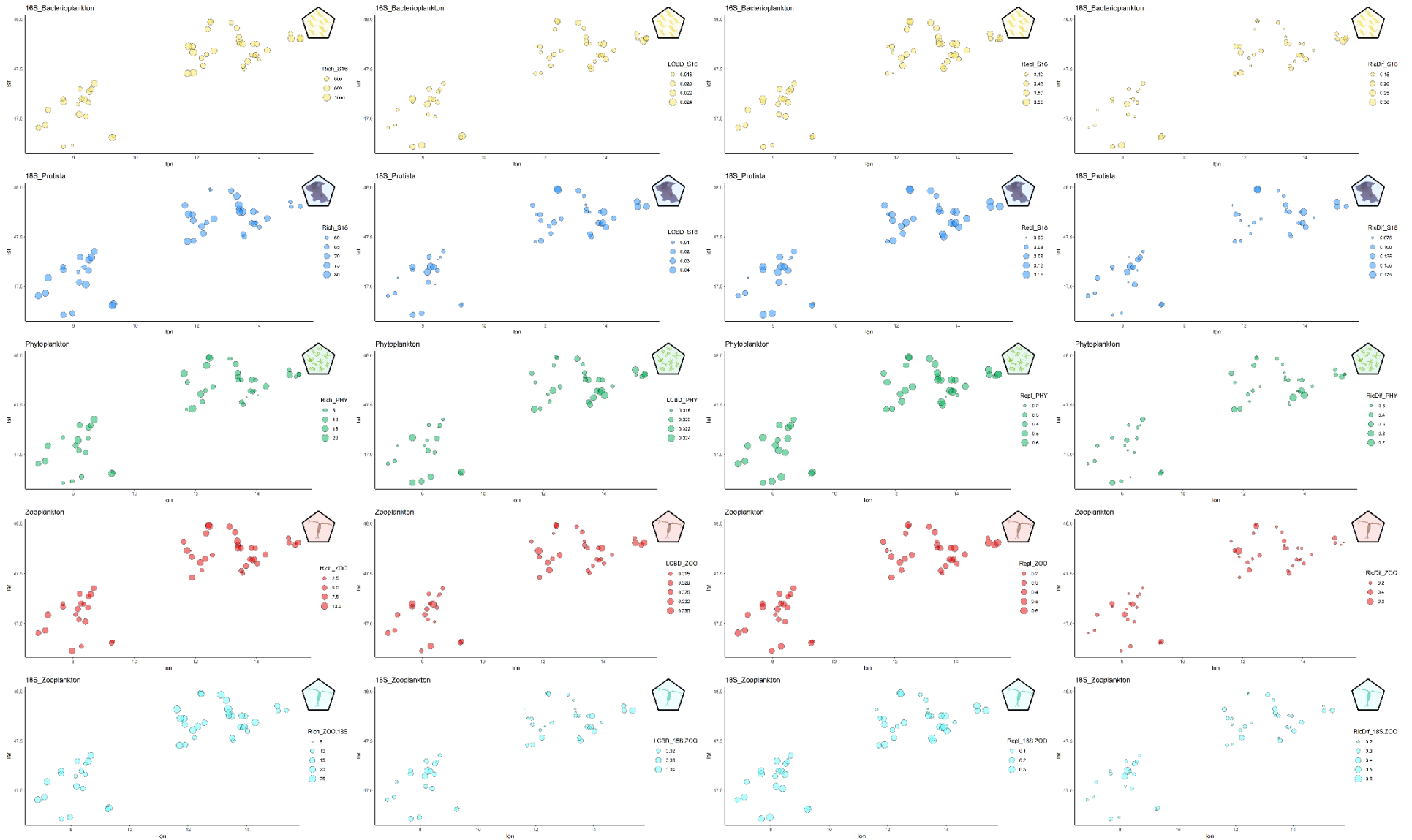
Hubertussee Phytoplankton	6	0,020	0,558	0,316
Irrsee Phytoplankton	12	0,019	0,563	0,295
Kirchsee Phytoplankton	20	0,019	0,444	0,425
Klostersee Phytoplankton	18	0,019	0,461	0,392
Krotensee Phytoplankton	12	0,019	0,566	0,294
Lag_Grond Phytoplankton	18	0,019	0,457	0,397
Langbuegner_See Phytoplankton	19	0,019	0,441	0,412
Lunzer_Obersee Phytoplankton	16	0,018	0,471	0,367
Lunzer_Untersee Phytoplankton	5	0,022	0,599	0,335
Melchsee Phytoplankton	8	0,021	0,643	0,267
Mondsee Phytoplankton	10	0,020	0,600	0,275
Murtensee Phytoplankton	15	0,019	0,511	0,343
Neuenburgersee Phytoplankton	11	0,019	0,561	0,287
Offensee Phytoplankton	12	0,020	0,604	0,287
Reintalersee Phytoplankton	21	0,019	0,400	0,453
Rotsee Phytoplankton	9	0,020	0,611	0,270
Schwarzensee_Strobl Phytoplankton	5	0,021	0,561	0,342
Seitenarm_Hubertussee Phytoplankton	6	0,022	0,618	0,302
Sempachersee Phytoplankton	20	0,018	0,406	0,435
Soppensee Phytoplankton	11	0,018	0,547	0,289
Steirersee Phytoplankton	1	0,024	0,226	0,744
Tegernsee Phytoplankton	7	0,018	0,543	0,298
Thunersee Phytoplankton	3	0,022	0,427	0,495
Toplitzsee Phytoplankton	2	0,022	0,318	0,611
Tuerlersee Phytoplankton	13	0,018	0,517	0,311
Vierwaldstaettersee Phytoplankton	9	0,019	0,586	0,275
Vorderer_Gosausee Phytoplankton	9	0,020	0,618	0,267
Walchsee Phytoplankton	5	0,022	0,594	0,335
Wallersee Phytoplankton	5	0,021	0,565	0,345
Weitsee Phytoplankton	9	0,020	0,599	0,271
Wolfgangsee Phytoplankton	7	0,020	0,591	0,287
Zuerichsee Phytoplankton	10	0,018	0,568	0,279
Zugersee Phytoplankton	6	0,020	0,581	0,309
Zooplankton				
Almsee Zooplankton	5	0,031	0,601	0,174
Ausseer_See Zooplankton	5	0,016	0,338	0,207
Baldeggersee Zooplankton	7	0,016	0,366	0,174
Bielерsee Zooplankton	8	0,021	0,384	0,233
Brienzersee Zooplankton	7	0,016	0,371	0,176
Brunnsee Zooplankton	7	0,024	0,501	0,162
Burgschisee Zooplankton	6	0,022	0,499	0,147
Caumasee Zooplankton	3	0,022	0,227	0,417
Erlaufsee Zooplankton	6	0,024	0,526	0,145

Gleinkersee Zooplankton	6	0,015	0,369	0,159
Greifensee Zooplankton	6	0,016	0,385	0,157
Grundlsee Zooplankton	7	0,018	0,396	0,175
Hallstaettersee Zooplankton	6	0,015	0,374	0,158
Halwilersee Zooplankton	6	0,016	0,395	0,157
Hechtsee Zooplankton	8	0,024	0,441	0,225
Hinterer_Gosausee Zooplankton	4	0,015	0,227	0,305
Hintersteiner_See Zooplankton	3	0,029	0,359	0,385
Hubertussee Zooplankton	6	0,029	0,604	0,139
Inkwilersee Zooplankton	3	0,029	0,375	0,381
Irrsee Zooplankton	7	0,018	0,408	0,171
Kirchsee Zooplankton	6	0,015	0,381	0,158
Klostersee Zooplankton	11	0,021	0,213	0,415
Krotensee Zooplankton	6	0,019	0,439	0,154
Lag_Grond Zooplankton	5	0,018	0,378	0,205
Langbuegner_See Zooplankton	7	0,012	0,299	0,185
Lunzer_Obersee Zooplankton	5	0,029	0,572	0,178
Lunzer_Untersee Zooplankton	4	0,015	0,227	0,305
Melchsee Zooplankton	4	0,028	0,475	0,262
Mondsee Zooplankton	9	0,013	0,182	0,322
Murtensee Zooplankton	7	0,018	0,407	0,175
Neuenburgersee Zooplankton	6	0,023	0,502	0,146
Offensee Zooplankton	6	0,016	0,395	0,158
Reintalersee Zooplankton	7	0,018	0,405	0,172
Rotsee Zooplankton	5	0,014	0,308	0,214
Rumensee Zooplankton	3	0,032	0,428	0,371
Schliersee Zooplankton	1	0,037	0,116	0,757
Schwarzensee_Strobl Zooplankton	7	0,016	0,378	0,172
Sempachersee Zooplankton	7	0,019	0,430	0,167
Soppensee Zooplankton	3	0,021	0,200	0,427
Spitzingsee Zooplankton	6	0,018	0,416	0,156
Steirersee Zooplankton	5	0,016	0,345	0,205
Tegernsee Zooplankton	8	0,011	0,217	0,253
Toplitzsee Zooplankton	6	0,015	0,367	0,159
Tuerlersee Zooplankton	6	0,012	0,314	0,165
Vierwaldstaettersee Zooplankton	7	0,014	0,343	0,175
Vorderer_Gosausee Zooplankton	5	0,018	0,378	0,201
Walchsee Zooplankton	7	0,018	0,400	0,174
Wallersee Zooplankton	7	0,016	0,366	0,174
Weitsee Zooplankton	4	0,024	0,385	0,280
Wolfgangsee Zooplankton	8	0,011	0,217	0,253
Zuerichsee Zooplankton	7	0,012	0,306	0,183
Zugersee Zooplankton	6	0,016	0,385	0,157

18S Zooplankton				
Achensee 18S_Zooplankton	22	0,016	0,188	0,236
Almsee 18S_Zooplankton	14	0,028	0,353	0,211
Ausseer_See 18S_Zooplankton	15	0,020	0,277	0,201
Baldeggersee 18S_Zooplankton	5	0,047	0,173	0,618
Bielensee 18S_Zooplankton	22	0,014	0,171	0,238
Brienzersee 18S_Zooplankton	15	0,025	0,329	0,198
Brunnsee 18S_Zooplankton	18	0,021	0,306	0,185
Burgschisee 18S_Zooplankton	13	0,026	0,306	0,237
Caumasee 18S_Zooplankton	24	0,013	0,115	0,281
Gleinkersee 18S_Zooplankton	25	0,014	0,094	0,304
Greifensee 18S_Zooplankton	20	0,016	0,215	0,214
Grundlsee 18S_Zooplankton	15	0,018	0,252	0,204
Halwilersee 18S_Zooplankton	14	0,023	0,292	0,217
Hechtsee 18S_Zooplankton	21	0,014	0,178	0,223
Hinterer_Gosausee 18S_Zooplankton	11	0,031	0,297	0,300
Hintersteiner_See 18S_Zooplankton	10	0,028	0,219	0,353
Hubertussee 18S_Zooplankton	10	0,036	0,332	0,332
Inkwilersee 18S_Zooplankton	15	0,021	0,281	0,202
Irrsee 18S_Zooplankton	21	0,013	0,159	0,227
Kirchsee 18S_Zooplankton	25	0,011	0,061	0,309
Klostersee 18S_Zooplankton	18	0,020	0,289	0,188
Krotensee 18S_Zooplankton	25	0,013	0,084	0,304
Lag_Grond 18S_Zooplankton	15	0,023	0,305	0,200
Lunzer_Obersee 18S_Zooplankton	12	0,021	0,211	0,279
Lunzer_Untersee 18S_Zooplankton	16	0,020	0,284	0,192
Mondsee 18S_Zooplankton	26	0,012	0,042	0,335
Murtensee 18S_Zooplankton	17	0,017	0,244	0,193
Neuenburgersee 18S_Zooplankton	20	0,017	0,231	0,207
Offensee 18S_Zooplankton	19	0,017	0,245	0,197
Reintalersee 18S_Zooplankton	16	0,022	0,304	0,190
Rotsee 18S_Zooplankton	19	0,019	0,270	0,195
Rumensee 18S_Zooplankton	13	0,025	0,296	0,237
Schliersee 18S_Zooplankton	21	0,017	0,214	0,221
Schwarzensee_Strobl 18S_Zooplankton	22	0,014	0,165	0,237
Sempachersee 18S_Zooplankton	8	0,034	0,175	0,459
Spitzingsee 18S_Zooplankton	18	0,017	0,241	0,193
Steirersee 18S_Zooplankton	11	0,028	0,262	0,306
Tegernsee 18S_Zooplankton	23	0,012	0,118	0,262
Thunersee 18S_Zooplankton	12	0,025	0,257	0,273
Toplitzsee 18S_Zooplankton	18	0,022	0,313	0,185
Tuerlersee 18S_Zooplankton	10	0,027	0,195	0,359
Vierwaldstaettersee 18S_Zooplankton	22	0,016	0,190	0,234

Vorderer_Gosausee 18S_Zooplankton	16	0,021	0,292	0,191
Walchsee 18S_Zooplankton	23	0,011	0,111	0,262
Wallersee 18S_Zooplankton	25	0,014	0,096	0,304
Weitsee 18S_Zooplankton	17	0,018	0,256	0,193
Wolfgangsee 18S_Zooplankton	16	0,017	0,248	0,195
Zuerichsee 18S_Zooplankton	13	0,023	0,271	0,243
Zugersee 18S_Zooplankton	13	0,023	0,273	0,240

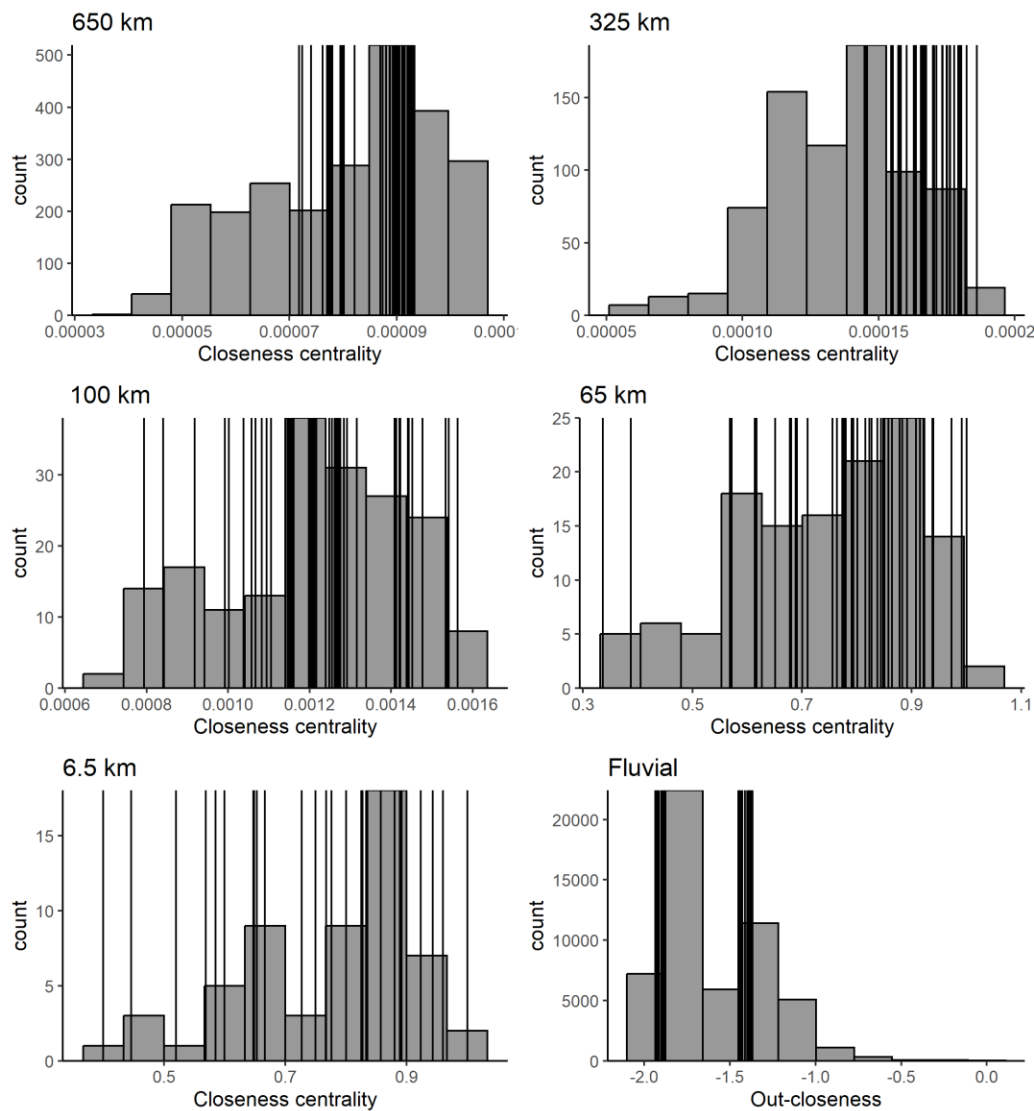
Supplementary S4: Plots showing diversity metrics distribution for each one of the studied groups. Size indicates metrics values. Colours correspond to the different groups: bacterioplankton, protist, phytoplankton, zooplankton and 18S zooplankton respectively.



Supplementary S5: Network descriptive parameters calculated for each one of the constructed networks. Note that Fluvial network corresponds to a dendritic network and some of the values (e.g. degree) must be understood correspondingly.

	Linkage density	Connectance	Diameter	Number of nodes	Mean CC	CC sd	Max. CC	Min. CC
650 km	183,986	0,077	16,000	2406,000	0,000	0,000	0,000	0,000
325 km	28,363	0,037	34,000	771,000	0,000	0,000	0,000	0,000
100 km	21,189	0,115	14,000	185,000	0,001	0,000	0,002	0,001
65 km	12,016	0,095	11,000	127,000	0,739	0,165	1,000	0,336
6.5 km	11,931	0,209	7,000	58,000	0,773	0,154	1,000	0,400
Fluvial	2,000	0,000	34,693	53580,000	0,990	0,006	1,000	0,963

Supplementary S6: Network centrality values distribution within each one of the constructed networks. Black lines correspond to the sampled lakes that appear well distributed along the range of centrality values capturing its main variability or a wide part of it.



Supplementary S7: Generalized additive values model summary for each combination of group, network, and diversity metric residuals. Highlighted rows correspond to the significant relationships, also represented in Figure 4. Find below the model summary results the plots corresponding to each one of the detected relationships (both significant and non-significant ones) grouped in panels of 4 corresponding to the four diversity metrics for the same organism group (bacterioplankton in yellow, protists in blue, phytoplankton in green, zooplankton in red and 18S zooplankton in cyan) and network scales (650, 325,100,65,6.5, and Fluvial).

Group	Network	Variable	Intercept	Std.Err.	t-value	p-value	Smooth F-value	Smooth p-value	Adj R-sqr	Expl.Deviance
16S Bacterioplankton	650 km	Rich_S16	2.46E-14	18.78416	1.31E-15	1	2.988091	0.090098	0.03756	0.056446
16S Bacterioplankton	650 km	LCBD_S16	-1.99E-19	0.000225	-8.86E-16	1	0.271371	0.604746	-0.01449	0.005401
16S Bacterioplankton	650 km	Repl_S16	3.23E-18	0.005442	5.94E-16	1	1.483755	0.22893	0.009395	0.02882
16S Bacterioplankton	650 km	RicDif_S16	-5.11E-19	0.005876	-8.70E-17	1	2.590844	0.11379	0.030251	0.049267
16S Bacterioplankton	325 km	Rich_S16	1.31E-14	17.59118	7.47E-16	1	9.677281	0.009489	0.155927	0.187234
16S Bacterioplankton	325 km	LCBD_S16	-1.15E-19	0.000219	-5.26E-16	1	1.853679	0.221218	0.0363	0.062649
16S Bacterioplankton	325 km	Repl_S16	-1.56E-19	0.005274	-2.97E-17	1	4.529	0.104204	0.069681	0.102987
16S Bacterioplankton	325 km	RicDif_S16	1.61E-18	0.005935	2.71E-16	1	1.829116	0.465038	0.010852	0.03864
16S Bacterioplankton	100 km	Rich_S16	2.53E-14	17.07044	1.48E-15	1	13.46609	0.002105	0.205161	0.235085
16S Bacterioplankton	100 km	LCBD_S16	-8.84E-20	0.000216	-4.09E-16	1	3.963857	0.054796	0.062238	0.082247
16S Bacterioplankton	100 km	Repl_S16	-2.43E-18	0.005242	-4.63E-16	1	5.026377	0.077847	0.080742	0.113838
16S Bacterioplankton	100 km	RicDif_S16	3.96E-18	0.005865	6.76E-16	1	3.15254	0.273498	0.034017	0.065469
16S Bacterioplankton	65 km	Rich_S16	2.09E-14	18.88115	1.11E-15	1	2.447281	0.124048	0.027596	0.046664
16S Bacterioplankton	65 km	LCBD_S16	-1.61E-19	0.000224	-7.20E-16	1	0.804965	0.680146	-0.00294	0.025021
16S Bacterioplankton	65 km	Repl_S16	1.80E-19	0.005484	3.29E-17	1	0.696057	0.408155	-0.006	0.01373
16S Bacterioplankton	65 km	RicDif_S16	1.61E-18	0.005903	2.73E-16	1	2.541507	0.348819	0.021419	0.048985
16S Bacterioplankton	6.5 km	Rich_S16	1.18E-14	18.60598	6.36E-16	1	4.010076	0.050669	0.055733	0.074249
16S Bacterioplankton	6.5 km	LCBD_S16	-1.81E-19	0.000218	-8.32E-16	1	3.169334	0.199853	0.045146	0.078334
16S Bacterioplankton	6.5 km	Repl_S16	1.28E-18	0.005377	2.38E-16	1	2.732672	0.104598	0.032856	0.051821
16S Bacterioplankton	6.5 km	RicDif_S16	-2.21E-18	0.005809	-3.80E-16	1	4.591565	0.165665	0.052361	0.080743
16S Bacterioplankton	Fluvial	Rich_S16	1.93E-14	18.36238	1.05E-15	1	6.355628	0.08568	0.080297	0.110775
16S Bacterioplankton	Fluvial	LCBD_S16	-1.12E-19	0.000218	-5.13E-16	1	3.715371	0.210423	0.044188	0.076341

16S Bacterioplankton	Fluvial	Repl_S16	6.01E-20	0.005474	1.10E-17	1	0.874706	0.354151	-0.00246	0.017193
16S Bacterioplankton	Fluvial	RicDif_S16	1.20E-18	0.005886	2.04E-16	1	2.408715	0.126974	0.026879	0.04596
18S Protista	650 km	Rich_S18	2.02E-16	1.002246	2.02E-16	1	1.285468	0.26268	0.005915	0.026629
18S Protista	650 km	LCBD_S18	-1.85E-19	0.001604	-1.15E-16	1	0.972307	0.344298	0.008356	0.032211
18S Protista	650 km	Repl_S18	2.68E-19	0.006658	4.03E-17	1	0.040816	0.885571	-0.01738	0.005948
18S Protista	650 km	RicDif_S18	-1.14E-18	0.004123	-2.77E-16	1	0.36428	0.770329	-0.00813	0.020852
18S Protista	325 km	Rich_S18	1.03E-16	1.009662	1.02E-16	1	0.577975	0.450943	-0.00885	0.012175
18S Protista	325 km	LCBD_S18	2.38E-19	0.001613	1.48E-16	1	0.829462	0.367303	-0.00293	0.018191
18S Protista	325 km	Repl_S18	3.59E-18	0.006541	5.49E-16	1	1.890092	0.175734	0.018236	0.038699
18S Protista	325 km	RicDif_S18	-6.81E-19	0.00414	-1.65E-16	1	0.226408	0.636477	-0.01638	0.004794
18S Protista	100 km	Rich_S18	-4.64E-16	0.997386	-4.65E-16	1	1.757898	0.191527	0.015531	0.036048
18S Protista	100 km	LCBD_S18	1.37E-18	0.001588	8.63E-16	1	2.395497	0.128484	0.028242	0.048492
18S Protista	100 km	Repl_S18	4.83E-18	0.006512	7.42E-16	1	2.324701	0.134181	0.026844	0.047124
18S Protista	100 km	RicDif_S18	2.29E-18	0.0041	5.59E-16	1	1.141727	0.290782	0.002943	0.023717
18S Protista	65 km	Rich_S18	8.15E-16	0.99788	8.17E-16	1	2.008367	0.438053	0.014555	0.044574
18S Protista	65 km	LCBD_S18	-7.87E-19	0.001599	-4.92E-16	1	1.87328	0.448533	0.014948	0.047259
18S Protista	65 km	Repl_S18	1.73E-18	0.00667	2.60E-16	1	0.018578	0.892195	-0.02087	0.000395
18S Protista	65 km	RicDif_S18	-7.89E-19	0.004113	-1.92E-16	1	0.800276	0.683211	-0.00337	0.02621
18S Protista	6.5 km	Rich_S18	-3.41E-16	0.960239	-3.55E-16	1	1.612425	0.210564	0.012589	0.033165
18S Protista	6.5 km	LCBD_S18	3.10E-19	0.001604	1.93E-16	1	1.418588	0.239677	0.008642	0.029297
18S Protista	6.5 km	Repl_S18	1.24E-18	0.006511	1.90E-16	1	2.75875	0.333612	0.027304	0.058847
18S Protista	6.5 km	RicDif_S18	-8.67E-19	0.004133	-2.10E-16	1	0.388434	0.536182	-0.01291	0.008198
18S Protista	Fluvial	Rich_S18	-7.93E-16	0.963599	-8.23E-16	1	1.273522	0.264841	0.005666	0.026382
18S Protista	Fluvial	LCBD_S18	5.42E-19	0.001615	3.36E-16	1	0.764226	0.386468	-0.00494	0.016
18S Protista	Fluvial	Repl_S18	2.23E-18	0.006641	3.36E-16	1	0.421826	0.519196	-0.01219	0.008895
18S Protista	Fluvial	RicDif_S18	-1.92E-18	0.004134	-4.65E-16	1	0.365683	0.548282	-0.01339	0.00772
Phytoplankton	650 km	Rich_PHY	-4.61E-16	0.68543	-6.72E-16	1	1.77536	0.373186	0.02201	0.055434
Phytoplankton	650 km	LCBD_PHY	-9.61E-21	0.000216	-4.45E-17	1	0.866122	0.669626	-0.00377	0.023751
Phytoplankton	650 km	Repl_PHY	-5.64E-18	0.01435	-3.93E-16	1	0.41857	0.520773	-0.01201	0.008645
Phytoplankton	650 km	RicDif_PHY	6.90E-18	0.015236	4.53E-16	1	0.154362	0.696167	-0.01756	0.003206
Phytoplankton	325 km	Rich_PHY	-5.81E-16	0.692554	-8.39E-16	1	1.076304	0.304747	0.001576	0.021961

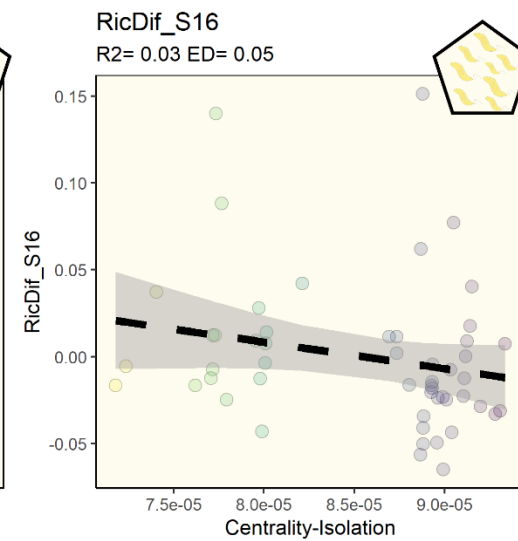
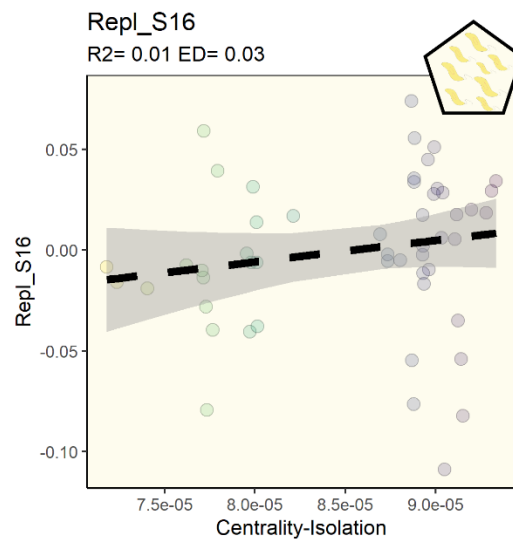
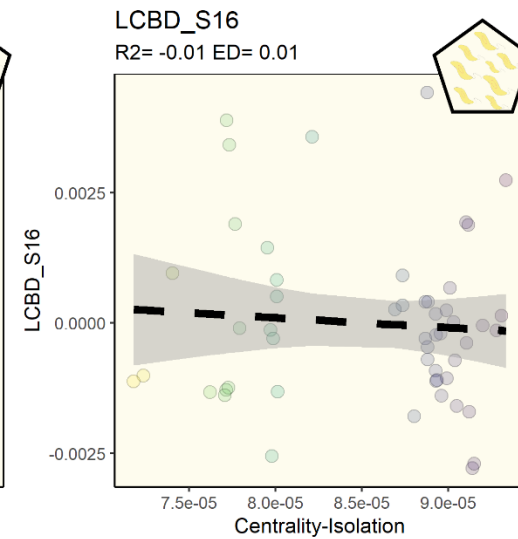
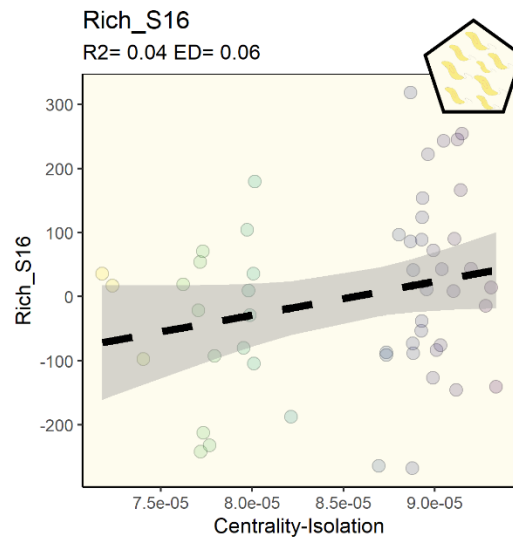
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Phytoplankton	325 km	Repl_PHY	-1.05E-23	0.01464	-7.16E-22	1	0.000339	0.985544	-0.02083	7.14E-06
Phytoplankton	325 km	RicDif_PHY	3.23E-18	0.015258	2.12E-16	1	0.013356	0.90856	-0.02055	0.000278
Phytoplankton	100 km	Rich_PHY	-5.81E-16	0.68681	-8.46E-16	1	1.898493	0.17467	0.018068	0.038125
Phytoplankton	100 km	LCBD_PHY	-9.48E-20	0.000214	-4.42E-16	1	0.784592	0.455645	0.010932	0.039014
Phytoplankton	100 km	Repl_PHY	-1.10E-18	0.014374	-7.68E-17	1	0.272893	0.603823	-0.01506	0.005654
Phytoplankton	100 km	RicDif_PHY	2.25E-18	0.015254	1.48E-16	1	0.039512	0.843323	-0.01999	0.000823
Phytoplankton	65 km	Rich_PHY	-9.42E-17	0.698987	-1.35E-16	1	0.178205	0.674884	-0.01706	0.0037
Phytoplankton	65 km	LCBD_PHY	-9.20E-20	0.000213	-4.32E-16	1	1.684349	0.340515	0.026121	0.059027
Phytoplankton	65 km	Repl_PHY	-5.89E-18	0.013917	-4.23E-16	1	2.267745	0.191124	0.048186	0.077487
Phytoplankton	65 km	RicDif_PHY	5.44E-18	0.01489	3.65E-16	1	1.614923	0.326568	0.028016	0.060145
Phytoplankton	6.5 km	Rich_PHY	-4.97E-16	0.678369	-7.33E-16	1	2.747935	0.22724	0.042056	0.07629
Phytoplankton	6.5 km	LCBD_PHY	-1.08E-19	0.000215	-5.04E-16	1	0.919669	0.501365	0.009948	0.041275
Phytoplankton	6.5 km	Repl_PHY	1.72E-18	0.01452	1.18E-16	1	0.797696	0.376252	-0.00415	0.016349
Phytoplankton	6.5 km	RicDif_PHY	1.76E-18	0.015249	1.15E-16	1	0.068858	0.794169	-0.01937	0.001433
Phytoplankton	Fluvial	Rich_PHY	-1.59E-16	0.696957	-2.27E-16	1	0.145829	0.818112	-0.01116	0.015364
Phytoplankton	Fluvial	LCBD_PHY	-1.99E-19	0.00021	-9.46E-16	1	2.634646	0.201024	0.048036	0.081212
Phytoplankton	Fluvial	Repl_PHY	-1.23E-19	0.014398	-8.52E-18	1	0.111116	0.740335	-0.01848	0.00231
Phytoplankton	Fluvial	RicDif_PHY	1.76E-18	0.015198	1.16E-16	1	0.394884	0.532724	-0.0125	0.00816
Zooplankton	650 km	Rich_ZOO	-1.19E-16	0.206279	-5.78E-16	1	5.591359	0.038291	0.110792	0.138912
Zooplankton	650 km	LCBD_ZOO	3.82E-19	0.00075	5.09E-16	1	2.947505	0.311003	0.028234	0.057616
Zooplankton	650 km	Repl_ZOO	-4.33E-18	0.014064	-3.08E-16	1	1.103251	0.299034	0.002009	0.021587
Zooplankton	650 km	RicDif_ZOO	-8.42E-18	0.015002	-5.61E-16	1	0.780232	0.381322	-0.00433	0.015365
Zooplankton	325 km	Rich_ZOO	2.50E-18	0.215426	1.16E-17	1	1.56648	0.270662	0.03018	0.057222
Zooplankton	325 km	LCBD_ZOO	-3.03E-19	0.000732	-4.14E-16	1	6.027606	0.099308	0.074382	0.104066
Zooplankton	325 km	Repl_ZOO	-2.47E-17	0.01275	-1.93E-15	1	12.18382	0.001018	0.179838	0.195923
Zooplankton	325 km	RicDif_ZOO	-1.53E-23	0.0148	-1.03E-21	1	2.175822	0.146466	0.022536	0.041702
Zooplankton	100 km	Rich_ZOO	2.43E-18	0.216137	1.12E-17	1	1.331607	0.302298	0.023768	0.04988
Zooplankton	100 km	LCBD_ZOO	-4.23E-19	0.000747	-5.66E-16	1	3.595426	0.243603	0.037689	0.066711
Zooplankton	100 km	Repl_ZOO	-3.32E-17	0.012765	-2.60E-15	1	13.79142	0.006254	0.17789	0.204908
Zooplankton	100 km	RicDif_ZOO	3.85E-18	0.014868	2.59E-16	1	1.69912	0.198384	0.013522	0.032865

Zooplankton	65 km	Rich_ZOO	-8.08E-17	0.220912	-3.66E-16	1	0.007875	0.930004	-0.01984	0.000158
Zooplankton	65 km	LCBD_ZOO	-6.90E-20	0.000756	-9.13E-17	1	1.671957	0.201963	0.013003	0.032357
Zooplankton	65 km	Repl_ZOO	-1.60E-17	0.013665	-1.17E-15	1	4.131772	0.047559	0.057822	0.076307
Zooplankton	65 km	RicDif_ZOO	-5.05E-18	0.015114	-3.34E-16	1	0.029518	0.864289	-0.0194	0.00059
Zooplankton	6.5 km	Rich_ZOO	-1.08E-16	0.220555	-4.89E-16	1	0.16984	0.682597	-0.01655	0.003391
Zooplankton	6.5 km	LCBD_ZOO	2.69E-19	0.000751	3.59E-16	1	2.411738	0.126763	0.026933	0.046014
Zooplankton	6.5 km	Repl_ZOO	-6.37E-18	0.01409	-4.52E-16	1	0.913404	0.343833	-0.0017	0.01794
Zooplankton	6.5 km	RicDif_ZOO	-6.25E-18	0.015042	-4.16E-16	1	0.512519	0.477397	-0.00965	0.010146
Zooplankton	Fluvial	Rich_ZOO	-6.54E-17	0.2111	-3.10E-16	1	4.764395	0.03378	0.068737	0.086998
Zooplankton	Fluvial	LCBD_ZOO	2.69E-19	0.000763	3.53E-16	1	0.755905	0.388774	-0.00481	0.014893
Zooplankton	Fluvial	Repl_ZOO	-1.10E-17	0.013991	-7.83E-16	1	1.753844	0.467579	0.012369	0.042727
Zooplankton	Fluvial	RicDif_ZOO	-6.77E-18	0.015017	-4.51E-16	1	0.740929	0.654087	-0.0063	0.017749
18S Zooplankton	650 km	Rich_ZOO.18S	-3.78E-16	0.632723	-5.98E-16	1	7.521453	0.012499	0.145303	0.168781
18S Zooplankton	650 km	LCBD_18S.ZOO	7.43E-19	0.000848	8.76E-16	1	8.127145	0.006477	0.129469	0.147637
18S Zooplankton	650 km	Repl_18S.ZOO	5.45E-18	0.010747	5.07E-16	1	2.85114	0.09794	0.037133	0.057193
18S Zooplankton	650 km	RicDif_18S.ZOO	2.29E-18	0.010688	2.14E-16	1	1.349889	0.251171	0.007242	0.027927
18S Zooplankton	325 km	Rich_ZOO.18S	-2.07E-16	0.617167	-3.35E-16	1	10.11419	0.006206	0.186815	0.216689
18S Zooplankton	325 km	LCBD_18S.ZOO	4.49E-19	0.000826	5.44E-16	1	9.303321	0.008709	0.174291	0.204602
18S Zooplankton	325 km	Repl_18S.ZOO	9.54E-18	0.010446	9.13E-16	1	5.757853	0.020433	0.090184	0.109139
18S Zooplankton	325 km	RicDif_18S.ZOO	-1.19E-18	0.010812	-1.10E-16	1	0.067529	0.917131	-0.01607	0.00916
18S Zooplankton	100 km	Rich_ZOO.18S	-1.19E-15	0.638708	-1.86E-15	1	8.111195	0.00651	0.129058	0.147209
18S Zooplankton	100 km	LCBD_18S.ZOO	1.86E-18	0.000847	2.20E-15	1	8.383854	0.005733	0.133366	0.151429
18S Zooplankton	100 km	Repl_18S.ZOO	1.69E-17	0.010588	1.59E-15	1	4.356643	0.042324	0.065357	0.08483
18S Zooplankton	100 km	RicDif_18S.ZOO	2.54E-18	0.010819	2.34E-16	1	0.185183	0.669051	-0.01726	0.003943
18S Zooplankton	65 km	Rich_ZOO.18S	1.71E-16	0.651787	2.63E-16	1	5.665227	0.063839	0.093023	0.128055
18S Zooplankton	65 km	LCBD_18S.ZOO	1.79E-19	0.000868	2.06E-16	1	5.264864	0.073217	0.087863	0.12291
18S Zooplankton	65 km	Repl_18S.ZOO	4.87E-19	0.010961	4.44E-17	1	0.970458	0.646479	-0.00167	0.027363
18S Zooplankton	65 km	RicDif_18S.ZOO	6.51E-18	0.010713	6.08E-16	1	0.586624	0.492443	0.002566	0.028361
18S Zooplankton	6.5 km	Rich_ZOO.18S	-2.06E-16	0.669043	-3.08E-16	1	3.228301	0.078817	0.044364	0.064274
18S Zooplankton	6.5 km	LCBD_18S.ZOO	4.03E-19	0.000882	4.57E-16	1	4.012238	0.051003	0.059138	0.078761

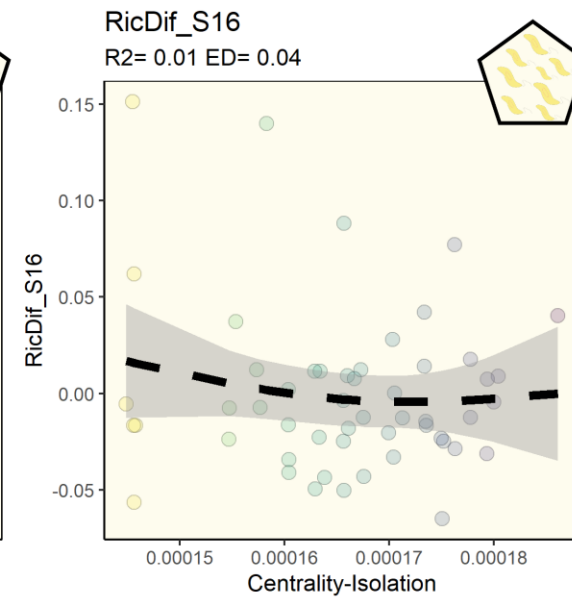
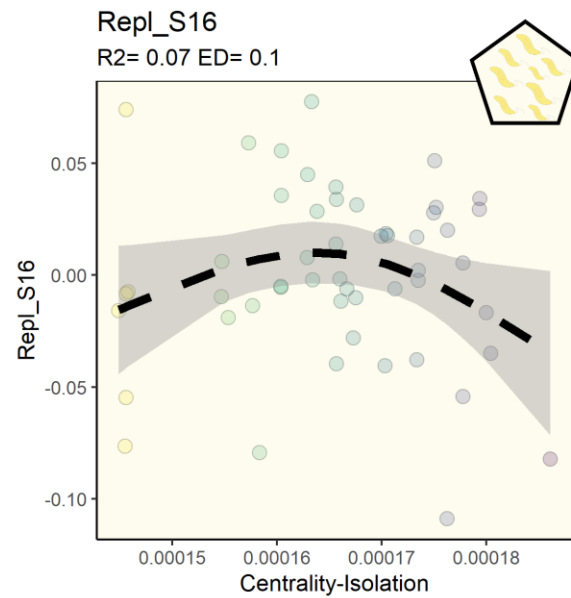
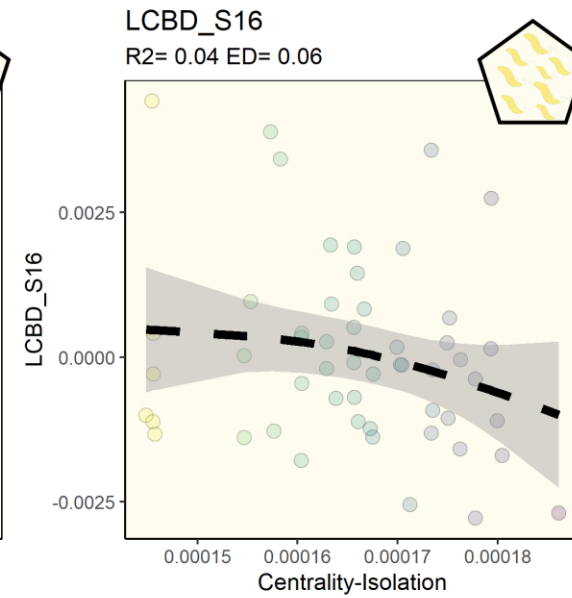
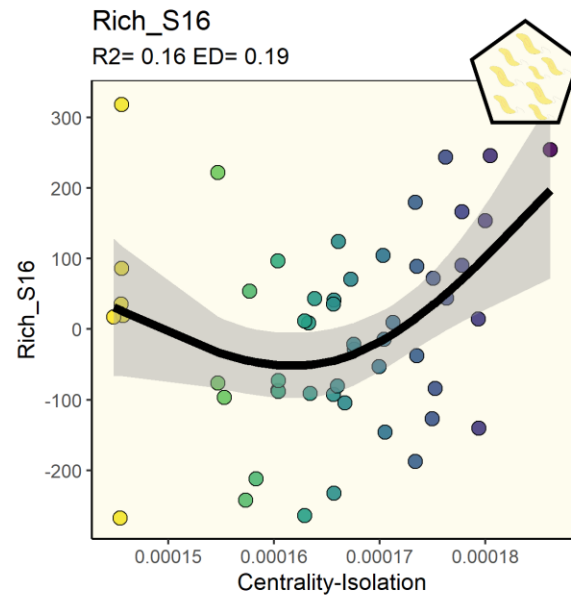
18S Zooplankton	6.5 km	Repl_18S.ZOO	2.11E-18	0.011037	1.91E-16	1	0.263013	0.610517	-0.01559	0.005565
18S Zooplankton	6.5 km	RicDif_18S.ZOO	1.92E-18	0.010623	1.81E-16	1	1.084562	0.364103	0.019299	0.047605
18S Zooplankton	Fluvial	Rich_ZOO.18S	2.85E-16	0.63861	4.47E-16	1	8.129726	0.00645	0.129326	0.147465
18S Zooplankton	Fluvial	LCBD_18S.ZOO	6.20E-20	0.000842	7.36E-17	1	9.045048	0.004222	0.143546	0.161389
18S Zooplankton	Fluvial	Repl_18S.ZOO	-1.61E-18	0.010767	-1.50E-16	1	2.662263	0.109458	0.033469	0.053606
18S Zooplankton	Fluvial	RicDif_18S.ZOO	-3.21E-18	0.010605	-3.03E-16	1	1.994803	0.165258	0.022521	0.043483

Bacterioplankton

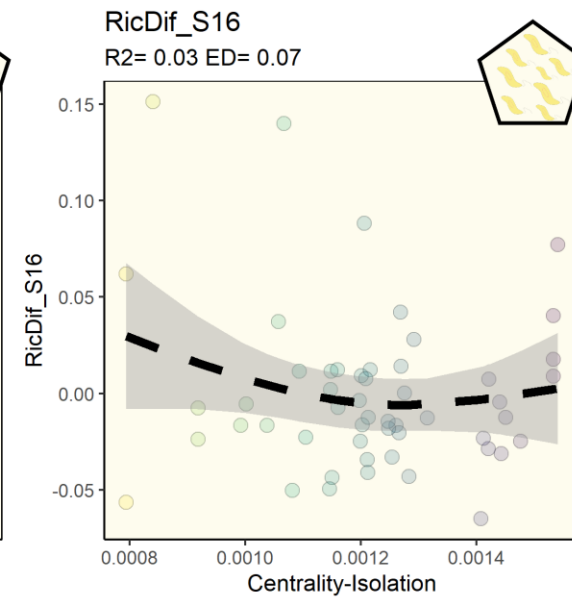
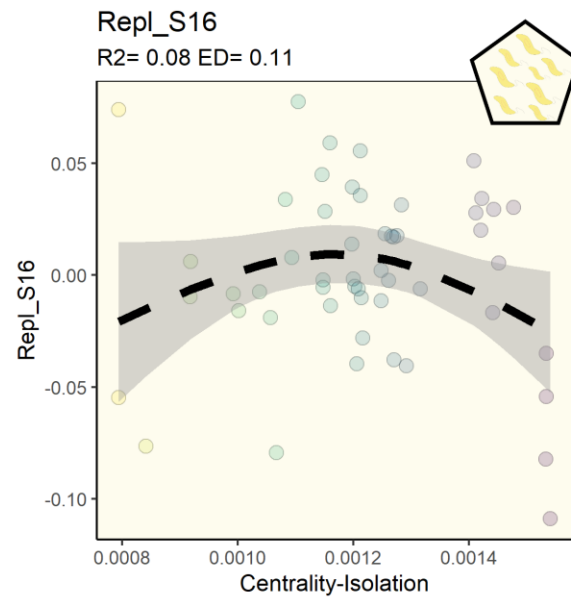
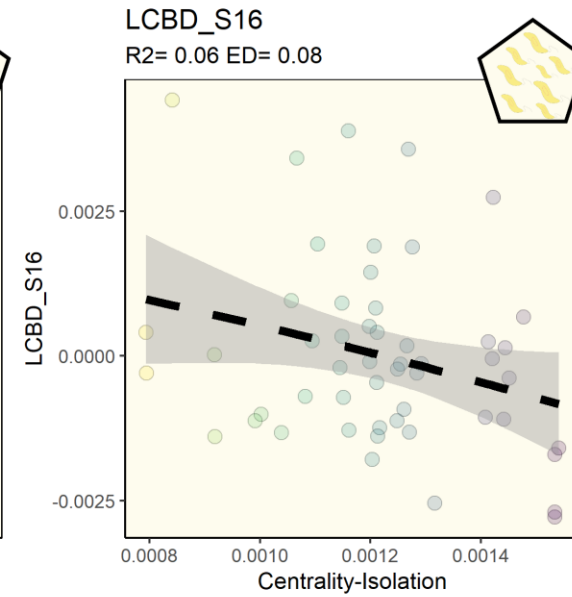
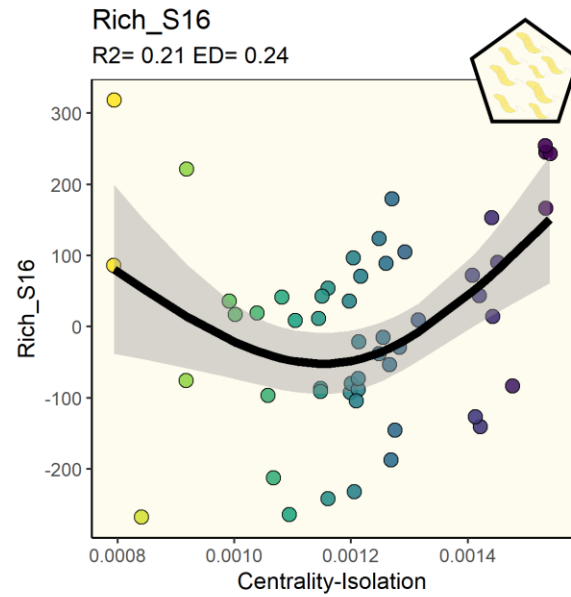
650 km



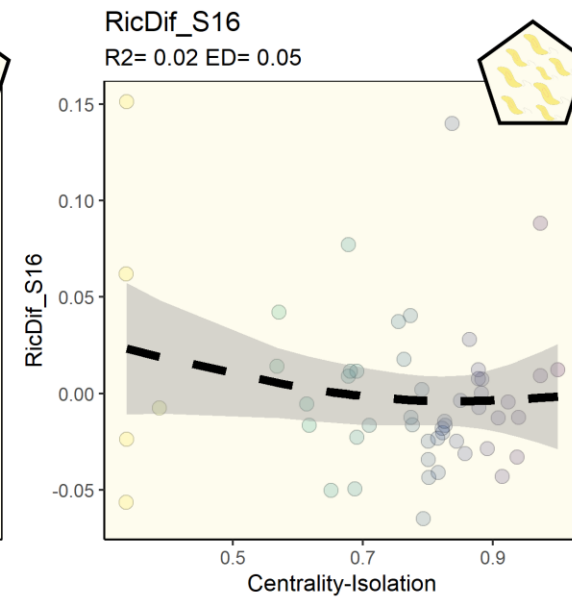
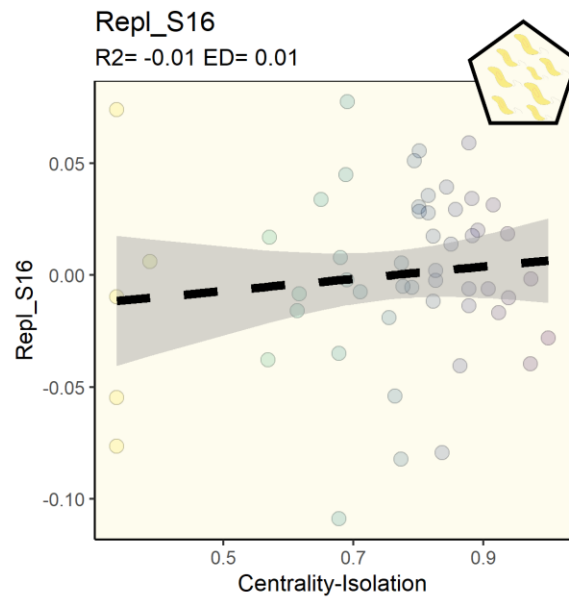
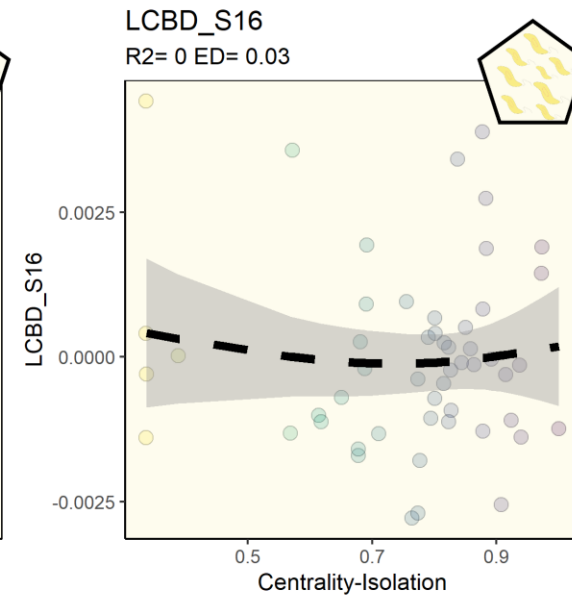
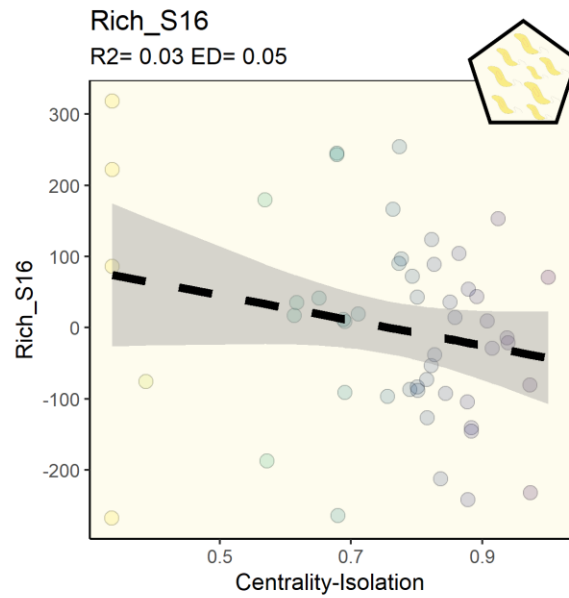
325 km



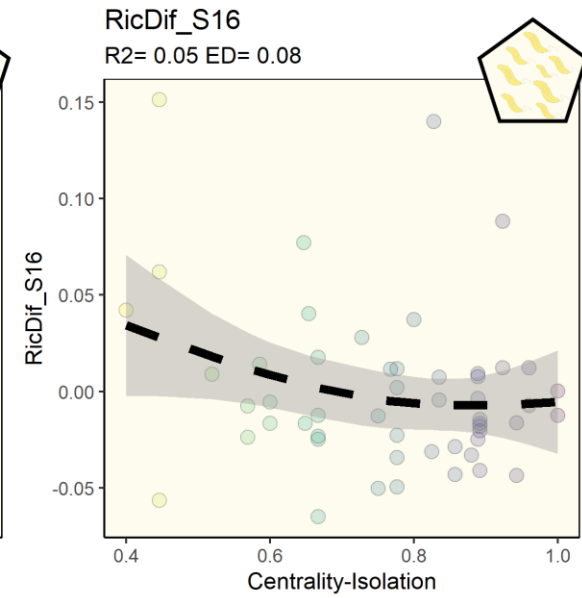
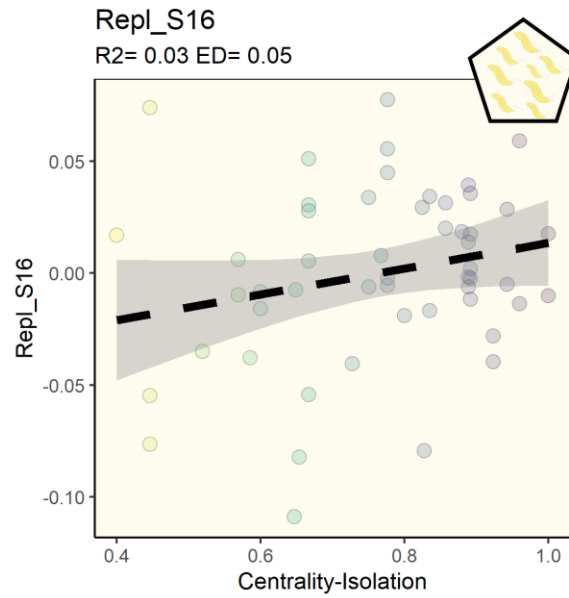
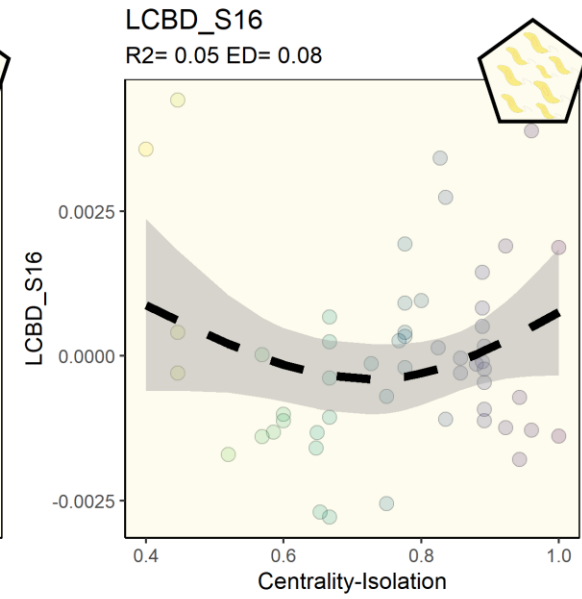
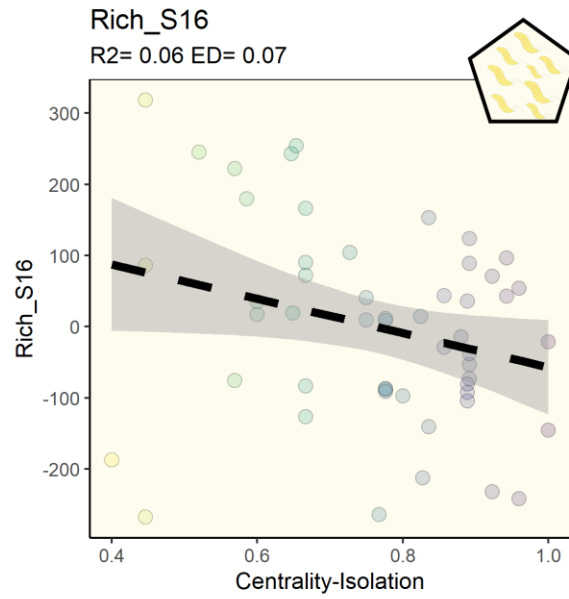
100 km



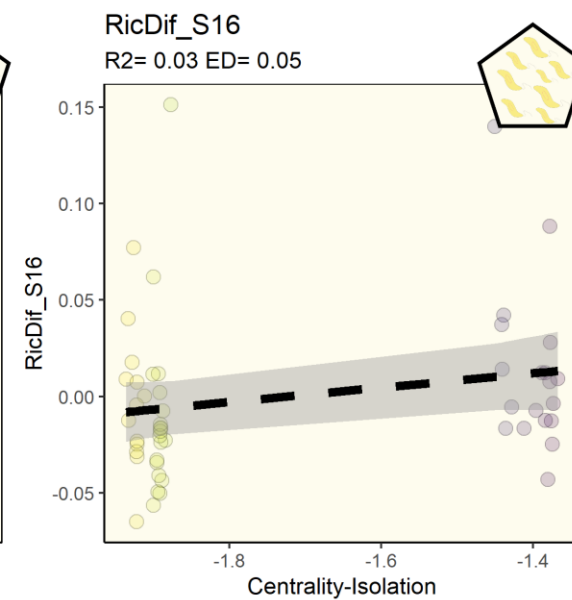
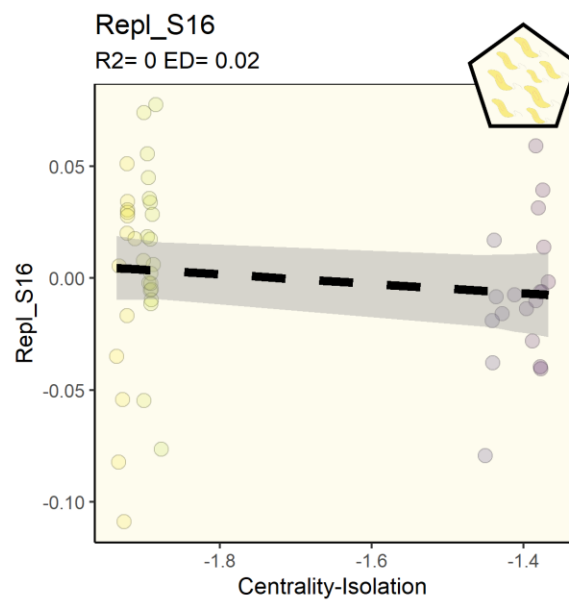
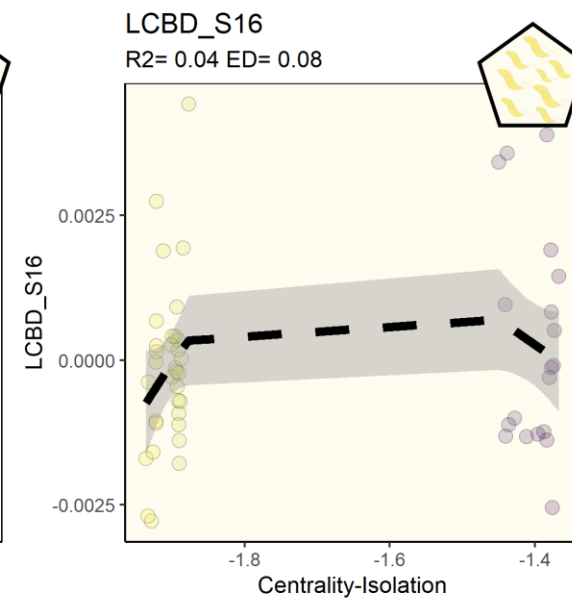
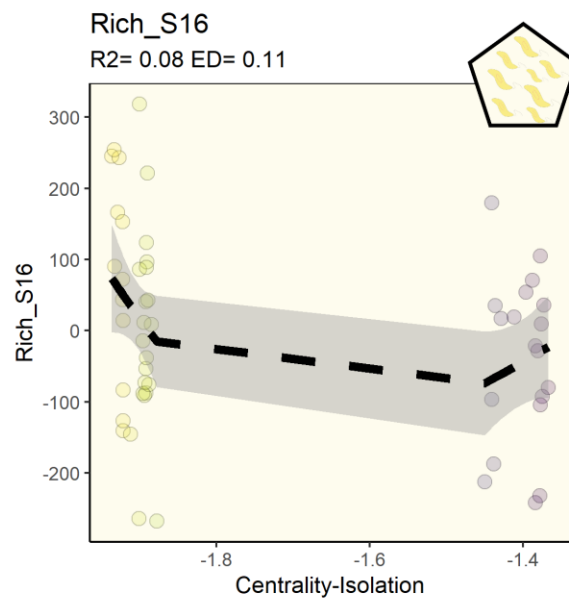
65 km



6.5 km

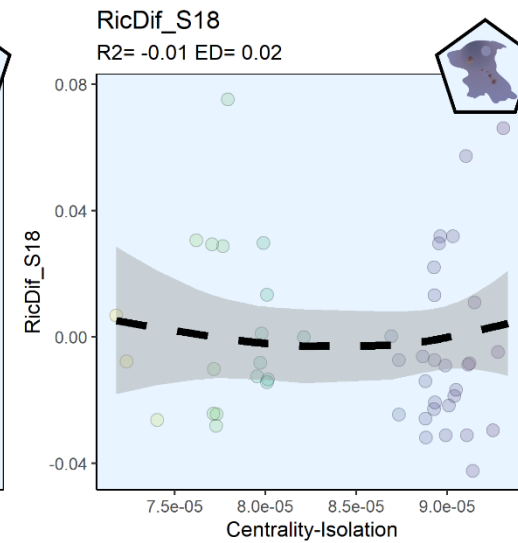
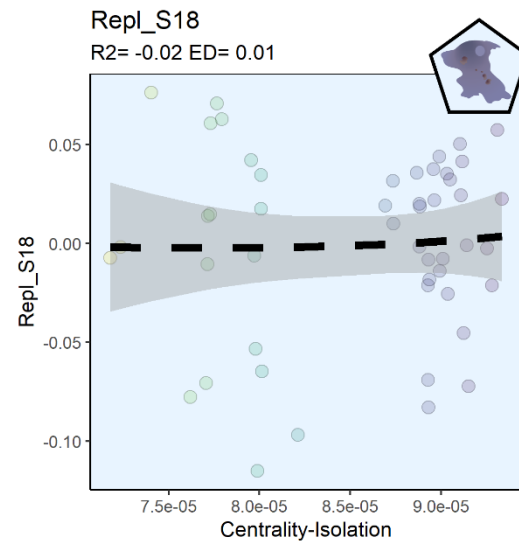
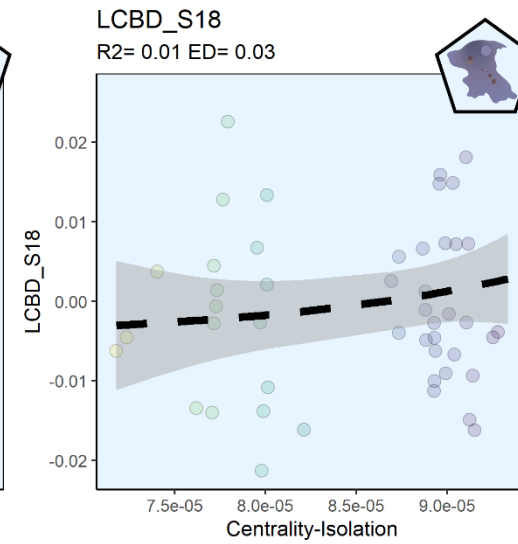
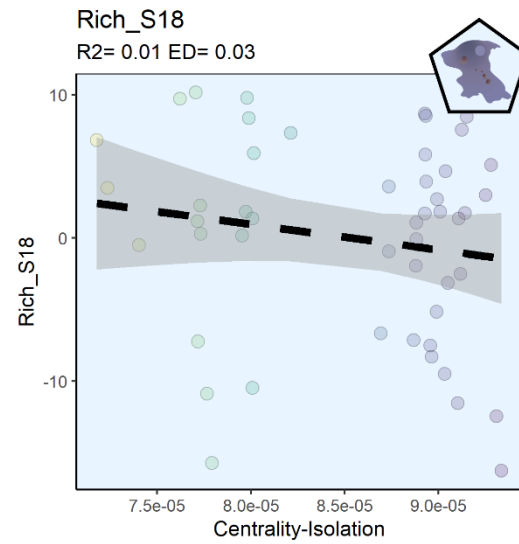


Fluvial network

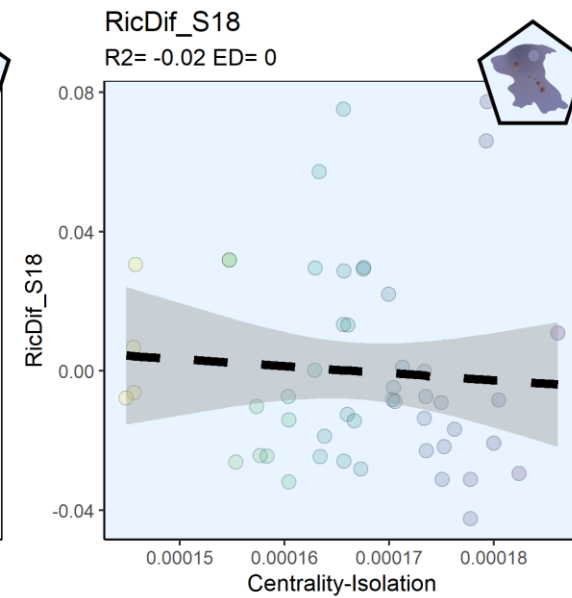
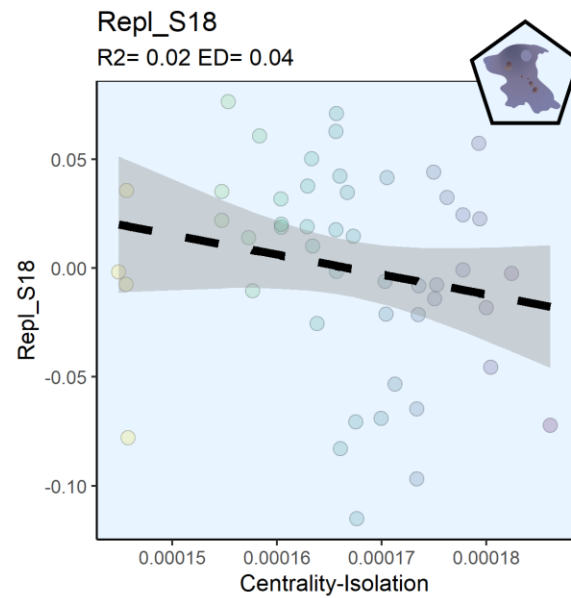
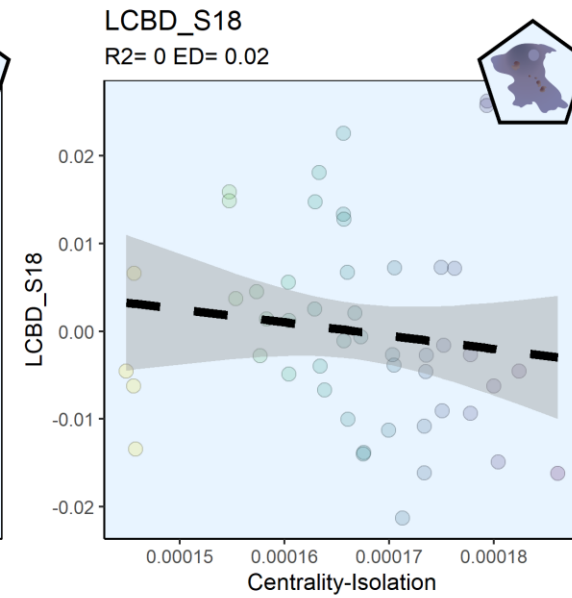
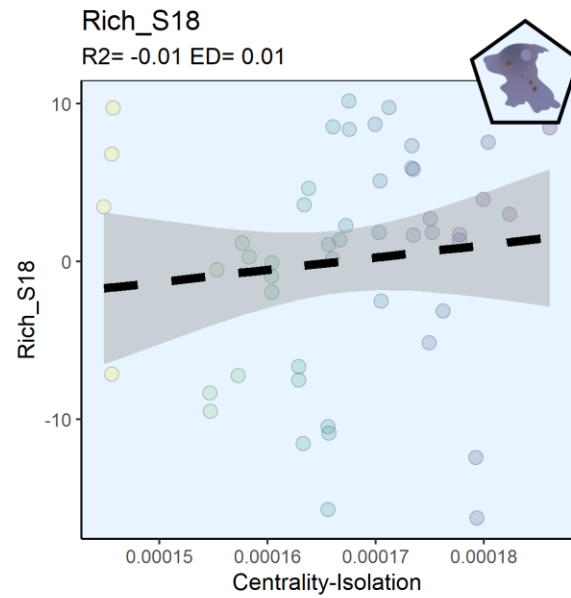


Protista

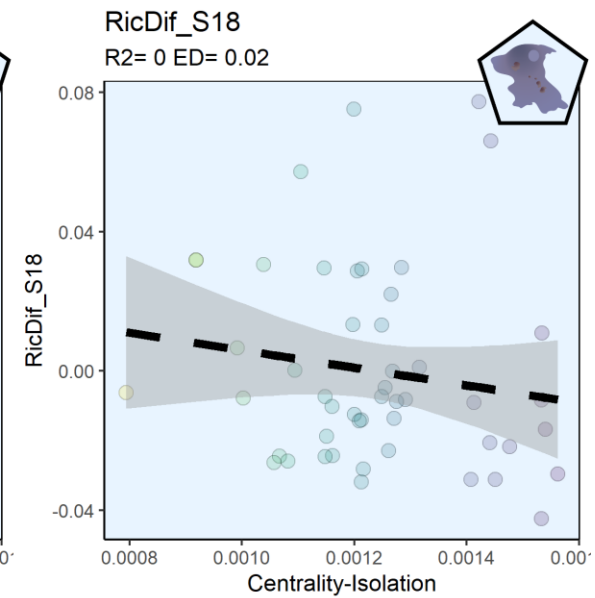
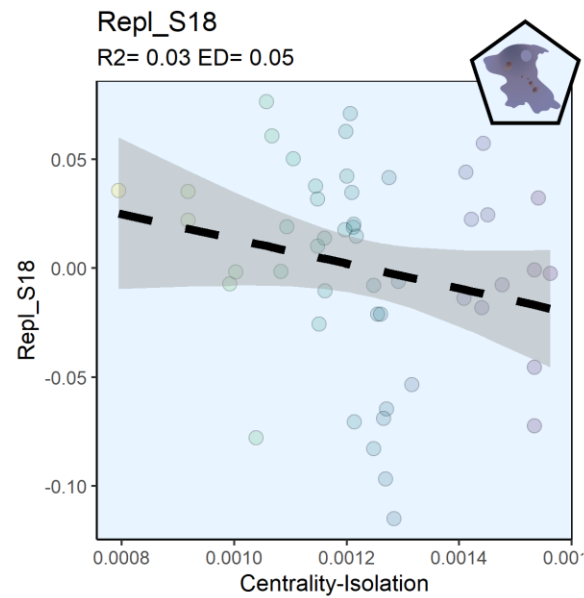
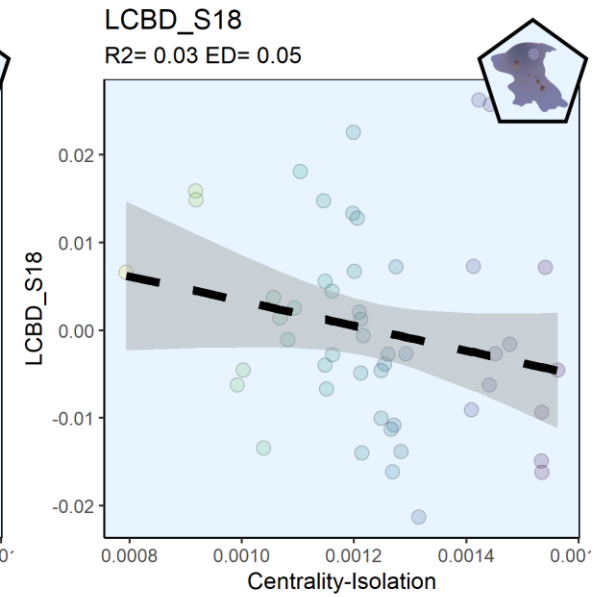
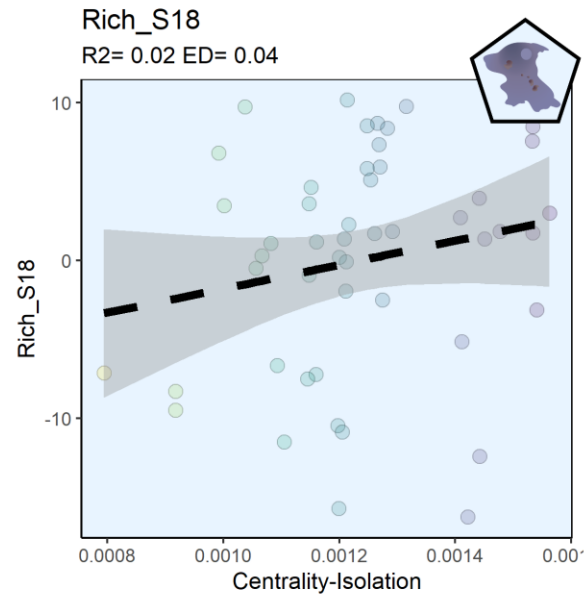
650 km



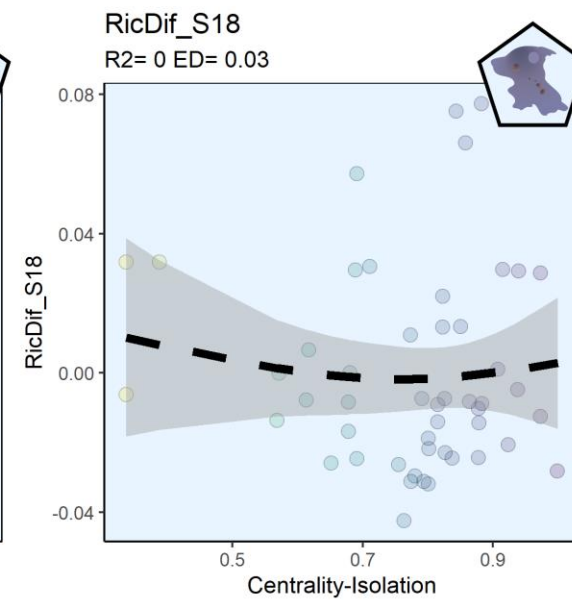
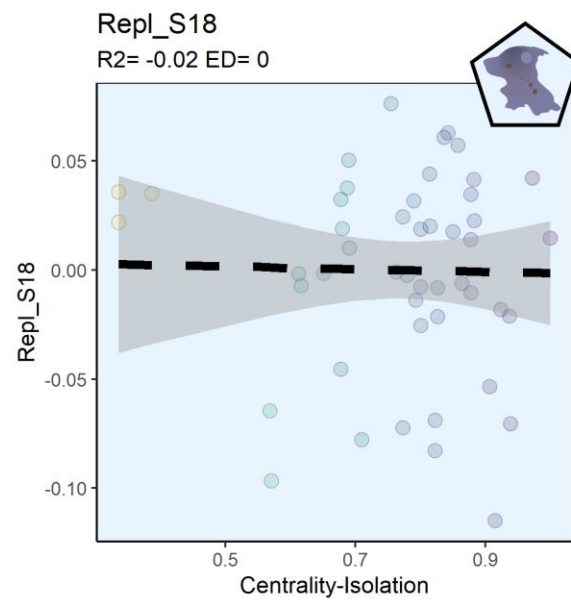
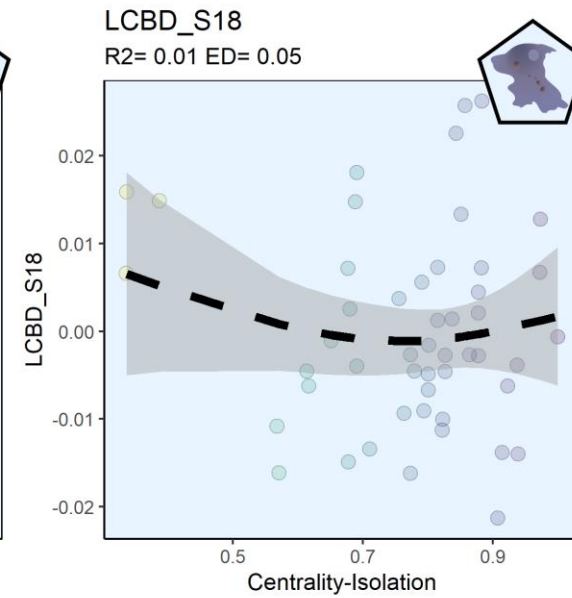
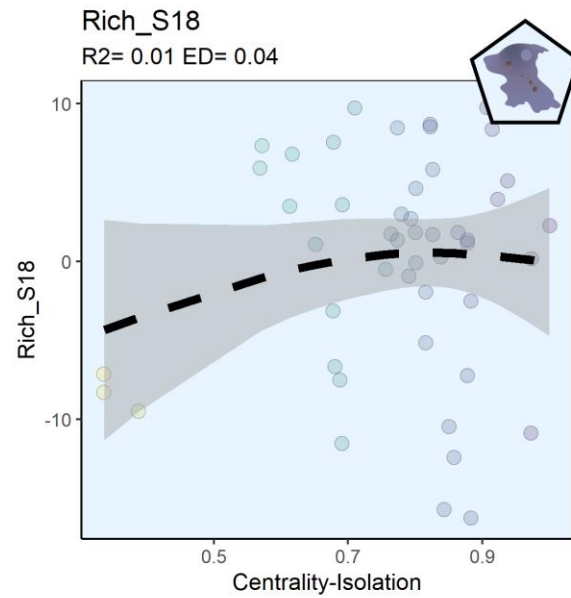
325 km



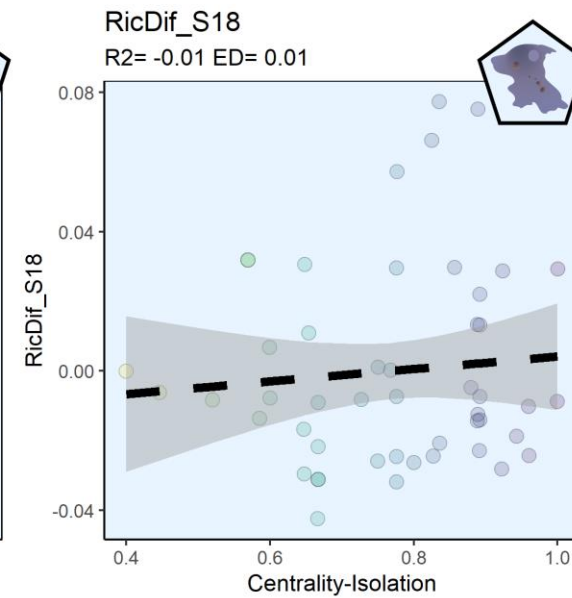
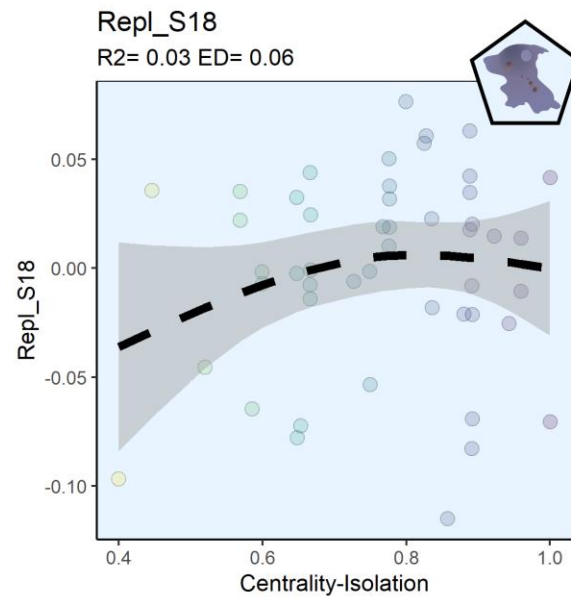
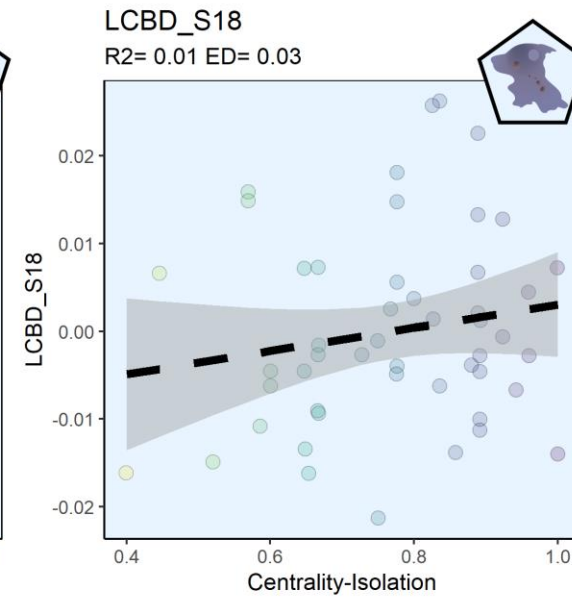
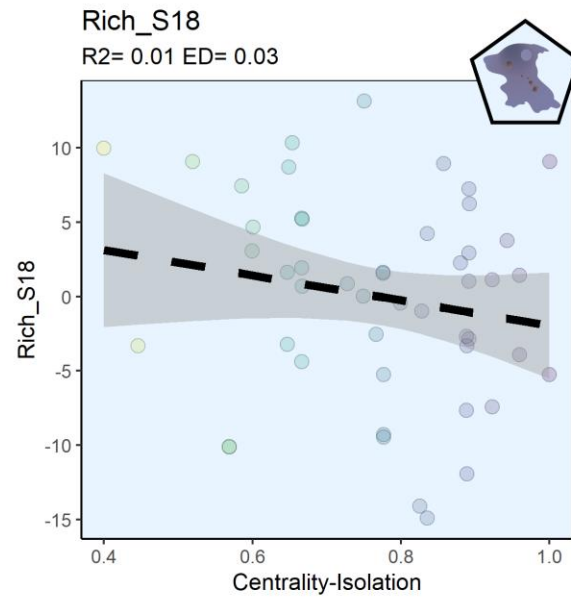
100 km



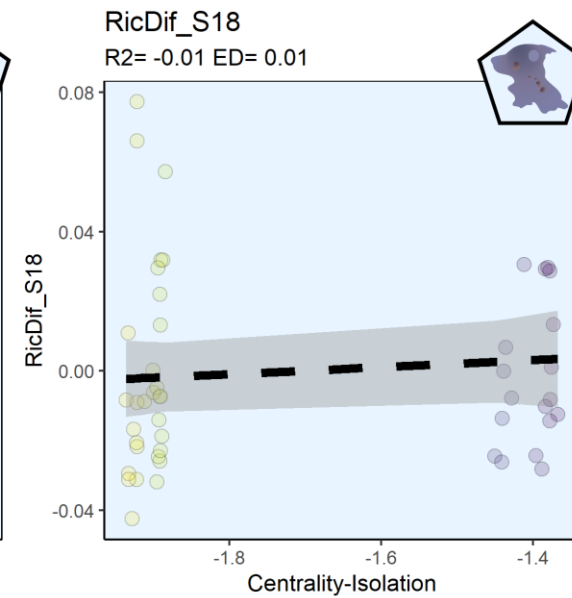
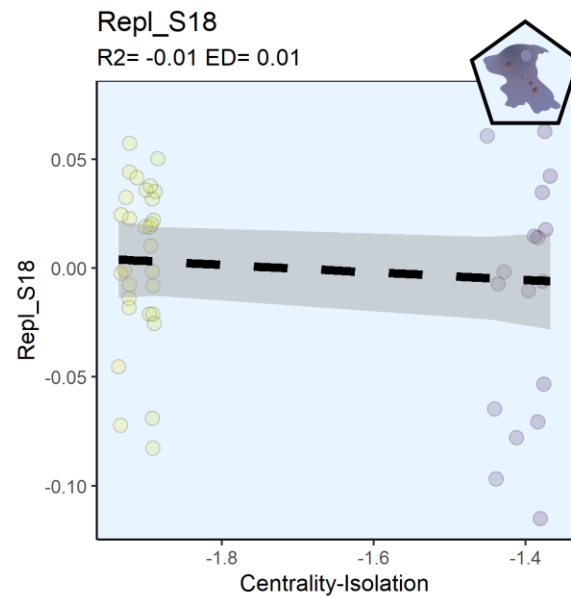
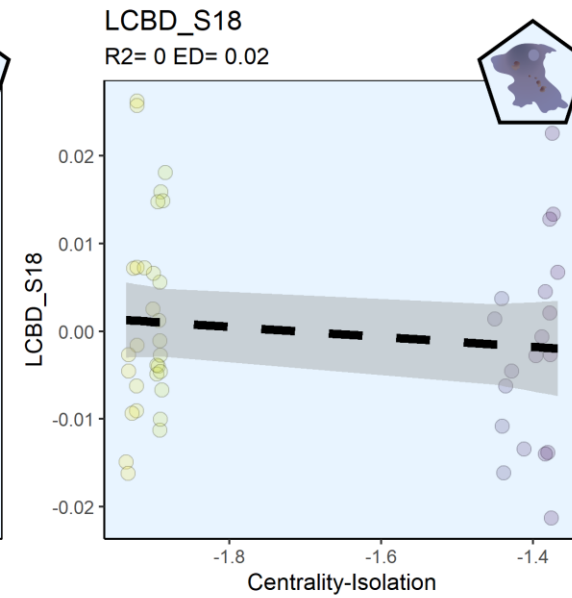
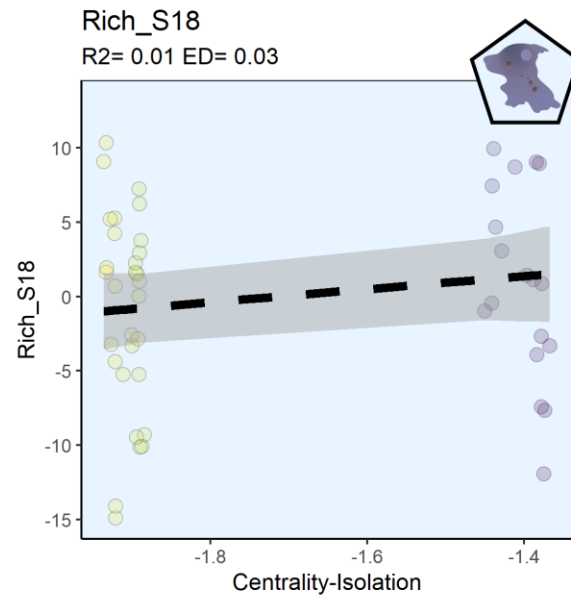
65 km



6.5 km

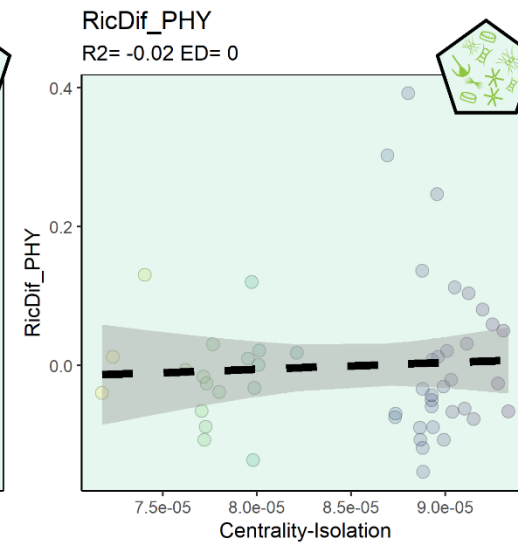
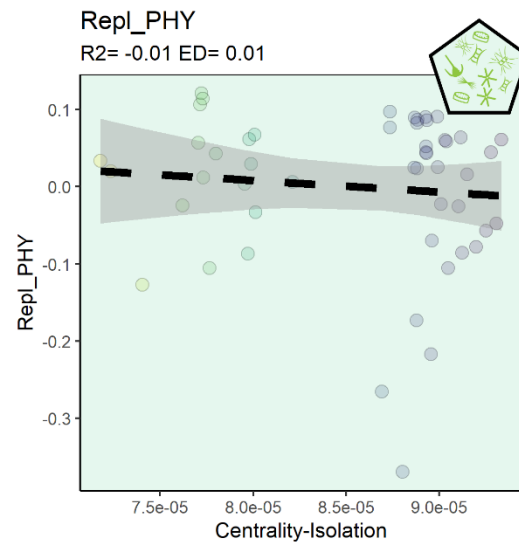
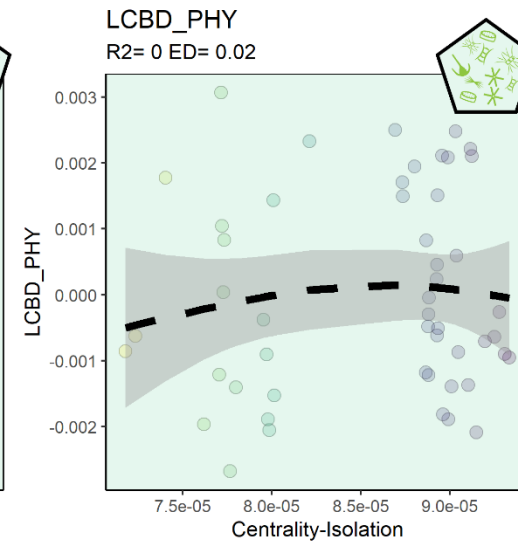
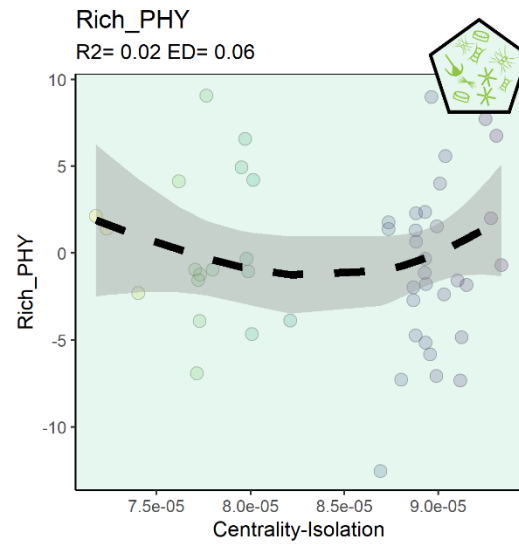


Fluvial network

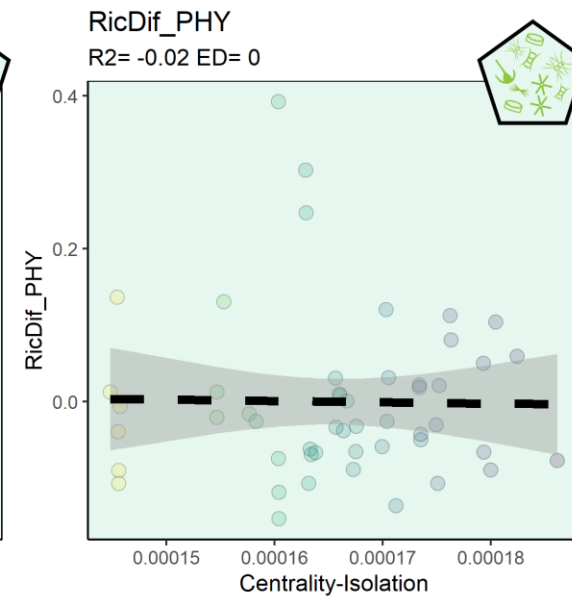
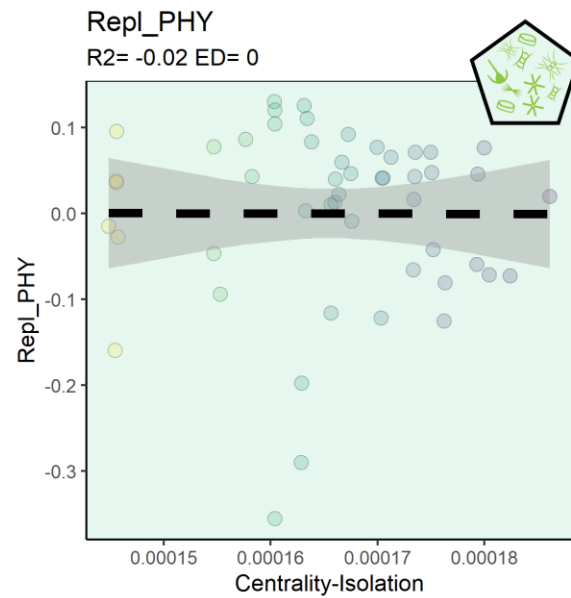
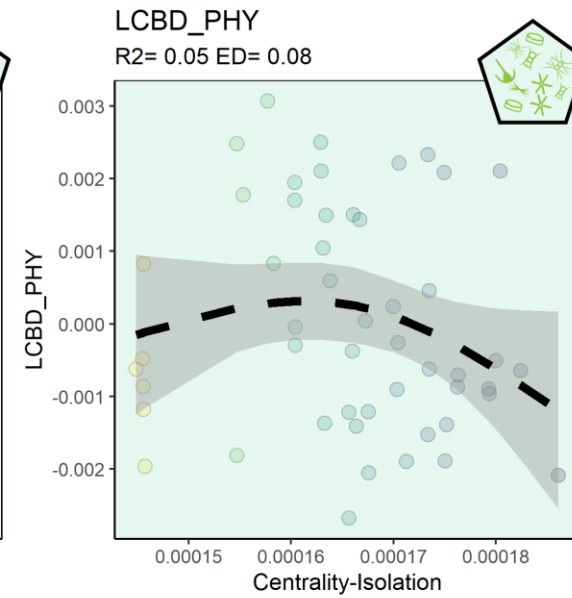
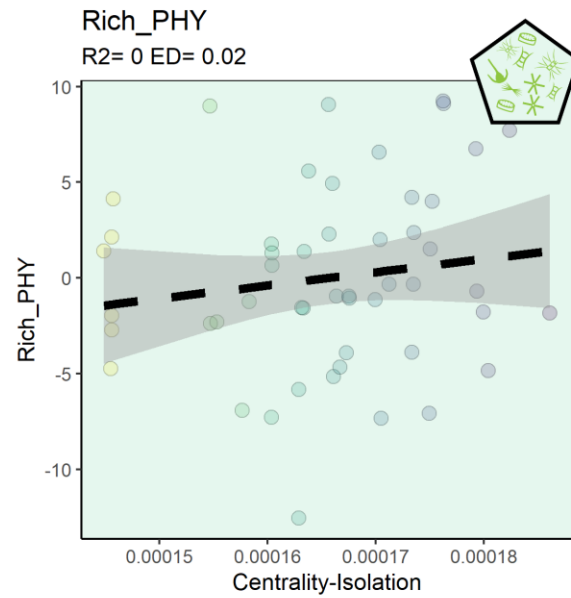


Phytoplankton

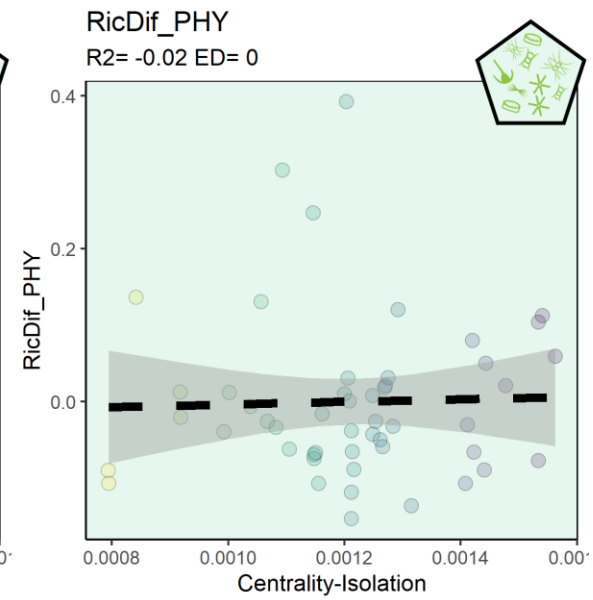
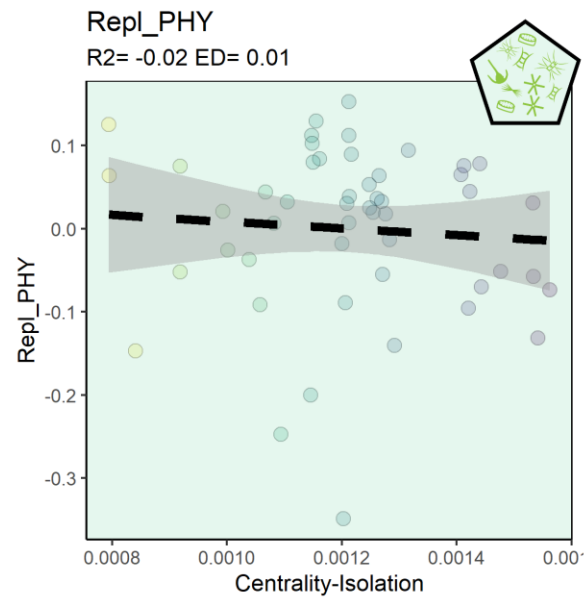
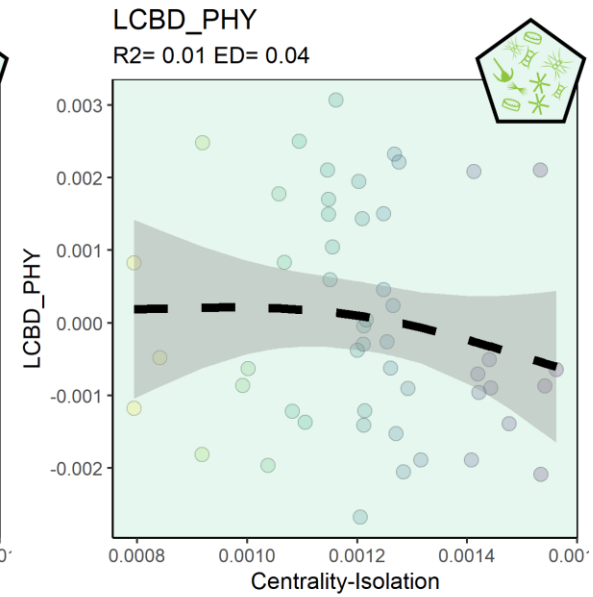
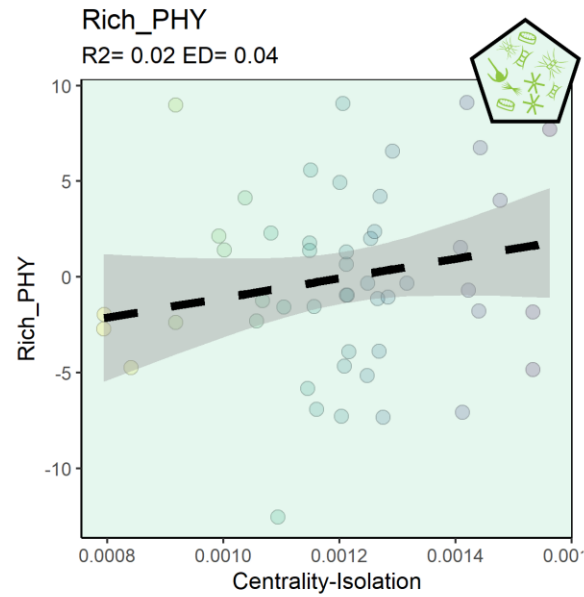
650 km



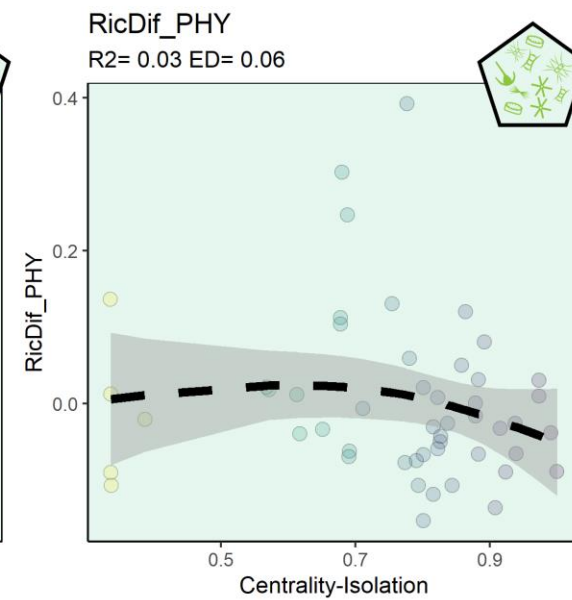
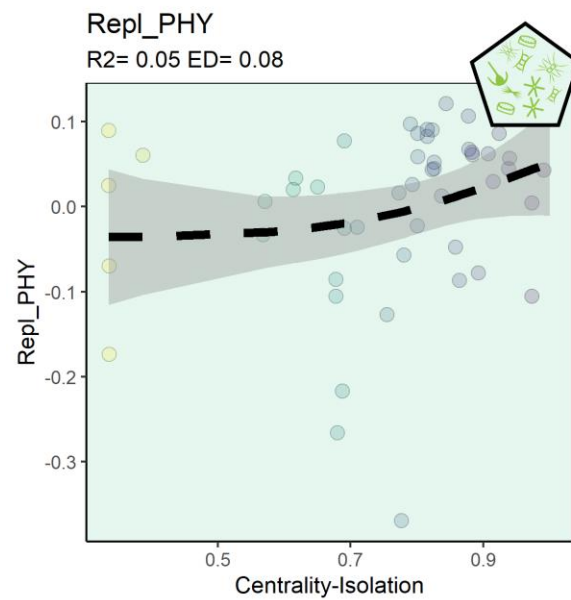
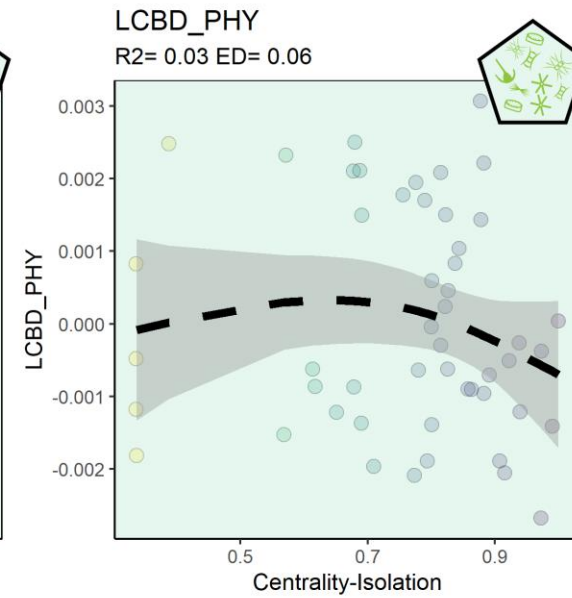
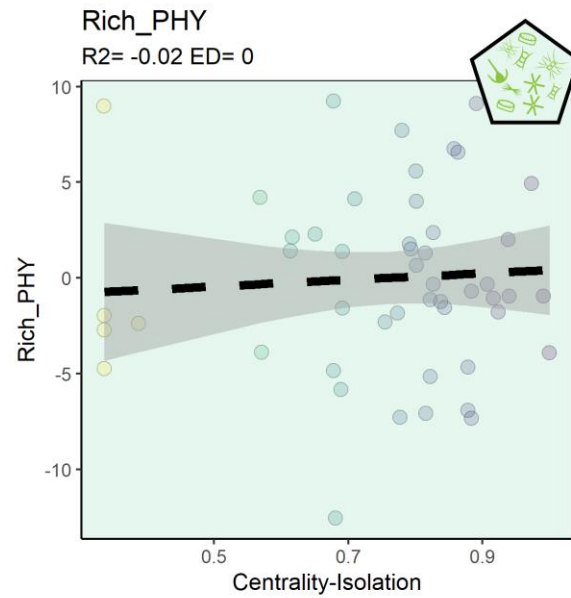
325 km



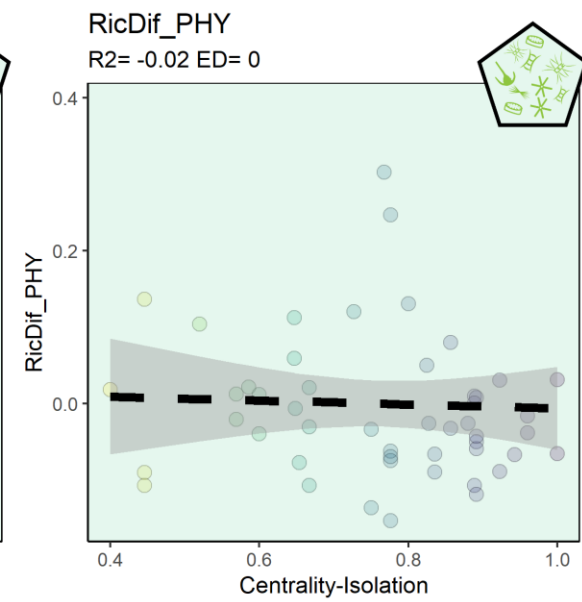
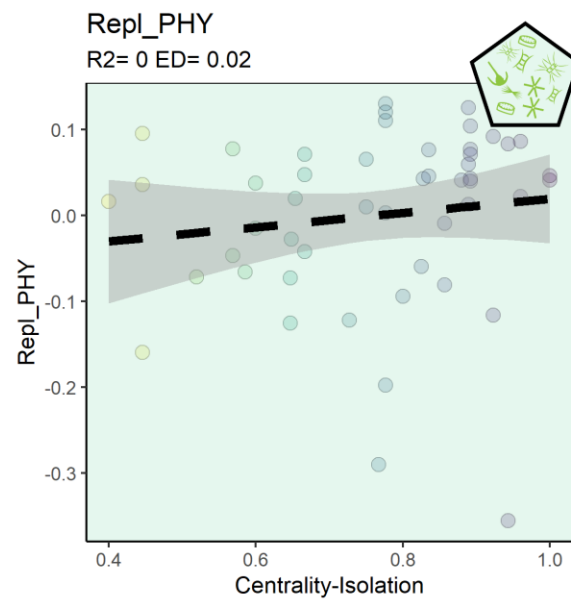
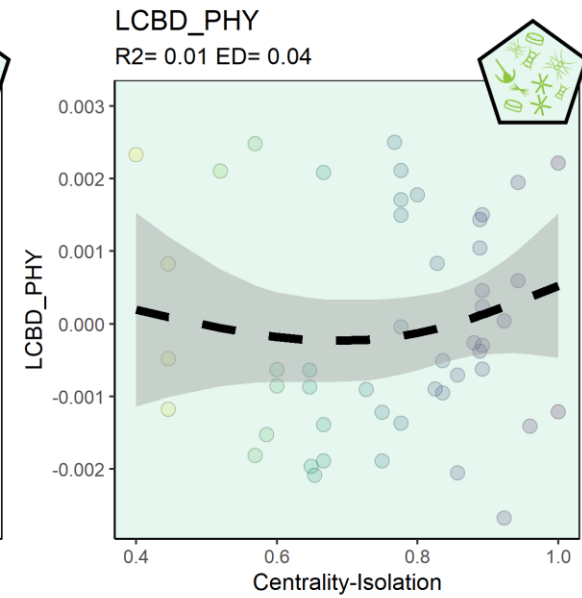
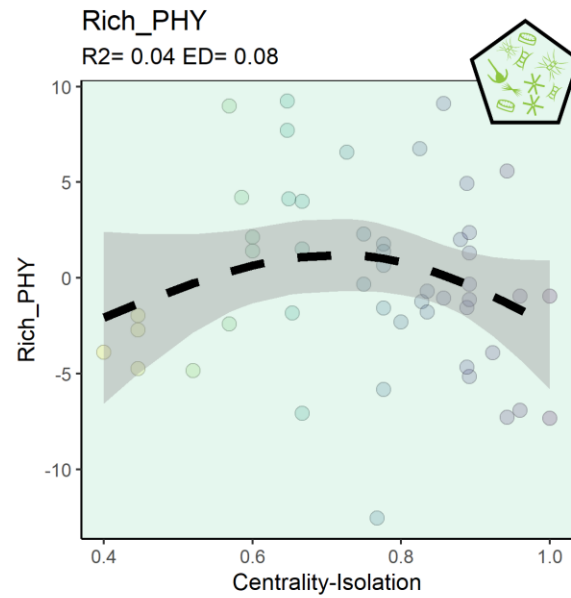
100 km



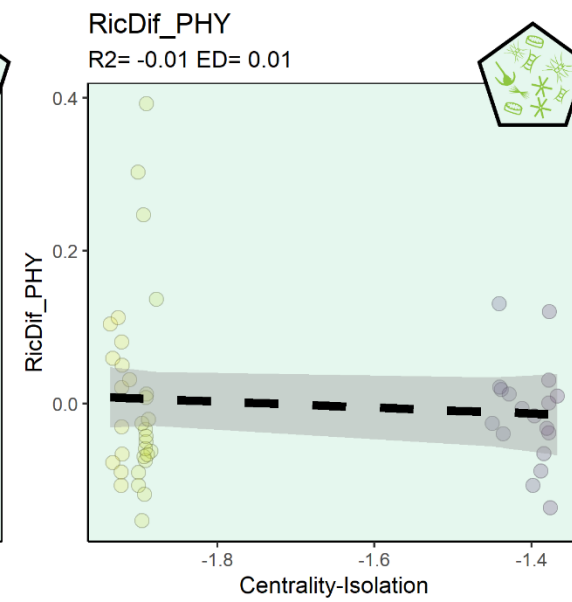
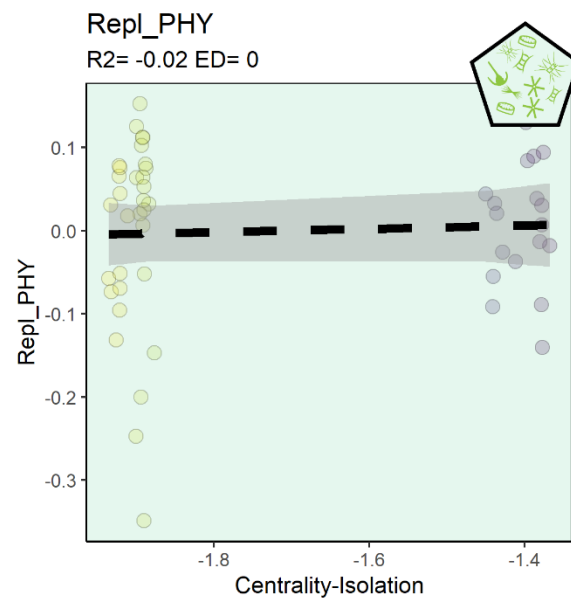
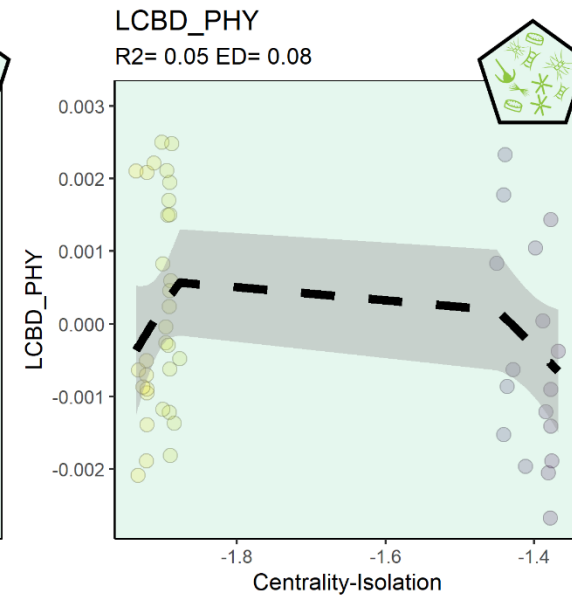
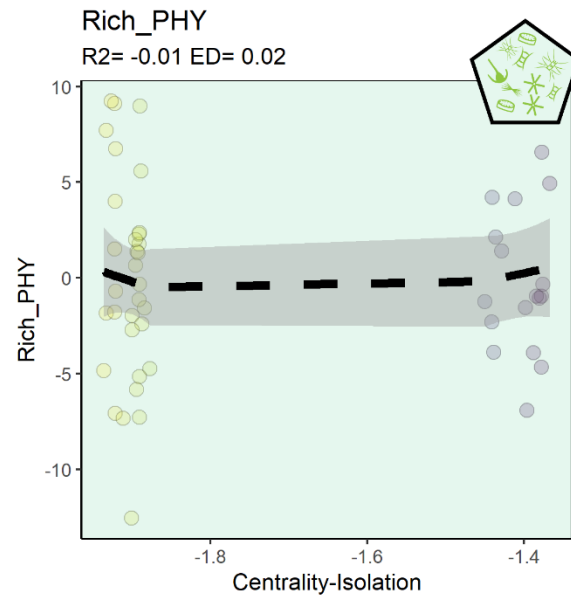
65 km



6.5 km

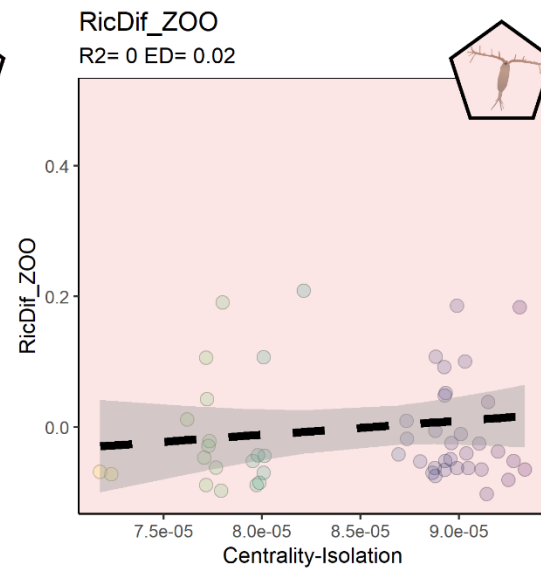
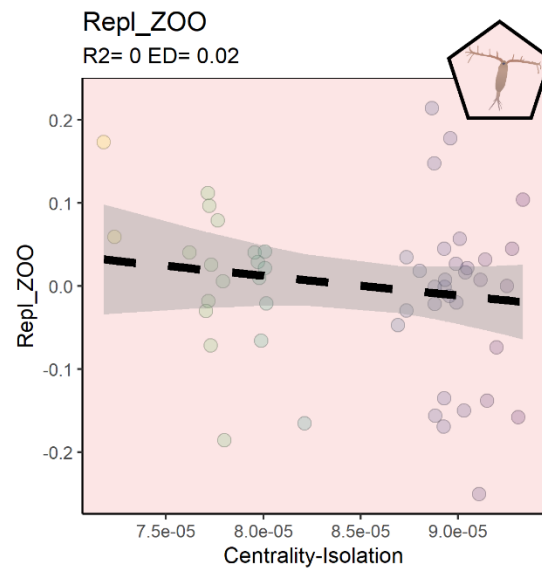
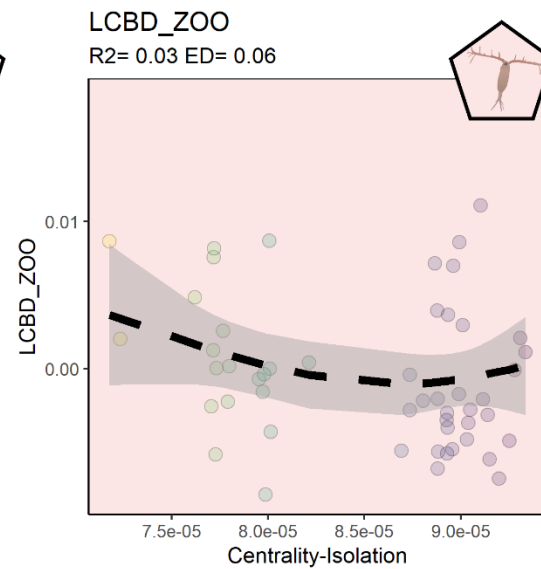
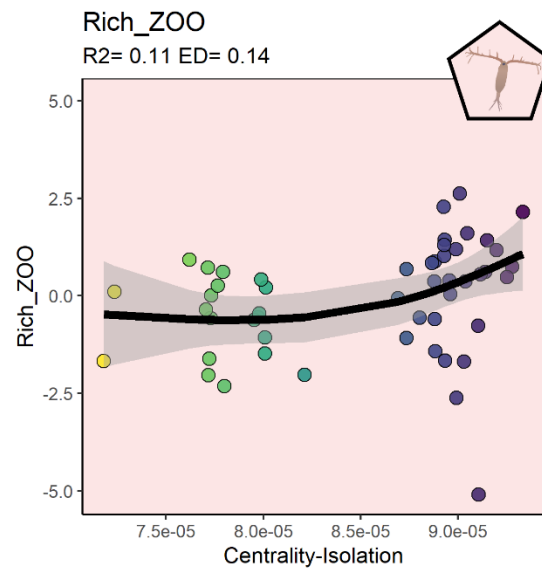


Fluvial network

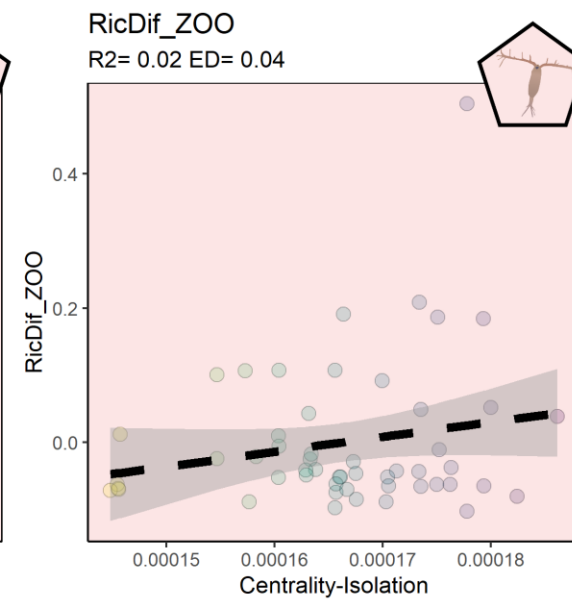
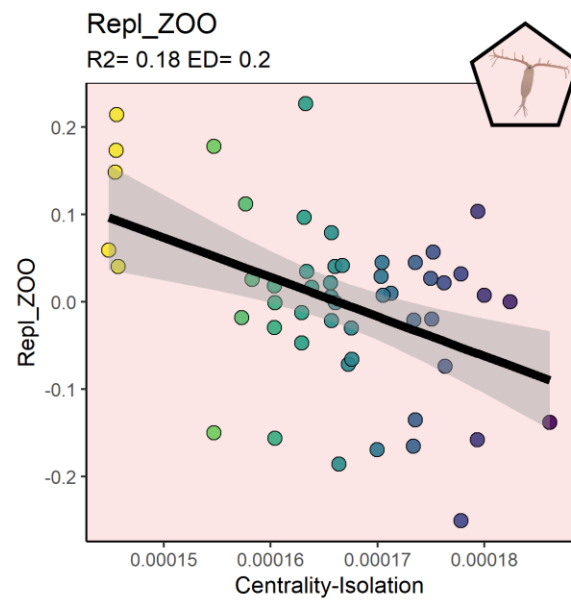
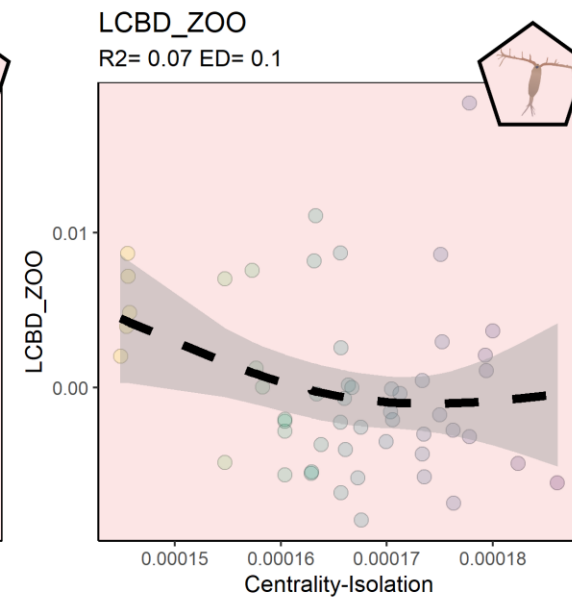
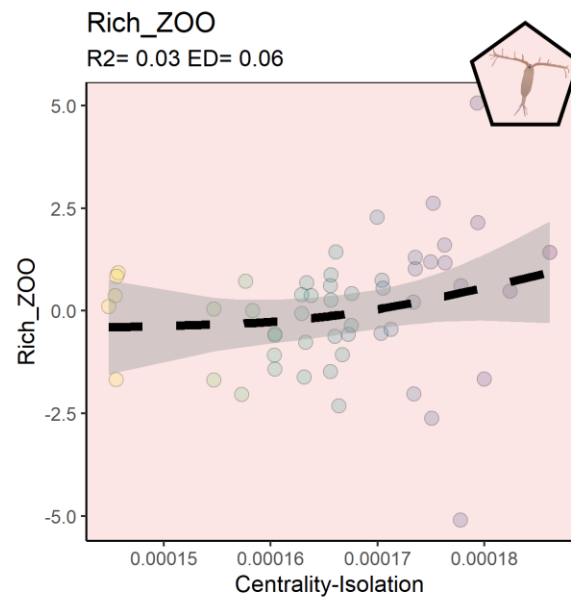


Zooplankton

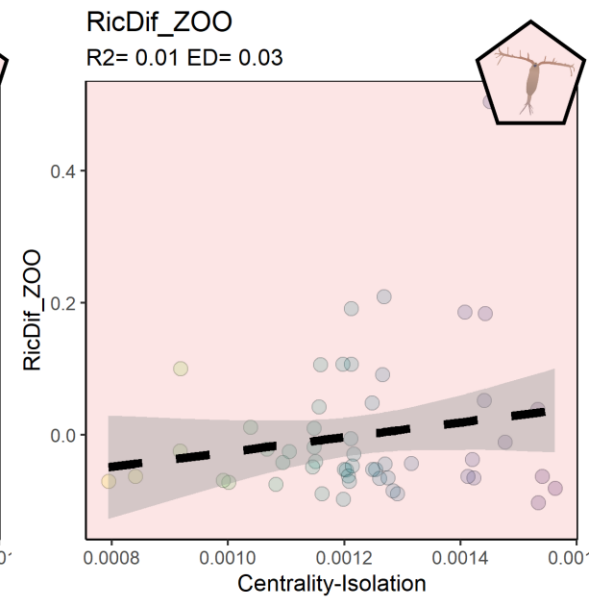
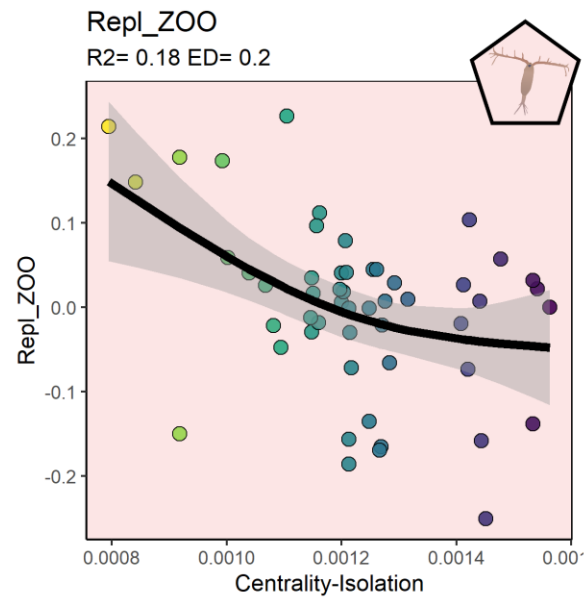
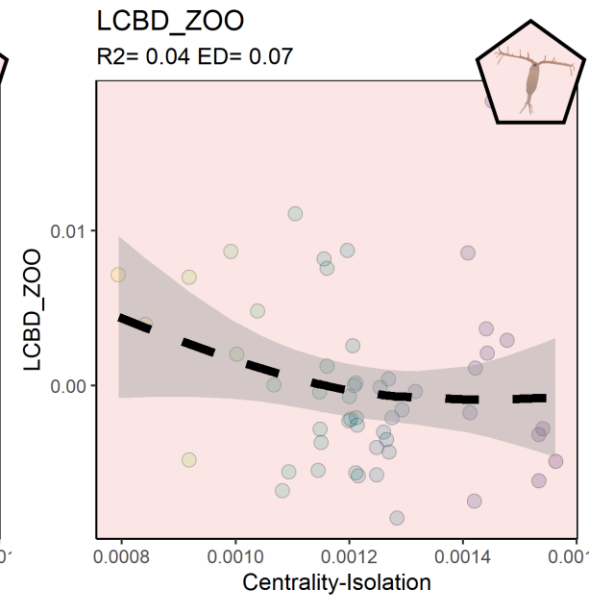
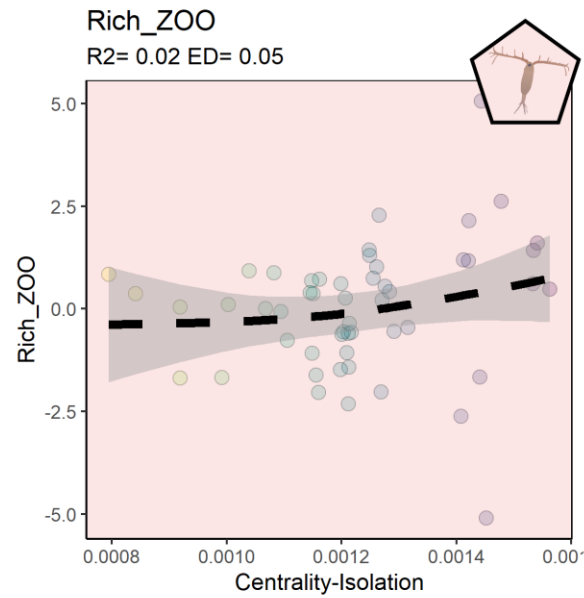
650 km



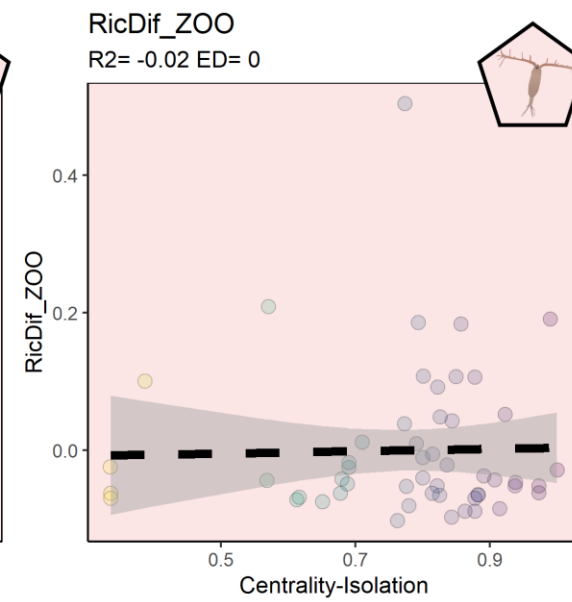
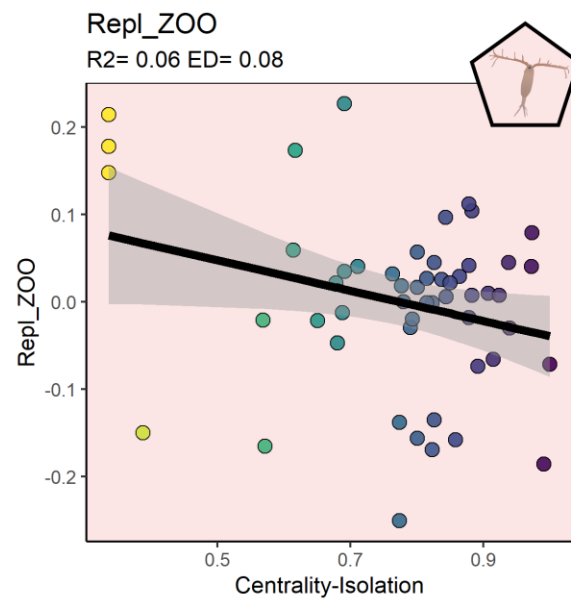
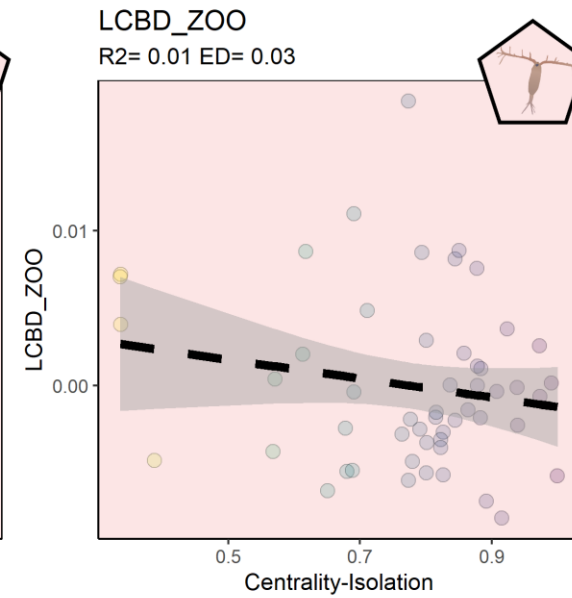
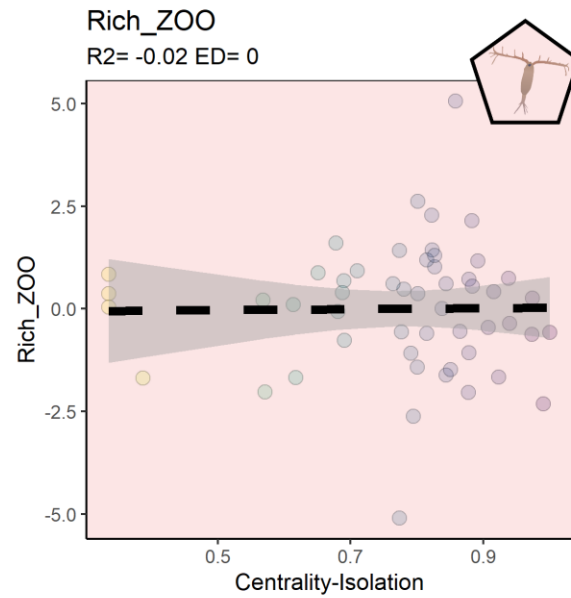
325 km



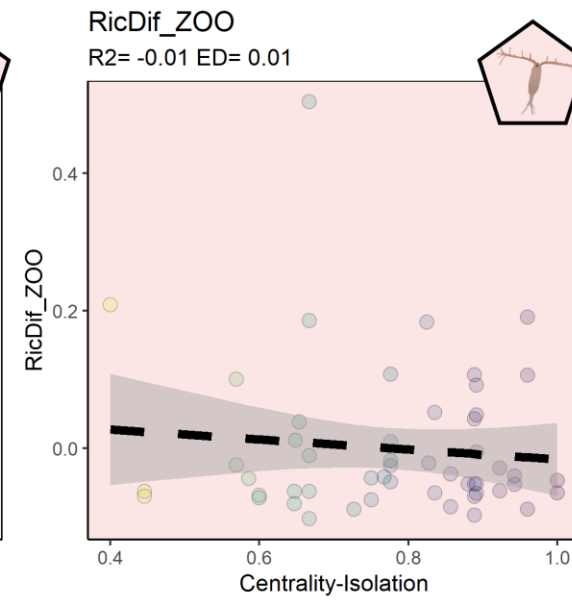
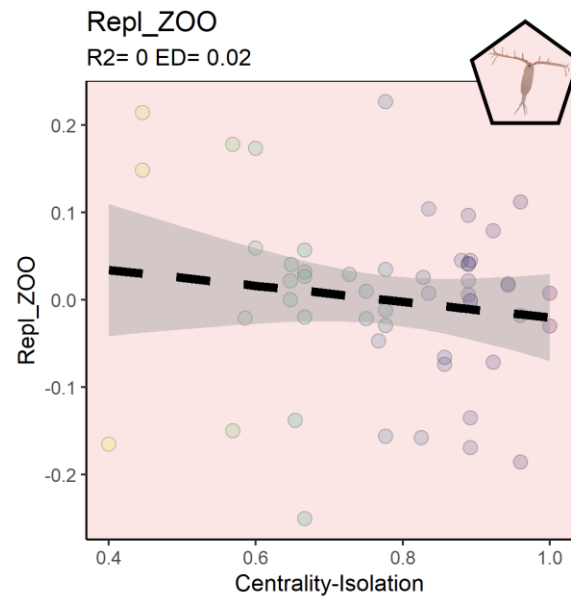
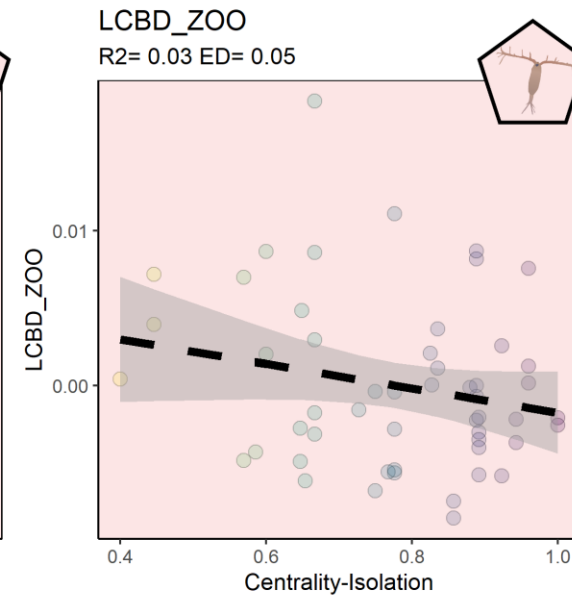
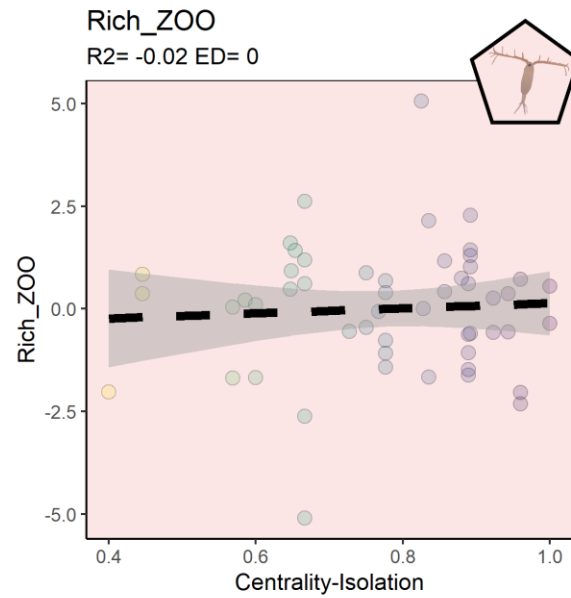
100 km



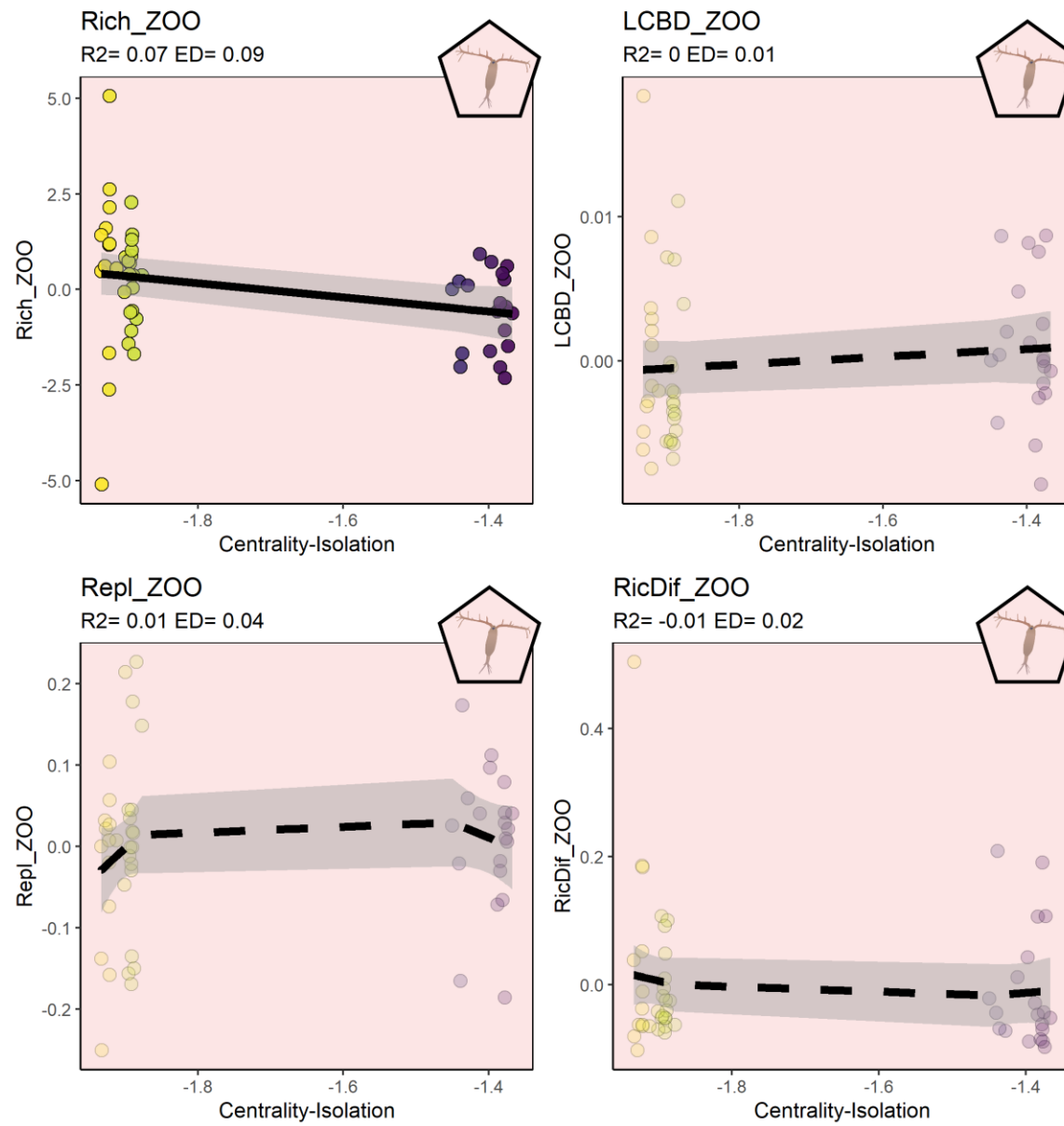
65 km



6.5 km

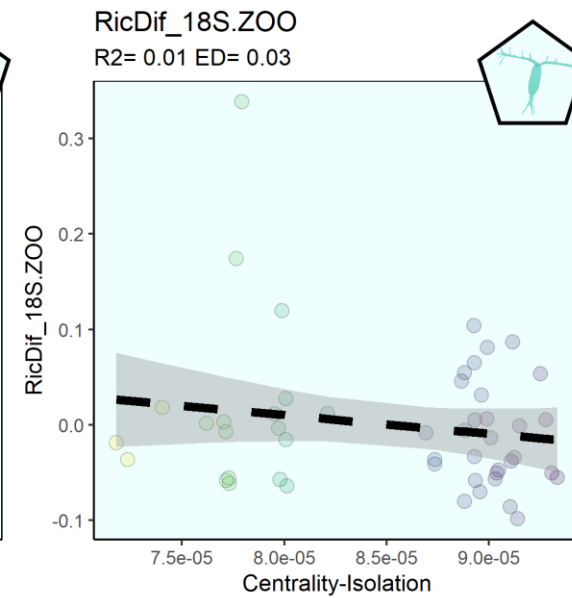
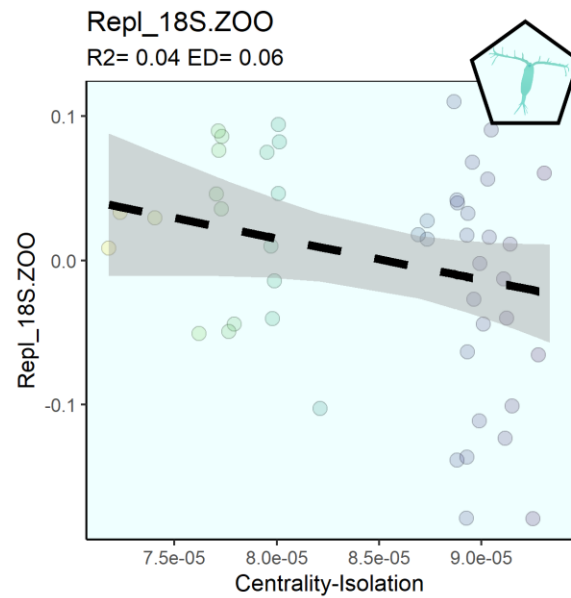
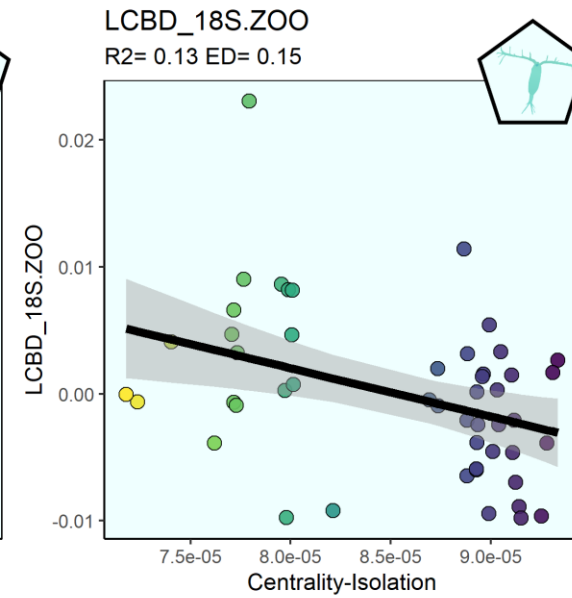
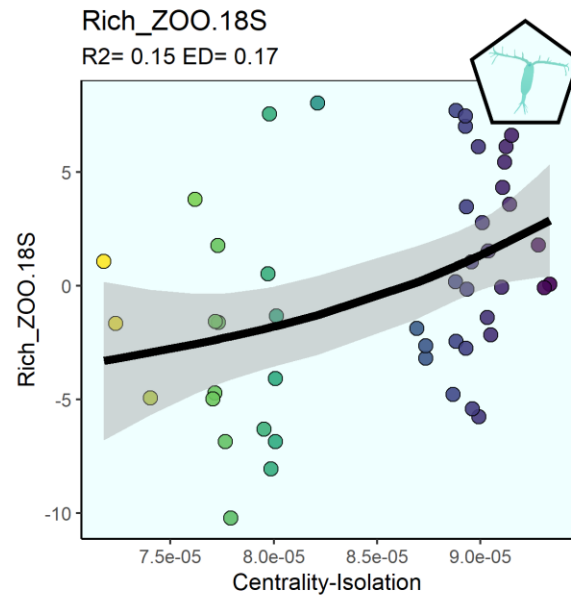


Fluvial network

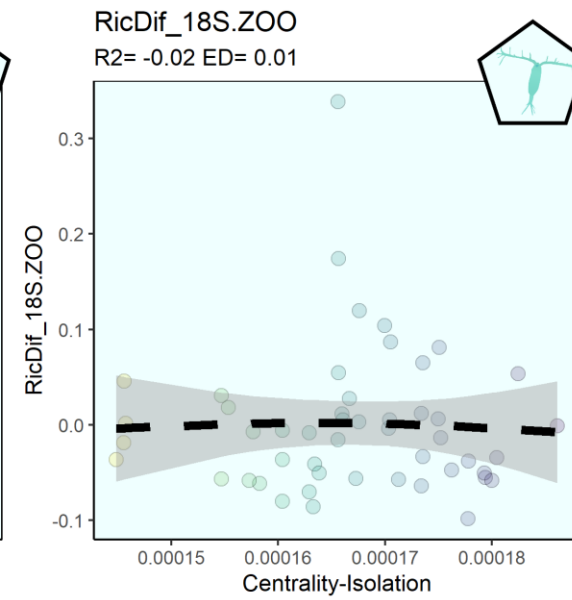
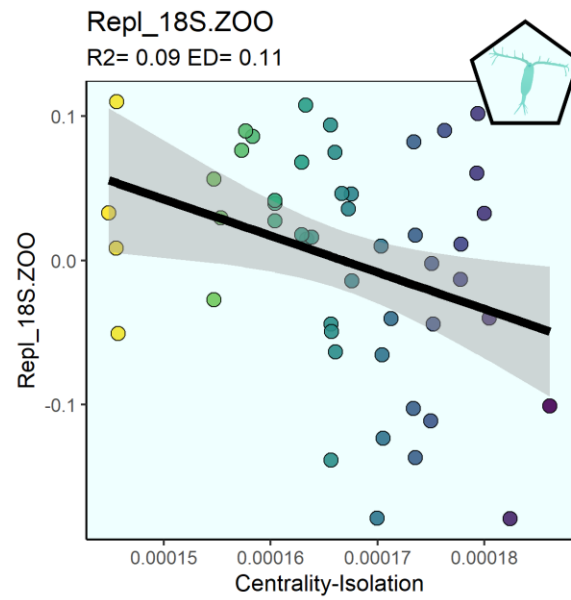
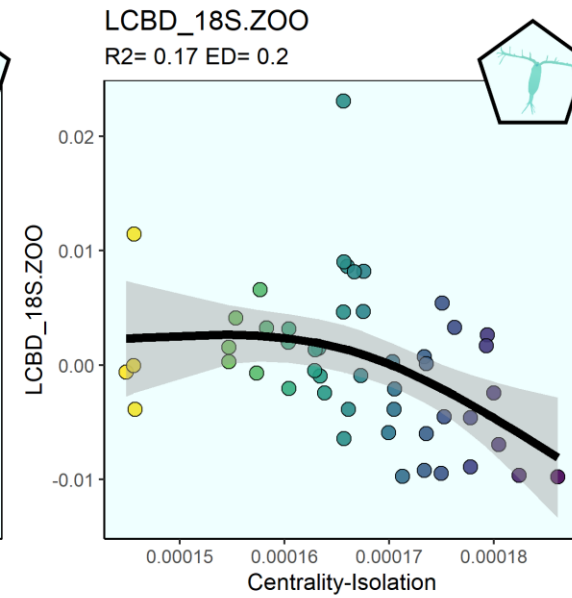
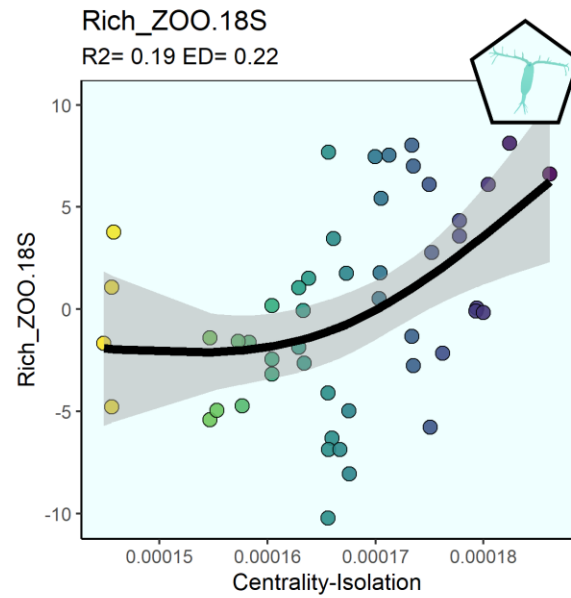


18S Zooplankton

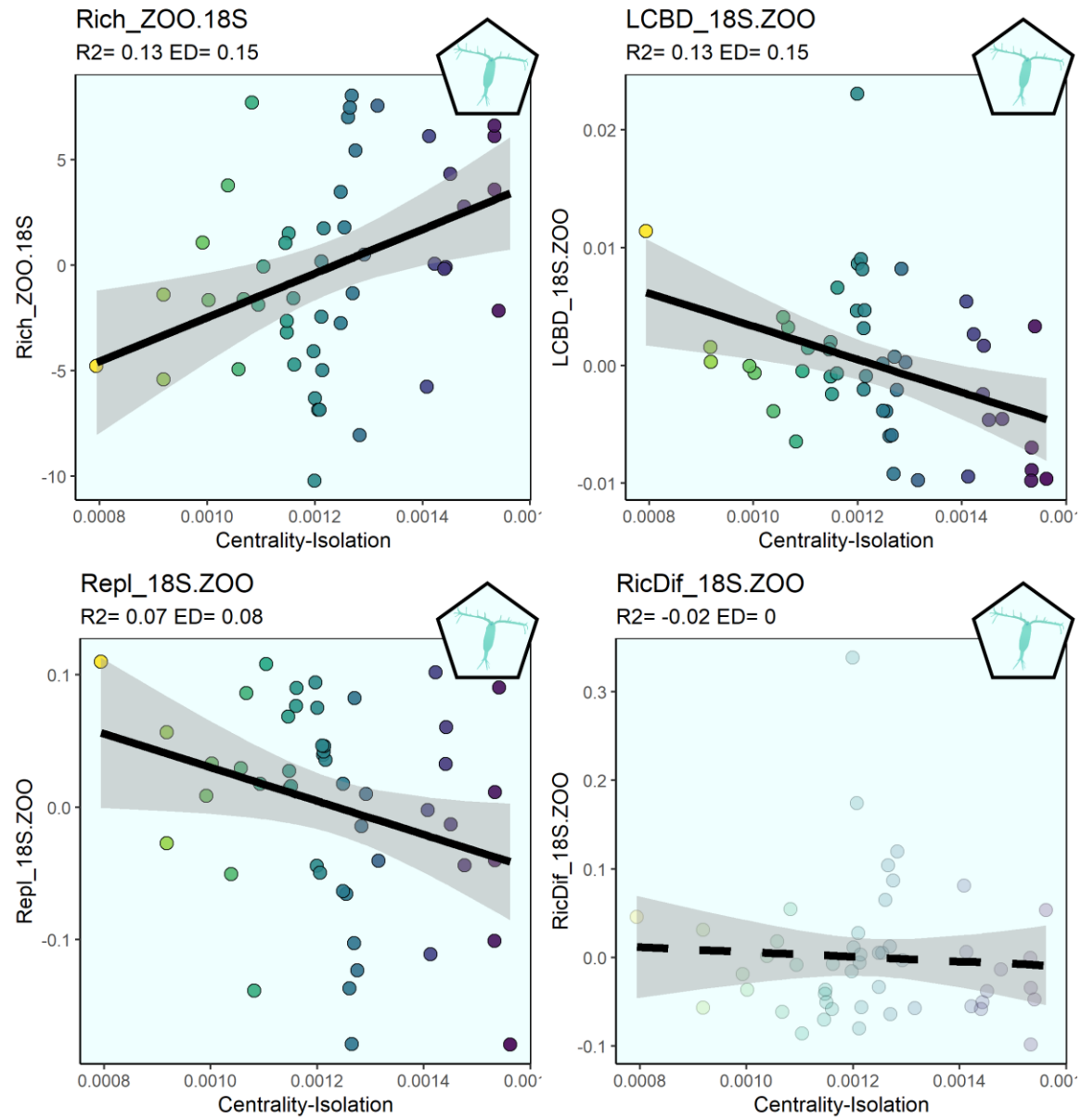
650 km



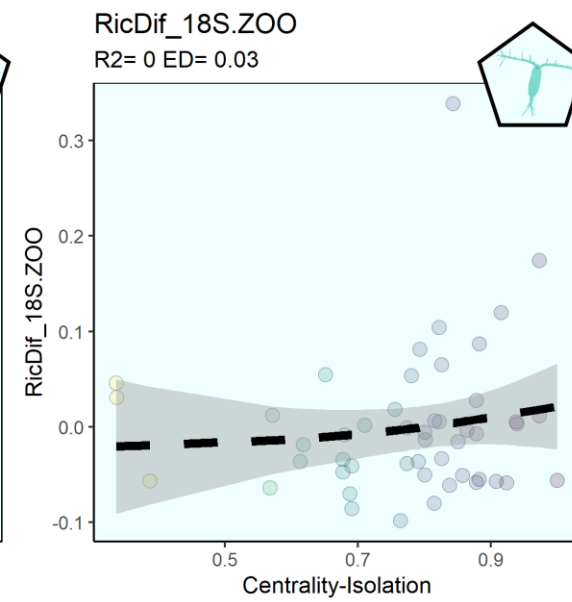
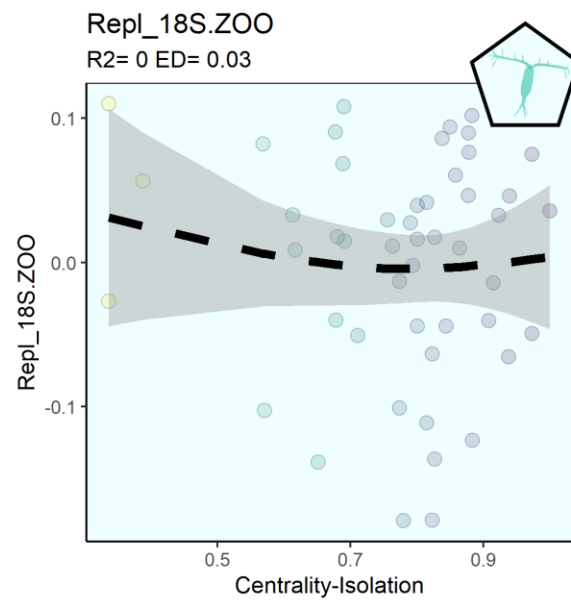
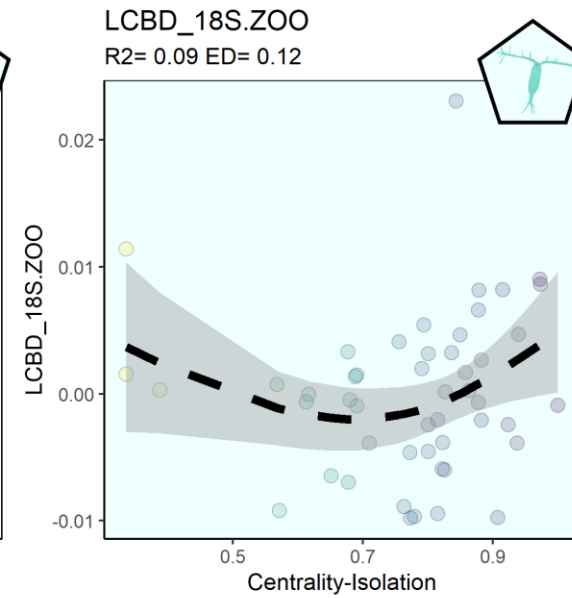
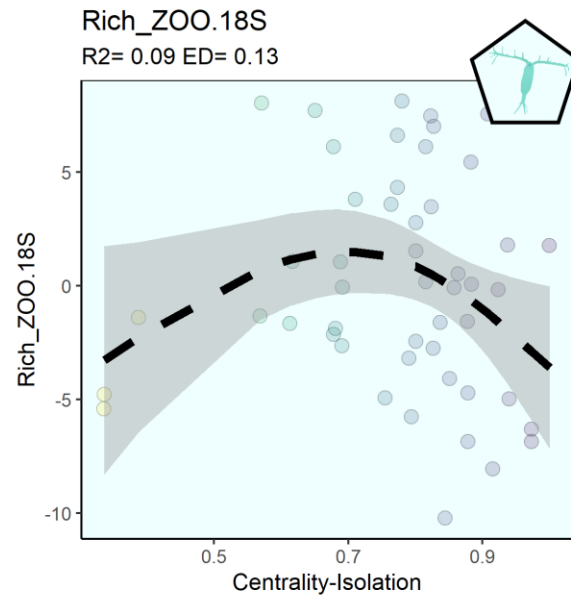
325 km



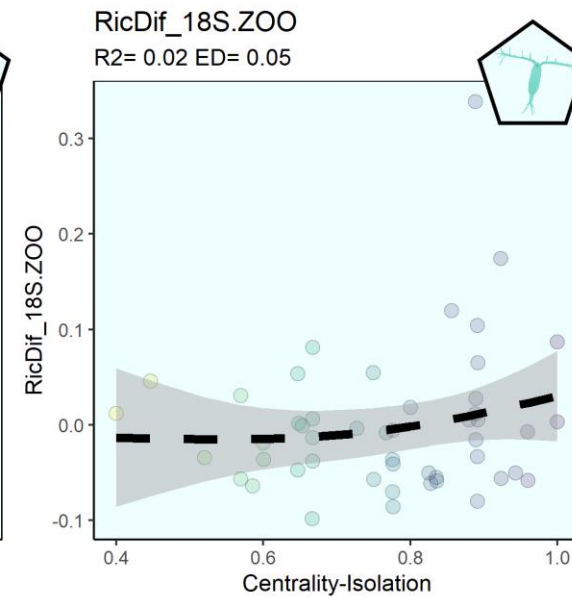
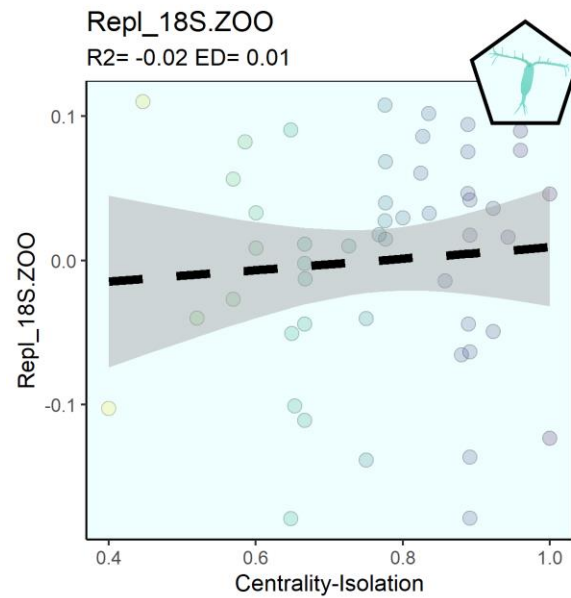
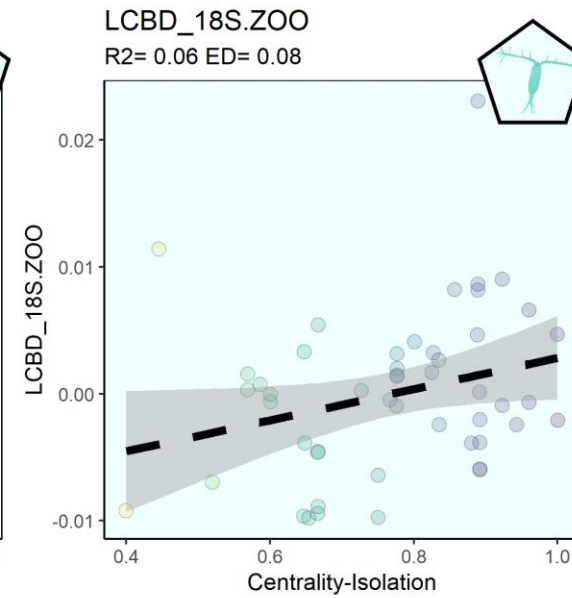
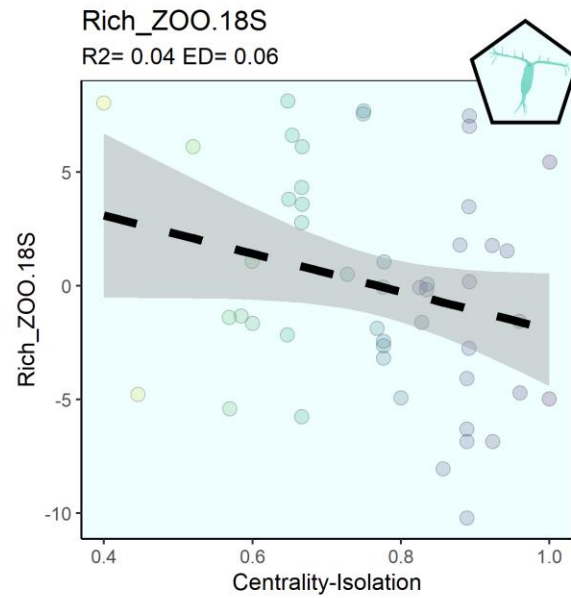
100 km



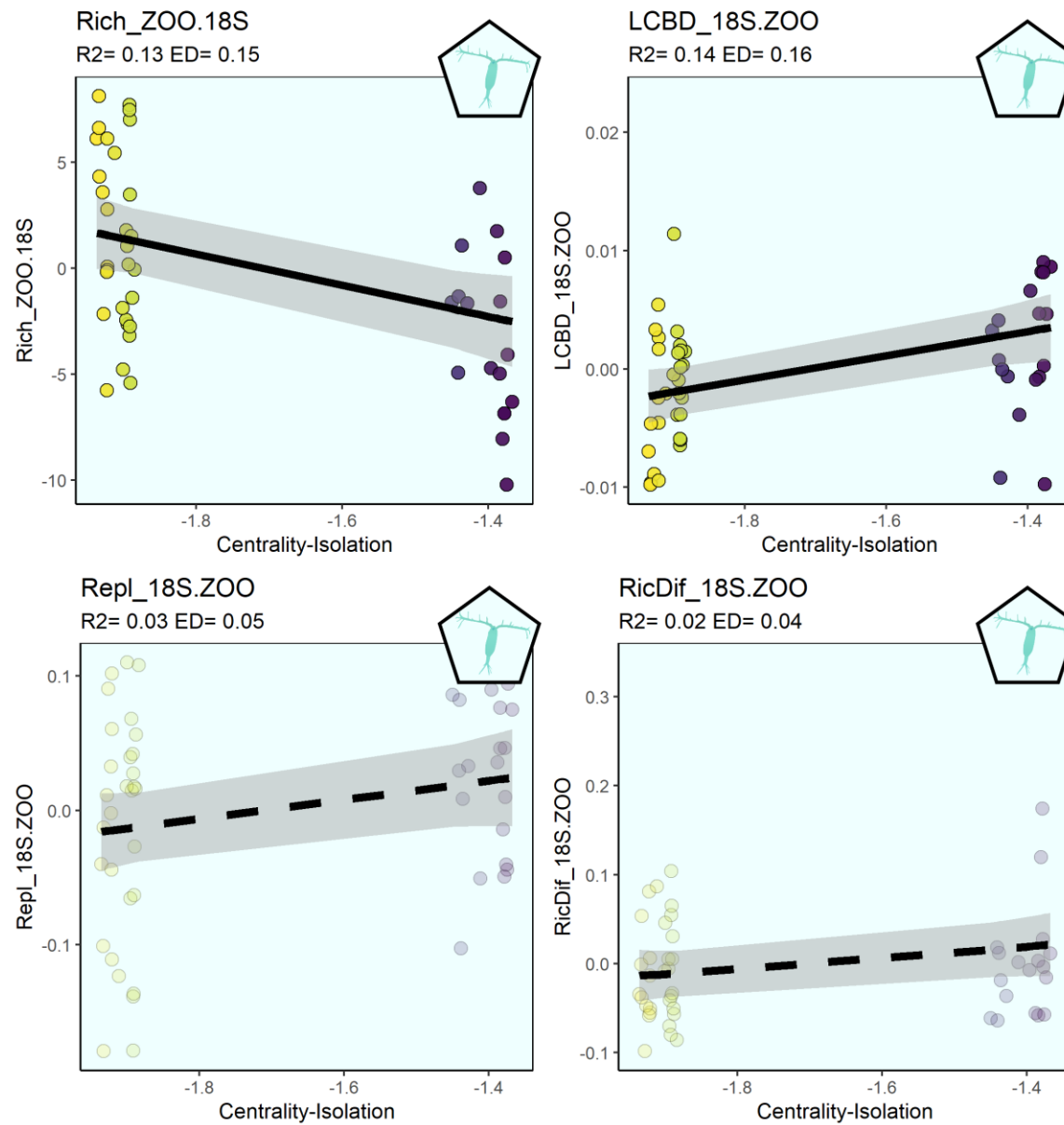
65 km



6.5 km



Fluvial network



Supplementary S8: Generalized additive model summary corresponding to the smooth surfaces for each combination of group, network, and unexplained dbRDA. Highlighted rows correspond to the significant relationships, also represented in Figure 5. Find below the model summary results the plots corresponding to each one of the detected relationships (both significant and non-significant ones) for the same organism group (bacterioplankton in yellow, protists in blue, phytoplankton in green, zooplankton in red and 18S zooplankton in cyan) and network scales (650, 325,100,65,6.5, and Fluvial).

Group	Network	Variable	Intercept	Std.Err.	t-value	p-value	Smooth F-value	Smooth p-value	Adj R-sqr	Expl.Deviance
16S Bacterioplankton	650 km	dbRDA	8.55E-05	8.02E-07	106.5382	1.77E-58	8.813516	0.024166	0.147345	0.200985
16S Bacterioplankton	325 km	dbRDA	0.000166	1.33E-06	124.7219	1.11E-62	8.836002	0.011649	0.147662	0.186148
16S Bacterioplankton	100 km	dbRDA	0.001217	2.20E-05	55.44932	4.69E-44	18.88969	0.001721	0.270279	0.336214
16S Bacterioplankton	65 km	dbRDA	0.758547	0.01931	39.28189	8.71E-37	24.5673	0.000603	0.325105	0.397099
16S Bacterioplankton	6.5 km	dbRDA	0.763943	0.01911	39.9751	6.93E-38	14.48389	0.00577	0.221182	0.283803
16S Bacterioplankton	Fluvial	dbRDA	-1.72034	0.031453	-54.6961	9.96E-45	9.211756	0.02082	0.152989	0.206983
18S Protista	650 km	dbRDA	8.53E-05	8.94E-07	95.45488	1.14E-54	2.603288	0.233255	0.051427	0.08813
18S Protista	325 km	dbRDA	0.000167	1.39E-06	120.2013	4.80E-60	2.483456	0.117577	0.049184	0.07114
18S Protista	100 km	dbRDA	0.001237	2.43E-05	50.9636	1.35E-42	3.643877	0.069622	0.070552	0.095563
18S Protista	65 km	dbRDA	0.773128	0.021396	36.13349	2.23E-36	0.184857	0.343673	0.003836	0.007349
18S Protista	6.5 km	dbRDA	0.768984	0.020754	37.05228	5.68E-37	1.13E-05	0.634949	-3.42E-08	4.71E-07
18S Protista	Fluvial	dbRDA	-1.71022	0.03527	-48.4901	1.09E-41	1.399676	0.31285	0.028333	0.051869
Phytoplankton	650 km	dbRDA	8.55E-05	8.93E-07	95.73458	2.17E-57	0.000603	0.652192	5.94E-06	2.46E-05
Phytoplankton	325 km	dbRDA	0.000166	1.49E-06	111.4366	1.32E-60	0.000367	0.797904	-1.05E-06	1.50E-05
Phytoplankton	100 km	dbRDA	0.001214	2.65E-05	45.87776	6.40E-42	0.000513	0.658066	3.17E-06	2.09E-05
Phytoplankton	65 km	dbRDA	0.758995	0.024716	30.70813	1.15E-33	0.000118	0.411156	2.17E-06	4.81E-06
Phytoplankton	6.5 km	dbRDA	0.762997	0.022339	34.15466	7.87E-36	4.67E-05	0.635907	5.08E-07	1.90E-06
Phytoplankton	Fluvial	dbRDA	-1.72348	0.034533	-49.9081	1.12E-43	6.01E-06	0.661613	5.60E-08	2.45E-07
Zooplankton	650 km	dbRDA	8.54E-05	7.14E-07	119.5417	1.94E-59	24.47214	0.000241	0.324254	0.385027
Zooplankton	325 km	dbRDA	0.000166	1.11E-06	149.6749	2.43E-63	27.37309	0.000159	0.349266	0.414765

Zooplankton	100 km	dbRDA	0.001228	2.07E-05	59.19011	2.49E-45	18.90584	0.001659	0.270447	0.336813
Zooplankton	65 km	dbRDA	0.7748	0.022382	34.61728	4.29E-37	3.66E-05	0.636296	3.80E-07	1.44E-06
Zooplankton	6.5 km	dbRDA	0.777988	0.020288	38.34767	2.14E-38	2.215916	0.255153	0.04164	0.072645
Zooplankton	Fluvial	dbRDA	-1.70941	0.030401	-56.2283	3.45E-45	15.60226	0.001704	0.23426	0.285286
18S Zooplankton	650 km	dbRDA	8.53E-05	8.09E-07	105.4857	1.07E-54	13.79674	0.006129	0.223253	0.285598
18S Zooplankton	325 km	dbRDA	0.000167	1.31E-06	127.6789	4.48E-59	8.959357	0.021516	0.157294	0.212972
18S Zooplankton	100 km	dbRDA	0.001237	2.27E-05	54.37939	9.89E-43	10.79992	0.007535	0.18365	0.233795
18S Zooplankton	65 km	dbRDA	0.773128	0.021438	36.06412	1.99E-36	1.82E-06	0.991691	-2.28E-07	7.58E-08
18S Zooplankton	6.5 km	dbRDA	0.768984	0.020604	37.32296	7.69E-37	0.703918	0.268633	0.014452	0.025144
18S Zooplankton	Fluvial	dbRDA	-1.71022	0.031348	-54.5556	4.21E-42	14.53112	0.004983	0.232382	0.295183

