High dispersal levels and lake warming are emergent drivers of cyanobacterial community assembly over the Anthropocene

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Authors contributions

M-E.M., F.P. and P.S. designed the study. M-E.M. collected data and performed data analysis. M-E.M. and F.P. wrote the manuscript, which was commented and edited by P.S.

Conflict of Interest

The authors declare no competing financial interests.

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Abstract

Disentangling the relative importance of deterministic and stochastic processes in shaping natural communities is central to ecology. Studies on community assembly over broad temporal and spatial scales in aquatic microorganisms are scarce. Here, we used 16S rDNA sequence data from lake sediments to test for deterministic and stochastic assembly patterns in cyanobacterial phylogenies across ten European peri-Alpine lakes and over a century of eutrophication and climate warming. We studied phylogenetic structure and dissimilarity in cyanobacterial assemblages over spatial, temporal, and environmental gradients. We found limited evidence for deviation of lake communities from a random assembly model and no significant effects of geographic distance on phylogenetic similarity, suggesting no dispersal limitation and high levels of stochastic assembly. We did not detect a significant effect of phosphorus and nitrogen levels on deviation of community phylogenies from random. We found however a significant decay of phylogenetic similarity for non-random communities over a gradient of air temperature and water column stability. We show how phylogenetic data from sedimentary archives can improve our understanding of microbial community assembly processes, and suggest that climate warming has been the strongest environmental driver of cyanobacterial community assembly over the Anthropocene.

Introduction

Understanding the mechanisms that determine changes in the structure and composition of natural communities over large spatial and temporal scales is critical, given the impacts that human activities have on biodiversity and ecosystem functions (Cardinale et al 2012). The relative importance of stochastic and deterministic processes driving community assembly might vary over space and time: dispersal, demography, ecological interactions and evolutionary processes can all influence the structure of natural communities across scales (Chase 2010, Hillerislambers et al 2012, Segura et al 2011, Siepielski et al 2010, Vergnon et al 2012, Wagner et al 2012). It is an on-going challenge to understand how anthropogenic environmental changes might influence the mechanisms determining community assembly, particularly in aquatic microbes whose dispersal appears to have no boundaries (Patterson 2009, Whittaker and Rynearson 2017).

Community assembly studies focusing on lake cyanobacteria have been neglected due to lack of data at the appropriated spatial and temporal scale, despite the importance that these organisms have acquired over the past decades for freshwater ecosystem functioning and services (Huisman et al 2018). Over the last century, the frequency and severity of cyanobacteria-dominated communities have increased in lakes and reservoirs worldwide despite remediation measures applied at the regional and international scale (Carey et al 2012, Taranu et al 2012). Cyanobacterial blooms are often dominated by toxic species, and there is a global concern that environmental changes are promoting the geographic expansion of some potentially harmful taxa (Salmaso et al 2015, Sinha et al 2012), due to a combined effect of increasing temperature and nutrient loads (Carey et al 2012, Monchamp et al 2017, Rigosi et al 2014). Toxic species have indeed widened their geographic distribution, supporting the idea that harmful cyanobacteria are spreading across temperate lakes (Monchamp et al 2017). The role of geographic dispersal (where distance limits the establishment of new taxa) relative to selection by environmental gradients remains unresolved in the assembly of these globally important microorganisms.

In this study, we analysed cyanobacterial community composition data spanning over a hundred years and across ten lakes. We used 16S rDNA sequences from sediment cores of European peri-Alpine lakes (Fig. S1) that underwent directional environmental change characterised by climate warming and eutrophication (Monchamp et al 2017). The aim was to test for emergent deterministic (environment-driven) and stochastic (dispersal-driven) patterns in the phylogenetic structure of cyanobacterial assemblages across these different lakes of the same region (Chase 2010, Ruokolainen et al 2009).

We used a null-model that accounted for temporal changes in the size of the species pool to simulate random assembly. We then tested for deviation from random patterns as phylogenetic clustering and overdispersion: the tendency for taxa to co-occur with larger or smaller expectancy, respectively, than predicted by the null-model (Fig. 1A) (Cadotte et al 2013, Emerson and Gillespie 2008, Gotelli and McCabe 2002, Kathleen Lyons et al 2016, Pomati et al 2017). In most cases, dispersal-driven assembly would generate random taxa co-occurrence patterns, while environmental drivers would lead to deviation from random (Cavender-Bares et al 2009, Emerson and Gillespie 2008, Kathleen Lyons et al 2016, Kraft et al 2011). There can be interactions among assembly mechanisms that generate exceptions to these predictions (Bell et al 2005, Mayfield and Levine 2010). We however expect that comparison of phylogenetic structures to null-model simulations, combined with the patterns of community phylogenetic similarity across lakes and spatial or ecological distance, will allow us testing for deterministic and stochastic signatures in cyanobacterial community assembly.

Specifically, when dispersal of cyanobacterial taxa among lakes is not limited (Fig. 1B), we expect that phylogenetic community similarity will decrease over an environmental gradient, while no change is expected when the system is driven only by dispersal (Fig. 1C) (Chase 2010). If there are barriers to dispersal of cyanobacteria, we predict differences in similarities among lake communities that are only dependent on the geographic distance (Fig. 1B), and no effects driven by ecological gradients (Fig. 1C) (Chase 2010). The environmental-driven

decrease in phylogenetic community similarity will not be influenced by dispersal limitation (Fig. 1B), and will vary deterministically as a consequence of the gradient itself (Fig. 1C) (Chase 2010). This is because we expect that, under environment-driven assembly, the turnover of taxa along the ecological gradient will determine community structure in each lake. Here, we investigated whether cyanobacterial community phylogenetic structures within and across lakes over time matched these expectations from assembly processes, and what patterns dominate.

Materials and methods

Data collection

We used high-resolution 16S rDNA sequence data from ten European peri-Alpine lakes, spanning between early 1900s and 2016, to estimate phylogenetic diversity of cyanobacterial communities (Monchamp et al 2016, Monchamp et al 2017). Briefly, sediment cores were collected in ten lakes between 2013 and 2016 using a gravity corer, and layers were dated by varve counting and, in most cases, with radionuclide (Pb^{210}, Cs^{237}) measurements (Monchamp et al 2016, Monchamp et al 2017). Based on the sediment age models, sediment sub-samples were collected at various depths in cores from each lake to capture the cyanobacterial community composition over the last ~100 years. DNA was extracted from bulk sediments in a clean laboratory facility, and the DNA extract were used for PCR and high-throughput sequencing of the cyanobacterial 16S rRNA gene (Table S1) on a MiSeq Illumina platform as previously described (Monchamp et al 2016, Monchamp et al 2017).

The clean, primmer-trimmed sequences were clustered in operational taxonomic units (OTUs) with a 97% threshold of sequence similarity in QIIME (Caporaso et al 2010) using the UPARSE workflow (Edgar 2013). PyNast (Caporaso et al 2010) and the Greengenes microbial sequence database (McDonald et al 2012) were used for sequence alignment, and FastTree (Price et al 2010) was used to estimate a phylogeny based on maximum-likelihood containing all OTUs found in the lakes. OTUs were taxonomically assigned with a confidence

threshold of 85% and the ones assigned to phyla other than photosynthetic cyanobacteria were removed from the dataset. Each sample was rarefied to 2,744 sequences (cyanobacteria only) prior to phylogenetic analyses.

The physical (air temperature) and chemical (nitrogen [NO_3^--N], total phosphorus [TP]) data were collected over several decades consist of several decades of monitoring of the ten lakes (Monchamp et al 2017) and the annual maximal Schmidt Stability Index (SSI; the maximal strength of the water column stratification) was derived from water temperature and hypsometry data (Monchamp et al 2017, Schmidt 1928). Euclidean distances for each environmental variable were calculated among lakes to derive environmental gradients used in the linear models in the R package 'vegan' version 2.4.4 (Oksanen et al 2013).

Phylogenetic analyses

To derive the phylogenetic structure of each community, we quantified the mean pairwise phylogenetic distance (MPD) (Webb 2000) using *mpd* and *ses.mpd* in the package 'picante' version 1.6.2 for R (Swenson 2014) and used null-model simulations of random assembly that account for temporal changes in the size of the species pool (Kathleen Lyons et al 2016). We calculated a standardised effect size of MPD (SES_{MPD}) within each local community subtree based on the comparison of the observed MPD values with the values in the random distribution using 999 randomisations of the species at the tip of the phylogenetic tree, while species richness was maintained (Erickson et al 2014, Hardy and Senterre 2007, Swenson 2014): $SES_{MPD} = \text{Mean}(MPD_{Observed} - MPD_{Randomized})/SD(MPD_{Randomized})$. The SES_{MPD} values were multiplied by −1 to be equivalent to the net relatedness index (NRI) (Webb 2000).

We derived the Unifrac phylogenetic distance (Lozupone and Knight 2005) between all pairs of samples using the *dist* function in the Bioconductor package 'phyloseq' (McMurdie and Holmes 2013) based on the OTU table and the fasta files from amplicon sequencing. The geographic distance-decay relationship was measured on binned communities each representing a period of one decade (from the 1930s to the 2010s; decades 1900s, 1910s

and 1920s were excluded due to insufficient number of samples). The binning was done to remove the factor time from the analysis, as it would introduce a bias when comparing multiple samples from single lakes over time. The temporal distance-decay of phylogenetic similarity was studied plotting log-transformed Unifrac distances against natural log-transformed time distances (years) for each lake in the dataset. Significance of the distance-decay relationship at each decade was tested using Mantel tests in the R package 'ade4' with a significance threshold of $p \leq 0.05$. To test whether the environment (physical and chemical parameters) play a role in driving community assembly, we used the samples that were identified as phylogenetically non-random (i.e., those which SES_{MPD} values were outside the 90% confidence interval of the null model simulation) in linear ordinary least square (OLS) regressions where physical and chemical lake data were the explanatory variables.

Results

Community phylogenetic structure. Based on the SES_{MPD} values, a large number of cyanobacterial communities did not show a phylogenetic structure that significantly differed from the null (random) expectation (Fig. 2). In fact, only two communities were significantly phylogenetically clustered, whereas eighteen out of seventy-six communities showed significant phylogenetic overdispersion, with SES_{MPD} values outside the 90% confidence interval of the null model simulation. Although the remaining forty-six communities analysed did not show significant signal of non-randomness, most (especially since the 1980s) of the SES_{MPD} values were negative, suggesting a tendency towards overdispersion. The samples that displayed significant non-random phylogenetic structure and their corresponding MPD and SES_{MPD} values are listed in Table S2 of the Supplementary Materials.

Distance-decay relationships. We estimated the phylogenetic similarity (beta-diversity) across all pairs of communities reconstructed from the sedimentary archives of the ten lakes at each time-period and investigated the role of geographical and temporal distance (Fig. 3). Our analysis did not reveal an increase in phylogenetic beta-diversity with geographic

distance (Fig. 3A), suggesting no dispersal limitation of cyanobacteria at the regional (peri-Alpine) scale. On the contrary, we observed for all lakes a clear decay of phylogenetic similarity along the temporal gradient representing the history of each lake (Fig. 3B), with the exception of lakes Geneva and Annecy (the latter due to insufficient data points) (Fig. S2).

Community similarity over environmental gradients. All non-random samples identified in Fig. 2 using the SES_{MPD} metric were used to investigate the role of chemical (TP and NO_3^--N) and physical (air temperature and water column stability) drivers in explaining cyanobacterial community deviation from a random assembly. We found no evidence for a role of nutrients (TP and NO_3^--N) in explaining non-random community structure (Fig. 4). On the other hand, OLS regression showed a significant decrease in community similarity along with both air temperature (p = 0.0003, adjusted R^2 = 0.057) and SSI gradients (p = 0.019, adjusted R^2 = 0.058) (Fig. 4). This suggests that communities in lakes characterized by similar physical characteristics related to lake water temperature are more similar in cyanobacterial community composition compared to lakes that display greater differences in temperature and stratification.

Discussion

Most of the cyanobacterial communities obtained in this study from sedimentary archives did not show significant deviation from a random phylogenetic structure, suggesting a strong signal of stochastic (dispersal-driven) community assembly in lake cyanobacteria. Our previous work has shown that DNA-based reconstructions of cyanobacterial communities are robust (Monchamp et al 2016, Monchamp et al 2017), therefore the observed patterns are unlikely to be driven by biases in sedimentary DNA-based community reconstructions. On the contrary, it has been noted that a strong effect of stochastic relative to deterministic processes is expected in the community assembly of microalgae, particularly in highly productive (eutrophic) environments (Chase 2010). The decay in phylogenetic similarity over time coupled with the lack of a geographic distance-decay relationship across lake communities (Fig. 3) suggest temporally dynamic communities with no limitation to dispersal

at the regional (peri-Alpine) scale. In a recent study on genetic divergence among populations of a marine diatom, no significant relationship was found between genetic and geographic distances at regional and global scales (Whittaker and Rynearson 2017). Most reports about microbial dispersal so far did no show clear evidence for geographic distance-decay patterns at the local (0 - 100 km) and regional (101 - 5,000 km) scales (Hanson et al 2012). The scale of distances in our study was not suited to capture dissimilarity changes among cyanobacterial communities along very large geographical distances (e.g. continental), where an effect of geographical isolation might emerge (Papke et al 2003). Nevertheless, our research suggests that cyanobacterial communities present weak dispersal limitation among lakes of the same region, even around and across barriers such as the European Alpine mountain range.

Previous work has shown that communities of cyanobacteria have become more homogeneous in terms of composition across peri-Alpine lakes over the last decades, in favour of a few clades of bloom-forming and potentially toxic taxa (Monchamp et al 2017, Salmaso et al 2015). This could result in an increase of phylogenetic clustering over time, if the traits under selection by environmental changes are phylogenetically conserved (Emerson and Gillespie 2008). Our data show that the phylogenetic structure of assemblages is, in most cases, not clustered. Only two out of seventy-six tested communities displayed significant clustering, which strongly suggests that the environmental driving forces of cyanobacterial assembly in the lakes are not acting on phylogenetically conserved traits. Coloniality and buoyancy regulation are in fact multiphyletic traits that have been associated to the invading taxa, which belong to different cyanobacterial phylogenetic lineages within the orders *Chroococcales*, *Nostocales* and *Oscillatoriales* (Carey et al 2012, Huisman et al 2018, Monchamp et al 2017). The more prevalent signal of overdispersion in the community phylogenies might support this hypothesis of environmental selection for convergent traits.

Gradients of NO_3^--N and TP concentrations across lakes did not significantly explain deviation from random assembly in the investigated cyanobacterial communities (Fig. 4). It is important to note that the most of the lakes investigated here classify as meso-eutrophic to eutrophic (Oecd 1982) (see average P and NO_3^--N concentrations reported by (Monchamp et al 2017)). Significant patterns of phylogenetic dissimilarity might emerge across communities characterized by a broader nutrient gradient, but this remains to be tested by surveys or experimentally. Rather, the difference in physical conditions, such as temperature and strength of the water column stratification, seemed in our study to explain a significant proportion of the observed variance in phylogenetic relatedness among lake cyanobacterial communities. The increasing trend in air temperatures, which has accelerated since the 1980s across the peri-Alpine region, has caused modifications in thermal characteristics of lakes, e.g., via changes in the duration and strength of the water column stratification (Monchamp et al 2017, Posch et al 2012), which in turn affects recirculation and availability of nutrients for phytoplankton growth (Huisman et al 2018, Pomati et al 2017, Yankova et al 2017). This effect has been amply documented and has favoured, as mentioned above, buoyant cyanobacterial forms that are able to control their vertical position in the water column to reach optimal nutrient and light conditions (Monchamp et al 2017, Pomati et al 2017, Posch et al 2012, Salmaso et al 2015, Yankova et al 2017). Our findings therefore support previous evidence and suggest that climate warming is the strongest environmental driver of the assembly of lake cyanobacterial communities, and might select for specific traits such as, for example, buoyancy regulation.

In conclusion, this is the first study to our knowledge that explicitly tests for assembly patterns in cyanobacterial communities across regional scales and over the Anthropocene. We successfully reconstructed the phylogenetic diversity in seventy-six cyanobacterial communities over a period of ca. 100 years using DNA from sediment cores collected in ten lakes. Our study shows that both stochastic (dispersal-driven) and deterministic (environmental-driven) processes are important in assembling cyanobacterial communities across lakes of the European peri-Alpine region. Cultural eutrophication and climate change

are the most notable environmental factors favouring cyanobacterial growth, but the processes governing community composition and phylogenetic structure appeared in our study to be more significantly driven by lake warming. Our results are relevant for basic understanding of microbial community assembly processes, and for the management of aquatic ecosystems whose services are threatened by an increasing prevalence of potentially toxic cyanobacteria.

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Figure legends

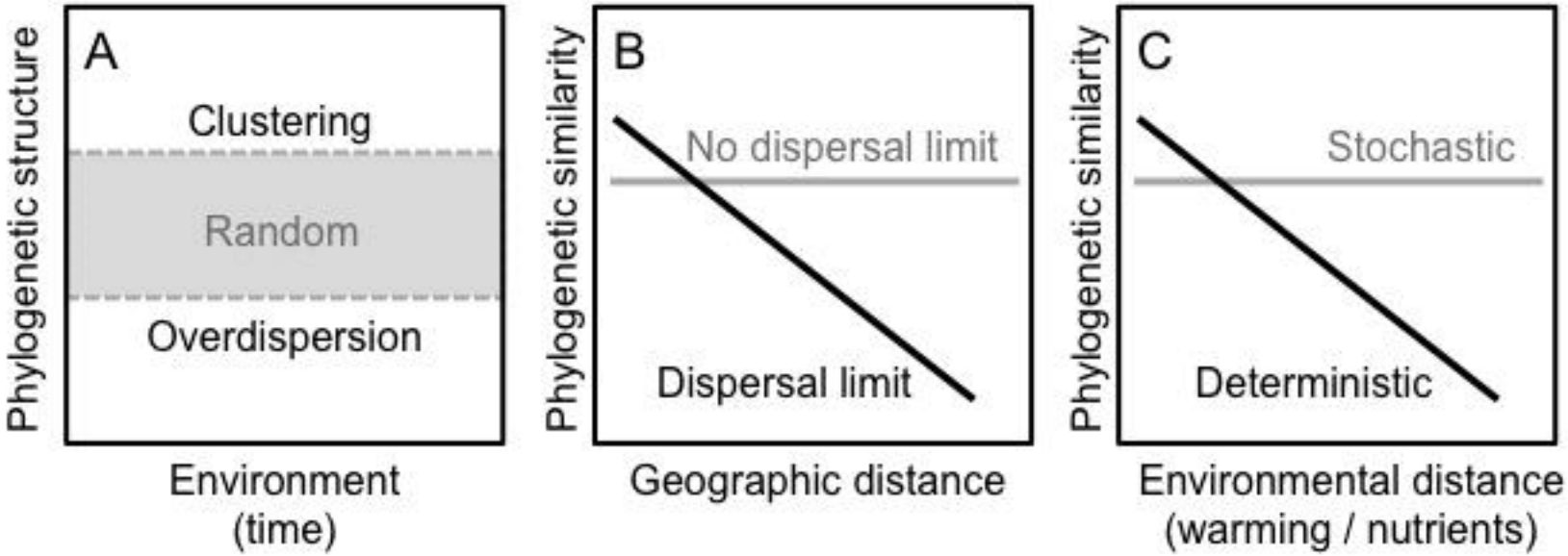
Figure 1. Schematic description of the theoretical expectations for phylogenetic community assembly within and between communities, based on stochastic (dispersal-driven) and deterministic (environment-driven) processes. **(A)** Taxa associations are analysed using their mean pairwise phylogenetic distance (MPD) for each date of each time-series and by comparing it to expected patterns from null-model simulations of random assembly (grey box): clustering and overdispersion (above and below the random expectation, respectively) signal communities that are composed of species phylogenetically closer or further apart than expected by chance, respectively, as a sign of deterministic processes. **(B)** Predicted patterns in phylogenetic community similarity depending on limitation (black line) and no limitation (grey line) in taxa dispersal among sites. **(C)** Predicted change in phylogenetic similarity for completely stochastic (grey) and deterministic (black) models of community assembly along an ecological environmental gradient (e.g. lake physics and chemistry).

Figure 2. Time series of the standardised effect size of mean pairwise phylogenetic distances (SES_{MPD}) values multiplied by −1 for the equivalent of the NRI index (Webb 2000), calculated for each local community compared with null model simulations. The samples outside the central area delimited by the dashed lines show significant community structure (above or below the 95% [grey lines] and 90% [red lines] confidence intervals of the null-model simulation). Negative values signal phylogenetic overdispersion, whereas positive values signal phylogenetic clustering.

Figure 3. Distance-decay in cyanobacterial communities. A) Natural log-transformed phylogenetic (Unifrac) similarity between all pairwise cyanobacterial communities at each decade between the 1900s to the 2010s plotted against a gradient of natural log-transformed geographic distances between lakes. A null distance signifies that the pairwise phylogenetic dissimilarity was calculated between samples of the same lake at a given period. The vertical dashed lines mark the distances of 50 km and 130 km for reference (the absolute pairwise distances separating all lakes are summarized in Table S2 of Supplementary Information). **B)**

Natural log-transformed Unifrac distances plotted against the natural log-transformed temporal gradient (years) for each lake (colour coding).

Figure 4. Cyanobacterial beta-diversity over environmental gradients. Phylogenetic (Unifrac) similarity between samples are plotted against environmental distances (euclidean) in **A)** TP (n = 104) and **B)** NO_3^--N (n = 77) concentrations, **C)** air temperature (n = 209), and **D)** maximal annual Schmidt Stability Index (SSI) (n = 65). Only significant regressions ($p \leq 0.05$) are shown. The number of samples in each analysis depends on the availability of lake monitoring data (details on the time-series of monitoring data are found in (Monchamp et al 2017)). Samples used in the regression analysis are the non-random communities (i.e., showing significant phylogenetic structure based on SES_{MPD} deviation from the null model expectation).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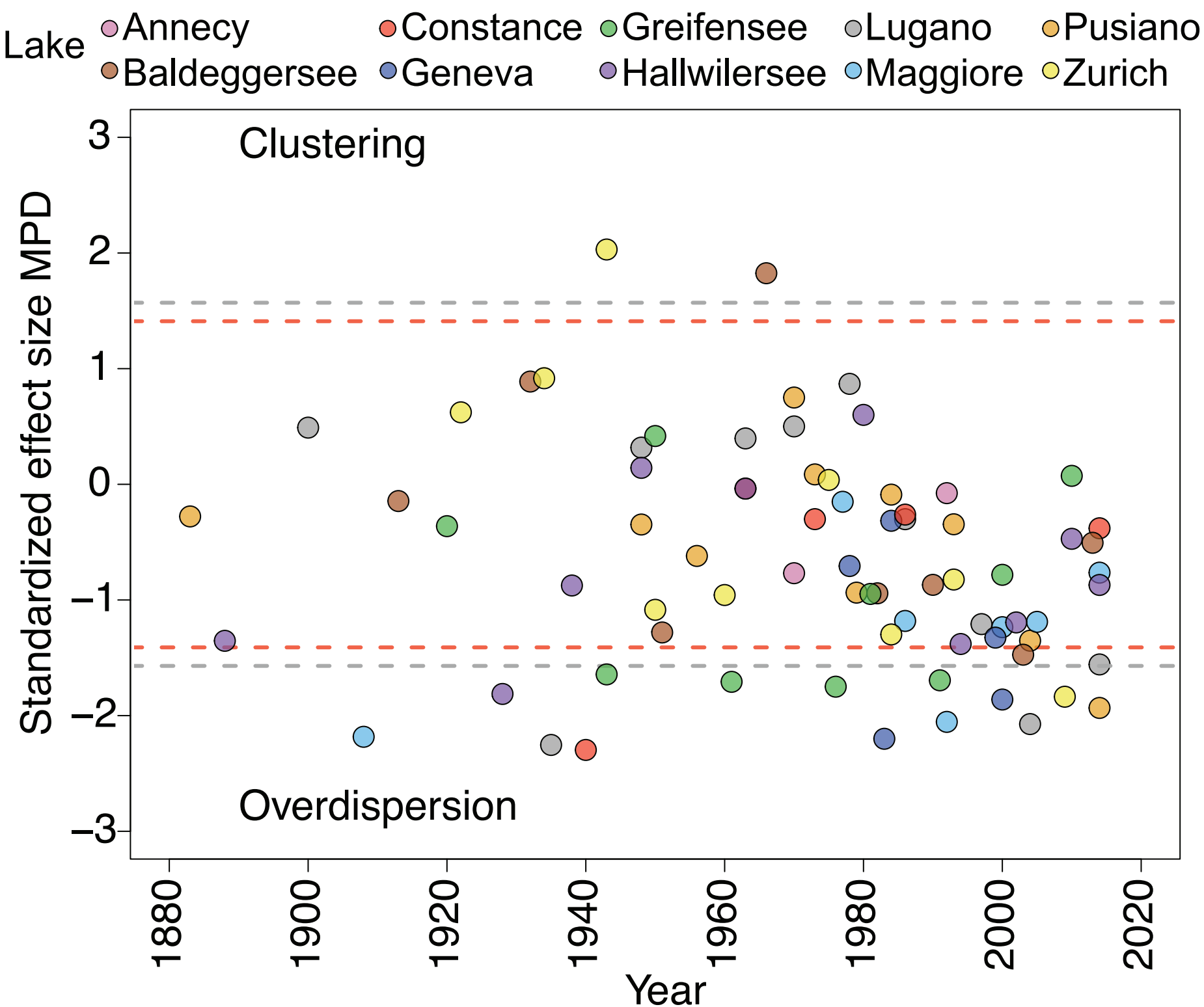
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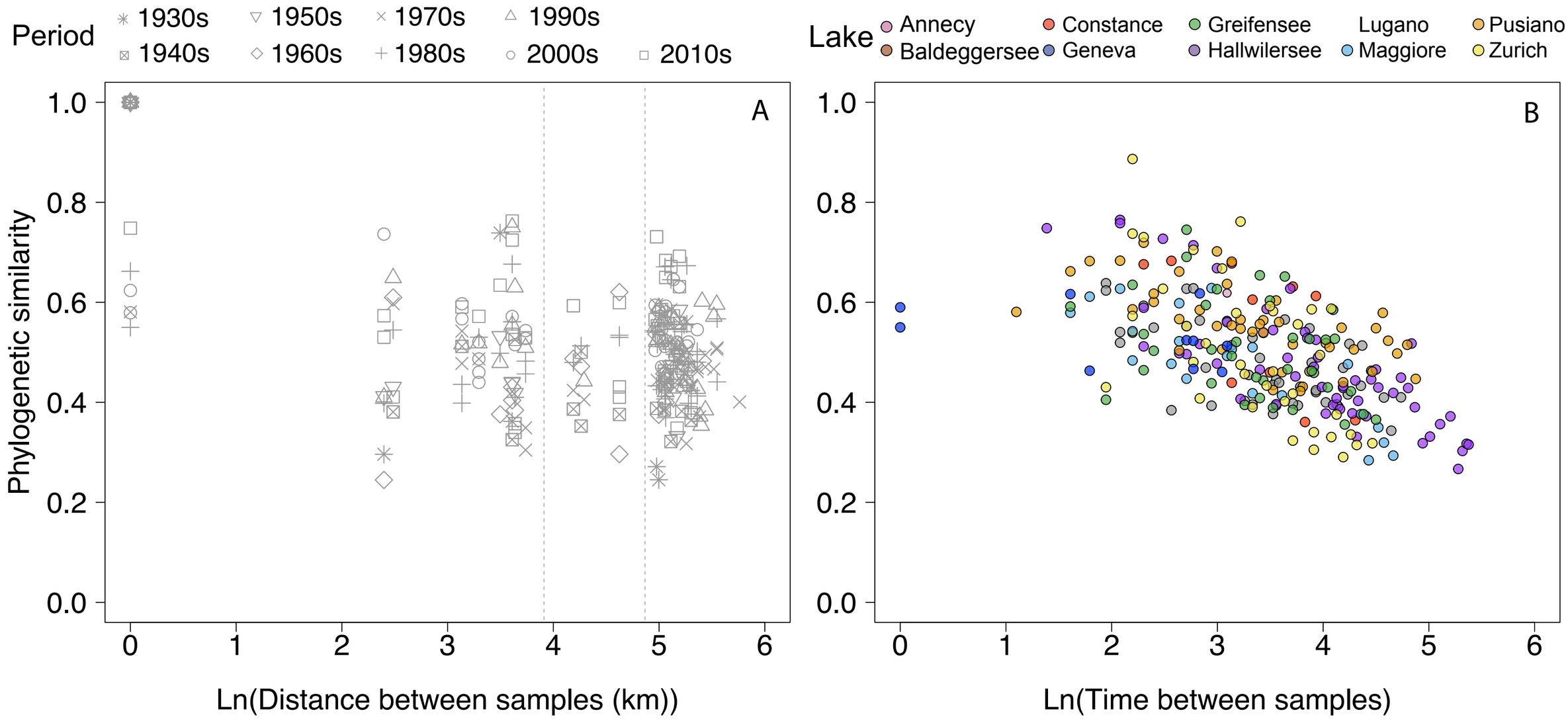
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1.0
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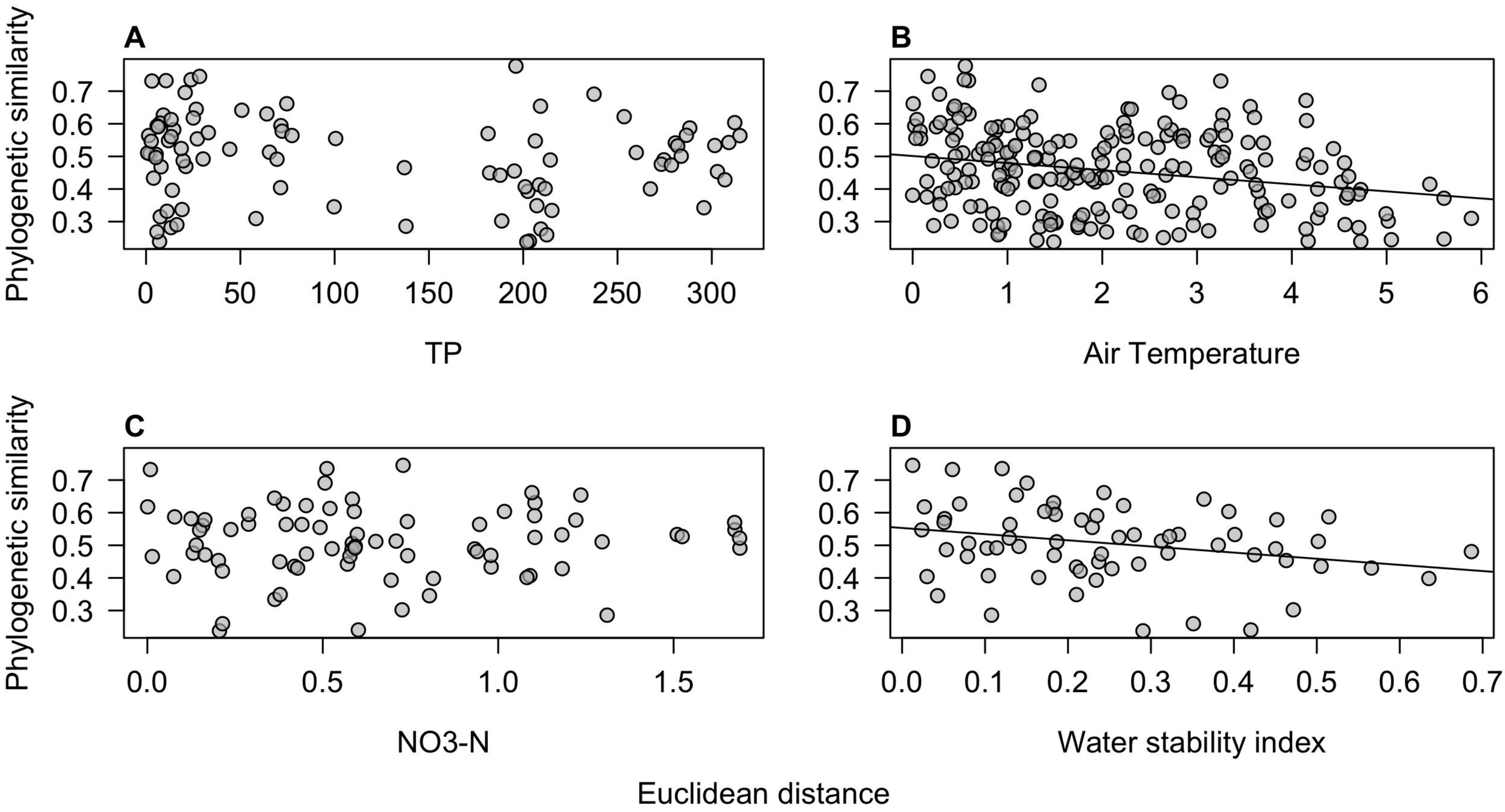
Ln(Distance between samples (km))
Ln(Time between samples)


A
B
C
D
Phylogenetic similarity
0.7
0.6
0.5
0.4
0.3
0
50
100
150
200
250
300
TP
1
2
3
4
5
6
Air Temperature
0.0
0.5
1.0
1.5
NO3-N
0.1
0.2
0.3
0.4
0.5
0.6
0.7
Water stability index
Euclidean distance