

Research

Association between temporal and spatial beta diversity in phytoplankton

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The rates of temporal and spatial species turnover have been compared in different organisms and scales, revealing that both are not independent but, rather, associated. However, the knowledge is limited for the association between spatial turnover and temporal turnover. Here, we performed two investigations of the phytoplankton composition in the lakes of the Yangtze River catchment in China in the spring and summer of 2012, which covered regional spatial scale and two-season temporal scale. We analysed the association between temporal and spatial species turnover in phytoplankton. The results showed that 1) the two-season temporal turnover of phytoplankton varied based on the mean values and the coefficient of variance of environmental variables, and pH was the most important variable negatively affecting the temporal turnover; 2) the spatial beta diversity of phytoplankton in summer was higher than that in spring, and the distance decay pattern was significant in summer, but not in spring; 3) the variation in spatial turnover in spring and summer was attributed to the primary environmental variables (nitrogen, phosphorus and underwater available light) and broader-scale spatial variables; 4) the proportion of jointly explained variation of spatial Bray–Curtis dissimilarity by the environment and space increased from ~38% (spring) to ~55% (summer), which was mainly due to the variation in spatially structured environmental variables during the two-season temporal turnover, such as pH and ion concentrations; 5) the community compositions in summer were more similar between the lakes with similar two-season temporal turnover. These results indicate that the spatial turnover of phytoplankton composition in summer was partially predetermined by the variation in environmental variables and phytoplankton composition during the process of two-season temporal turnover, and highlight the understanding of temporal variations in spatial beta diversity as well as the underlying assembly mechanisms in phytoplankton.

Introduction

Beta diversity, the spatial and temporal changes in species composition among sampling units, is a measure quantifying the change or turnover in species composition across space and time (Whittaker 1960, 1972). Beta diversity is a key concept for understanding ecosystem function and biodiversity conservation because it helps

describe the distribution of diversity (Legendre et al. 2005). In recent decades, there has been a remarkable increase in the number of studies on beta diversity, involving different study goals, such as the scaling of diversity (Legendre et al. 2009, Barton et al. 2013), the distribution of species (Qian and Ricklefs 2007, Wang et al. 2012), metacommunity structure (Astorga et al. 2012, De Bie et al. 2012), ecosystem stability (O’Gorman and Emmerson 2009), conservation planning (Gering et al. 2003) and the development of ecological theories (Condit et al. 2002, Kraft et al. 2011). These studies focus on two dimensions, space and time, to study beta diversity across ecosystems, geographical gradients and organism groups. However, there is little knowledge about the association between spatial and temporal beta diversity.

In general, the similarity of species composition typically decreases with increasing distance, known as distance (space, time or environment) decay (Nekola and White 1999). The distance-decay pattern of spatial beta diversity is driven by multiple factors related to species functional traits or characteristics (body size, thermoregulation and dispersal type), geographical gradients and general ecosystem properties (spatial extent, geographical position, region, realm, migrations and dispersal routes) (Soininen et al. 2007a). Temporal beta diversity is simultaneously governed by ecological, physical, and geographical variables (sampling duration, ecosystem size and type, organism size and latitude) (Korhonen et al. 2010). These factors have been integrated into two main explanations, niche theory and neutral theory (Astorga et al. 2012), a framework shared by many authors (Duque et al. 2002, Soininen et al. 2004, Cottenie 2005, Jones et al. 2006, Thompson and Townsend 2006, Nogueira et al. 2010). Niche theory predicts that community similarity decreases with environmental distance, irrespective of geographic proximity, as a result of species differences along environmental gradients (Tilman 1982). Neutral theory, by contrast, predicts that the decay of community similarity is caused by spatially limited dispersal, independent of environmental differences between sites (Hubbell 2001). Furthermore, niche theory and neutral theory are correlated with environment and geographic distance, respectively.

The relative importance of the two explanations is often linked to the spatial extent of the study (Soininen et al. 2007b) or the functional traits of the organisms, such as the body size, life-history type and dispersal capacity of different organism groups (Astorga et al. 2012, De Bie et al. 2012). Even within the same organism group, especially in groups of small organisms, there are different arguments regarding the relative importance of niche theory and neutral theory, such as in the phytoplankton community. Some studies showed that the phytoplankton composition or beta diversity was controlled by only pure environmental effects (Vanormelingen et al. 2008), or both pure environmental and pure spatial effects (Soininen et al. 2007a, Teittinen et al. 2016). Others showed that neither environmental nor spatial effects structured phytoplankton communities (Beisner et al. 2006, Nabout et al. 2009). Compared with larger organisms, small organisms have relatively short generation times and

high population growth rates. These traits mean that the composition of their communities can quickly track changes in the local environment seasonally (Korhonen et al. 2010), and their demographic characteristics should enable efficient species sorting and weaken the potential of dispersal limitation to generate spatial patterns in metacommunities (Van der Gucht et al. 2007). Therefore, the relative importance of environmental and spatial fractions to spatial turnover may be affected by the temporal turnover, and addressing this possibility requires further time series spatial-snapshot studies to achieve a more comprehensive understanding of community dynamics (Langenheder et al. 2012, Hatosy et al. 2013).

The turnover of community composition across space is influenced by different assembly mechanisms, such as environmental conditions and dispersal (Langenheder et al. 2012), which varied depending on temporal turnover process. Therefore, spatial beta diversity can be associated with temporal turnover by analyzing the variations and their relationship to spatial and temporal beta diversity. However, due to the lack of data involving simultaneously variations in time, space, environment, and biotic assemblages, there is still limited knowledge about the temporal variation in spatial beta diversity and the association between spatial and temporal turnover. Shallow lakes are excellent model systems in which to investigate spatial interactions because of their island-like nature and discrete boundaries, and phytoplankton communities experience dramatic seasonal shifts, especially from spring to summer. To overcome the hindrance from non-synchronization data (such as that in meta-analysis) for analysis, we implemented two synchronous field investigations in spring and summer (as short as possible sampling campaign for each investigation, almost same interval between two campaigns for each lake, completely same variables for each investigation) at a regional scale and examined the variation in temporal and spatial beta diversity in phytoplankton in the lakes located in the Yangtze River catchment, China. We would use these simultaneously data to investigate how the temporal turnover affects the spatial beta diversity. Specifically, we hypothesize that 1) phytoplankton composition will be similar (low spatial beta diversity) in the lakes with similar temporal turnover, 2) spatial variability of environmental variables driving temporal turnover also will contribute to the spatial beta diversity, and 3) the effect of dispersal on the spatial beta diversity will increase from spring to summer due to flood pulses.

Methods

Study lakes

This study investigated 49 floodplain lakes (all areas > 1 km², median/interquartile range of lake area: 16.1/27.8 km²) along the Yangtze River in China, from the middle reaches to the lower reaches (Supplementary material Appendix 1 Table A1, Fig. 1). All of these lakes are shallow and polymictic freshwater lakes that span a trophic gradient from oligotrophy to

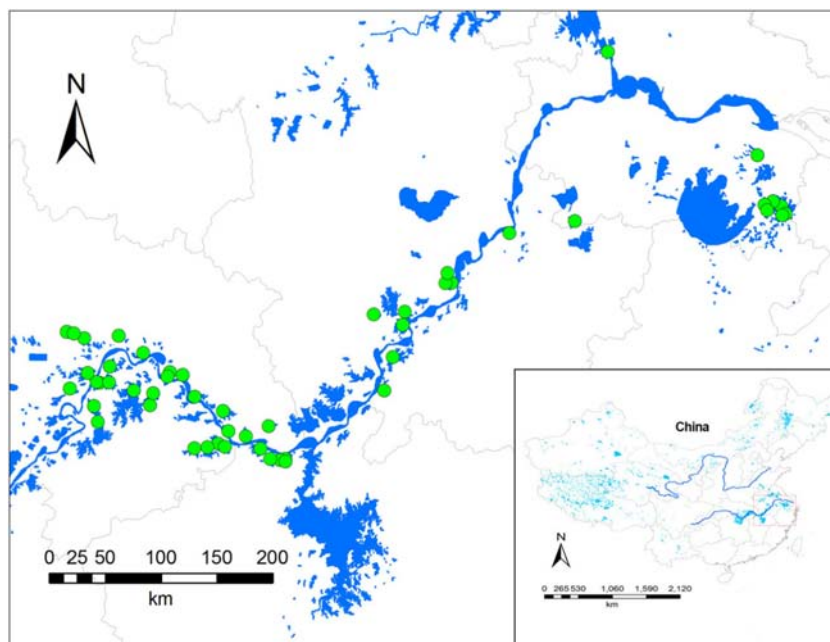


Figure 1. Map of the study lakes in China. The blue polygons indicate all lakes (area > 1 km²) in China, and the green ones indicate the investigated lakes in the case.

hypereutrophy due to different human population levels and different environmental backgrounds (Supplementary material Appendix 1 Table A2).

Sampling and analyses

Sampling was carried out in April and August 2012, representing spring and summer, respectively. Each sampling campaign was performed over a short timeframe (approximately 3 weeks) to obtain a snapshot view of the phytoplankton communities in the selected lakes. In each lake, the sampling duration (the interval between two sampling campaigns) was approximately 120 d, and three sampling sites were established to integrate spatial heterogeneity. For each sampling site, integrated water samples (5 l) were collected by mixing the surface (50 cm below the surface), middle and bottom (50 cm above the bottom) samples taken with a Uwitec water sampler (Uwitec, Mondsee, Austria). The mixed layer depth was determined from the vertical temperature profiles.

Vertical profiles of physical and chemical parameters (temperature, pH, dissolved oxygen (DO) and conductivity) were measured at every sampling site to calculate the mean values and determine the depth of the mixed layer using a multiparameter meter (model 6600V2; Yellow Springs Instruments, Yellow Springs, OH, USA). Transparency (SD) was measured with a Secchi disk. Five liters of water were collected for laboratory analyses. Ammonium (NH₄⁺), nitrate (NO₃⁻), nitrite (NO₂⁻) and dissolved inorganic phosphorus (PO₄⁻) were measured using a continuous flow analyser (Skalar SA 1000, Breda, the Netherlands). Dissolved anions (Cl⁻, SO₄²⁻, K⁺, Na⁺, Ca²⁺, Mg²⁺) were analysed using

ion chromatography, inductively coupled plasma atomic emission spectroscopy or inductively coupled plasma mass spectrometry. Total nitrogen (TN) and total phosphorus (TP) were analysed using peroxodisulphate oxidation and the spectrophotometric method. Chlorophyll *a* was extracted with 90% acetone and measured on a spectrofluorometer (Shimadzu RF-5301PC, Japan) (Yan et al. 2004). The diurnal mean light during the sampling period was obtained from the closest meteorology stations of the China Meteorological Administration.

Plankton analysis

Integrated 500-ml phytoplankton samples were collected at each site and fixed with acid Lugol. Identification was performed at the species or genus level using the most recent literature (Hu and Wei 2006). Counts were made in random fields (more than 30 fields) in sedimentation chambers (30 ml) using an inverted microscope following the criteria of Utermöhl (1958). For dominant species, at least 100 individuals were counted. For all lakes, we considered the organism as the unit (unicell, colony, or filament) to facilitate the calculation of the biovolume. Cell numbers per colony as well as organism dimensions, including maximum linear dimension were estimated. The biovolume was calculated from the measurements of 30 organisms of each species at each site according to Hillebrand et al. (1999). The biomass was determined as algal volume for each lake and converted to fresh weight assuming a specific gravity of 1 g cm⁻³. The species richness is the total number of species recorded during counts, which was standardized to count size.

Data analysis

Calculating and comparing the temporal and spatial beta diversity

The variability in species composition among sampling units can be measured with beta diversity (Anderson et al. 2006). The most widely used ecological measures of compositional dissimilarity include the classic Jaccard index (Jaccard 1900), Sørensen index (Sørensen 1948) for presence–absence data (Chao et al. 2005), and the Bray–Curtis index (Bray and Curtis 1957) for relative abundance information (Magurran 2004, Hatosy et al. 2013, Teittinen et al. 2016). The Sørensen index is monotonically related to Jaccard index, and its value is lower than that of Jaccard index. The difference between the two indices is that the Sørensen index gives double value to shared species. The Bray–Curtis index is considered to be an extension of the Sørensen index; it varies from 0 to 1, and if data are reduced to presence/absence, then the Bray–Curtis index is equal to Sørensen index. In the present study, the Bray–Curtis and Jaccard dissimilarity indices were chosen as beta biodiversity metrics reflecting the variation in phytoplankton communities. We calculated the two metrics to assess the temporal (from spring to summer) and spatial (among lakes and within lakes) variation of phytoplankton composition using the R package ‘vegan’ (Okasanen et al. 2012). The temporal beta diversity of each lake and the spatial beta diversity among lakes were calculated with the data of the mean values of three sites in each lake. To diminish the effect of rare species, we selected the data of the phytoplankton contributing > 1% of the total community biomass and occurring in at least 3 lakes before completing the calculation. For the Bray–Curtis index, we calculated the metric with no transformation data, log transformation data and square root transformation data. The results were very similar; therefore, only the results from the square root transformation data were used in the study. In addition, there were slight difference in the sampling intervals (119.8 ± 2.88 d) of all lakes from spring to summer. To diminish the effect of sampling intervals on temporal turnover and make the turnover to be comparable, we modified the values of the two metrics by dividing by the sampling intervals, which were transformed to mean = 1. After the temporal and spatial beta diversity were obtained, the difference among them were compared with Tukey HSD post-hoc test. The spatial beta diversity along the lakes was shown in a heat map ranked by increasing temporal turnover to present the association between them.

Analysing the primary factors driving the variation in temporal beta diversity

To identify the primary reasons for the variation in temporal beta diversity, the relationships between the temporal beta diversity indices and potential explanatory variables were analysed with generalized linear models (GLMs) and boosted regression trees (BRTs). Both the mean levels and the discrepancy of explanatory variables between spring and summer might affect the variation of phytoplankton composition. Therefore, we chose the mean values and the coefficient of

variance (CV) of environmental variables as explanatory variables. Before the two analyses, we first integrated and performed principal components analysis (PCA) to reduce the dimensions of the environmental variables (water depth, transparency, water temperature, diurnal mean light, pH, DO, electronic conductivity, TN, TP, Cl⁻, SO₄²⁻, K⁺, Na⁺, Ca²⁺, Mg²⁺, PO₄³⁻, NH₄⁺, NO₂⁻, NO₃⁻), and to decrease the degrees of freedom below the number of sampled lakes. First, we integrated NO₂⁻ and NO₃⁻ as NO_x by adding them together. Second, we calculated the mean light (I_m) using the following formula (Riley 1957):

$$I_m = I \frac{1 - e^{-KZ_m}}{KZ_m}$$

Here, we used the diurnal mean light during the sampling period as the surface light (I). We estimated extinction coefficients (K) using Secchi disk transparency (Z_{sd}) with the relationship, $K = 1.54/Z_{sd}$ (Sterner 1990). The mixing depth (Z_m), defined as the greatest depth at which the temperature differed from the lake surface temperature by not more than 1°C, was determined from the temperature profile. Finally, by performing PCA with the R package ‘psych’, the mean values and CV values of electronic conductivity and the concentration of dissolved ions (Cl⁻, SO₄²⁻, K⁺, Na⁺, Ca²⁺, Mg²⁺) were reduced to one principal component, Ion (PC1, Supplementary material Appendix 1 Table A3) and cvIon (PC1, Supplementary material Appendix 1 Table A4), respectively, as explanatory variables. The mean nutrients were reduced to their first two principal components: P (PC2), including TP and PO₄³⁻; N (PC3), including TN, NH₄⁺, NO_x (Supplementary material Appendix 1 Table A3). The CV values of nutrients were also reduced to their first two principal components: cvP (PC2), including cvTP and cvPO₄³⁻; cvN (PC3), including cvTN, cvNH₄⁺ and cvNO_x (Supplementary material Appendix 1 Table A4). The remaining variables were used as explanatory variables without a PCA step. Explanatory variables (temperature, DO and I_m) were log-transformed [$\log_{10}(x + 0.0001)$] before analysis to reduce distributional skew.

GLMs with Gaussian error distribution were used to examine temporal beta diversity in relation to the explanatory variables. The GLM results show the importance of variables in a multivariate setting. The best approximating model was selected with Akaike’s information criterion (AIC; Akaike 1974). In addition to GLM, we determined the effects of explanatory variables on temporal beta diversity with a BRT method to ensure the independence of the methods. BRT is an ensemble method for fitting statistical models that differs fundamentally from conventional techniques that aim to fit a single parsimonious model (Elith et al. 2008). BRT is based on the combination of the strengths of two algorithms: regression trees (models that relate a response to their predictors by recursive binary splits) and boosting (an adaptive method for combining many simple models to provide improved predictive performance). The final BRT model can

be understood as an additive regression model, in which the individual terms are simple trees fitted in a forward, stage-wise fashion (Elith et al. 2008). Due to relatively low sample size, we fitted the BRT (interaction depth = 2, bagging fraction = 0.5, learning rate = 0.0005) using the function 'gbm' in the R package 'gbm' with a Gaussian error distribution. The optimal number of trees was produced with cross-validation.

Analysing the reasons explaining the variation in spatial beta diversity

To examine the variation in beta diversity of phytoplankton among lakes (spatial beta diversity), we first detected the spatial autocorrelation patterns of the species dissimilarity matrix and environmental variables in phytoplankton communities. A Mantel correlogram (Borcard and Legendre 2012) was implemented with the function 'mantel.correlog' in the R package 'Vegan'. The geographical distance matrix was divided into fifteen distance classes according to Sturge's rule (Scott 2009) to set the range of pairwise distance in each class (Legendre and Legendre 2012). Mantel correlation coefficients were calculated at each distance class and tested for significance with a permutation test (using 9999 permutations) based on a sequential Bonferroni correction ($\alpha = 0.05$; Legendre and Legendre 2012).

Next, we used a distance-based approach (Wang et al. 2013), where the dissimilarity is related to the spatial and environmental distance between lakes. Environmental distance was measured as Euclidean distance using all environmental variables standardized to have a mean of zero and a standard deviation of one. Bray–Curtis and Jaccard dissimilarities were regressed against spatial or environmental distances using a Gaussian generalized linear model. Significance was determined using Mantel tests (Spearman's correlation) with 9999 permutations (Legendre et al. 2005). Furthermore, partial Mantel tests were used to assess the relationship between beta diversity and spatial or environmental distance after controlling for environmental distance or spatial distance, and the significance was assessed using 9999 permutations. Subsequently, variation partitioning analysis was performed to quantify the contribution of environmental and spatial distance to the community dissimilarities (Martiny et al. 2006). These analyses were performed in the R environment with the Vegan package (Okasanen et al. 2012).

In addition, we estimated the degree of variation in spatial beta diversity that can be attributed to spatial patterns and the distance of environmental variables (Ion, pH, P, N and log-transformed temperature, I_m and DO). Before the analysis, the spatial pattern was decomposed to a set of variables using principal coordinates of neighbour matrices (PCNM; Borcard and Legendre 2002). For this step, a geographic distance matrix was produced from the locations of the lakes. This matrix was then truncated using a threshold distance equal to the maximum distance from the minimum spanning tree created from the inter-site distances, and all distances greater than this threshold were replaced with a value of four times the threshold distance. A principal coordinates analysis (PCoA) was performed on the truncated geographic distance

matrix, and all eigenfunctions with positive eigenvalues were retained. Subsequently, variation partitioning was performed using the 'varpart' function in the Vegan package to disentangle the contributions of spatial and environmental distance to the dissimilarities.

Furthermore, multiple regression on distance matrices (MRM, $nperm = 999$) (Lichstein 2007) was implemented using the ecodist package in R (Goslee and Urban 2007) to estimate the significant variables including environmental variables and PCNM eigenfunctions. To reduce the effect of spurious relationships between variables, we ran the MRM test, removed the non-significant variables, and then reran the tests until all variables were significant (Martiny et al. 2011). We report the final model results. The relative importance (lmg value) of these significant variables was calculated with the relaimpo package (Grömping 2006). All statistical analyses were conducted in R (R Core Team).

Results

Comparison of temporal and spatial beta diversity

In the case, we totally identified 214 species in these lakes (Supplementary material Appendix 1 Table A5). The mean richness was 35. The results of temporal and spatial beta diversity in the lakes showed that, for the Bray–Curtis dissimilarity index, the temporal beta diversity (dissimilarity between spring and summer, 0.79 ± 0.16) and the beta diversity among lakes in summer (0.76 ± 0.16) were the highest, followed by the beta diversity among lakes (0.59 ± 0.14) in spring. The beta diversities within lakes in spring (0.35 ± 0.12) and summer (0.38 ± 0.17) were lowest (HSD-test, $p < 0.05$), and there was no significant difference between them. For the Jaccard dissimilarity index, the pattern was similar to that of the Bray–Curtis index, except that the beta diversity within the lakes in summer was higher than in spring (Supplementary material Appendix 1 Fig. A1). Moreover, there was no relationship between the beta diversity among lakes in summer and spring ($p > 0.05$). In the heat map, the low values of spatial beta diversity indices mainly distributed along the top-right to bottom-left diagonals, and high values mainly distributed in the top-left and bottom-right corners in summer (Fig. 2). In spring, there was no obvious distribution patterns for these values. Furthermore, the values of the spatial beta diversity indices in summer were lower in the lakes with similar two-season temporal turnover (especially the turnover in the range of 0.4–0.7 and 0.9–1.0) than in those with very different two-season temporal turnover.

The temporal variation of beta diversity

The phytoplankton composition dynamically changed from spring to summer according to the Bray–Curtis and Jaccard dissimilarity values. The difference between the Bray–Curtis and Jaccard dissimilarity values decreased with increasing two-season temporal turnover (Supplementary material

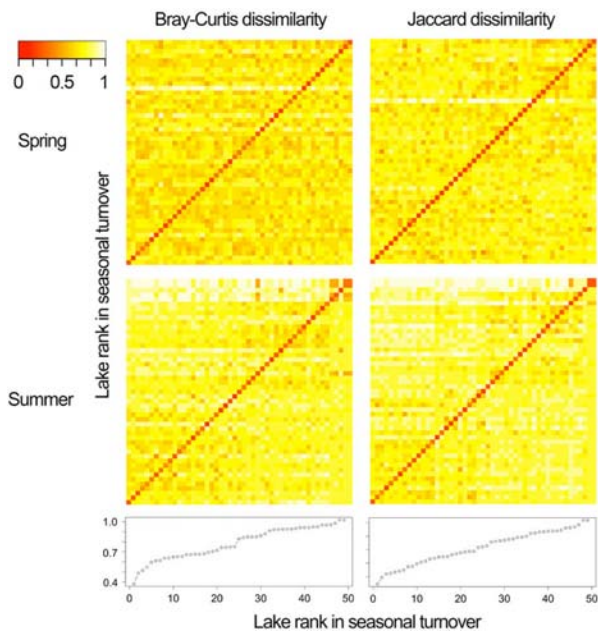


Figure 2. The heat maps of spatial beta diversity (Bray–Curtis and Jaccard dissimilarity) in spring and summer along the lake rank of increasing two-season temporal turnover. Hot colors represent high dissimilarity between two samples. Cool colors represent low dissimilarity between two samples. The red diagonals represent the dissimilarity of each sample compared to itself. The panels under the heat maps are two-season temporal turnover in different lakes ranked with increasing two-season temporal turnover.

Appendix 1 Fig. A2). The result of best approximating GLM showed that the averaged nitrogen level ($p=0.020$) and the CV value of DO ($p=0.013$) explained the variation in Bray–Curtis dissimilarity significantly, and pH ($p=0.052$) also slightly contributed to the variation (AIC=-51.4, $D^2=69.7\%$, Supplementary material Appendix 1 Table A6). The pH ($p=0.002$) and CV values of DO ($p=0.007$) were primary explanatory variables for the Jaccard dissimilarity (AIC=-79.7, $D^2=44.1\%$, Supplementary material Appendix 1 Table A6). The importance of pH was further emphasized in the results of BRT, in which it had the highest relative influence on the Bray–Curtis dissimilarity (22.0%), followed by the CV of temperature (14.1%), nitrogen level (9.6%), lake area (9.4%), the CV of pH (8.3%) and the other factors ($< 7\%$). The pH also had the highest relative influence on the Jaccard dissimilarity (37.4%), followed by the CV of temperature (11.4%), the CV of pH (9.6%), lake area (8.3%), the CV of pH (8.3%) and other factors ($< 5\%$) (Fig. 3). The temporal dissimilarity values of phytoplankton decreased with increasing pH and increased with increasing nitrogen level and the CV of temperature (Supplementary material Appendix 1 Fig. A3 and A4).

The spatial variation of beta diversity

Mantel's autocorrelogram of the environmental variables in spring showed that spatial autocorrelation was typically non-significant except in the first distance class for temperature

and nitrogen and in the first several classes for Ion and I_m . Mantel's autocorrelogram of the environmental variables in summer showed that spatial autocorrelations of temperature, nitrogen, phosphorus, dissolved oxygen and I_m were significant in the first through third distance classes. Ion and pH were significantly positively autocorrelated in the sites closer than 150 and 100 km, respectively. pH was negatively autocorrelated in the sites farther than 200 km (Supplementary material Appendix 1 Fig. A5 and A6). Mantel's autocorrelogram of community dissimilarities showed a decreased trend in Mantel correlation statistical values. Spatial autocorrelation in the two indices was not significant in the most distant class scale in spring except in the first distance class (ca 12 km), and it was positively autocorrelated in the sites closer than 100 km in summer (Supplementary material Appendix 1 Fig. A7). In other words, closer sites were more similar in phytoplankton composition in summer ($p < 0.05$). The spatial autocorrelogram indicated that phytoplankton compositions became less similar as geographical distances increased. In addition, Mantel's autocorrelogram of two-season temporal turnover showed that spatial autocorrelation was typically non-significant except in the first distance class (Supplementary material Appendix 1 Fig. A8).

Mantel tests showed that phytoplankton community dissimilarities based on both the Bray–Curtis and the Jaccard indices increased significantly with environmental and spatial distance in summer, and no significant relationship was found in spring (Fig. 4). The gradient magnitude of the Bray–Curtis dissimilarity increased from 0.81 (0.18–0.99) in spring to 0.96 (0.04–1.00) in summer, and that of the Jaccard dissimilarity increased from 0.76 (0.20–0.96) in spring to 1.00 (0.00–1.00) in summer. The maximum environmental distance (Euclidean distance) increased substantially from 4.18 in spring to 6.99 in summer (Fig. 4). In summer, the relationships between community dissimilarity and environmental distance were consistently weaker than those between community dissimilarity and spatial distance according to the r values (Table 1). Based on partial Mantel tests, the pure effects of environmental and spatial characteristics on community dissimilarities were also significant only in summer, and the pure spatial effects were more significant than environmental effects according to the r and p values (Table 1).

The spatial pattern was broken down into 21 PCNM eigenfunctions with positive eigenvalues, which were used for modelling community dissimilarities as well as environmental variables. The results of variation partitioning showed that environmental and spatial characteristics jointly explained more of the variation in the Bray–Curtis dissimilarity than of the Jaccard dissimilarity. While 27% of the variation of the Bray–Curtis dissimilarity in spring was spatially structured and explained by the PCNM eigenfunctions, 45% of that amount was explained by the environmental variables. The effect of the environment was highly spatialized (51% of environmental effect) (Fig. 5a). In addition, PCNM eigenfunctions and environmental variables explain 15% of the variation in the Jaccard dissimilarity in spring, respectively. 47% of spatial effect was also explained by the environmental

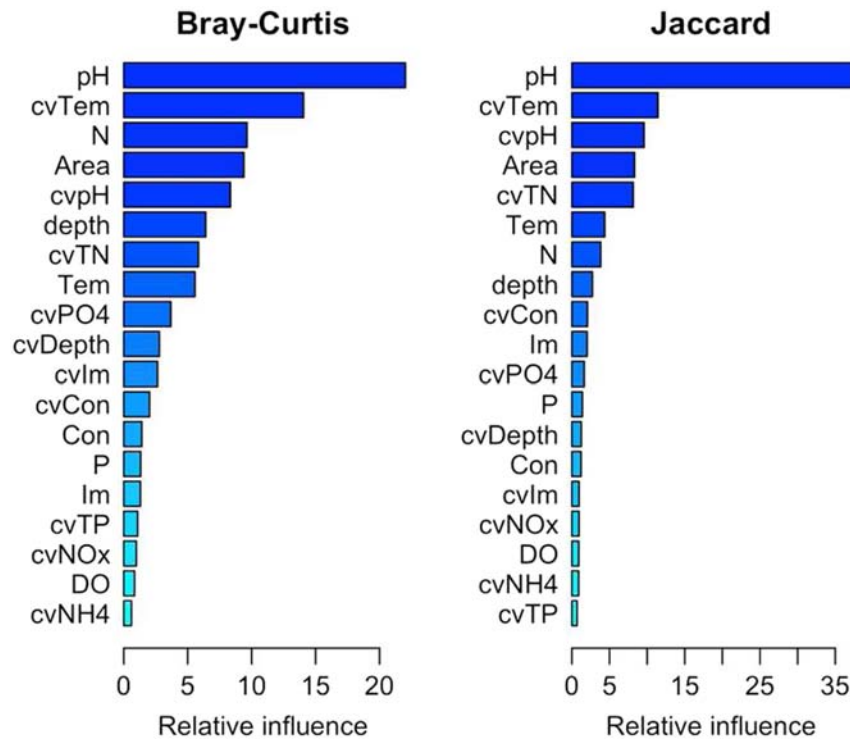


Figure 3. The environmental factors related to Bray–Curtis and Jaccard dissimilarity of phytoplankton between spring and summer (turn-over rate) identified with Boosted Regression Trees. The values of the relative contribution (%) of each variable for each dissimilarity metric can be found in parentheses on the x-axes of Supplementary material Appendix 1 Fig. A3 and A4. pH: the pH mean values in spring and summer; N: the principal component scores of nitrogen nutrients including the mean values of total nitrogen, dissolved total nitrogen, nitrite, nitrate and ammonia; Tem: mean values of the water temperature, Im: the mean values of the underwater available light; P: the principal components of phosphorus nutrients including the mean values of total phosphorus, dissolved total phosphorus, phosphate; DO: the mean values of the dissolved oxygen; Con: the mean values of conductivity; depth: the mean values of the depth; cvTem: the coefficient of variation (CV) of temperature between spring and summer; cvpH: the CV of pH; cvTN: the CV of total nitrogen; cvNOx: the CV of nitrite and nitrate; cvPO4: the CV of phosphate; cvIm: the CV of underwater available light; cvCon: the CV of conductivity; cvDepth: the CV of depth; cvNH4: the CV of ammonia; cvTP: the CV of total phosphorus.

variables, and 47% of environmental effect was spatialized (Fig. 5b).

In summer, the variation of Bray–Curtis dissimilarity was explained by PCNM eigenfunctions (44%) and environmental variables (37%). The explaining amount of the spatial and environmental variables was up to 55%, and the unexplained portion was approximately 45%. In addition, 60% of the explaining amount by PCNM eigenfunctions was explained by environmental variables. The effect of environmental variables on dissimilarity was spatialized (71% of environmental effect) (Fig. 5c). For the Jaccard dissimilarity in summer, spatial and environmental variables explained 32% and 31% of its variation, respectively. Finally, 82% of the explaining amount by PCNM eigenfunctions was also explained by environmental variables, and 86% of environmental effect was spatialized (Fig. 5d).

The results of MRM showed the significant variables that contribute to the variation in dissimilarity indices in spring and summer (Supplementary material Appendix 1 Table A7, ordination diagrams for the significant PCNM vectors were shown in Supplementary material Appendix 1

Fig. A9). In summer, the significant variables were P, I_m , PCNM1, PCNM2, and PCNM3 contributing to the variation of Bray–Curtis dissimilarity, and P, PCNM1, PCNM2, and PCNM3 for Jaccard dissimilarity. PCNM1 was mainly related to pH (74% of explained variation, Table 2). PCNM2 was related to Ion (62%, Table 2). PCNM3 was weakly related to water temperature (7%, Table 2). The spatial variables were more important than the environmental variables according to the regression coefficients and lmg values. In spring, N, P, PCNM2, PCNM3 and PCNM15 were significant variables determining the variation in the Bray–Curtis dissimilarity and P, I_m , and PCNM3 were significant variables for the variation of Jaccard dissimilarity. PCNM2 was mainly related to Ion (65%, Table 2). PCNM3 was mainly related to nitrogen level (12%, Table 2). PCNM15 was related to phosphorus level (13%, Table 2). Environmental variables were relatively important in the variation of dissimilarities compared with those in summer. In addition, all the PCNM eigenfunctions with relatively high importance were low order, which represented spatial structure at broader scales (Dray et al. 2006).

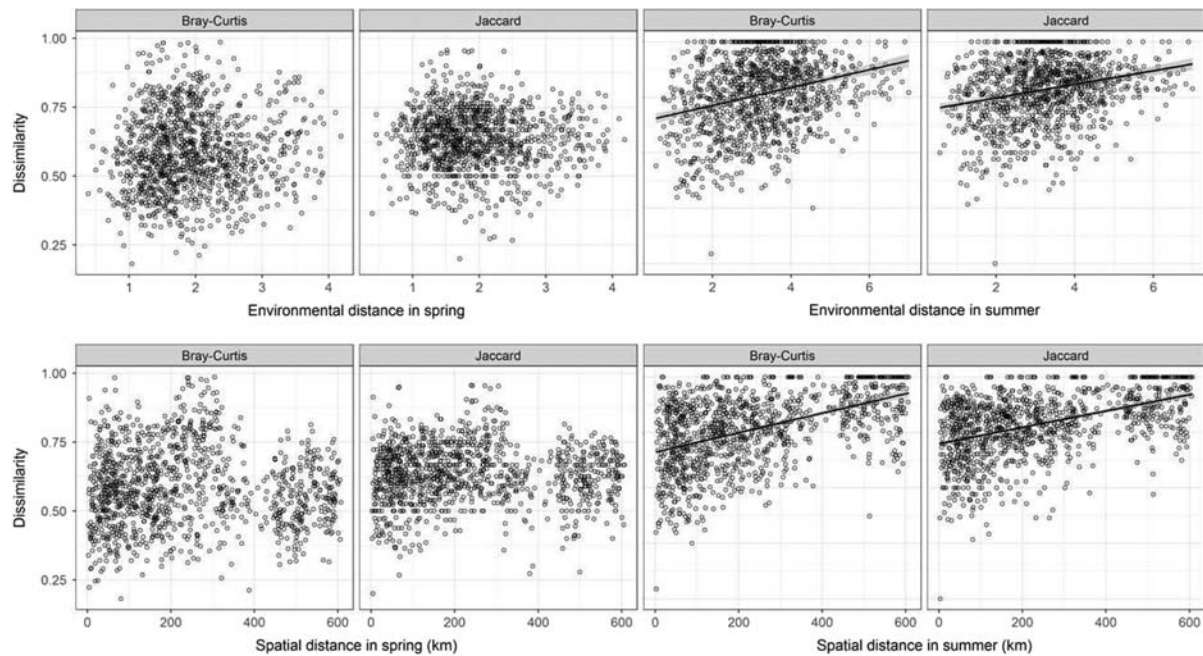


Figure 4. The relationship between beta diversity of phytoplankton (Bray–Curtis and Jaccard dissimilarity) among lakes and environmental and spatial distance. The trends along environmental distance were modeled with linear models. The significant trends ($p < 0.05$) were showed as solid line.

Discussion

Comparison of spatial and temporal beta diversity

Our study showed that beta diversity in summer (wet season) was significantly higher than that in spring (dry season) (Supplementary material Appendix 1 Fig. A1). In floodplain lakes, high environmental heterogeneity (differences in origin, morphometry, hydrology, and limnology) is expected to cause high beta diversity (Neiff 1996), and flood pulses have a homogenizing effect, increasing similarity between lakes (Thomaz et al. 2007). However, this effect was not found in the phytoplankton community in the investigated lakes, which was consistent with the results from the Araguaia River tropical floodplain lakes (Nabout et al. 2007). This finding might be due to the extensive sampling scale, in which the lakes keep relatively isolated. The rainfall events only partially homogenized the environmental heterogeneity

and were not sufficient to decrease the dissimilarity of the phytoplankton composition. The beta diversity within lakes was significantly lower than that among lakes. The connectivity of water body within lakes was obviously better than that among lakes, which might contribute to the high similarity of the phytoplankton composition within lakes. The data also indirectly confirmed the importance of lake isolation to the high beta diversity among lakes.

Explaining the temporal turnover

The temporal turnover varied among the investigated lakes in the study. According to the review by Rosenzweig (1995), the patterns in temporal turnover are mostly driven by the sampling effect at short timescales, and ecological or (especially) evolutionary factors do not have enough time to shape the assemblage. However, for short-lived organisms, the sampling effect may influence the turnover on a time scale

Table 1. Results of Mantel and partial Mantel tests for the correlation between phytoplankton community dissimilarity among lakes (Jaccard and Bray–Curtis) and spatial distance, and environmental distance (Euclidean) in each season. The significant Mantel and partial Mantel correlations were shown as bold.

Phytoplankton	Index	Environmental		Spatial		Environmental-spatial		Spatial-environmental	
		r	p	r	p	r	p	r	p
Spring	Bray–Curtis dissimilarity	0.098	0.074	0.034	0.268	0.093	0.090	0.006	0.432
	Jaccard dissimilarity	0.021	0.336	0.049	0.176	0.007	0.438	0.045	0.197
Summer	Bray–Curtis dissimilarity	0.310	< 0.001	0.448	< 0.001	0.120	0.023	0.359	< 0.001
	Jaccard dissimilarity	0.313	< 0.001	0.435	< 0.001	0.131	0.014	0.341	< 0.001

Environmental-spatial = the effects of environmental distance on community dissimilarity while controlling for spatial distance; spatial-environmental = the effects of spatial distance on community dissimilarity while controlling for environmental distance.

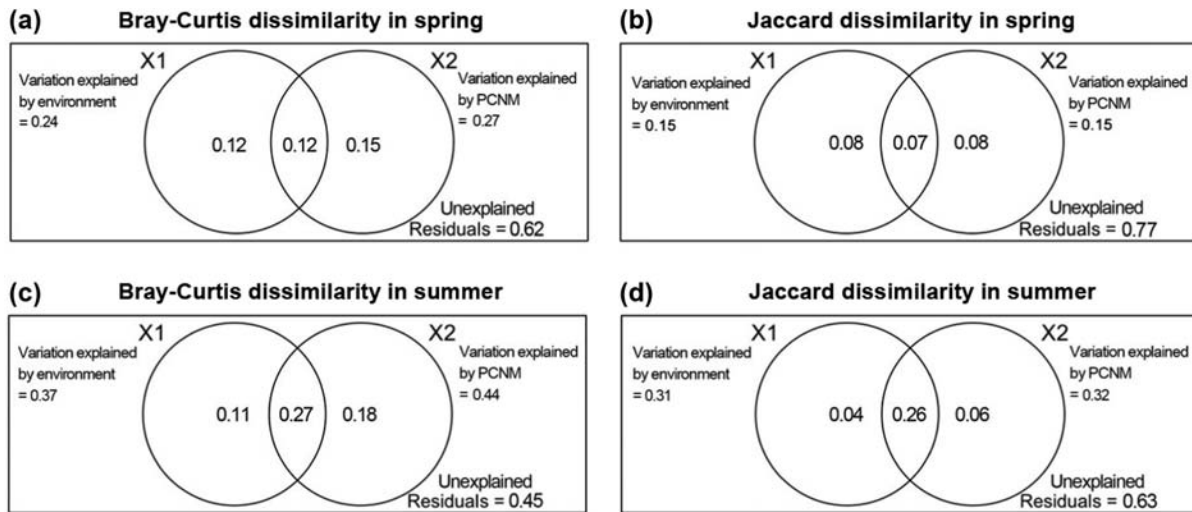


Figure 5. The Venn diagrams representing the partition of the variation Bray–Curtis and Jaccard dissimilarity in spring and summer between environmental variables (left circle, X1) and PCNM eigenfunctions (right circle, X2). Each box represents 100% of the variation in the corresponding response variable. The reported fractions are adjusted R².

of only days (Soininen 2010), and the temporal turnover of phytoplankton should be affected not only by sampling effect (sampling duration) but also by a number of ecological factors (ecosystem size, latitude gradient) (Korhonen et al. 2010). In this case, the investigated lakes are almost all located in the same latitude, and we also controlled the sampling interval of each lake and duration for each campaign at the almost same level. All synchronous investigating protocols effectively limited the sampling effect. Therefore, the ecological factors, including environmental variables and lake area, might be the primary explanatory variables. According to the results of GLM and BRT, the mean pH was the principal contributor to the variation of two-season temporal turnover of phytoplankton among the investigated lakes. In the low pH lakes, the turnover of phytoplankton was more dramatic than in the high pH lakes (Supplementary material Appendix 1 Fig. A3 and A4), which was consistent with the results of experimental acidification (Brettum 1996).

Table 2. Significant environmental variables related to the significant PCNM vectors in MRM analysis. Forward regression based on permutation procedure was used to select the environmental variables. Adj-R²=adjusted coefficient of determination. For the spatial patterns of each PCNM variable, see Supplementary material Appendix Fig. A6.

	Spatial vectors	Environmental variables	Adj-R ²	F	p
Spring	PCNM2	Ion	0.653	91.526	0.001
		P	0.065	11.819	0.003
	PCNM3	N	0.120	7.518	0.012
		DO	0.077	5.514	0.024
Summer	PCNM15	P	0.131	8.231	0.004
	PCNM1	pH	0.739	136.760	0.001
		DO	0.084	23.387	0.001
		P	0.034	12.080	0.001
	PCNM2	Ion	0.615	77.734	0.001
	PCNM3	Temperature	0.065	4.329	0.042

The importance of pH for diatom composition was also found in some streams (Teittinen et al. 2016, Wang et al. 2017). The two-season temporal turnover was also remarkably affected by the difference in temperature and pH between spring and summer, lake areas and nitrogen levels, and increased with these variables. In particular, the contribution of nitrogen level to beta diversity based on abundance data was higher than that to presence–absence data. These results suggested that decreasing pH, increasing CV of temperature and pH, and nitrogen enrichment will increase the two-season temporal turnover and the crisis of decreasing aquatic ecosystem stability (Haines 1981). The two-season temporal turnover rate also increased with the increase of lake area, which is consistent with the findings of Korhonen et al. (2010) and does not support the general species-time-area relationship (Adler et al. 2005).

Variation in explaining factors contribution to spatial beta diversity

It has been recognized that community similarity will decay (or dissimilarity will increase) with increasing geographical or environmental distance. However, there is no consensus on the distance decay relationship across organism groups, geographic gradients and environments (Soininen et al. 2007b). We found that the distance decay pattern of phytoplankton community similarity was not significant in spring, while it was significant in summer, which was confirmed by the results of the Mantel test. The non-significant pattern in spring was consistent with the findings of 18 lakes in Canada (Beisner et al. 2006) and in the floodplain lakes of Brazil (Nabout et al. 2009). The significant pattern in summer agreed with the studies reviewed by Soininen et al. (2007b) and recent studies in diatoms (Teittinen et al. 2016). The significant environmental distance decay in summer was also in agreement with the results of Vanormelingen et al. (2008).

The lack of consistency in distance decay pattern between spring and summer could be explained by comparing the effects of the environmental and spatial variables on beta diversity (based on abundance and presence–absence data). First, we differentiated the reasons of the variation from being non-significant in spring to being significant in summer. The variation in the geographical distance decay pattern could be attributed to the increase in the phytoplankton composition gradient due to a lack of variation in the geographical distance. The variation in the environmental distance decay pattern should be attributed to both the increasing environmental distance and the phytoplankton composition gradient. Based on the partial Mantel test (Table 1), the relationship between both the pure environmental and spatial distance and phytoplankton community dissimilarity became significant in summer. However, the pure effect of environmental distance on the two community dissimilarities was consistently weaker than that of spatial distance, suggesting that environmental filtering did not account for much of the among-site differences in species composition. This finding may be due to the relatively small ranges in the measured environmental variables or the fact that we missed some spatially structured abiotic or biotic factors that may have been influential to the distance decay patterns (Teittinen et al. 2016).

Furthermore, we analysed the changes in the proportion of explained variation from spring to summer. According to the results of variation partitioning, the proportions of explained variation in the Jaccard dissimilarity index and the Bray–Curtis dissimilarity index increased obviously, which indicated that the effect of environmental and spatial variables on the phytoplankton presence–absence and abundance composition significantly increased. The environment-controlled effect on the Bray–Curtis dissimilarity index increased from 24% in spring to 37% in summer, and that on the Jaccard dissimilarity index increased from 15% in spring to 31% in summer. John et al. (2007) suggested that the increasing environment-controlled effect might be attributed to the involvement of different environmental or biological variables between two analysis. However, in our case, we used the same variables to perform the analysis in spring and summer. The effect of difference in variables could be excluded, and the altered proportion should be from the variation of environment and species composition. From spring to summer, the variation of environmental variables, especially the spatially structured environmental variables (Fig. 5c, d), such as pH (Supplementary material Appendix 1 Fig. A6, Table 2), resulted in the changes (two-season temporal turnover) in species composition (Fig. 3), which increased the correlation between environmental distance and spatial dissimilarity of phytoplankton composition (Fig. 4) and indicated the increasing species sorting (Leibold et al. 2004, Langenheder et al. 2012). The pure spatially structured variation for the Jaccard dissimilarity index did not change significantly from spring to summer and that for the Bray–Curtis dissimilarity index increased from 15% in spring to 18%, which was a relatively slight variation. The pure spatially structured variation is generally

considered to be as neutral processes, such as dispersal, and the effect of unobserved variables, which are not correlated with the observed environmental variables but are spatially structured (Legendre et al. 2009, Legendre and Legendre 2012). We can expect an increased dispersal process among the floodplain lakes in the wet season. However, the dispersal process seems to be limited to lakes closer than approximately 100 km, which did not decrease the magnification of spatial beta diversity from spring to summer in the broader spatial scale (Supplementary material Appendix 1 Fig. A1). In addition, the unobserved environmental variables were the same in spring and summer. The variables should be spatially structured during the temporal turnover process if these variables contribute to the increase in the proportion. Overall, it is difficult to distinguish the contribution of dispersal from unobserved variables to the 3% variation at the current time.

Finally, as both environmental and spatial variables explained significant portions of the variation in phytoplankton dissimilarity based on abundance and presence–absence data, we further evaluated which of these environmental variables and spatial eigenfunctions were most important for each dissimilarity index in each season. We found that all the significant environmental variables are the primary variables for determining the growth rates and composition of phytoplankton, such as nitrogen, phosphorus and light (Reynolds 2006). The most important spatial eigenfunctions were the broader scale variables (Borcard and Legendre 2002, Dray et al. 2006). Furthermore, the relative importance of spatial eigenfunctions was similar to that of environmental variables for the two dissimilarity indices in spring. However, the spatial variables were of greater importance than environmental variables in summer, which confirmed the results of the partial Mantel tests.

Association of temporal and spatial beta diversity

The rates of temporal and spatial species turnover have been compared in different organisms, revealing that temporal and spatial species turnover are not independent but, rather, are associated (Adler et al. 2005, Hatosy et al. 2013). Our results further showed how the temporal and spatial species turnover in phytoplankton were associated. In spring, there was no relationship between the spatial beta diversity and two-season temporal turnover. After experiencing the two-season temporal turnover, the community assemblies in summer were more different in space than those in spring. In particular, in the lakes with low two-season temporal turnover (0.4–0.7 of dissimilarity), the phytoplankton composition was relative stable. During the two-season temporal turnover process, some spring species were replaced and some shifted in abundance, the ultimate composition of species in summer was approximately 50% similar to the spring population. In the lakes with high two-season temporal turnover (0.9–1.0 dissimilarity), almost all the species were replaced, and the new community assemblies presented partial similarity. The species composition in summer was quite different between the lakes

with low and high two-season temporal turnover. The spatial turnover rates were relatively low between the lakes with similar two-season temporal turnover. These results suggested that the spatial turnover of phytoplankton composition in summer was partially predetermined based on the variation in environmental variables and phytoplankton composition during the process of two-season temporal turnover. The jointly explained proportion of spatial dissimilarity in phytoplankton by environmental and spatial variables increased significantly from spring to summer, which indicated that the environmental variables and community composition varied towards the increasing correlation with spatial variables. For example, pH, the primary factor affecting two-season temporal turnover, was spatially structured accompanying with the temporal turnover process, and contributed to the spatial turnover of phytoplankton in summer.

In summary, our results demonstrate the association between the spatial and temporal beta diversity of phytoplankton in lakes, which spatial beta diversity was low in the lakes with similar temporal turnover. The association mainly was linked by the variation of environmental variables. The environmental variables controlling the temporal turnover were spatially structured over time, which further determine the spatial beta diversity. These results suggested that species sorting is the main assembly process during the temporal shift process. The contribution of dispersal process to spatial beta diversity was limited in the regional spatial scale and seasonal temporal scale. Thus, our study would be helpful to understanding the inconsistency in the explanation of spatial beta diversity by emphasizing the association between temporal and spatial turnover, and shows the need to integrate spatial and temporal process to achieve a more comprehensive understanding of phytoplankton dynamics.

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Supplementary material (Appendix ECOG-03340 at <www.ecography.org/appendix/ecog-03340>). Appendix 1.