Water quality drives the regional patterns of an algal metacommunity in interconnected lakes

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The metacommunity approach provides insights into how the biological communities are assembled along the environmental variations. The current study presents the importance of water quality on the metacommunity structure of algal communities in six river-connected lakes using long-term (8 years) monitoring datasets. Elements of metacommunity structure were analyzed to evaluate whether water quality structured the metacommunity across biogeographic regions in the riverine ecosystem. The algal community in all lakes was found to exhibit Clementsian or quasi-Clementsian structure properties such as significant turnover, grouped and species sorting indicating that the communities responded to the environmental gradient. Reciprocal averaging clearly classified the lakes into three clusters according to the geographical region in river flow (upstream, midstream, and downstream). The dispersal patterns of algal genera, including *Aulacoseira*, *Cyclotella*, *Stephanodiscus*, and *Chlamydomonas* across the regions also supported the spatial-based classification results. Although conductivity, chemical oxygen demand, and biological oxygen demand were found to be important variables (loading > |0.5|) of the entire algal community assembly, water temperature was a critical factor in water quality associated with community assembly in each geographical area. These results support the notion that the structure of algal communities is strongly associated with water quality, but the relative importance of variables in structuring algal communities differed by geological regions.

The metacommunity concept is an important approach for community ecology because it allows both local (e.g., nutrient, biotic interaction) and regional (e.g., dispersal) factors that contribute to community assembly to be identified1. Interest in community assembly is increasing because the local community is constantly reassembled in response to changes in the local environment, and the diversity and functionality of the community are controlled by the spatial distribution and interaction of species in the community2,3. To understand the role of the community assembly in the field, focusing on the community level (such as the metacommunity concept), rather than the species level, can provide new insights to associate the environmental factors with the community4.

Elements of metacommunity structure (EMS) is an useful tool that evaluates the assembly process of the community and determines the effects of environmental factors on the community assembly by assessing community patterns5,6. The EMS calculates three elements (coherence, turnover, and boundary clumping) to identify the idealized metacommunity pattern (e.g. checkerboard, random, evenly spaced, Gleasonian, or Clementsian pattern)7. The patterns facilitate the search for general rules determining metacommunity structure6. EMS approaches have been applied to terrestrial and aquatic systems for various organisms. Most studies on fish communities have been focused on freshwater ecosystems, and only a few studies have dealt with insects and zooplankton8–12. The algal community has largely been neglected when applying the EMS approach. Although the abundance of algal species is affected by water quality, such as phosphorus and nitrogen levels in the water, it has not been proven whether the assembling mechanism of algal communities is also affected by water quality.

The incidence of algal species is influenced by complex relationships between biological and environmental factors such as species dispersion, competition, water quality, and topography13,14. Although independent biological and environmental factors have been identified for the incidence of a single algal species in laboratory conditions, the study of factors affecting the algal community is limited to freshwater environment15. Relationships between these factors and the algal community have been found to vary across regions and spatial scales16.

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A few studies have researched on the algal community in the river-connected lakes, where is an aquatic system in which species disperse naturally and share many algal species. The structures of algal community are simultaneously determined by changes in environmental factors, even in the same regions\(^4\).\(^5\).

There are also reports of the importance of biotic interaction, such as increases in algal species, biotoxin production and changes in bacterial community in determination of algal community in previous studies\(^6\)\(^7\). As algal community change is a complex process determined by biotic and abiotic variables, understanding changes at the community level, rather than understanding individual algal species or population, can be important in responding to various environmental problems caused by algal community in the riverine ecosystem.

The goal of this study was to understand how environmental variables influenced algal community assembly in six river-connected lakes in South Korea. More specifically, we studied whether the algal metacommunity structure respond to water qualities in the river-connected lakes and how well can explained variability in the algal community-water quality relationships across the multiple lakes. The algal community was examined for the idealized metacommunity structures at each lake using long-term (8 years) monitoring datasets and how environmental factors (water qualities) in each of the EMS analyses were associated with algal community assembly in the lakes. Our present study provides new comparative information about the response of the algal community to local environmental factors, although the metacommunity structures are largely invariable at different biogeographic scales in river-connected lakes.

**Materials and methods**

**Algal community sampling and data acquisition.** Field samplings were performed at six lakes of the North Han River, Paldang (PD), Cheongpyeong (CP), Uiam (UM), Chuncheon (CC), Soyang (SY), and Hwacheon (HC) (Fig. 1). The North Han River (37°06′–38°06′N, 127°16′–127°49′E) located on the warm temperate zone of humid continental climate with mean annual temperature from 14.4 to 15.6 and total annual precipitation of 976–1581 mm. The monsoon season generally occurs between June to August, accounting for 73% of the annual precipitation. In detail, monthly water samples were collected using from 2008 to 2016 (except...
Algal diversity was highly influenced by hydrogeochemical factors. The diversity analysis was conducted using Random Forest classification and Canonical Correspondence Analysis (CCA). Six key indicator genera were selected based on the mean decrease Gini value, indicating the contribution of each variable to the overall metacommunity structure. The metacommunity structure was classified into three groups: upstream, middle, and downstream, based on the hierarchical clustering of site scores and water quality parameters. The results suggest that algal diversity is highly influenced by hydrogeochemical factors.
ranges of algal genera contributing most to these patterns (Fig. 3A). The Clementsian structure indicates that the community was assembled by the environmental gradient. Most individual lakes also exhibited the Clementsian structure as a best-fit pattern of metacommunity structure (Table 1, Fig S1). In contrast, PD exhibited a quasi-Clementsian structure due to its non-significance in turnover. Even though all lakes were analyzed by season, they were identified as Clementsian or quasi-Clementsian as the same as the abovementioned results (Table S1). These results support the algal communities were strongly associated with environmental factors regardless of variation in biogeographic units or seasons.

The Clementsian structure across all datasets had three compartment-by-site scores, which were determined by an EMS ordination procedure for ordering algal genera and sites (Fig. 3B). CP, UM, and CC, located...
midstream, were between 100 and 300 in the rank of site scores, and significantly different from upstream (SY and HC) and downstream (PD) (Kruskal Wallis test followed by Dunnett test, \( P < 0.05 \)). These results are differentiated from the beta-diversity results, which were divided into two groups. Although genera dispersed through river hydrologic connections and six lakes shared considerable numbers of genera, the occurrence of some genera was unique geographically. The indicator analysis confirmed that the abundances of key indicator genera were clearly varied depending on the location of river networks (Fig. 4). The distribution of *Aulacoseira*, *Cyclotella*, and *Stephanodiscus* increased proportionally from upstream to downstream, while *Chlamydomonas* decreased. The distribution of *Asterococcus* was unique to the upstream group. These results support the contention that metacommunity analysis is capable of analyzing the assembly of algal communities in detail at the community level as well as at the genus level. Lakes located downstream could be classified into two additional clusters (down: PD, and mid: CP, UM, and CC) according to the assembly characteristics.

**Environmental drivers.** The water quality of all lakes is summarized in Table S2. Although clear regional differences were not observed in algal diversity and EMS results, the water quality of the downstream (PD) and upstream (SY and HC) groups was statistically different, except for pH. The midstream (CP, UM, and CC) varied regionally within the range of water quality values between upstream and downstream, while COD and TN gradually increased from downstream to upstream. Seasonal or annual temperatures and precipitation, which are known to be important for algal growth, could not be seen as significant differences between lakes (Table S3 and S4).

To identify the environmental drivers of algal community, the association between water quality and site scores generated from EMS analysis was evaluated. The CCA axes were defined by reciprocal averaging, which is the same ordination method used to identify the main gradient of algal distribution in the EMS framework. Site score and CCA axes were highly correlated (Spearman’s \( \rho = 0.92, P < 0.001 \)), indicating that axes from both analyses represent variations in the same latent environmental gradients. The variation in temperature was most highly associated with the CCA1 axes along with the metacommunities structure in each location (Table 2), whereas temperature was not important in all lakes (loading = -0.061). Temperature was positively related to the EMS ordination axes of upstream (loading = 0.893), but negatively related to axes of downstream (loading = -0.801) and midstream (loading = -0.547). Moreover, other environmental variables which were highly associated with EMS ordination axes (i.e. loading < 0.500 or > 0.500) were significantly different by location. Conductivity and COD were the environmental variables highly associated with ordination axes for upstream, but pH or BOD were associated downstream and midstream. Compared to the individual analyses of lakes, these results tended to be similar (Table S5).
Discussion

We used EMS analysis combined with CCA to identify the relationship between water quality and assembly of algal communities in river-connected lakes. Most of the algal metacommunities for each lake follow a Clementsian structure, characterized by a continual change in algal composition at the genus level along environmental gradients. EMS produced three regional compartments (upstream, midstream, and downstream) by reciprocal averaging score. CCA revealed that three compartments were associated with different variables of water quality.

Table 2. Contribution of environmental variables in first axis of canonical correspondence analysis (CCA). Each value indicated loading value of first axis in CCA using corresponding algal community and environmental variables data according to groups. The bold values mean highly environmental variables highly correspond (< 0.5) to first axis of CCA. BOD, Biochemical oxygen demand; COD, Chemical oxygen demand; TN, Total nitrogen; NH₄⁺, Ammonium; TP, Total phosphorus; PO₄⁻, Phosphate (unit: mg/L).

| All | Up | Mid | Down |
|-----|----|-----|------|
| Temperature (℃) | − 0.061 | 0.893 | − 0.547 | − 0.801 |
| Conductivity (μS/cm) | 0.743 | 0.546 | 0.237 | 0.408 |
| pH | 0.354 | 0.308 | 0.413 | 0.625 |
| BOD | 0.57 | 0.138 | 0.598 | 0.659 |
| COD | 0.711 | 0.655 | 0.214 | 0.361 |
| TN | 0.355 | 0.245 | 0.193 | 0.168 |
| NH₄⁺ | 0.072 | 0.102 | 0.234 | 0.125 |
| TP | 0.189 | 0.219 | − 0.027 | − 0.095 |
| PO₄⁻ | 0.012 | 0.481 | − 0.155 | − 0.257 |

Figure 4. The abundance distribution of key indicator genera (A) Asterococcus, (B) Chlamydomonas, (C) Rhodomonas, (D) Aulacoseira, (E) Cyclotella and (F) Stephanodiscus. The genera with the top 10% mean decrease Gini value was selected as key indicator genera. Figures were created by R 4.0.2 (https://www.R-project.org) and the labels were adjusted using Adobe Photoshop CS6 13.0.6×64 (https://www.adobe.com/products/photoshop.html).
Therefore, algal communities along the river were generally assembled depending on the water quality of the region, even though algal communities were dispersed and genera were shared through hydrological connections.

The EMS and the conventional diversity approach were compared to understand the importance of biogeographical features on the algal community in river-connected lakes. The alpha diversity (richness) varied significantly depending on individual lakes (Fig. 2A), but the beta diversity and EMS approach could provide clear clustering by biogeographical features (Figs. 2B and 3B). Since beta diversity measures the changes in diversity of species from one site to another22, beta diversity should provide similar clustering results to the EMS approach. Nevertheless, it is worth noting that the number of regional partitions was different in the two approaches. Because EMS is based on site-by-species incidence, matrices consider whether the community responds to environmental gradients by measuring the proportional species turnover1, thus the EMS approach could provide discriminatory information compared to beta diversity.

Metacommunities in biogeographical regions or individual lakes were either Clementsian or quasi-Clementsian (Table 1 and S1). Clementsian structures arise when communities are actually changing consistently through groups of species that respond in a similar way to environmental gradients23. These results are consistent with the previous reported that metacommunity structure of diatoms showed Clementsian in river-connected mountain stream24. According to the river continuum concept (RCC), the physical properties of the riverine ecosystem were determined by flowing water from upstream to downstream. The physical properties changed the chemical system and biological communities in the responded or induced environmental gradient25. Synchronous species turnover is a phenomenon that occurs in ecosystems that share a significant proportion of species26. Clementsian structure is not rare, and they have already been reported for other aquatic organisms9,27. Most species found in riverine ecosystems are generally regulated by species dispersal and sorting11, so that the downstream sites shared high proportions of genera, while upstream sites showed significant differences in this study (Fig. 2B and Fig. S2).

The lakes located in midstream (CP, UM, and CC) shared highly similar distributions of genera but were significantly different from downstream (PD). PD, at the confluence of three rivers, is prone to dispersal of other genera from other rivers. These partially explain the quasi-Clementsian structure and distinct patterns compared to midstream.

One of the advantages of the EMS approach is identifying the environmental variables that influence community assembly by correlating reciprocal averaging and environmental variables. CCA, which is based on reciprocal averaging and multiple regression, was used to determine which environmental variables were associated with gradients along which metacommunities were structured22. The algal communities across broad geographical gradients showed consistent Clementsian structure. Clementsian structure emphasizes discrete ‘community types’ along ecological gradients, such that subgroups of species replace other subgroups in space23. Such variation also suggests that subgroups of species either respond similarly to environmental variation or are affected by similar historical effects such as drought, flood and other environmental perturbation that occurred before28. Conductivity, COD, and BOD were found to be the most important variables (Loading > |0.5|) of the entire algal community assembly. Conductivity is an indicator of overall variation in water chemistry, associating with levels of nutrients such as phosphate, nitrate and ammonia. COD and BOD is the most commonly used organic pollution indicator in water bodies29. The amount or type of organic matter has a significant effect on microbial community structure. In this study, we also found that beta diversity of algal community varied significantly depending on the lake specific concentration of COD (Fig. 2B and Table S2). The association between COD concentration and beta diversity suggests that COD make a significant contribution to the structure of algal communities. Previous reports also identify conductivity, COD, and BOD as the main drivers of the algal community composition14,30,31, indicating the importance of these factors as a driver of algal composition in the rivers. This contradicts, in part, the work of Padišak et al.32 who found TN and TP to be important drivers of functional groups in the river, while conductivity and COD were not significantly correlated with functional groups. However, untangling these communities and analyzing each lake type classified by the EMS approach revealed that the algal community could be distinguished by presenting a different relationship with temperature. The compositions of algal communities are remarkably influenced by temperature in a single lake15,33. Since lakes classified through the EMS approach had a similar algal composition (Figs. 2, 3), it is possible to explain that temperature acted as an important variable, unlike the results where the entire algal community is analyzed. Besides temperature, the variables strongly related to algal communities were conductivity, COD, and BOD, which concurs with the entire algal community analysis, but that importance differs depending on the location of the lake. Depending on land use and population density along the river, the types and concentrations of organic matter flowing into rivers vary, and the algal communities, which are strongly affected by differences in organic matter, are sensitive to regional differences28. This may explain why environmental variables were found to regionally influence the algal community assembly in river-connected lakes.

The relationship between the main structure of the entire metacommunity and the three lake types classified by biogeographical regions (up-, mid-, and downstream) reveals the role of spatially structured factors on algal composition. Previous research on lakes has shown that geographical distance strongly influences the algal community distribution16. The results of the current study also provide evidences that more than half of the genera are shared regardless of the lake location as species dispersal is a main driver of community assembly in a riverine ecosystem. For example, *Stephnaodiscus* and *Cyclotella*, were reported as ‘weedy’ genera that highly dispersed and their abundances were known to be affected by level of nutrients35–37. Our results also showed the abundance of *Stephnaodiscus* and *Cyclotella* were closely related to the concentration of TP and COD along the river (Fig. 4 and Table S2). The lake specific genus was also observed such as *Asterococcus* in upstream (HC and SY). This unique genus has known to be associated with the presence of freshwater organisms (e.g. fish and bivalve) as well as nutrients level35. The ecological and limnological properties of upstream may accommodate the unique genus. The uniqueness of the algal communities in each lake supports that the assembly of algal community is affected by species sorting. These results are consistent with previous findings that algal communities
are determined by species dispersal when habitats are shared in aquatic environments. The EMS approach is powerful in detecting compartmentalized structures according to spatial distribution and provides a fruitful interpretation of algal communities at the species and community levels.

Conclusion
River-connected lakes were used to address patterns and the underlying process of metacommunity organization of algal communities in freshwater. The approach based on metacommunity used ecological features, providing a fruitful starting point for more sophisticated analyses of variation in algal community structure. Our findings strongly suggest that algal metacommunities showed Clementsian structures over long spatial extents through the water body. The EMS approach combined with CCA facilitated the interpretation of the effect of environmental variables on the variation of the algal community assembly, and its effects across biogeographic regions in riverine ecosystem. In addition, the results also provide insight into biogeographical patterns of algal community structure in freshwater by comparing the beta diversity and EMS approach. This finding may also be applicable in aquatic ecosystems when studying local communities across large spatial scales.

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Author contributions

M.S.K.: Data curation, methodology, formal analysis, writing-original draft. S.H.A.: Data curation, formal analysis, validation, writing-original draft. I.J.J: Formal analysis, validation. T.K.L.: Conceptualization, supervision, writing-review and editing.

Competing interests

The authors declare no competing interests.

Additional information

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