Biodiversity increases integrated trophic position of macroinvertebrate communities in coastal food webs: testing the vertical diversity hypothesis

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Introduction

Study on relationships between biodiversity and ecosystem functioning (BEF) has attracted social as well as ecological interests because the biodiversity can affect ecosystem processes, especially productivity, which determines provisioning service for humanity. Because of difficulty in accurate measurement of the productivity, however, biomass has been traditionally used as its proxy to assess the BEF. Positive correlations between biodiversity and biomass-based productivity indices have been reported for many plants both in terrestrial and aquatic ecosystems. Such correlations are also true for consumers in terrestrial systems. In aquatic ecosystems, in contrast, the biomass-based BEF relationships are inconsistent among consumer communities: some are positive or convex and others non-significant (Waide et al. 1999).

Such an inconsistency can be explained by vertical diversity, i.e., diversity of trophic positions. In systems with multitrophic interactions, in theory, consumer biomass exponentially decreases with the increasing trophic position, while underlying more primary products. The use of the consumer biomass as a proxy of its productivity is, therefore, inappropriate to view the BEF relationships in complex multitrophic systems, as in the case of aquatic food webs. Considering the multitrophic and multifunctional nature of real food webs, Wang & Brose (2018) recently have constructed a theoretical model to test vertical diversity hypothesis (VDH), predicting that functional diversity across the TPs can enhance trophic biomass flows from basal resources to top predators.

In the multitrophic and multifunctional systems, one of better ways for full-understanding of the BEF is to estimate trophic biomass flows, using carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope analysis, which is a powerful tool for the food web analysis. Taking advantage of this analysis, Ishikawa et al. (2017) have proposed a novel index of food web properties, integrated trophic position (hereafter, *i*TP), defined as the summed TPs of all taxa in a focal food web weighed by the relative biomass of each taxon. The *i*TP can provide appropriate estimate for ecosystem functioning of vertical diversity because it indicates how many times consumer biomass experiences metabolic turnover as a whole of community within its food web. Here we test how the biodiversity can affect *i*TP for benthic macroinvertebrates in coastal waters of Lake Biwa, focusing on within-lake variation in coastal environments which can alter their local communities and thus food web properties.

Materials & Methods

We collected benthic macroinvertebrates and their basal food sources from 33 shallow coastal waters of Lake Biwa. For each sampling site, the macroinvertebrates were sorted, identified and counted to calculate Shannon-Wiener diversity index (*H*′). For each taxon at each site, its dry mass was measured to calculate its biomass per unit area. Individual taxa and their basal foods at each site were provided for $\delta^{13}C$ and $\delta^{15}N$ stable isotope analysis. After this analysis, we calculated *i*TP, according to Ishikawa et al. (2017).

Results & Discussion

A total of 27 benthic macroinvertebrate taxa were found in coastal waters of Lake Biwa. In the coastal communities, oligochaetes and chironomids are the most dominant taxa in numerical abundance, while gazing snails and a suspension-feeding bivalve were the most dominant in biomass abundance. Most taxa of grazers and deposit feeders located around TP=2, while carnivorous leeches and a freshwater prawn had the highest TP, regarded as top predators of macroinvertebrate communities.
The community biomass tended to increase significantly but weakly with macroinvertebrate diversity *H*’. By contrast, *i*TP of coastal macroinvertebrate communities markedly increased when they have the higher *H*’ (Fig. 1). The within-lake variation in their *i*TPs was better accounted for not only by the relative biomass abundance of top predators with highest TPs and lower numerical abundance but also by that of deposit feeders with lower TP and highest numerical abundance: the former can increase the relative contribution of predator TPs to the *i*TP, while the latter can have negative effects not only on the *i*TP but also on *H*’ because of its numerical abundance. This is possible explanation for such a correlational pattern of BEF found in the coastal macroinvertebrate communities, empirically supporting the VDH. Our study demonstrated that the *i*TP rather than the consumer community biomass can be a promising indicator for BEF related to vertical diversity in aquatic food webs with multitrophic interactions.

Keywords: Biodiversity-Ecosystem functioning, Food web, Integrated trophic position, Lake Biwa, Stable isotope analysis, Vertical diversity

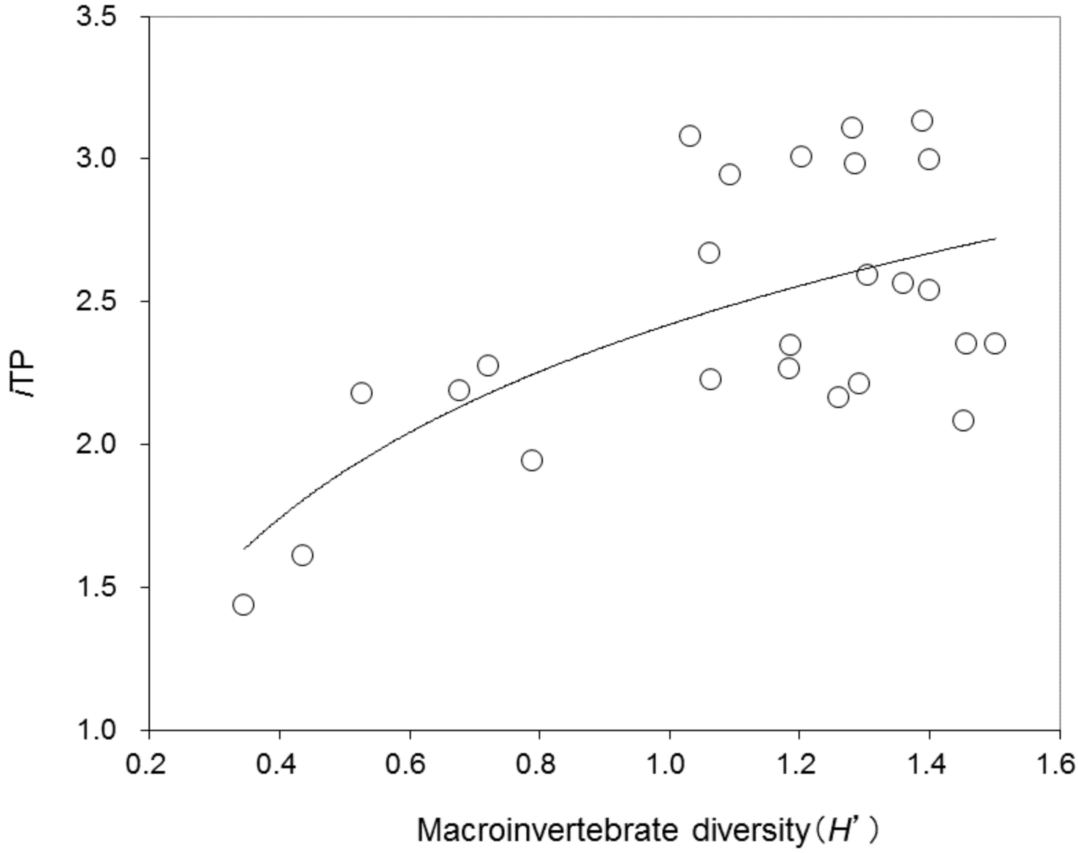

Fig. 1 A positive correlation between diversity (*H'*) and integrate trophic position (*i*TP) for benthic macroinvertebrate communities in coastal waters of Lake Biwa.