



Original research article

Environmental and spatial controls of macroinvertebrate functional assemblages in seagrass ecosystems along the Pacific coast of northern Japan



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ABSTRACT

The relative contributions of environmental and spatial processes in macroinvertebrate community structure (i.e., β -diversity) for three functional groups classified on the basis of dispersal ability and microhabitat selection (seagrass-associated [SA], drift-faunal [DF], and benthic-faunal [BF] groups) were examined in a seagrass ecosystem along the Sanriku coast of Japan. Variation partitioning was conducted to explain the environmental heterogeneity and spatial arrangement of local communities (i.e., degree of variation in the community) for each functional group. Processes determining community structure and metacommunity type differed among the functional groups. The SA group was under greater influence of environmental control, whereas the fractions of β -diversity in the DF and BF groups were explained by only spatial predictors. Thus, even if macroinvertebrate communities live in the same ecosystem, different mechanisms may determine the functional community structure, which depends on ecological traits such as dispersal ability and microhabitat. Ecological processes underlying community assembly differ among functional groups, indicating that the existence and/or dynamics of seagrass patches may affect the variation of faunal functions in an ecosystem.

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1. Introduction

In faunal communities inhabiting plant leaves and rhizomes (e.g., macro- and microinvertebrates), the quantity and/or quality of environmental variations (including microhabitat structures on living plants) as well as the dynamics of the spatial distribution pattern of the vegetation determine the dynamics of species diversity, functional diversity, and/or the composition (i.e., β -diversity) of the faunal communities (e.g. Wiens, 1976; Bascompte et al., 2003; Pandit et al., 2009). Especially, when vegetation has a heterogeneous and patchy distribution pattern, differences in ecological traits among faunal species, such as the capability of dispersing among patches and the degree of association with the vegetation as habitat (i.e., generalists vs. specialists), have strong effects on the relative contributions of environmental and spatial processes in determining faunal community structures (e.g. Hovel, 2003; Leibold et al., 2004; Boström et al., 2006). A faunal community living in such patchily distributed habitat has been given to the set of local communities linked by the dispersal of multiple

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potentially interacting species, that is, the metacommunity (e.g., Hubbell, 2001; Holyoak et al., 2005; Logue et al., 2011; Martiny et al., 2011; Chust et al., 2013a,b).

The relative importance of environmental and spatial processes in determining community structures has been evaluated in various local community forms patches in both terrestrial and coastal landscapes, such as ponds, lakes, streams, estuaries, marine pelagic areas, tide pools, and intertidal rocky shores (Cottenie, 2005; Mykrä et al., 2007; Lindo and Winchester, 2009; Pandit et al., 2009; Pinto and MacDougall, 2010; Fiorentino et al., 2012; Chust et al., 2013a). In these studies, the relative contributions of environmental and spatial processes were evaluated in each taxonomic group (e.g., phytoplankton, zooplankton, macro-algae, molluscs), because the relative importance of these two mechanisms varied depending on community characteristics such as ecological traits (e.g., dispersal ability, habitat type, life history, and trophic level). Therefore, each taxonomic group has been defined as an ecological trait group (Beisner et al., 2006; Okuda et al., 2010; Heino et al., 2012). However, mechanism of community assembly (e.g., metacommunity type) in case of evaluation in each taxonomic group are often difficult to explain, because formation of taxonomic groups results in interaction between phylogenetic and ecological responses in conflict between adaptive divergence and convergence (e.g. Wardle and Zackrisson, 2005; Wright et al., 2006; Hájek et al., 2011; De Bie et al., 2012; Brooks et al., 2012).

For example, the species-sorting (SS) + mass-effect (ME) metacommunity type is likely to emerge when using taxonomic groups (Pinto and MacDougall, 2010; Logue et al., 2011). This is because the differences in ecological traits among higher taxonomic groups has ensured evolutionarily sufficient variation in a heterogeneous environment with associated niche differentiation (SS) and/or source-sink population dynamics (ME) among the species in each taxonomic group of the communities (e.g., Holyoak et al., 2005; Pandit et al., 2009). Actually, Cottenie (2005) grouped four types of metacommunities in a meta-analysis by collecting 158 published datasets of higher taxonomic groups (e.g., phytoplankton, plants, zooplankton, macroinvertebrates, fishes, and birds) and found that most datasets (73%) were structured by a mixed SS+ME type, with only 8% showing the neutral model (NM) and/or patch dynamics (PD) type (NM/PD type). Many other studies focusing on higher taxonomic groups, such as birds, fishes (Logue et al., 2011; De Bie et al., 2012), diatoms, bryophytes, invertebrates (Mykrä et al., 2007; Hájek et al., 2011; De Bie et al., 2012; Heino et al., 2012; Chust et al., 2013b), macro-algae, sessile invertebrates, and mobile molluscs (Pandit et al., 2009; Okuda et al., 2010), also concluded that environmental heterogeneity related to niche explanations tended to be more important to community structure than spatial arrangement associated with dispersal processes (i.e., the SS+ME metacommunity type was most prevalent). However, these suggestions are being intensely debated in community ecology as considerable controversy surrounding neutral theory (i.e., NM/PD dynamics). Considering importance of the species assembly process in neutral theory, reports of only a limited fraction of the NM/PD dynamics in real metacommunities is incongruous against theoretical progression of neutral theory in community ecology (Hubbell, 2001; Logue et al., 2011; Martiny et al., 2011; Chust et al., 2013b). For example, it is possible that NM/PD dynamics (i.e., stochastic dynamics) of metacommunities may be contained within SS+ME dynamics (i.e., deterministic dynamics) in empirical studies.

Here, we expect that communities should be distinguished based on pure ecological traits, because ecological traits such as dispersal ability and/or microhabitat selection among species of the same taxonomic group are not necessarily similar and are sometimes quite different. In addition, there are numerous reports of similar ecological traits among species in different taxonomic groups due to evolutionary convergence (e.g., Wardle and Zackrisson, 2005; Wright et al., 2006; Hájek et al., 2011; De Bie et al., 2012; Brooks et al., 2012). Therefore, rather than classifying community members based on taxonomy, we focus on ecological traits and functions to classify specific ecological groups to evaluate the relative roles of environmental and spatial processes in determining community structure.

By using groups and diversity based on ecological traits, i.e., “functional group” and “functional diversity”, that is the value and range of functional traits and ecosystem function of organisms present in a community (e.g., Moullot et al., 2013; Storkey et al., 2013), can lead to elucidate community assembly rules and/or ecosystem processes (Yamada et al., 2011; Matsuzaki et al., 2013; Sasaki et al., 2014). Functional diversity was measured based on the values and range of ecological traits of species such as microhabitat, dispersal ability, habitat type, life history, and trophic level (e.g., Schleuter and Daufresne, 2010). Particularly in the measurement of functional groups, these ecological traits are used as criteria for classifying functional subgroups (e.g., Bellwood et al., 2004; Wardle and Zackrisson, 2005; Wright et al., 2006; Yamada et al., 2007a, 2010; Brooks et al., 2012). In this study, we focus on the functional groups when evaluating the relative roles of environmental and spatial factors in determining community structure. We expect that the relative importance of these two processes will differ depending on functional groups rather than taxonomic groups (e.g., Cottenie, 2005; Hájek et al., 2011; De Bie et al., 2012). If the relative importance of environmental and spatial processes differs among functional groups in determining community structure, then the mechanisms involved in community assembly also differ among functional groups. For example, the functional group community dynamics may be explained by the SS+ME type as well as other types (e.g., the NM/PD type). Furthermore, based on differences in community structure patterns among groups with different ecological functions, we can also discuss differences in the utilization of plant patches as habitat by each functional group, that is, the variation (i.e., dynamics) of functions.

Seagrass forms patches on the sandy bottom in shallow estuaries and marine coastal habitats (e.g. Vellend and Geber, 2005; Phinn et al., 2008; Yamakita et al., 2011). The presence of seagrass increases habitat complexity and provides living space, shelter, and feeding and nursery grounds for a greater variety and abundance of faunal species than in adjacent unvegetated habitats (Connolly and Hindell, 2006; Horinouchi, 2007). Thus, seagrass beds are highly productive near-shore habitats and are commonly regarded as distinct from adjacent ecosystems. Many faunal species move from one seagrass

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