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Spatial variation in community dynamics in intertidal sessile assemblages

Thesis
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Summary

One of the essential issue in ecology is to reveal the causes and consequences of temporal variability in assemblages sharing the same resources. In this study, I examined the spatial variation in community dynamics and its processes by analyzing decadal time series data of rocky intertidal sessile assemblages along the Pacific coast of eastern Hokkaido, Japan.

In chapter2, I examined two fundamental questions in community ecology regarding the relationship between seasonal changes in community structure and environmental gradient:

(i) How does the magnitude of seasonal changes in community structure vary along an environmental gradient? (ii) How do the processes driving seasonal changes in community structure vary along an environmental gradient? I found that the magnitude of seasonal changes in community structure was the largest at mid shore. The major processes driving seasonal changes in community structure changed vertically, reflecting the indirect influence of vertical distributions of species. An unexpected finding was that the magnitude of seasonal changes in community structure did not reflect the strength of seasonal variation in the physical environment.

In chapter 3, I examined the underlying mechanisms of compositional dynamics and its spatial variation by parameterizing discrete Lotka-Volterra model. First, to evaluate how the species compositions were regulated, I examined the strength of correlation between the compositional turnover and the temporal compositional variance, and the relative strengths of intra- versus interspecific density dependence. Then, I tested a hypothesis that the compositional turnover of community should

strongly depend on the magnitude of community-wide endogenous population fluctuations. Lastly, to reveal the cause of spatial variation in underlying mechanism of compositional dynamics of communities, I examined the relative contribution of demographic and environmental stochasticities in determining the magnitude of endogenous population fluctuations, then how those two stochasticities varied among species and sites. I found that compositional dynamics was under strong density-dependent processes. I also found that the spatial variation in the compositional dynamics largely depended on community-wide magnitude of endogenous population fluctuation, where most part is environmental stochasticity.

The implications of this study are twofold. First, the paths of the causal relationship from abiotic environment to community dynamics were different among time scales in rocky intertidal sessile assemblages. Second, our knowledge about spatial variation in community dynamics will be greatly improved by elucidation of the population response to physical environment.

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1 General introduction

One of the essential issues in ecology is to reveal the causes and consequences of temporal variability in assemblages sharing the same resource. This chapter addresses the background of community dynamics and this thesis. First, I briefly introduce rocky intertidal sessile assemblages, which are the study system of this thesis. Then, I review community dynamics in the aspects of seasonal and long-term dynamics of this system. Lastly, I outline the objectives of this thesis.

1.1 Intertidal sessile assemblages and its contributions to community ecology

Rocky intertidal sessile assemblages have contributed to offering general hypotheses which are applicable for various ecosystems, and to developing ecological theories as a model system for research in community ecology. In this section, I introduce their ecological features and review previous studies.

1.1.1 Sessile assemblages in intertidal rocky shore

Intertidal sessile assemblages are an ideal system to investigate community dynamics and its processes. Intertidal sessile assemblages consist of two contrasting functional groups: sessile invertebrates and algae (Raffaelli & Hawkins 1996). These organisms compete with each other for space which is a common resource for them (Branch1984). Their population size can be easily quantified as the proportion of occupied area (Roughgarden et al. 1985), i.e. coverage, which is increased by recruitment of larvae or propagules (Raimondi 1988; Kæhler & Williams 1997; Noda et al. 2003; Pineda et al. 2010), and by individual body growth (McCourt 1984; Sanford et al. 1994; Noda et al. 2003; Chomsky et al. 2004; Schneider 2008), and is decreased by intra- and inter-specific competition (Connell 1961a,b; Paine 1966; Lubchenco1980), by consumption (Paine 1966; Lubchenco 1980), and by physical disturbance (Sousa 1979a,b).

Rocky intertidal habitats are characterized by two dominant gradients in physical conditions. First, there is a notable vertical gradient of the physical environment due to the effects of tides and waves (Connell 1972; Raffaelli & Hawkins 1996). Toward the upper intertidal zone, where the immersion period is shorter than in the lower intertidal zone, the physical harshness is greater due to the longer period of exposure to high temperature and desiccation (Menge 2001; Helmuth 2001). Second, there is also a horizontal gradient of the physical environment due to the effects of wave exposure (Raffaelli & Hawkins 1996; Menge2001). Toward the tips of rocky headlands, the forces of waves and swells are greater.

1.1.2 Previous studies of rocky intertidal sessile assemblages

Research on intertidal sessile assemblages has a long history. From 1800s to mid 1900s, the subject of these studies was to understand the distribution patterns of sessile organisms (Audouin & Milne-Edwards 1832; Vaillant 1891; Baker 1909; Walton 1915; Colman 1933; Stephenson & Stephenson 1949; Lewis 1964; Stephenson 1972). These studies which were conducted using a qualitative approach, revealed that vertical patterns of sessile organisms along environmental gradient (i.e. zonation) were universal around the world. These patterns were thought to be determined by the physiological tolerance of each species directly (Engelmann 1884; Oltmann 1892; Colman 1933;

Doty1946; Evans1947).

After the mid 1900s, field manipulative experiments involving the transplantation or removal of focal organisms, had increased. Up to the 1980s, not only the physical environment (Connell 1961a; Foster 1971; Crisp 1974; Dayton 1975; Schonbeck & Norton 1978; Swinbanks 1982; Hawkins & Hartnoll 1985; Norton 1985) but also biotic processes, such as predation (Paine 1966; Paine 1969; Paine 1974; Southward & Southward 1978; Underwood 1980; Underwood & Jernakoff 1981; Ojeda & Santelice 1984; Hawkins & Jones1992) and competition, (Connell 1961a,b; Connell 1970; Hruby 1976; Lubchenco 1980; Schonbeck & Norton1980; Hawkins & Hartnoll 1985) were focused on as the factors affecting community structure. These studies suggested that the upper limitation of species distribution was mainly determined by the physical environment, whereas the lower limitation of species distribution was determined by species interactions, such as predation and competition.

In the 1990s, environmental factors relating primary productivity, such as nutrient concentration (Wootton et al. 1996; Menge et al. 1997; Worm et al. 2000; Noda et al. 2003; Masterson et al. 2008) and amount of phytoplankton (Menge et al. 1997; Noda et al. 2003), and biotic processes, such as recruitment of larvae and propagules (Gaines & Roughgarden 1985; Menge et al. 1985; Menge 1990; Menge 1992; Gaines & Bertness 1992; Delany et al. 2003; Noda et al. 2003; Forde & Raimondi 2004; Satheesh & Wesley 2008), and facilitation (Bertness & Callaway 1994; Bertness et al. 1999; Miyamoto & Noda 2004), were focused on as the factors affecting community structure. These studies revealed that the effects of abiotic and biotic factors on community structure were very complex and varied spatiotemporally, representing strong context dependency.

In the 2000s, much more attention was paid to how community structure and its determining factors, such as abiotic environment (Menge 2000; Nielsen et al. 2004; Menge et al. 2015) and biotic processes (Noda 2004; Lagos et al. 2005; Tsujino et al. 2010; Menge et al. 2015), varied with spatial scale. These studies found that in abiotic environments, recruitment processes and community structure varied at a scale of 10s of km, suggesting that abiotic and biotic processes varying at mesoscales can play an important role to determine community structure in rocky intertidal sessile assemblages.

1.2 Temporal variability of community structure in intertidal sessile assemblages

Elucidation of temporal variability of community structure (e.g. species richness, species composition, and total biomass) and its underlying mechanisms contribute to deepening our understanding of the essential issues in community ecology, such as species coexistence mechanisms, community stability, and ecosystem function. The studies on temporal variability of community structure were mainly conducted in two aspects: seasonal and long-term fluctuations.

1.2.1 Seasonal community dynamics

Understanding of the patterns and processes of seasonal changes in community structure contributes to increasing our knowledge of species coexistence through temporal niche differentiation among species in environments that flactuate cyclically. It also improves predictability of the response ecosystems have to changes in seasonal patterns of the environment caused by climate change. Although studies focusing on seasonal dynamics in rocky intertidal sessile assemblages have been reported since the 1950s, the seasonal changes in community structure have not been received attention prior to 1980s; alternatively, the major objective was to reveal the seasonal changes in effects of herbivores on sessile assemblages (Aleem 1950; Lawson 1957; Castenholz 1961; Lawson 1966; Haven 1973). These studies using observation (Lawson 1957; Lewis 1964) or manipulative experiments (Castenholz 1961; Haven 1973) reported that algal coverage was effected by herbivores but decreasing algal coverage during the harshest season was directly caused by mortality from physical stress.

After the 1980s, most studies aimed at how both species interaction other than grazing and the abiotic environment, contributed to seasonal dynamics in sessile assemblages. The major objective of early studies was to reveal the effects of herbivores on seasonal changes in sessile assemblages (Lubchenco & Cubit 1980; Underwood 1980; Cubit 1984; Underwood & Jernakoff 1984; Jernakoff 1985). These studies using manipulative experiments suggested that seasonal fluctuations in algal coverage was caused by seasonal variation in rates of algal growth and rates of algal loss by physical stress and herbivory (Underwood 1980; Underwood 1981; Cubit 1984). It was found that the effects of removing herbivores from algal assemblages were different from those caused by the physical environment, such as wave exposure and tidal height (Lubchenco & Cubit 1980; Underwood & Jernakoff 1984; Jernakoff 1985).

After the 1990s, the major objectives were to reveal not only the effects of consumption and the abiotic environment (Kæhler & Williams 1998; Jenkins et al. 2001; Kim

2001), but also the effects of biotic processes such as recruitment (Delany et al. 2003; Noda et al. 2003; Forde & Raimondi 2004; Satheesh & Wesley 2008) and interspecific competition (Noda et al. 2003). Various physical factors driving seasonal changes in sessile assemblages, such as light intensity (Clarke 1988; Wiencke 1996; Jenkins et al. 2001), water and air temperature (Jenkins et al. 2001; Noda et al. 2003), ice foot and ice scour (Kim2001), nutrient concentrations (Menge et al. 1997; Worm et al. 2000; Noda et al. 2003; Masterson et al. 2008), and phytoplankton (Menge et al. 1997; Noda et al. 2003), were given attention. These studies using field experimental approaches pointed out that variation in recruitment intensity during the recruitment season affected community structure, but its effect did not remain for a longer period (Forde & Raimondi 2004) because post-settlement mortality differed among species and sites (Delany et al. 2003). In addition, an experimental study demonstrated that seasonal changes in community structure was caused by recruitment of early-appearing species during seasons with more bare rock, and subsequently transition for late-appearing species (Noda et al. 2003).

After the mid 2000s, many studies focused on spatial variation in seasonal changes of sessile assemblages, especially the differences in those patterns among sites where the physical environment was distinct (Prathep 2005; Satheesh & Wesley 2008; Bertocci et al. 2012; Titlyanov et al. 2014). The studies using an observational approach reported that seasonal changes in various community properties such as abundance of each species (Bertocci et al. 2012), total biomass (Satheesh & Wesley 2008) and the number of species (Titlyanov et al. 2014) were different (Prathep 2005; Titlyanov et al. 2014), or similar (Bertocci et al. 2012) among sites where the physical environment such as wave exposure and tidal height was distinct.

In summary, the above findings suggest that seasonal changes and these spatial variations in sessile assemblages of intertidal rocky shores, were caused by seasonal fluctuations in the abiotic environment directly and indirectly through abiotic processes, and the spatial variations in these direct and indirect processes, respectively. Several questions, however, remain to be unanswered. First, quantitatively patterns of seasonal changes at the community level are not known because previous studies were conducted on seasonal changes in abundance of each species without time replicates. Second, driving processes of the quantitatively patterns of seasonal changes and spatial variations are not known at the community level.

1.2.2 Long-term community dynamics

The knowledge of community dynamics in long-term temporal scales, generally, contributes to understanding slow, rare, or complex changes in natural systems. Further, these processes (e.g. climate change, anthropogenic disturbance, and stochastic events) aid to our understanding of community dynamics which are not detectable on short-term scales. Up to the 1990s, the subject of studies was to reveal the inter-annual fluctuations in sessile organisms and these driving processes (Southward & Crisp 1954; Southward & Crisp 1956; Southward 1967; Boalch et al. 1974; Oliveira 1978; Southward 1991; Berchez & Oliveira 1992; Evans et al. 1993; Southward 1995a,b). These studies were conducted by observation of the coverage of each species in transects and quadrats. Major studies were inter-annual variations in four species of barnacles and driving factors (Southward & Crisp 1954; Southward & Crisp 1956; Southward 1967; Southward

1991). These studies suggested that the population fluctuations of these barnacles was derived from the variation in recruitment intensity through the fluctuation in water temperature.

After the mid 1990s, major attention was paid to prediction and understanding of ecological consequence of anthropogenic alternation of the environment, such as climate change (Barry et al. 1995; Sagarin et al. 1999; Franke et al. Gutow 2004; Rindi & Guiry 2004; Simkanin et al. 2005; Lima et al. 2007; Sagarin et al. 2008), anthropogenic disturbance, such as eutrophication and water pollution (Roos et al. 2003; Oliveira & Qi 2003), and the invasion of alien species (Robinson et al. 2007; Branch et al. 2008). Thus, there was an increase in studies which aimed to examine how rocky intertidal sessile assemblages changed between the present and decades ago. In most cases, these studies conducted by resurvey occurrence of species and the abundance of each species using the same methods in the same site, compared with the previous and resurvey data. For the aspect of impact of climate change on species distribution, species' ranges shifted northward and abundance of each species increased among southern species, whereas species' ranges and abundance was reduced in northern species, which related to the geographic ranges of each species. Many studies were concerned that these results were caused by increasing water temperatures with climate change (Barry et al. 1995; Ohgaki et al. 1999; Sagarin et al. 1999; Franke & Gutow 2004; Simkanin et al. 2005; Lima et al. 2007). On the aspect of impact of water pollution on species diversity, the number of species increased with eutrophication through bottom-up effects (Roos et al. 2003), whereas the number of species decreased and went extinct as a result of water pollution, and recovered by building a submarine sewage terminal (Oliveira &

Qi 2003). On the aspect of impact of biological invasion on endemic assemblages, alien mussel ameliorated the physical stress and modified habitat complexity, consequently abundance and the number of species in native species increased, this differed with tidal height (Robinson et al. 2007) and wave exposure (Branch et al. 2008).

In summary, the above findings suggest that long-term community dynamics in rocky intertidal sessile organisms were caused by fluctuation of the abiotic environment such as water temperature. Several questions, however, remain to be answered yet. First, the temporal pattern of community properties such as turnover and variation had not been quantitatively examined in previous studies. Second, the role of biotic processes on long-term community dynamics are almost un-understood, except for Dye (1998) which suggested that temporal variation in recruitment intensity affected long-term community dynamics.

1.3 Objectives of this thesis

In this study, I examined the spatial variation in community dynamics and its processes by analyzing decadal time series data of rocky intertidal sessile assemblages along the Pacific coast of eastern Hokkaido, Japan.

In chapter 2, I examine how seasonal changes in community structure vary along a vertical gradient. Specific questions are: (i) How does the magnitude of seasonal changes in community structure change vertically? (ii) How does the processes driving seasonal changes in community structure change vertically? I found that the magnitude of seasonal changes in community structure was the largest at mid shore. I also found that the major processes driving seasonal changes in community structure changed vertically, reflecting the indirect influence of vertical distributions of species.

In chapter 3, I examine the underlying mechanisms of compositional dynamics and its spatial variation by parameterizing a discrete Lotka-Volterra model. First, to evaluate how the species compositions were regulated, I examine the strength of correlation between the compositional turnover and the temporal compositional variance, and the relative strengths of intra- versus interspecific density dependence. Then, I test the hypothesis that the compositional turnover of communities should strongly depend on the magnitude of community-wide endogenous population fluctuations. Lastly, to reveal the cause of spatial variation in underlying mechanisms of compositional dynamics of communities, I examine the relative contribution of demographic and environmental stochasticities in determining the magnitude of endogenous population fluctuations, then how those two stochasticities varied among species and sites. I found that compositional dynamics was under strong density-dependent processes. I also found that the spatial variation in the compositional dynamics largely depended on the community-wide magnitude of endogenous population fluctuations, where most part is environmental stochasticity.

In chapter 4, I synthesize the results of previous chapters and provide future prospects for researchers in community ecology.

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2 Seasonal changes in community structure along a vertical gradient: patterns and processes in rocky intertidal sessile assemblages

2.1 Introduction

To improve our understanding of ecosystem, it is important to understand the seasonal changes in communities along environmental gradients. The pattern and processes of seasonal changes in community structure vary along environmental gradients because species composition (e.g., Austin 1985) and seasonal variability of the physical environment (e.g., Blume et al. 2002) vary along environmental gradients. Several fundamental questions, however, remain to be answered about the relationship between seasonal changes in community structure and environmental gradients. First, how does the magnitude of seasonal changes in community structure, in terms of the total variance in the species abundance among seasons (Legendre and Cáceres 2013), vary along an environmental gradient? It is widely assumed that the magnitude of seasonal changes in community structure should increase with the seasonal variation of the physical environment (Robles 1982; Titlyanov et al. 2014) because community dynamics is mainly driven by temporal changes in the physical environment (Elton 1958; Verhoef and Morin 2010). Second, how do the processes driving seasonal changes in community structure vary along an environmental gradient? The seasonal changes in community structure result from seasonal changes in population processes such as birth, mortality, and dispersal.

Rocky intertidal sessile assemblages are an ideal system for investigating the seasonal changes in community structure along an environmental gradient. Numerous studies have investigated the seasonality of the physical environment of rocky shores and the community structure of intertidal sessile assemblages, as well as their interrelationship. In intertidal habitats, the strength of larval and propagule fluxes (Raimondi 1988; Kaehler and Williams 1997; Noda et al. 2003; Pineda et al. 2010), body growth rate (McCourt 1984; Sanford et al. 1994; Noda et al. 2003; Chomsky et al. 2004; Schneider 2008; Bownes and McQuaid 2010), and predation pressure (Castenholz 1961; Lubchenco and Cubit 1980; Cubit 1984; Jernakoff 1985; Hori and Noda 2001; Sanford 2002; Noda et al. 2003) vary seasonally, reflecting the seasonality of physical environmental factors, such as temperature and moisture (Sutherland 1970; Helmuth and Hofmann 2001; Hori and Noda 2001; Noda et al. 2003; Schneider 2008). The seasonal variability of the physical environment increases with elevation (Bertness et al. 1999). In northern Pacific coast of North America, for example, intertidal species are exposed to high air temperature and desiccation at low tide in summer (Frank 1965; Sutherland 1970; Dayton 1971; Cubit 1984). There is also a notable vertical environmental gradient due to the effects of tides and waves in rocky intertidal habitats (Connell 1972; Raffaelli and Hawkins 1996). In the upper intertidal zone, where the immersion period is shorter than in the lower intertidal zone, the physical harshness is greater due to the longer period of exposure to high temperature and desiccation (Menge and Branch 2001; Helmuth and Hofmann 2001). In addition, the strength of larvae and propagule fluxes for sessile assemblages decreases in the upper intertidal zone (Raimondi 1988; Bownes and McQuaid 2006, 2009; Munroe and Noda 2009) because larvae and propagule are passively transported there by waves. On the other hand, in the lower intertidal zone, more species interactions occur and thus the predation pressure (Paine 1971; Menge 1978a, 1978b; Bazterrica et al. 2007; Rilov and Schiel 2011) and species competition (Connell 1961a, 1961b; Lubchenco 1980; Chapman 1990; Rius and McQuaid 2006) increase. Consequently, these direct and secondary effects result in vertical zonation, which is the distribution pattern of observable as successive bands of sessile species from the low shore to high shore (Lewis 1964; Dayton 1971; Stephenson and Stephenson 1972; Menge 1976).

In this study, I examined how seasonal changes in community structure vary along a vertical gradient in rocky intertidal sessile assemblages. Specific questions I addressed were: (i) How does the magnitude of seasonal changes in community structure change vertically? (ii) How do the processes driving seasonal changes in community structure change vertically? In intertidal rocky shores, the magnitude of seasonal changes in community structure is expected to increase with shore level because the seasonal variability of the physical environment increases with elevation (Bertness et al. 1999). In addition, the processes driving seasonal changes in community structure vary along the shore level.

2.2 Methods

2.2.1 Study area

The study area is located along the Pacific coast of eastern Hokkaido, Japan (Fig. 1). The area is within the subarctic zone and is impacted by the cold Oyashio current

(Briggs 1995; Asakura 2003; Alam et al. 2014); ice scour occurs once every few years (Alam et al. 2014). The maximum tidal amplitude of this area is roughly 160 cm (Alam and Noda 2016). Low tides, which increase environmental stress for intertidal sessile organisms such as that from high temperature and desiccation, occur during the day from late March to early September and during at night from late September to early March, so that the environmental stress is likely to be intense in summer and weak in winter (Fukaya et al. 2013).

2.2.2 Census design

A hierarchical sampling design (Noda 2004) was applied. I chose five shores (Mochirippu, 43° 1′ N, 145° 1′ E; Mabiro, 42° 59′ N, 144° 53′ E; Aikappu, 43° 1′ N, 144° 50′ E; Monshizu, 43° 2′ N, 144° 46′ E; and Nikomanai, 42° 56′ N, 144° 40′ E) separated by 10 - 24 km along the Pacific coast of eastern Hokkaido (Fig. 1). Within each shore, five permanent rectangular plots were established. Each plot was 50 cm wide by 100 cm high (vertical extent cover 63% of the maximum tidal amplitude of this area), and the mean tidal level corresponded to the vertical midpoint; thus the vertical position and vertical extent of plots can be regarded as the unified index of the vertical environmental gradient in the study area. I divided each plot vertically into four parts, height 1 (upper), height 2 (middle-upper), height 3 (middle-lower), and height 4 (lower), where the upper and lower parts correspond to marginal areas of intertidal sessile assemblages. Hereafter, I refer to the four subsections of a plot along the vertical gradient as "quadrats". In each quadrat, 50 grid points were placed on the rock surface at 5 cm intervals in both the vertical and horizontal direction, and the species occupying each grid point were identified and recorded. Censuses were carried out at each plot twice a year, in spring (April or May) and in autumn (October or November), from autumn of 2002 to autumn of 2014. All measurements were made at low tide.

2.2.3 Data analysis

Transition probability matrix model

Discrete-time Markov chain models are commonly used to quantify the processes driving community dynamics of sessile assemblages (e.g., Tanner et al. 1994; Hill et al. 2004). These models assume that the state of a point in space is given by one of a set of species or functional groups of species. Suppose that there are s possible states. Given a column state vector $\mathbf{x}_t = (x_1, x_2, \ldots, x_s)$ representing the relative frequency of each possible state in a community at time t, the model is defined by transition probability matrix $\mathbf{P}$ containing the conditional probabilities p_{ij} that a point in state j at time t will be in state i at time t+1:

$$\mathbf{x}_{(t+1)} = \mathbf{P}\mathbf{x}_{(t)},$$

where $\mathbf{P}$ is the column stochastic transition matrix (i.e., each column sums to 1). Using perturbation analysis, I can calculate the effect of changes in the elements on the state vector (Tanner et al. 1994; Caswell 2001; Hill et al. 2004).

Estimation of the transition probabilities and state vector

A total of 9 sessile animals and 45 algal species were recorded in the quadrats during

12 years of research. In this study, to reduce the transition matrices used in the models to a tractable size, I classified these benthic species into eight ecological states: (1 - 5) the five dominant species *Chthamalus dalli* Pilsbry (barnacle), *Corallina pilulifera* Postels et Ruprecht (crustose coralline algae), *Gloiopeltis furcata* Postels et Ruprecht (red algae), *Analipus japonicus* Harvey (brown algae), and *Chondrus yendoi* Yamada et Mikami in Mikami (red algae); (6) Annual species including *Neosiphonia yendoi* Segi (red algae), *Urospora penicilliformis* Roth (green algae), and *Cladophora opaca* Sakai(green algae); (7) other Perennial species including *Balanus glandula* Darwin (barnacle), *Hildenbrandia rivularis* Liebmann (red algae), and *Neorhodomela oregona* Doty (red algae); and (8) Bare rock. Here I defined the five dominant species as the five species most frequently observed (in raw total grid points) during the research, and others are classified into annual species or perennial species based on their life cycle.

To estimate transition probabilities and state vectors, I used a multistate dynamic occupancy model proposed by Fukaya and Royle (2013), in which the effect of observation errors on the estimation of transition probabilities and state vectors is taken into account. I obtained two transition probability matrices depicting the community transition from spring to autumn and from autumn to spring (the summer and winter transition probability matrices, $\mathbf{P}^{\text{summer}}$ and $\mathbf{P}^{\text{winter}}$, respectively) for each quadrat (Tables S1 and S2 in Appendix). Furthermore, I obtained two state vectors describing relative frequencies of each of the eight ecological states in spring and autumn (the spring and autumn state vectors, $\mathbf{x}^{\text{autumn}}$ and $\mathbf{x}^{\text{spring}}$, respectively) for each quadrat every year. The model was fitted to the data by using the Markov chain

Monte Carlo method run in JAGS [?] through the R2jags package for R (Plummer 2003). To ensure independence of the posterior probability on initial values, three independent iterations were executed. Estimates were obtained from 10,000 iterations after a burn-in of 5,000 iterations, thinning at intervals of 3. I used spatial medians of posterior samples as point estimates for transition probabilities and state vectors. By using these state vectors, I addressed the first question (described further below in *The magnitude of seasonal changes in community structure*). By using these transition probability matrices, I estimated the eigenvector sensitivities to examine the second question (described further in *The process driving seasonal changes in community structure*).

Magnitude of seasonal changes in community structure

I investigated how the magnitude of seasonal changes in community structure and seasonal dynamics of each ecological state vary vertically. First, I estimated the magnitude of seasonal changes in community structure. The magnitude of seasonal changes in community structure at height h, $SS_{\mathrm{total},h}$, was estimated as follows:

$$SS_{\mathrm{total},h} = \sum_i SS_{\mathrm{ecological\,state}\,i,h}, \tag{1}$$

where $SS_{\mathrm{ecological\ state}\,i,h}$ is the seasonal difference in relative frequencies of ecological state i at height h, which was obtained as the sum of squares in ANOVAs treating season as a fixed effect and year as a random effect. Cochran ' s C test was conducted prior to each ANOVA to test the assumption of homoscedasticity. When homoscedasticity was rejected, I used permutation ANOVA with 100,000 replicates instead of conventional ANOVA.

Then, to detect the ecological states exhibiting significant seasonal changes in relative frequencies at each height, I compared the mean value of relative frequencies of each ecological state at each height. If the results of Cochran ' s C test were significant, then I performed ANOVA treating season as a fixed effect and year as a random effect for each ecological state, otherwise I used permutation ANOVA with 100,000 replicates.

Finally, for those ecological states revealed to exhibit significant seasonal changes in relative frequencies at each height by ANOVA or permutation ANOVA, I examined the vertical pattern of the magnitude of seasonal changes in relative frequencies within the ecological state and qualitative pattern of the mean of relative frequencies within the ecological state. To identify how the magnitude of seasonal dynamics within ecological states varies vertically, I compared $SS_{\text{ecological state } i,\ h}$ in Eq(1). among heights. To examine whether the qualitative pattern of seasonality (i.e., the season with larger relative frequency) within an ecological state varies vertically, I compared the mean of relative frequencies within each ecological state among heights.

The processes driving seasonal changes in community structure

To evaluate the contribution of the seasonal change in transition probabilities among seasons to the seasonal change in the state vector, I applied a life table response experiment, which evaluates the effect of environmental or biological factors on changes in the vital rates at the population level (Caswell 2001). The seasonal change in the sate vector among seasons is approximated by

$$\mathbf{u}^{\text{autumn},n,h} - \mathbf{u}^{\text{spring, }n,\ h} \approx \sum_{ij}(p_{ij}^{(\text{summer, }n,\ h)} - p_{ij}^{(\text{winter, }n,\ h)})\frac{\partial \mathbf{u}^{(n,h)}}{\partial p_{ij}^{(n,h)}}\ |_{\mathbf{P}^{\dagger}} \tag{2}$$

where

$$\mathbf{P}^{\dagger} = (\mathbf{P}^{(\text{summer},n,h)} + \mathbf{P}^{(\text{winter},n,h)})/2.$$

Here, $\mathbf{u}^{(\text{autumn},n,h)}$ and $\mathbf{u}^{(\text{spring},n,h)}$ are dominant right eigenvectors of transition probability matrices $\mathbf{P}^{(\text{summer},n,h)}$ and $\mathbf{P}^{(\text{winter},n,h)}$, respectively, in quadrat n of height h. $p_{ij}^{(\text{summer},n,h)}$ and $p_{ij}^{(\text{winter},n,h)}$ are the elements of transition probability matrices $\mathbf{P}^{(summer,n,h)}$ and $\mathbf{P}^{(winter,n,h)}$, respectively, in quadrat n of height h. The transition probability matrices $\mathbf{P}^{(\text{summer},n,h)}$ and $\mathrm{P}^{(\text{winter},n,h)}$ were estimated as described above (see "*Estimation of the transition probabilities and state vectors*"). $\frac{\partial \mathbf{u}^{(n,h)}}{\partial p_{ij}^{(n,h)}}\ |_{\mathbf{P}^{\dagger}}$ represents the eigenvector sensitivity evaluated at $\mathbf{P}^{\dagger}$, which can be calculated from scaled eigenvector sensitivity analysis [**?**, **?**, **?**]; see "*Eigenvector sensitivity analysis*" in Appendix for details). The each term in the summation in Eq(2). can be rewritten as,

$$(p_{ij}^{(\text{summer},n,h)} - p_{ij}^{(\text{winter},n,h)})\frac{\partial \mathbf{u}^{(n,h)}}{\partial p_{ij}^{(n,h)}}\ |_{\mathbf{P}^{\dagger}} = (p_{ij}^{(\text{summer},n,h)} - p_{ij}^{(\text{winter},n,h)})\begin{pmatrix} \frac{\partial u_1^{(n,h)}}{\partial p_{ij}^{(n,h)}}\ |_{\mathbf{P}^{\dagger}} \\ \vdots \\ \frac{\partial u_i^{(n,h)}}{\partial p_{ij}^{(n,h)}}\ |_{\mathbf{P}^{\dagger}} \\ \vdots \\ \frac{\partial u_8^{(n,h)}}{\partial p_{ij}^{(n,h)}}\ |_{\mathbf{P}^{\dagger}} \end{pmatrix} = \begin{pmatrix} a_{1,ij}^{(n,h)} \\ \vdots \\ a_{i,ij}^{(n,h)} \\ \vdots \\ a_{8,ij}^{(n,h)} \end{pmatrix}.$$

The elements $a_{i,ij}^{(n,h)}$ mean the contributions of the seasonal change in transition probabilities (i.e., $p^{(\mathrm{summer},n,h)}$ minus $p^{(\mathrm{winter},n,h)}$) to the seasonal change in the state vector (i.e., $\mathbf{u}^{(\mathrm{autumn},n,h)}$ minus $\mathbf{u}^{(\mathrm{spring},n,h)}$).

The contributions $a_{i,ij}^{(n,h)}$ were classified into four ecological processes (Table 1): (1) recruitment, (2) disturbance, (3) persistence and (4) replacement. (1) For $i \neq 8$ (not " Bare rock "), recruitment element $a_{i,i8}^{(n,h)}$ corresponds to the contribution from Bare rock to species i. When $i = 1$ (*C. dalli*), for example, $a_{1,18}^{(n,h)}$ represents the contribution of the seasonal change in the transition probability that *C. dalli* occupies a previous unoccupied point (i.e., $p_{18}^{(\mathrm{summer},n,h)}$ minus $p_{18}^{(\mathrm{winter},n,h)}$) to the seasonal change in the relative frequencies of *C. dalli* (i.e., $u_1^{(\mathrm{autumn},n,h)}$ minus $u_1^{(\mathrm{autumn},n,h)}$; the first elements of $\mathbf{u}^{(\mathrm{autumn},n,h)}$ and $\mathbf{u}^{(\mathrm{spring},n,h)}$)(Table 1A). Recruitment occurs either by recruitment of larvae (or propagules) or individual growth from surrounding spaces, which could not be distinguished in this study. (2) For $i \neq 8$, disturbance element corresponds to the contribution from species i to Bare rock. When $i = 1$ (*C. dalli*), for example, $a_{i,8i}^{(n,h)}$ represents the contribution of the seasonal change in the transition probability that a point occupied by *C. dalli* at time t becomes Bare rock at t+1 (i.e., $p_{81}^{\mathrm{summer},n,h}$ minus $p_{81}^{\mathrm{winter},n,h}$) to the seasonal change in the relative frequencies of *C. dalli* (Table 1A). Disturbance occurs either by physical disturbance or biological processes such as predation, which could not be distinguished in this study. (3) For $i = 1$ to 8, persistence element $a_{i,ii}^{(n,h)}$ corresponds to the contribution from state i to itself. When $i = 1$ (*C. dalli*), for example, $a_{1,11}^{(n,h)}$ represents the contribution of the seasonal change in the transition probability that a point occupied by *C. dalli* at time t is still occupied by *C. dalli* at time t+1 (i.e., $p_{11}^{(\mathrm{summer},n,h)}$ minus $p_{11}^{(\mathrm{winter},n,h)}$) to the seasonal change in the relative frequencies of *C. dalli* (Table 1A). (4) For i, $j \neq 8$ and $i \neq j$, replacement elements $a_{i,ij}^{(n,h)}$ and $a_{i,ji}^{(n,h)}$ correspond to the contributions from species j to species i and from species i to species j, respectively. When $i = 1$ (*C. dalli*) and $j = 4$ (*A. japonicus*), for example, $a_{1,14}^{(n,h)}$ and $a_{1,41}^{(n,h)}$ represent the contribution of the seasonal change in the transition probabilities that a point occupied by *A. japonicus* at time t is occupied by *C. dalli* at time $t+1$ and a point occupied by *C. dalli* at time t is occupied by *A. japonicus* at time $t+1$ (i.e., $p_{14}^{(\mathrm{summer},n,h)}$ minus $p_{14}^{(\mathrm{winter},n,h)}$ and $p_{41}^{(\mathrm{summer},n,h)}$ minus $p_{41}^{(\mathrm{winter},n,h)}$) to the seasonal change in the relative frequencies of *C. dalli*, respectively (Table 1A). These two types of replacement occur by species competition, but are not the same process because the former increases species i and the latter decreases species i. Hereafter, I refer to the former as " replacement by " and the latter as " replacement of, " respectively. For $i = 8$ (" Bare rock "), I focused on the elements of recruitment, disturbance, and persistence (Table 1B) because replacement elements do not directly affect the seasonal increase and decrease of relative frequency on Bare rock. The absolute value of $a_{i,ij}^{(n,h)}$ means the magnitude of the contribution to seasonal changes in relative frequencies of each ecological state.

I investigated how dominant processes driving seasonal changes in community structure and seasonal dynamics of each ecological state vary vertically based on the contributions obtained by eigenvector sensitivity analysis. First, to detect the ecological states whose contribution to seasonal changes in relative frequencies were distinct among processes, I performed permutation ANOVA with 100,000 replicates treating process as a fixed effect. Then, for the statistically significant ecological states, significant differences among processes were assessed using a Wilcoxon rank sum test, with Bonferroni adjustment ($\alpha/10$) used to control for the familywise type I error rate. Finally, to determine the process driving seasonal changes in community structure at each height, I summed the processes driving seasonal population dynamics at each height.

All statistical analyses were executed with R 3.3.1 (R Development Core Team 2016). Cochran ' s *C* tests made use of the GAD package described by Sandrini-Neto and Camargo (2014). For permutation ANOVA and the Wilcoxon rank sum test, I made use of the lmPerm package described by Wheeler (2010) or exactRankTests package described by Hothorn and Hornik (2013), respectively. The eigenvector sensitivity analysis was numerically solved with Mathematica 10.2 (Wolfram Research, Champaign, IL, USA).

2.3 Results

The magnitude of seasonal changes in community structure exhibited a unimodal pattern along the vertical gradient (Table 2). The magnitude of seasonal changes in community structure was smallest at height 1 ($SS_{total,1} = 0.396$) and was largest at height 3 ($SS_{total,3} = 3.255$). The seasonal variation was similar at height 2 ($SS_{total,2} = 1.703$) and height 4 ($SS_{total,4} = 1.706$).

For those ecological states exhibiting significant seasonal changes in relative frequencies at each height, the qualitative pattern of seasonality (i.e., the season with larger relative frequency) within an ecological state differed among ecological states regardless of height (Fig. 2). No ecological state, however, reversed that pattern along the vertical gradient (Fig. 2). Annual species and Bare rock had larger relative frequencies in spring, whereas *C. dalli*, *C. pilulifera*, and perennial species had larger relative frequencies in autumn.

For those ecological states exhibiting significant seasonal change, the magnitude of seasonal dynamics varied vertically (Table 2). For *C. dalli*, the magnitude of seasonal change in relative frequency was similar at height 2 ($SS_{C.dalli,2} = 0.970$) and height 3 ($SS_{C.dalli,3} = 0.974$). For *C. pilulifera*, the magnitude of seasonal change in relative frequency was larger at height 4 ($SS_{C.pilulifera,4} = 0.300$) than at height 1 ($SS_{C.pilulifera,1} = 0.002$). For annual species, the magnitude of seasonal change in relative frequency was largest at height 1 ($SS_{\text{annualspecies},1} = 0.267$) and was smallest at height 3 ($SS_{\text{annualspecies},3} = 0.074$). For perennial species, the magnitude of seasonal change in relative frequency was larger at height 4 ($SS_{\text{perennialspecies},4} = 0.046$) than at height 2 ($SS_{\text{perennialspecies},2} = 0.004$). For Bare rock, the magnitude of seasonal change in relative frequency was largest at height 3 ($SS_{\text{Barerock},3} = 1.916$) and smallest at height 2 ($SS_{\text{Barerock},2} = 0.468$).

The dominant processes driving seasonal changes in community structure varied along the vertical gradient (Fig. 3). The seasonal changes of species group and Bare rock were driven by replacement and by persistence, respectively, at height 1; by recruitment, disturbance, and persistence and by colonization, respectively, at height 2; and by replacement and by recruitment and persistence, respectively, at height 3. At height 4, seasonal changes of species group were mainly driven by recruitment, disturbance, and persistence. For *C. dalli* and *G. furcata*, replacement also drove seasonal change. Seasonal change of Bare rock was driven by recruitment and persistence.

For each ecological state, the dominant processes driving seasonal change varied vertically (Fig. 3). For *C. dalli* and *G. furcata*, the processes driving seasonal population dynamics were replacement at heights 1 and 3; recruitment, disturbance, and persistence at height 2; and all processes at height 4. For *C. pilulifera* and *C. yendoi*, the processes driving seasonal population dynamics were replacement at heights 1, 2, and 3 and recruitment, disturbance, and persistence at height 4. For annual species, the process driving seasonal change was replacement at heights 1 and 3. For perennial species, the processes driving seasonal change were replacement at heights 1 and 3 and recruitment and persistence at height 2. For Bare rock, the processes driving seasonal change were persistence at height 2, recruitment at height 3, and recruitment and persistence at height 4.

2.4 Discussion

Pattern of the magnitude of seasonal changes in community structure

Although it has been widely assumed that the magnitude of seasonal changes in community structure should increase with the seasonal variation in the physical environment (Robles 1982; Titlyanov et al. 2014), our study demonstrated that the magnitude of seasonal change of rocky intertidal sessile assemblages in eastern Hokkaido did not asymptotically increase toward the upper shore, where seasonal variabilities in both temperature and desiccation stress are large (Menge and Branch 2001). This unexpected pattern might be explained by the hypothesis that sessile organisms living on the upper shore have a broad tolerance to environmental stress (Newell 1979; Norton 1985; Roberts et al. 1997), making them less sensitive to the large seasonal variation in physical stress. Species living on the upper shore are exposed to large environmental fluctuations at various time scales, including diel, seasonal, and interannual variations, and consequently have evolved tolerance for a broad range of environmental conditions. Indeed, several high-shore species such as *G. furcata* (Huan et al. 2014) and *Chthamalus stellatus* Poli (a closely related species of *C. dalli*) (Foster 1971), which did not show significant seasonal changes in population size in the present study, have high tolerance for heat and desiccation stresses. Like the rocky intertidal habitat, there is a positive covariance of amplitude among diel, seasonal, and interannual variations in several physical environmental factors in various habitats, such as temperature in mountains (Bird and Hodkinson 1999) and water temperature in rivers (Sinokrot and Stefan 1993). In such habitats, the magnitude of seasonal changes in community structure might not increase with the seasonal variation in the physical environment.

In general the magnitude of seasonal changes in community structure along an environmental gradient might be originated from changes in both species composition and intraspecific differences in the magnitude of seasonal population dynamics along an environmental gradient. In our study area which covered about 80% of entire vertical range of the intertidal zone, the magnitude of seasonal dynamics within an ecological state changed vertically even though the state vectors had the same ecological states among height. It may suggest that the vertical gradient of the magnitude of seasonal changes in community structure possibly originated from vertical changes in the magnitude of seasonal dynamics in intraspecies (Table 2). When determining the pattern of the magnitude of seasonal changes in community structure along an environmental gradient, the relative importance of the changes in community composition and changes in the magnitude of seasonal dynamics within species may depend on both the environmental range and spatial extent along the environmental gradient, and changes in community composition become more important as both ranges increase along the vertical gradient. This is because a wider environmental range ensures higher species turnover across the gradient, and a longer spatial extent of the environmental gradient inhibits dispersal across the gradient, which prevents species segregation along the gradient among species occupying different niche spaces. In regions where tidal amplitude is much larger than that in our study area, vertical changes in species composition should be more important in determining the pattern of the magnitude of changes in rocky intertidal sessile assemblages. Likewise, various habitats may have considerable differences in the environmental range and spatial extent within the environmental gradient, and these may be key properties for determining the magnitude of seasonal changes in community structure. On mountain slopes, the elevational extent of the slope from top to bottom and the degree of differences in temperature, humidity, and precipitation between both ends depend on the height of the mountain. Similarly, for rivers the degree of differences in water temperature and flow volume between the headwaters and river mouth depend on river size.

At height 3, where the magnitude of seasonal changes in community structure was largest, the seasonal change in community structure was mainly caused by seasonal changes in the relative frequency of Bare rock (Table 2), which increased during winter and decreased during summer (Fig. 2), suggesting that seasonal changes in community structure in the mid shore was dominated by the processes producing bare space, such as environmental stress (Sutherland 1970; Dayton 1971; Sousa 1979a; Seapy and Littler 1982), predation (Lubchenco and Cubit 1980; Cubit 1984; Jernakoff 1985), and physical disturbance (Hedgpeth 1957; Markham 1973; Sousa 1979b; Wethey 1979; Paine and Levin 1981; Taylor and Littler 1982). Among these processes, physical disturbance by ice scour matches the observed seasonality of bare space in our study. Indeed, pancake ice is ubiquitous in our study area (Y. Kanamori, personal observation), where ice scour occurs once every few years (Japan Meteorological Agency; http://www.jma.go.jp/jma/indexe.html).

Pattern of the processes driving seasonal changes in community structure

At the community level, the dominant processes driving seasonal changes in community structure did not show the vertical pattern relating to the notable environmental gradient (Fig. 3). On the other hand, at the species group level, the dominant processes driving seasonal dynamics were consistently different between the mode and the margins of their vertical distribution regardless of species group (Fig. 3). For species groups whose vertical mode of relative frequency was at height 2, *C. dalli* and *G. furcata*, and at height 4, *C. pilulifera* and *C. yendoi* (Fig. 2), recruitment, disturbance, and persistence drove seasonal change in relative frequency at the height of their vertical mode, whereas replacement was the driver at other heights (Fig. 3). These results at the community and species group level suggest that the vertical change in seasonal changes in community structure more strongly reflects the indirect influence that vertical changes in the physical environment have on the vertical distribution of species (Raffaelli and Hawkins 1996) than the direct effect caused by vertical differences in the physical environment (Connell 1972; Raffaelli and Hawkins 1996). Thus, the change in processes driving seasonal dynamics corresponding to the vertical distribution of species is important for predicting the process driving seasonal changes in community structure along an environmental gradient.

Utility of the transition probability matrix model

I evaluated the relative importance of processes driving seasonal changes in community structure along a vertical gradient by using eigenvector sensitivity analysis for transition probability matrices. This approach is useful for linking the changes in community structure to the processes underlying these changes and comparing the relative importance of these processes. This model could also be applied to an experimental approach (Paine 1976) and comparative experimental approach (Menge et al. 2002). In addition, this approach is the best way to compare communities with distinct species composition because it considers differences in the variability between elements in transition probability matrix, that is, transition probabilities (Horvitz et al. 1997; Caswell 2001).

Conclusion

The present study revealed that the magnitude of seasonal changes in community structure in rocky intertidal sessile assemblages was largest at mid shore. The major processes driving seasonal changes in community structure changed vertically, reflecting the indirect influence of the vertical change in the physical environment on the vertical distribution of species. An unexpected finding was that the magnitude of seasonal changes in community structure did not reflect the strength of seasonal variation in the physical environment. One hypothesis to explain this is that sessile organisms living on the high shore have a broad range of tolerance to environmental stress because they are exposed to large environmental fluctuations at various time scales, including diel, seasonal, and interannual variations, so that they are less sensitive to the large seasonal variation in physical stress.

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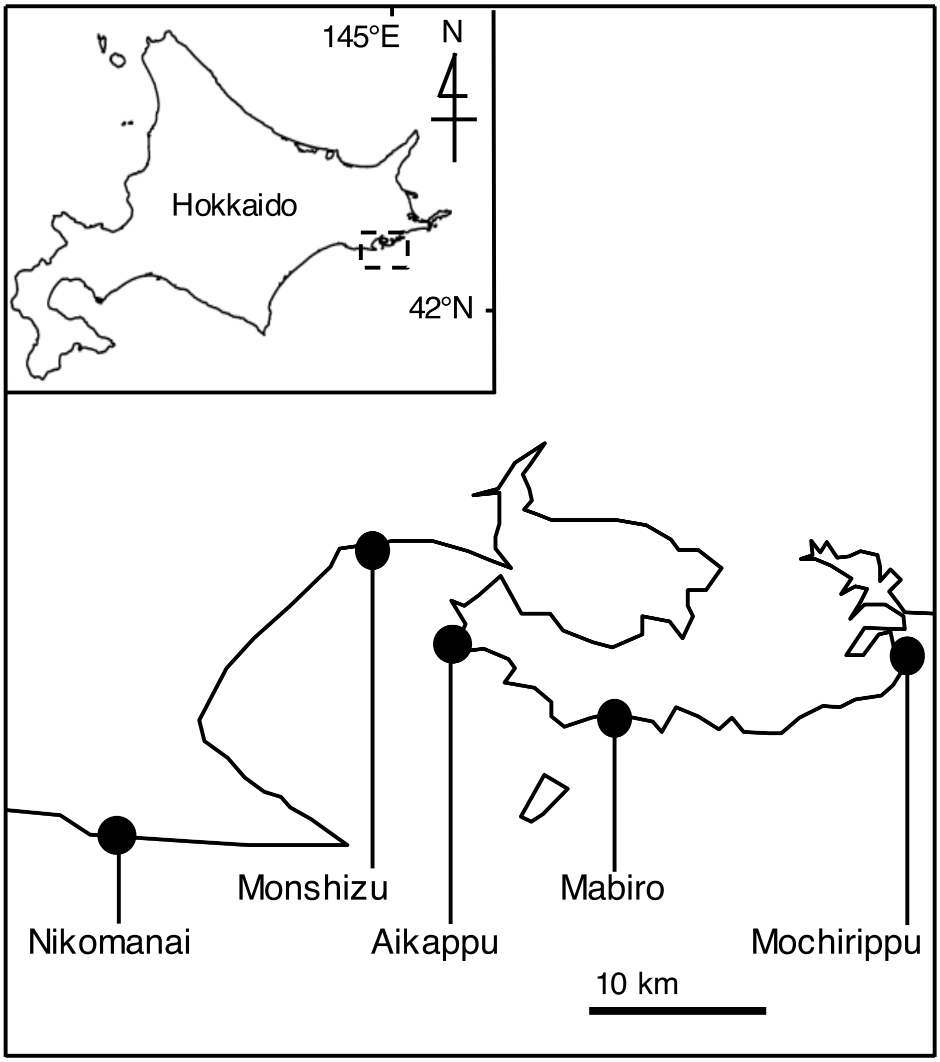

Fig. 1: Study site location. Five shores were chosen along the Pacific coast of eastern Hokkaido, Japan

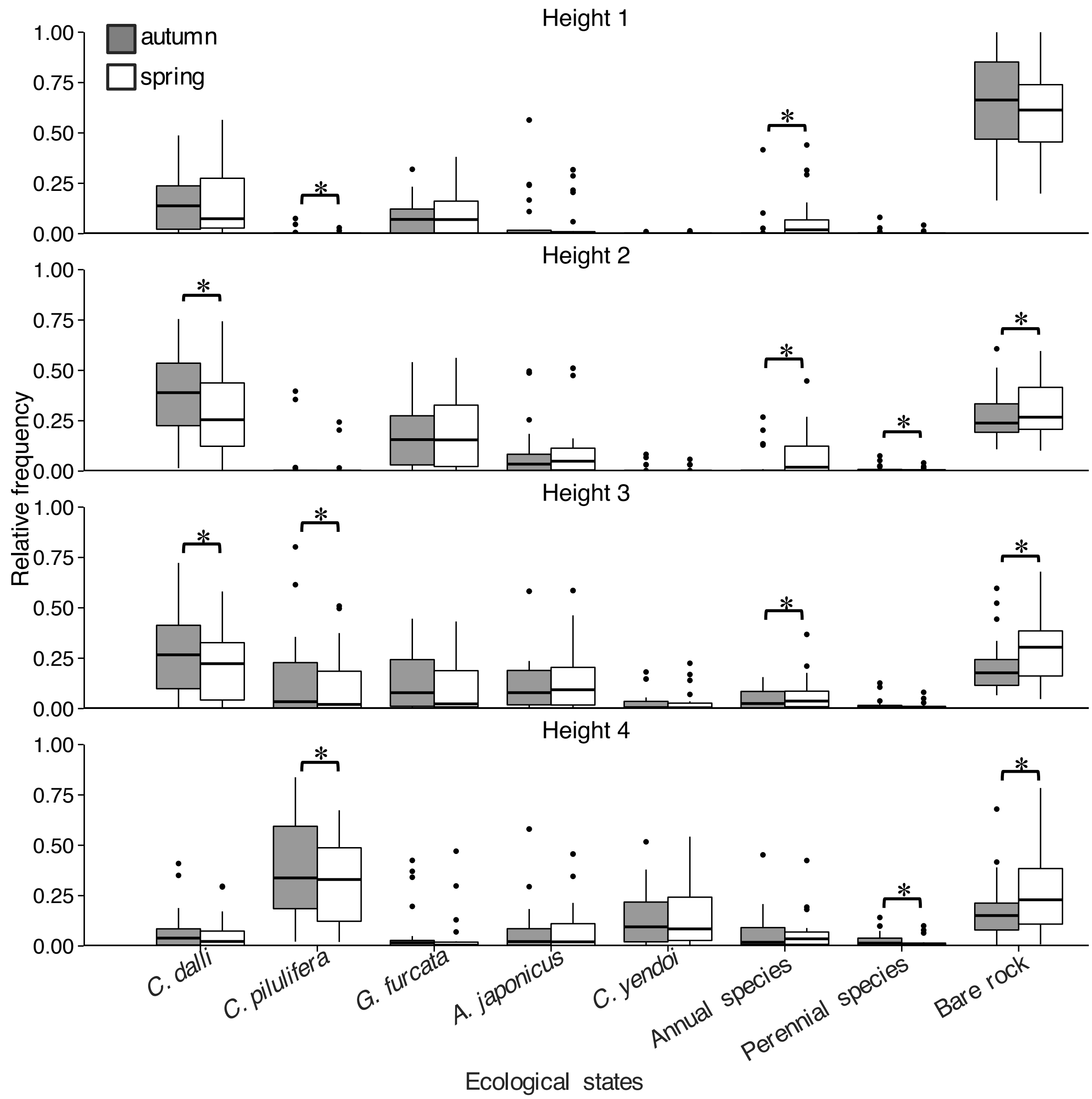

Fig. 2: Relative frequencies (mean±SE) of the eight ecological states (*Chthamalus dalli*, *Corallina pilulifera*, *Gloiopeltis furcata*, *Analipus japonicus*, *Chondrus yendoi*, annual species, other perennial species, and Bare rock) in spring and autumn at heights 1, 2, 3, and 4. Significant differences between the two seasons are denoted by an asterisk (*P $<$ 0.05), which corresponds to the data presented in Table 1

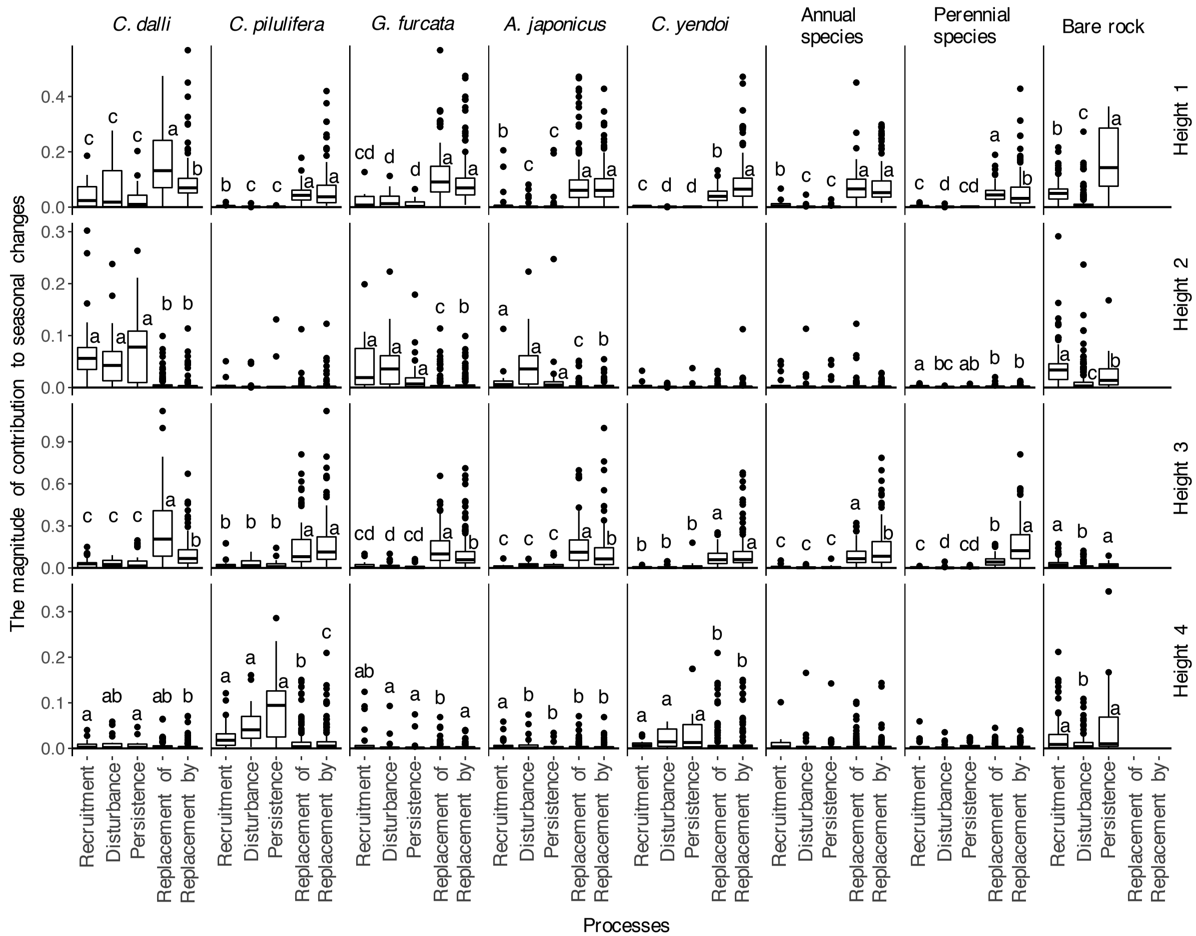

Fig. 3: Disturbance of the magnitude of the contribution to seasonal change in relative frequencies for each ecological state at heights 1, 2, 3, and 4. The magnitude of the contribution to seasonal changes in relative frequencies was estimated as the absolute value of $a^{(n,h)}{}_{i,ij}$ obtained from eigenvector sensitivity analysis. Box-and-whisker plots show the median (horizontal bold line inside the box), interquartile range (box), range (whiskers), and outliers (circles). Different letters denote significant differences among processes within an ecological state at each hright. The processes making the largest contribution in each ecological state

Table 1: Examples of the contributions at quadrat 1 of the Aikappu shore at height 2 for (A) *Chthamalus dalli* and (B) Bare rock

	C. dalli	*C. pilulifera*	*G. furcata*	*A. japonicus*	*C. yendoi*	Annual species	Perennial species	Bare rock
(A) *C. dalli*								
C. dalli	**-0.039**	**-0.001**	**-0.019**	**-0.008**	**-0.000**	**0.001**	**0.000**	-0.134*
C. pilulifera	-0.004	0.001	-0.002	-0.008	-0.000	0.001	-0.000	0.000
G. furcata	0.020	0.000	0.001	0.006	0.000	-0.003	0.000	-0.052
A. japonicus	0.008	0.002	-0.067	-0.070	-0.000	0.001	-0.000	0.044
C. yendoi	0.000	0.000	0.000	-0.000	-0.000	-0.000	-0.000	0.000
Annual species	-0.005	0.001	-0.002	0.001	0.000	-0.001	0.000	-0.002
Perennial species	0.000	0.000	0.000	-0.000	-0.000	0.000	0.000	0.000
Bare rock	***0.037***	-0.002	-0.157	-0.103	-0.000	0.000	-0.000	-0.260
(B) bare rock								
C. dalli	0.068	0.002	0.038	0.014	0.000	-0.002	-0.000	0.132*
C. pilulifera	-0.001	-0.000	0.000	0.001	0.000	-0.000	0.000	0.000*
G. furcata	0.020	-0.000	-0.000	-0.003	-0.000	0.001	-0.000	0.023*
A. japonicus	0.014	0.002	-0.079	-0.060	-0.000	0.001	-0.000	0.054*
C. yendoi	-0.001	-0.000	-0.000	-0.000	0.000	0.000	0.000	0.001
Annual species	0.005	-0.001	0.002	-0.001	-0.000	0.001	-0.000	0.005*
Perennial species	-0.001	-0.000	-0.000	-0.000	0.000	0.000	-0.000	0.001*
Bare rock	***-0.000***	***-0.000***	***-0.030***	***-0.037***	***-0.000***	***0.000***	***-0.000***	***0.019***

Table 2: Results of ANOVAs and permutation ANOVAs (100 000) for the differences in relative frequencies between seasons of the eight ecological states, with season as a fixed effect and year as a random effect

	C. dalli				*C. pilulifera*				*G. furcata*				*A. japonicus*			
species	*df*	SS	*F*	*P*	*df*	SS	*F*	*P*	*df*	SS	*F*	*P*	*df*	SS	*F*	*P*
Height 1																
season	1	0.026	0.762	0.38	1	0.002		**0.02**	1	0.014	0.36	1	0.066		0.12	
year	11	1.105			11	0.005			11	0.308			11	0.626		
residual	587	20.271			587	0.190			587	10.091			587	16.525		
Cochran's C test				0.65				<0.01				<0.01				<0.01
Height 2																
season	1	0.970	15.230	<**0.01**	1	0.034		0.09	1	0.025		0.46	1	0.001	0.014	0.91
year	11	1.616			11	0.144			11	1.115			11	0.764		
residual	587	37.450			587	6.773			587	23.041			587	21.174		
Cochran's C test				0.60				<0.01				<0.01				0.83
Height 3																
season	1	0.974		<**0.01**	1	0.185		**0.04**	1	0.081	2.869	0.009	1	0.018		0.49
year	11	1.510			11	0.382			11	0.327			11	0.574		
residual	587	34.466			587	25.967			587	16.604			587	22.017		
Cochran's C test				<0.01				<0.01				0.80				0.01
Height 4																
season	1	0.039		0.10	1	0.300	4.589	**0.03**	1	0.057		0.07	1	0.007		0.6
year	11	0.155			11	0.854			11	0.025			11	0.064		
residual	587	8.344			587	38.080			587	9.665			587	16.629		
Cochran's C test				<0.01				0.09				0.02				0.02

Table 2: Continued

species	*C. yendoi*				Annual species				Perennial species				bare rock				
	df	SS	*F*	*P*	*df*	SS	*F*	*P*	*df*	SS	*F*	*P*	*df*	SS	*F*	*P*	SS_{total}
Height 1																	
season	1	0.000		1	1	0.267		**<0.01**	1	0.001		0.19	1	0.020	0.241	0.62	0.396
year	11	0.001			11	0.390			11	0.015			11	3.514			
residual	587	0.017			587	11.169			587	0.470			587	45.310			
Cochran's C test				0.03				<0.01				<0.01				0.87	
Height 2																	
season	1	0.001	0.21	1	0.201		**<0.01**	1	0.004		**0.03**	1	0.468		**<0.01**	1.703	
year	11	0.015		11	0.938			11	0.047			11	4.767				
residual	587	0.549			587	9.7706			587	0.433			587	24.031			
Cochran's C test				<0.01				<0.01				<0.01				<0.01	
Height 3																	
season	1	0.000		0.09	1	0.074		**0.02**	1	0.007		0.07	1	1.916		**<0.01**	3.255
year	11	0.330			11	0.380			11	0.077			11	3.134			
residual	587	7.152			587	7.152			587	1.308			587	27.693			
Cochran's C test				<0.01				<0.01				<0.01				<0.01	
Height 4																	
season	1	0.025	0.82	0.37	1	0.000	0.009	0.93	1	0.046		**<0.01**	1	1.232		**<0.01**	1.706
year	11	0.526			11	0.156			11	0.054			11	0.898			
residual	587	17.654			587	8.816			587	1.576			587	27.310			
Cochran's C test				0.11				0.49				<0.01				<0.01	

2.5 Appendix

Table S1. Estimated summer transition probability matrices(transition provabilities: mean plus-minus SE) in Height 1, 2, 3, and 4 ($n = 25$). Columns represent the ecological states at time t (spring), and rows represent the ecological states at time t+1 (autumn).

	time *t*															
	Chthamalus dali		*Corallina pilulifera*		*Gloiopeltis fucata*		*Analipus japonicus*		*Chondrus yendoi*		Annual species		Perennial species		Bare rock	
time *t+1*	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE
Height 1																
C. dali	0.370	0.046	0.122	0.004	0.159	0.029	0.105	0.010	0.123	0.003	0.137	0.015	0.123	0.005	0.101	0.021
C. pilulifera	0.039	0.008	0.149	0.019	0.057	0.010	0.098	0.009	0.128	0.004	0.075	0.009	0.115	0.004	0.004	0.001
G. fucata	0.109	0.019	0.122	0.004	0.302	0.042	0.115	0.012	0.123	0.003	0.113	0.019	0.136	0.011	0.041	0.011
A. japonicus	0.064	0.019	0.121	0.003	0.104	0.020	0.239	0.046	0.127	0.004	0.095	0.013	0.128	0.008	0.047	0.024
C. yendoi	0.036	0.008	0.119	0.003	0.057	0.010	0.092	0.009	0.126	0.005	0.071	0.009	0.113	0.004	0.004	0.001
Annual species	0.041	0.009	0.124	0.001	0.064	0.013	0.119	0.021	0.126	0.004	0.104	0.020	0.122	0.007	0.012	0.007
Perennial species	0.038	0.008	0.120	0.004	0.061	0.010	0.106	0.010	0.122	0.002	0.089	0.018	0.141	0.016	0.004	0.001
Bare rock	0.302	0.031	0.124	0.004	0.195	0.025	0.124	0.008	0.124	0.002	0.316	0.050	0.121	0.004	0.787	0.034
Height 2																
C. dali	0.508	0.052	0.120	0.007	0.271	0.026	0.153	0.023	0.120	0.006	0.167	0.029	0.170	0.019	0.319	0.044
C. pilulifera	0.025	0.009	0.171	0.035	0.038	0.010	0.102	0.032	0.132	0.015	0.090	0.017	0.107	0.007	0.010	0.002
G. fucata	0.135	0.022	0.120	0.008	0.321	0.036	0.089	0.014	0.118	0.005	0.151	0.022	0.140	0.011	0.141	0.031
A. japonicus	0.077	0.029	0.116	0.007	0.073	0.016	0.302	0.045	0.117	0.005	0.113	0.029	0.112	0.007	0.072	0.034
C. yendoi	0.017	0.006	0.121	0.005	0.032	0.008	0.055	0.008	0.150	0.018	0.065	0.009	0.102	0.005	0.008	0.001
Annual species	0.043	0.020	0.116	0.006	0.037	0.009	0.067	0.009	0.121	0.004	0.133	0.029	0.105	0.005	0.023	0.010
Perennial species	0.022	0.005	0.111	0.007	0.040	0.008	0.069	0.010	0.114	0.006	0.066	0.009	0.142	0.010	0.012	0.002
Bare rock	0.173	0.022	0.125	0.008	0.187	0.022	0.162	0.018	0.128	0.007	0.215	0.028	0.123	0.008	0.415	0.039
Height 3																
C. dali	0.485	0.053	0.076	0.013	0.183	0.022	0.146	0.022	0.096	0.015	0.145	0.027	0.117	0.008	0.342	0.044
C. pilulifera	0.069	0.028	0.440	0.059	0.085	0.019	0.107	0.020	0.215	0.029	0.195	0.038	0.125	0.015	0.053	0.015
G. fucata	0.122	0.023	0.062	0.011	0.248	0.031	0.072	0.014	0.073	0.009	0.086	0.014	0.137	0.014	0.139	0.030
A. japonicus	0.076	0.012	0.067	0.012	0.128	0.015	0.315	0.041	0.091	0.012	0.108	0.026	0.107	0.010	0.098	0.036
C. yendoi	0.027	0.008	0.106	0.012	0.058	0.011	0.048	0.007	0.255	0.034	0.077	0.016	0.113	0.011	0.012	0.002
Annual species	0.047	0.008	0.102	0.014	0.077	0.009	0.092	0.017	0.088	0.009	0.147	0.022	0.121	0.011	0.052	0.012
Perennial species	0.032	0.006	0.059	0.010	0.058	0.008	0.056	0.011	0.081	0.009	0.058	0.010	0.140	0.022	0.021	0.004
Bare rock	0.142	0.019	0.087	0.015	0.164	0.021	0.163	0.016	0.100	0.012	0.185	0.026	0.140	0.025	0.283	0.035
Height 4																
C. dali	0.243	0.036	0.020	0.008	0.119	0.008	0.095	0.011	0.031	0.007	0.103	0.024	0.106	0.009	0.119	0.021
C. pilulifera	0.092	0.010	0.666	0.038	0.117	0.020	0.160	0.018	0.330	0.032	0.226	0.035	0.136	0.017	0.171	0.037
G. fucata	0.107	0.013	0.015	0.005	0.197	0.029	0.092	0.013	0.031	0.007	0.092	0.018	0.093	0.008	0.121	0.033
A. japonicus	0.099	0.011	0.029	0.010	0.114	0.009	0.227	0.034	0.034	0.008	0.074	0.009	0.094	0.008	0.106	0.033
C. yendoi	0.071	0.010	0.152	0.019	0.089	0.009	0.078	0.009	0.402	0.036	0.110	0.020	0.125	0.018	0.065	0.016
Annual species	0.089	0.009	0.046	0.011	0.104	0.011	0.108	0.014	0.064	0.019	0.161	0.036	0.124	0.020	0.063	0.011
Perennial species	0.104	0.014	0.035	0.007	0.101	0.008	0.092	0.011	0.057	0.010	0.096	0.013	0.208	0.027	0.061	0.011
Bare rock	0.194	0.025	0.037	0.009	0.159	0.015	0.148	0.008	0.051	0.009	0.138	0.026	0.113	0.011	0.294	0.043

Table S2. Estimated winter transition probability matrices(transition provabilities: mean plus-minus SE) in Height 1, 2, 3, and 4 ($n = 25$). Columns represent the ecological states at time t (autumn), and rows represent the ecological states at time t+1 (spring).

	time *t*															
	Chthamalus dali		*Corallina pilulifera*		*Gloiopeltis fucata*		*Analipus japonicus*		*Chondrus yendoi*		Annual species		Perennial species		Bare rock	
time *t+1*	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE	mean		mean	SE	mean	SE
							Height 1									
C. dali	0.400	0.049	0.122	0.006	0.093	0.009	0.110	0.014	0.125	0.002	0.115	0.007	0.137	0.013	0.120	0.030
C. pilulifera	0.038	0.008	0.129	0.012	0.058	0.010	0.090	0.010	0.120	0.002	0.110	0.006	0.110	0.005	0.004	0.001
G. fucata	0.103	0.024	0.118	0.005	0.389	0.052	0.122	0.016	0.124	0.002	0.115	0.006	0.122	0.006	0.040	0.009
A. japonicus	0.064	0.016	0.119	0.003	0.069	0.010	0.177	0.021	0.123	0.002	0.146	0.012	0.139	0.013	0.036	0.016
C. yendoi	0.038	0.008	0.116	0.003	0.058	0.010	0.089	0.009	0.122	0.003	0.111	0.006	0.111	0.005	0.004	0.001
Annual species	0.098	0.027	0.149	0.023	0.076	0.011	0.104	0.010	0.136	0.009	0.170	0.029	0.125	0.008	0.053	0.017
Perennial species	0.038	0.008	0.112	0.005	0.065	0.010	0.091	0.010	0.120	0.002	0.109	0.006	0.124	0.009	0.004	0.001
Bare rock	0.220	0.028	0.134	0.007	0.192	0.027	0.215	0.034	0.130	0.003	0.124	0.004	0.132	0.007	0.740	0.039
							Height 2									
C. dali	0.506	0.048	0.114	0.007	0.140	0.019	0.087	0.012	0.117	0.006	0.116	0.009	0.175	0.018	0.192	0.027
C. pilulifera	0.019	0.007	0.154	0.020	0.032	0.008	0.058	0.008	0.127	0.008	0.107	0.008	0.091	0.006	0.010	0.002
G. fucata	0.173	0.031	0.113	0.007	0.433	0.042	0.098	0.015	0.116	0.006	0.107	0.008	0.133	0.009	0.101	0.017
A. japonicus	0.047	0.013	0.131	0.012	0.053	0.012	0.332	0.034	0.117	0.005	0.149	0.023	0.124	0.020	0.089	0.034
C. yendoi	0.017	0.006	0.109	0.005	0.030	0.007	0.055	0.008	0.129	0.005	0.104	0.007	0.091	0.006	0.008	0.001
Annual species	0.044	0.012	0.142	0.014	0.061	0.016	0.081	0.010	0.149	0.018	0.182	0.030	0.105	0.009	0.055	0.013
Perennial species	0.024	0.007	0.106	0.007	0.034	0.007	0.058	0.008	0.113	0.006	0.102	0.008	0.111	0.007	0.011	0.002
Bare rock	0.170	0.019	0.131	0.007	0.217	0.026	0.230	0.024	0.132	0.011	0.132	0.009	0.170	0.015	0.533	0.033
							Height 3									
C. dali	0.468	0.043	0.069	0.012	0.123	0.011	0.092	0.015	0.079	0.011	0.086	0.010	0.125	0.008	0.164	0.022
C. pilulifera	0.025	0.007	0.421	0.052	0.056	0.010	0.050	0.008	0.208	0.029	0.125	0.018	0.122	0.011	0.027	0.005
G. fucata	0.155	0.036	0.055	0.010	0.294	0.042	0.108	0.025	0.074	0.010	0.074	0.008	0.096	0.007	0.062	0.014
A. japonicus	0.090	0.024	0.091	0.023	0.069	0.009	0.354	0.042	0.086	0.010	0.119	0.026	0.127	0.025	0.098	0.027
C. yendoi	0.023	0.007	0.113	0.016	0.051	0.009	0.045	0.008	0.261	0.041	0.064	0.008	0.092	0.007	0.015	0.002
Annual species	0.046	0.010	0.095	0.014	0.065	0.011	0.069	0.013	0.102	0.013	0.270	0.040	0.099	0.008	0.068	0.016
Perennial species	0.027	0.007	0.053	0.009	0.056	0.014	0.042	0.007	0.075	0.010	0.062	0.008	0.148	0.021	0.021	0.003
Bare rock	0.166	0.023	0.102	0.015	0.287	0.029	0.241	0.028	0.115	0.020	0.199	0.026	0.191	0.017	0.546	0.041
							Height 4									
C. dali	0.287	0.044	0.016	0.005	0.100	0.010	0.079	0.009	0.034	0.007	0.083	0.009	0.093	0.011	0.083	0.014
C. pilulifera	0.100	0.019	0.631	0.035	0.097	0.014	0.119	0.020	0.296	0.030	0.181	0.025	0.154	0.016	0.106	0.028
G. fucata	0.098	0.020	0.013	0.004	0.198	0.034	0.082	0.009	0.034	0.007	0.076	0.008	0.074	0.009	0.050	0.011
A. japonicus	0.091	0.010	0.037	0.012	0.114	0.011	0.274	0.042	0.043	0.011	0.111	0.019	0.083	0.013	0.083	0.017
C. yendoi	0.072	0.010	0.175	0.025	0.096	0.013	0.080	0.010	0.422	0.042	0.118	0.014	0.160	0.035	0.097	0.030
Annual species	0.103	0.019	0.034	0.008	0.085	0.007	0.088	0.010	0.046	0.009	0.198	0.037	0.101	0.013	0.058	0.009
Perennial species	0.068	0.009	0.017	0.004	0.085	0.011	0.077	0.010	0.036	0.007	0.079	0.008	0.154	0.030	0.039	0.007
Bare rock	0.180	0.025	0.078	0.018	0.226	0.032	0.201	0.020	0.090	0.025	0.155	0.019	0.180	0.023	0.483	0.055

Eigenvector sensitivity analysis

Dominant right eigenvector $\mathbf{u}_1$ was calculated from $\mathbf{P}^{\dagger}$. The sensitivity of this scaled eigenvector to seasonal differences in transition probabilities p_{ij} is

$$\frac{\partial \frac{\mathbf{u}_1}{\|\mathbf{u}_1\|}}{\partial p_{ij}} = \frac{\partial \mathbf{u}_1}{\partial p_{ij}} - \mathbf{u}_1 \sum_k \frac{\partial u_k}{\partial p_{ij}},$$

where

$$\frac{\partial \mathbf{u}_1}{\partial p_{ij}} = u_j^{(1)} \sum_{m \neq 1}^{s} \frac{\overline{v_i}^{(m)}}{\lambda_1 - \lambda_m} \mathbf{u}_m. \tag{S1}$$

Here, $u_j^{(1)}$ is the j-th element of $\mathbf{u}_1$, $\overline{v_i}^{(m)}$ is the i-th element of the complex conjugate of left eigenvector $\mathbf{v}_m$ and λ_m is the m-th eigenvalue. Eq (S1) cannot be directly applied to Markov chain models because any change in p_{ij} must be accompained by derivative I calculated is

$$\frac{\partial \frac{\mathbf{u}_1}{\|\mathbf{u}_1\|}}{\partial p_{ij}} = \frac{\partial \frac{\mathbf{u}_1}{\|\mathbf{u}_1\|}}{\partial p_{ij}} + \sum_{m \neq i}^{s} \frac{\partial \frac{\mathbf{u}_1}{\|\mathbf{u}_1\|}}{\partial p_{mj}} \frac{\partial p_{mj}}{\partial p_{ij}}. \tag{S2}$$

The derivative $\partial p_{mj}/\partial p_{ij}$ in Eq (S2) are determined such that the change in p_{ij} is compensated for by changes in the other entries in colomun j of $\mathbf{P}$. In this study, I followed Hill et al. (2004) and used proportional compensation although many compensation patterns are possible (Caswell 2001):

$$\frac{\partial p_{mj}}{\partial p_{ij}} = \frac{-p_{mj}}{1 - p_{ij}} \qquad m \neq i,$$

where the change in p_{ij} is distributed over the other column entries in proportion to their values.

References

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3 Spatial variation in compositional dynamics and mechanism in intertidal sessile assemblages

3.1 Introduction

One of the essential issues in ecology is to reveal underlying mechanism of both community dynamics within a community and its spatial variation, because they should tightly link to species coexistence mechanisms, community stability, and ecosystem function. The most common measurements of compositional dynamics of a community are the compositional turnover which can be treated as a temporal analog of beta-diversity (e.g. Whittaker 1972; Nekola 1999; Legendre et al. 2005; Jost 2007; Jaxon & Sax 2009), i.e. the temporal changes in species composition between neighboring time points, and the temporal compositional variance (e.g. Legendre et al. 2005; Anderson et al. 2006; Legendre 2013), i.e. the total community compositional variance through observation period (Vellend 2001; Legendre 2013)(Fig. 1(A)). Both properties tightly link to the concept of community stability; the resistance to environment variation increases with decreasing the temporal compositional variance, and the engineering resilience following a perturbation increases with increasing the compositional turnover (Pimm 1984; Ives 2007). On the other hand, the strength of correlation between these two measurements of compositional dynamics will tightly link degree of community regulation; the correlation will be low for a weakly regulated community, in which most populations behave like a random walk without equilibrium, conversely the correlation will be high for a strongly regulated community, in which most populations are regulated by intraspecific density dependence (Bagchi et al. 2017). Therefore, simultaneous measurements of both compositional turnover and temporal compositional variance in same communities has a great advantage to reveal feature of community dynamics and its underlying mechanism.

To clarify the underlying mechanism of community dynamics, understanding the population dynamics in community member offers great advantages. In general, population dynamics of competing species within a community can be described using discrete Lotka-Volterra model as follows:

$$\ln X_{i,t+1} - \ln X_{i,t} = r_i - \alpha_{ii} X_{i,t} - \sum_{n \neq i, n=1}^{N} \alpha_{in} X_{n,t} + \epsilon_{i,t},$$

Where X_i and r_i are population size and intrinsic growth rate, respectively. α_{ii} and α_{in} ($n \neq i, n = 1, 2, \cdots, N$) are , respectively, intraspecific and interspecific competition coefficients, i.e. the effect of species n on i, respectively. For long-term persistence of each population, it is necessary that the strength of intraspecific density dependence is larger than the strength of interspecific density dependence (i.e., $\alpha_{ii} > \alpha_{in}$) (Chesson 2000). ϵ_i is a random variable characterized by normal distribution with zero mean and variance σ_i^2. σ_i^2 represents the stochasticity of population growth rate, which is caused by both demographic stochasticity and environmental stochasticity (Royama 1992; Turchin 2003). Thus, by parameterizing discrete Lotka-Volterra model with a long-term time series data of a community, the compositional dynamics can be decomposed into endogenous (r_i, α_{ii} and α_{in}) (Fig. 1(B)) and exogenous (σ_i^2) processes (Fig. 1(C)).

The compositional turnover within a community should strongly depend on the magnitude of community-wide stochasticity, i.e. $\overline{\sigma^2} = 1/N \sum_i^N \sigma_i^2$ (Fig. 1(C)), because endogenous processes often play an important role in driving population dynamics (Royama 1999; Turchin 2003). Thus, focusing on the magnitude of stochasticity in each species σ_i^2 is the effective way to understand the underlying mechanism of compositional dynamics of communities and its spatial variation. First, the magnitude of stochasticity can be decomposed into two components by statistical procedure; demographic and environmental stochasticities (Fig. 1(D) and (E)). Assuming that the magnitude of stochasticity which is affected by mean population size as demographic stochasticity, coefficient of correlation, R^2, which is estimated by the regression of the effect of temporal mean population size on the magnitude of stochasticity means the magnitude of demographic stochasticity. Moreover, the magnitude of environmental stochasticity can be evaluated as residuals from that regression of y on x. Second, the cause of spatial variation in underlying mechanism of compositional dynamics of communities can be revealed by statistical comparison of both temporal mean population size and environmental stochasticity among species and sites (Fig. 1(F) and (G)). For example, if local community is high compositional turnover, its cause seems to be that the local community is consisted by species with low population size or high sensitivity for environment.

Intertidal sessile assemblages consist of perennials of two contrasting functional groups: sessile invertebrates such as barnacle and algae (Raffaelli & Hawkins 1996). These species compete to each other for space which is common resource for them (Branch 1984). Their population size can be easily quantified as the proportion of occupied area (Roughgarden et al. 1985), i.e. coverage, which increase by recruitment of larvae and propagules (e.g. Raimondi 1988; Kæhler 1997; Noda et al. 2003; Pineda et al. 2010), and by growth of individuals (e.g. McCourt 1984; Sanford et al. 1994; Noda et al. 2003; Chomsky et al. 2004; Schneider 2008), and decrease by intra- and interspecific competition (e.g. Connell 1961a,b; Paine 1966; Lubchenco 1980) and physical disturbance (Sousa 1979a,b; Menge & Branch 2001).

In this study, I examined the underlying mechanisms of compositional dynamics of intertidal sessile assemblages and its spatial variation by parameterizing discrete Lotka-Volterra model with a decadal time series data of rocky intertidal sessile assemblages from 25 sites along the Pacific coast of eastern Hokkaido, Japan. First, to evaluate how the species compositions were regulated, I examined the strength of correlation between the compositional turnover and the temporal compositional variance (Fig. 1(A)), and the relative strengths of intra- versus interspecific density dependence (Fig. 1(B)). Then, I tested a hypothesis that the compositional turnover of community should strongly depend on the magnitude of community-wide stochasticity (Fig. 1(C)). Lastly, to reveal the cause of spatial variation in underlying mechanism of compositional dynamics of communities, I examined the relative contribution of mean population size (Fig. 1(D)) and environmental stochasticity (Fig. 1(E)) in determining the magnitude of stochasticity, then how those two stochasticities varied among species and sites (Fig. 1(F) and (G)).

3.2 Methods

3.2.1 Study system

The study area is located along the Pacific coast of eastern Hokkaido, Japan (Fig. 2). The area is within the subarctic zone and is impacted by the cold Oyashio current (Briggs 1995; Asakura 2003; Alam et al. 2014). Ice scour occurs once every few years (Alam et al. 2014). In this study area, five perennial species dominate in sessile assemblage: *Chtamalus dalli* (barnacle), *Corallina pilulifera* (crustose coralline algae), *Gloiopeltis furcata* (red algae), *Analipus japonicus* (brown algae), and *Condrus yendoi* (red algae). Total coverage of them were nearly 90 % of the total coverage of all sessile assemblages.

3.2.2 Census design

A hierarchical sampling design (Noda 2004) was applied. The study area is located along the Pacific coast of eastern Hokkaido, Japan where there were the five shores (Mochirippu, 43°1′ N, 145°1′ E; Mabiro, 42°59′ N, 144°53′ E; Aikappu, 43°1′ N, 144°50′ E; Monshizu, 43°2′ N, 144°46′ E; and Nikomanai, 42°56′ N, 144°40′ E) separated by 10-24 km (Fig. 2). Five permanent rectangular plots were established within each shore. Each plot was 50 cm wide by 100 cm high and the mean tidal level corresponded to the vertical midpoint. 200 grid points were placed on the rock surface at 5 cm intervals in both the vertical and horizontal direction in each plot, and the sessile organisms occupying each grid point were identified and recorded. The coverage of each sessile organisms was calculated as total number of grid point at each plot every census. The censuses were carried out from 2002 to 2017 in summer (July or October). All measurements were made at low tide. 13 sessile animals and 36 algal species were recorded during 16 years of census. The total coverage of sessile organisms in each plot were approximately 60% and rarely reached 100%.

3.2.3 Data analysis

Species used for analyses was selected by two steps. In the first step, I excluded species whose total coverage at a plot was < 2 % to ensure estimation accuracy of population size. In the second step, I excluded species that the total of temporal occurrence in a plot was < 75 % (i.e., species which the total year observed coverage was < 12 years). This is because I considered that species with low temporal occurrence is considered to be a tourist species, and these species, therefore, should be treated as out of community member. Accordingly, the species used analyses was from 2 to 6 at each plot (Tables 1-1).

Measures of temporal variability in species composition

Two measures of compositional dynamics of a community, the compositional turnover, i.e. the temporal changes in species composition between neighboring time points, and the temporal compositional variance, i.e. the total community compositional variance through observation period, were obtained from each plot.

The compositional turnover, D_k, was estimated as the mean value of the Euclidean distance between all neighboring time points as follows:

$$D_k = \sum_{t=1}^{T} \sqrt{\sum_{i=1}^{N} (\ln N_{i,t+1,k} - \ln N_{i,t,k})^2 / (T-1)}.$$

$N_{i,t,k}$ is coverage of species i in plot k at year t.

The temporal compositional variance, BD_k, was estimated as the total community composition variance (Legendre and Cácers 2013) as follows:

$$\mathrm{BD}_k = \sum_{i=1}^{n} \sum_{t=1}^{T} s_{it,k}/(T-1),$$

where

$$s_{it,k} = (\ln N_{i,t,k} - \overline{\ln N_{i,k}})^2.$$

Here, $N_{i,t,k}$ is coverage of species i in plot k at year t.

Correlation analysis was used to examine the relationship between the rates and variabilities of each plot.

Population process model

The strengths of intra- and interspecific density dependence and the magnitude of stochasticity for each species at each plot were estimated using following formula:

$$\ln N_{i,t+1,k} - \ln N_{i,t,k} = \alpha_{i,k} - \beta_{i,k} N_{i,t,k} - \gamma_{i,k} M_{i,t,k} + \epsilon_{i,t,k}. \tag{1}$$

$N_{i,t,k}$ and $M_{t,k}$ are coverage of species i and of other species in plot k at year t, respectively. $\alpha_{i,k}$, $\beta_{i,k}$ and $\gamma_{i,k}$ are intrinsic growth rate, strengths of intra- and interspecific density dependence of species i at plot k, respectively. $\epsilon_{i,t,k}$ is a random variable characterized by normal distribution with zero mean and variance $\sigma^2_{i,k}$. $\sigma^2_{i,k}$ is the magnitude of stochastic population fluctuation of species i at plot k. The mean values of β, γ, and ϵ in each plot, $\overline{\beta}$, $\overline{\gamma}$, and $\overline{\epsilon}$, were obtained as surrogates of the community-level measures of the strength of intra- and interspecific density dependence and the magnitude of stochasticity.

Regression analysis was performed to examine how the turnover rates of each plot depend on the community-wide magnitude of stochasticity in each plot. All variables were log-transformed for the analyses.

Regression analysis of the effects of temporal mean coverage on the magnitude of stochasticity was performed to decompose the magnitude of stochasticity into demographic and environmental stochasticities for each species in each plot. I defined the magnitude of demographic and environmental stochasticity of each species in each plot as the coefficient of determination (R^2) of this regression and the residuals from this regression of y on x, respectively. All variables were log-transformed for the analyses.

The differences in the magnitude of demographic and environmental stochasticities among species and shores were examined by two-way ANOVAs, where the magnitude of demographic or environmental stochasticities were treated as dependent variable, and species and shores were treated as fixed effects. Species observed only in a shore were excluded in this analysis. The assumption of homoscedasticity was tested prior to each ANOVA by Bartlett test because the sample size was different among species and shores.

All statistical analyses were conducted by R 3.3.1 (R Development Core Team 2016).

3.3 Results

Relationship between compositional dynamics and mechanism of community regulation

There was a high and significant correlation between compositional turnover and temporal compositional variance of each plot ($r = 0.92$, $p < 0.001$, $n = 25$).

In all plots, community-wide strengths of intraspecific density dependence were positive and much larger than that of interspecific density dependence (Fig. 3).

Cause of spatial variations in compositional dynamics

The compositional turnover rates of each plot significantly and strongly depended on community-wide magnitude of stochasticity ($R^2 = 0.58$, $p < 0.001$, $n = 25$).

Demographic and environmental stochasticities

Although the endogenous population fluctuations of each species in each site significantly decreased with mean coverage, coefficient of determination of the regression, which reflect relative contribution of demographic stochasticity in determining the magnitude of stochasticity, was small ($R^2 = 0.10$).

The result of ANOVA showed that there was significant effect of species, shore, and their interaction on temporal mean coverage (Fig. 4 and Table 3). In contrast, there was significant effect of shore and the interaction of species and shore on the magnitude of environmental stochasticity (Fig. **??** and Table 3). This effects, however, disappeared for environmental stochasticity when I excluded the data of NN where the magnitude of environmental stochasticities of *C. dalli* and *A. japonicus* were appeared to be larger than other shores.

3.4 Discussion

Compositional dynamics and mechanism of community regulation

In present study, there was positive and strong correlation between the turnover rate and the temporal variance. In addition, community-wide strengths of intraspecific density dependence were positive in all plot, while community-wide strengths of interspecific density dependence were nearly zero (Fig. 3). These results suggest that intertidal sessile assemblage along the Pacific coast of eastern Hokkaido of Japan is under strong regulation by density-dependent processes. Even though the spatial variation in the compositional dynamics largely depended on community-wide magnitude of stochasticity, which largely depended on environmental stochasticity. It implies that even if the community is under strong regulation by density dependence, properties of community dynamics, such as the compositional turnover and the temporal compositional variance, largely depend on exogenous factors (i.e. environmental stochasticity). Previous studies have emphasized the importance of density-dependence as a cause of community stability (Henderson & Magurran 2014; Mutshinda et al. 2009) and paid less attention to environmental stochasticity if community is under strong regulation. My results suggest that environmental fluctuations, as well as density-dependence processes, play an important role in driving community dynamics even if community is under strong regulation.

Compensatory dynamics which stabilize community by differences in the magnitude and timing of species responses to physical environmental changes (McNaughton 1977; Patten 1975; Gonzalez 2009; Gotelli et al. 2017) has been long attention as a fundamental mechanism for stability in aggregate community properties such as species richness and biomass. A meta-analysis, however, represents that very few communities were regulated by compensatory dynamics (Houlahan et al. 2007). On the other hand, density-dependence can stabilize species richness and biomass through stabilizing compositional dynamics. Indeed, population dynamics are regulated by intraspecific density dependence in diverse types of communities (Mutshinda et al. 2009). In addition, present study demonstrated tight linkage between the domination of intraspecific density-dependence over interspecific one and temporal stability of species composition as it is predicted from general coexistence theory (Chesson 2000). These findings may imply that the intraspecific density-dependence play a more general role than compensatory dynamics do. Thus, revealing the strength of density-dependence and its underlying mechanism may offer great advantages in deepening our understanding not only about population dynamics and species coexistence mechanism but also about ecosystem function.

Demographic and environmental stochasticities

Since Hubbell (2001) had pointed out the importance of demographic stochasticity in community dynamics in the unified neutral theory of biodiversity, the relative importance of demographic and environmental stochasticities have been growing attention for community ecologists (Clark 2009; Chase 2011; Gravel et al. 2011; Rosindell et al. 2012; Vellend et al. 2014). Present study indicates that relative contribution of demographic stochasticity in determining the magnitude of endogenous population fluctuations was small. Although the importance of demographic stochasticity may be underestimated because I excluded rare species in this study, community dynamics of intertidal sessile assemblage along the Pacific coast of eastern Hokkaido in Japan may be strongly influenced by environmental stochasticity rather than demographic stochasticity as similar with other communities such as grassland (Lohier et al. 2016). To reveal generality and variability in the relative importance of demographic and environmental stochasticities is essential to deepen our knowledge about community dynamics, because their relative importance can vary depending on community size and degree of environmental variability.

Although there were significant effects of shores and interaction of species and shores on environmental stochasticity, this effect disappeared if data from a shore, NN, was excluded. These facts may be caused by ice scour. Indeed, drift ice was observed near the study site in the year when coverage of sessile assemblages dramatically decreased in NN, in 2008, 2013, and 2017 (Japan Metrological Agency): the reduction of coverage were large in *C. dalli* and *A. japonicus* with large magnitude of stochastic population fluctuations, and were small in *C. pilulifera* and *C. yendoi* with small magnitude of stochastic population fluctuations. Although, in general, intraspecific density dependence tends to be low under the condition with large intensity of disturbance (Menge 1976; Buss 1986; Townsend 1991), the community-wide intraspecific density dependence in NN is within the same range of it as other shores (Fig. 6). This fact suggest that the frequency of ice scour is not enough to decrease competition for space among sessile organisms because their coverage rapidly recovered after disturbance and reached the same level in following year (Kanamori et al., unpublished data).

Conclusion

In this study, I examined the underlying mechanisms of compositional dynamics of intertidal sessile assemblages and its spatial variation by parameterizing discrete Lotka-Volterra model with a decadal time series data of rocky intertidal sessile assemblages from 25 sites along the Pacific coast of eastern Hokkaido, Japan. I found that compositional dynamics was under strong regulation by intraspecific density-dependence. I also found that the spatial variation in the compositional dynamics largely depended on community-wide magnitude of stochasticity mainly caused by environmental stochasticity. These results suggest that even if the community is under strong regulation by density dependence, properties of community dynamics, such as the compositional turnover and the temporal compositional variance, largely depend on exogenous factors (i.e. environmental stochasticity).

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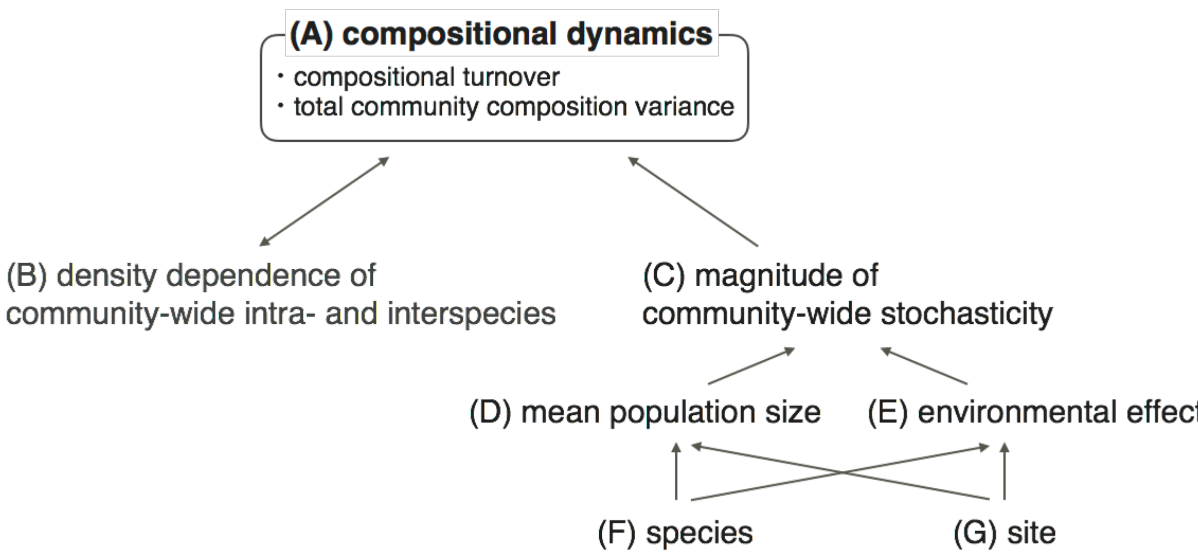

Fig. 1: Conceptual diagram of this study to understand compositional dynamics and its spatial variation

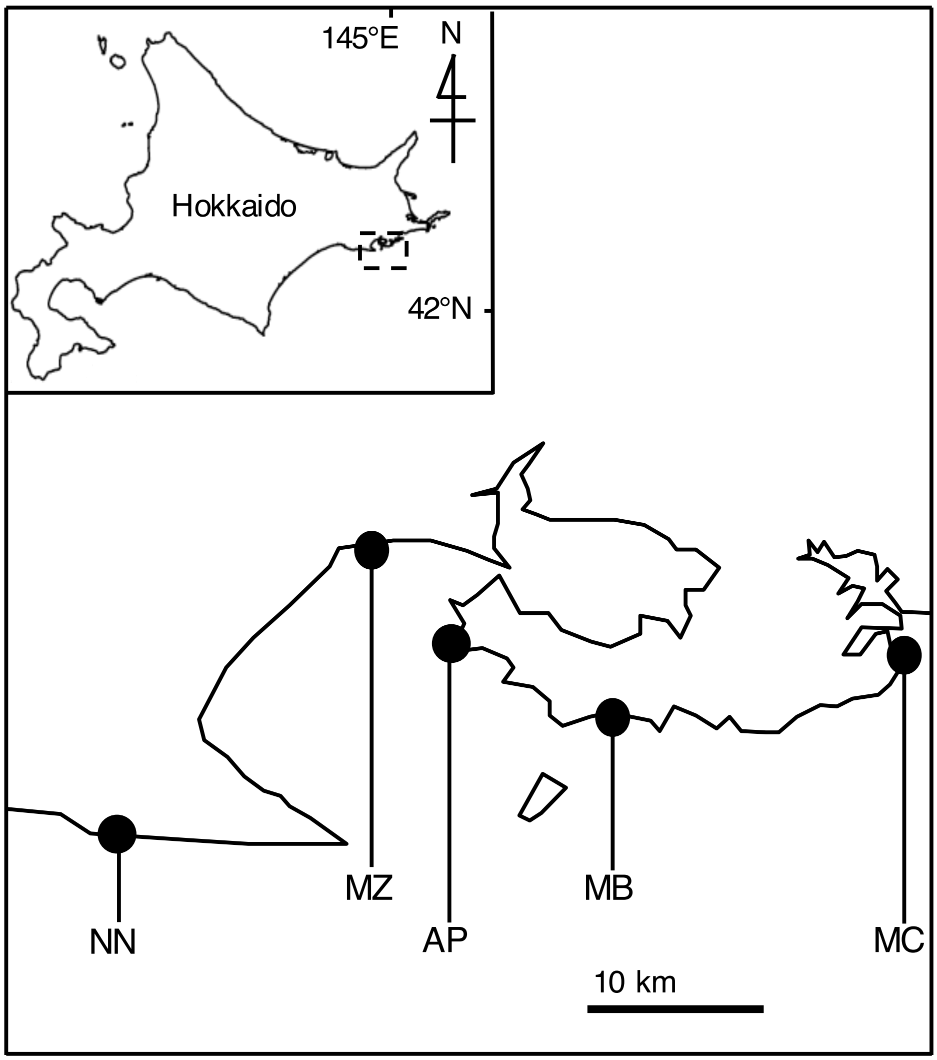

Fig. 2: Study site location. Five shores were chosen along the Pacific coast of eastern Hokkaido, Japan

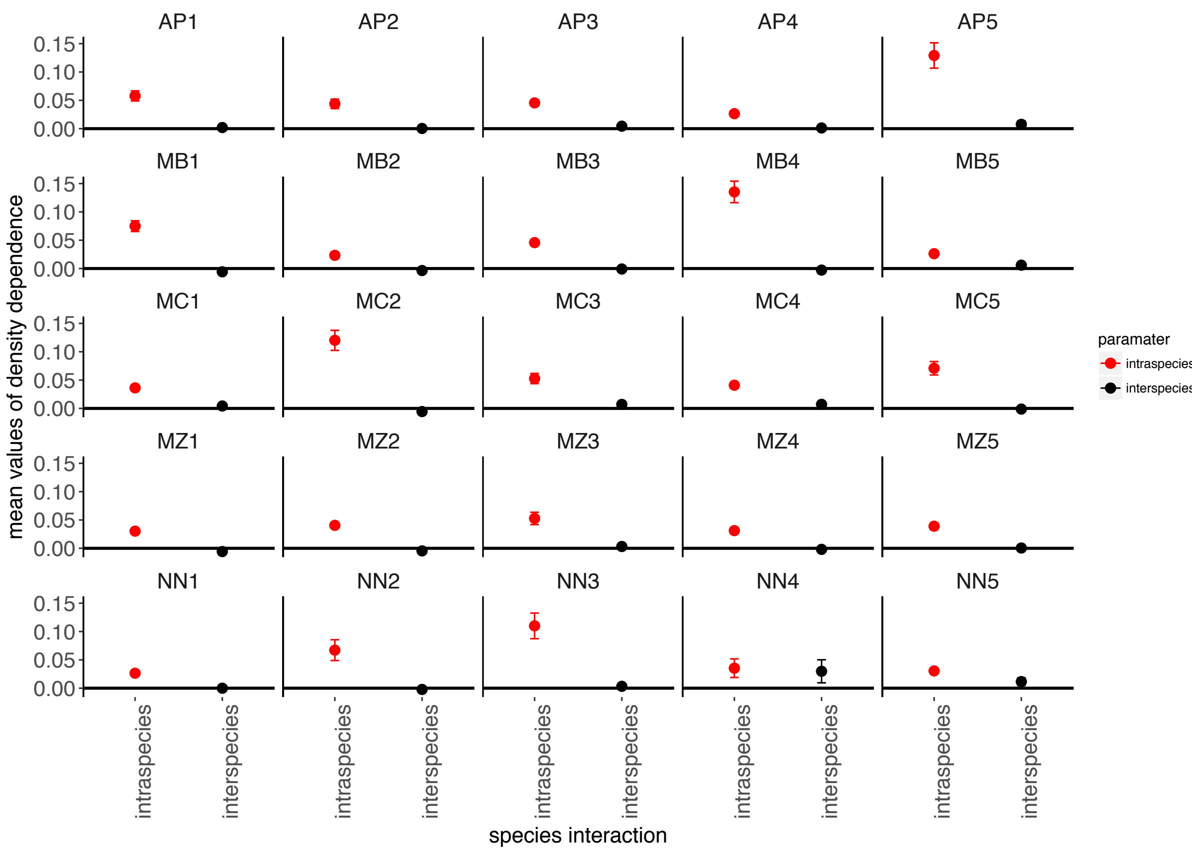

Fig. 3: The mean values of density effects from intra- and inter- species competition in community level

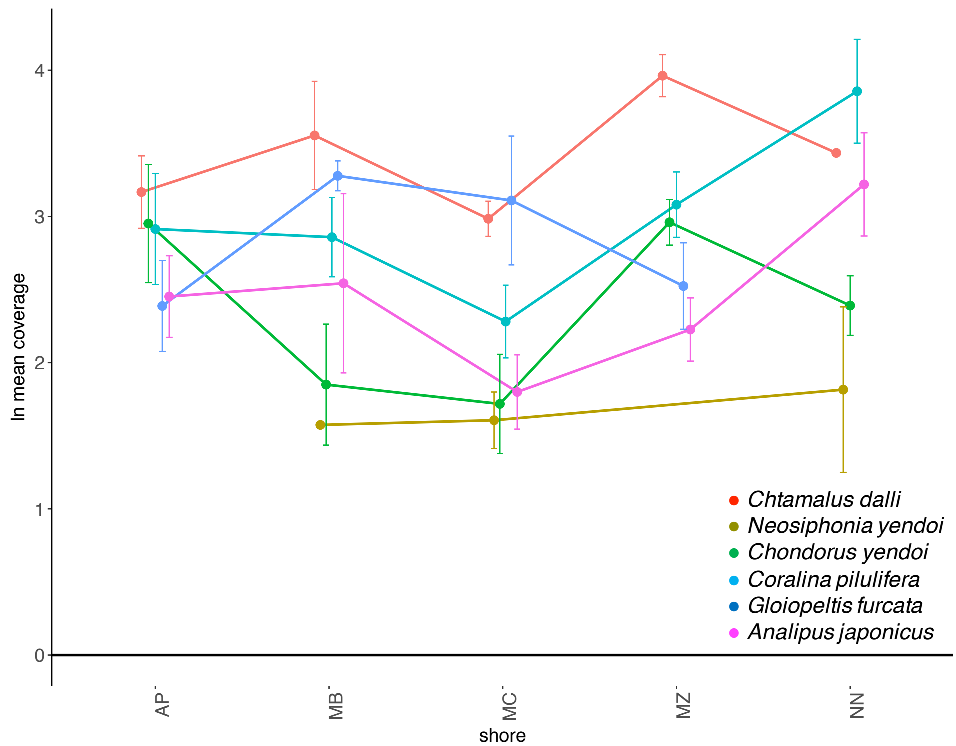

Fig. 4: The difference of demographic stochasticity among species and shores. This result corresponds to Table 3(A)

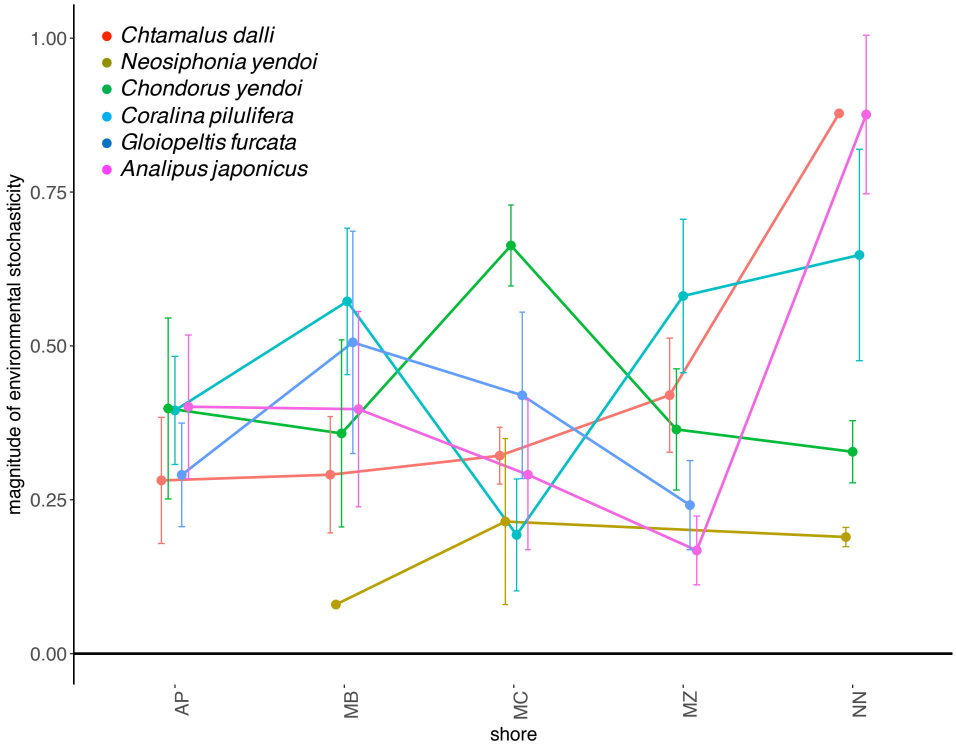

Fig. 5: The difference of environmental stochasticity among species and shores. This result corresponds to Table 3(B)

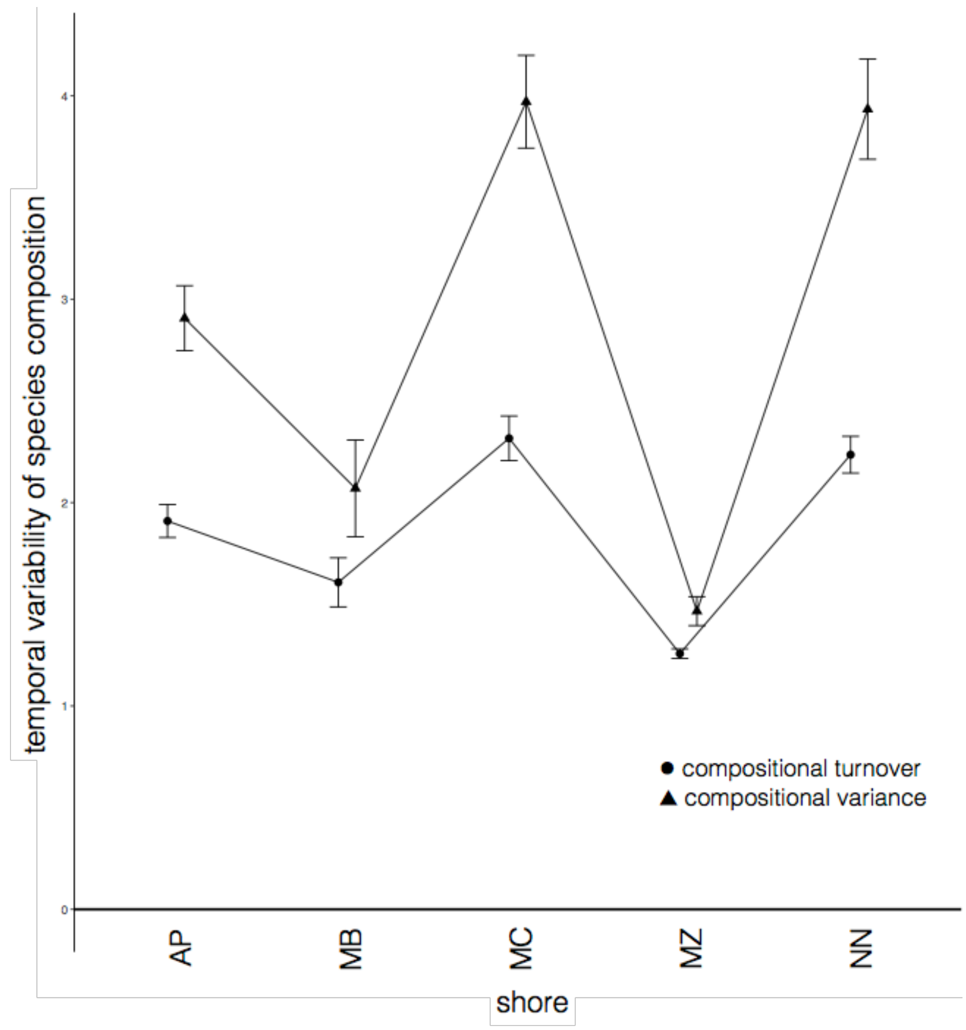

Fig. 6: The difference of the rate and variability among shores. x-axis is shores which coresponding to Fig. 2. The triangles and circles represent the rate and variability in temporal variability in species composition.

Table 1: Species list used for analysis in each plot. The criteria to select species is written in Data analysis

		AP					MB				
species	taxa	1	2	3	4	5	1	2	3	4	5
Chthamalus dalli	barnacle	●	●	●	●	●	●	●	●	●	●
Corallina pilulifera	coralline algae	●	●	●	●	●	●		●	●	
Gloiopeltis furcata	red algae	●	●	●	●	●	●	●	●	●	●
Analipus japonicus	blown,algae	●	●	●	●	●	●	●		●	●
Chondrus yendoi	red algae	●	●	●			●		●	●	
Neosiphonia yendoi	red algae						▲				
Cladophora opaca	green algae										
Pterosiphonia bipinnata	red algae										
Neorhodomela oregona	red algae										
Alaria praelonga	blown algae										
Hildenbrandia rubra	red algae									▲	
Leathesia difformis	blown algae	▲									

● Species was used for all statistical analysis

▲ Species was used for multi-regression model but excluded for two-way ANOVAs

Table 1: Continued

	MC					MZ					NN				
species	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
Chthamalus dalli	●	●	●	●	●	●	●	●	●	●	●				
Corallina pilulifera	●	●	●	●	●	●	●	●	●	●		●	●		●
Gloiopeltis furcata	●	●	●	●	●	●	●	●	●	●					
Analipus japonicus	●	●		●	●	●	●		●	●	●	●	●	●	●
Chondrus yendoi	●	●		●	●	●	●	●	●	●		●	●	●	●
Neosiphonia yendoi		▲	▲									▲	▲		
Cladophora opaca								▲							
Pterosiphonia bipinnata			▲												
Neorhodomela oregona				▲											
Alaria praelonga													▲		
Hildenbrandia rubra															
Leathesia difformis															

● Species was used for all statistical analysis

▲ Species was used for multi-regression model but excluded for two-way ANOVAs

Table 2: The results of two-way ANOVAs examining the differences among species and shores for (A) mean coverage and (B) magnitude of environmental stochasticity

SOV	*df*	SS	*F*	*P*
(A) mean coverage				
species	5	18.74	9.43	< 0.001
shores	4	4.06	3.41	0.02
species $\times$ shores	17	10.02	1.94	0.04
residuals	81	28.22		
(B) magnitude of environmental stochasticity				
species	5	0.43	1.59	0.17
shores	4	0.78	3.59	0.01
species $\times$ shores	17	2.04	2.22	0.009
residuals	81	3.85		

4 General discussion

One of the essential issues in ecology is revealing the mechanisms that determine spatial variation in community dynamics. Temporal variability in community structure (e.g. the number of species, species composition, and total biomass) and its spatial variation are mainly determined by three factors: abiotic environment (Fig. 1a-(1)), biotic processes, such as biological interaction (e.g. predation and competition) and dispersal (Fig. 1a-(2)), and spatial distribution of species (Fig. 1a-(3)). These factors affect community dynamics in an interactive way. The effects of biotic processes and spatial distribution of species on community dynamics are affected by the abiotic environment. In addition, biotic processes are affected by the spatial distribution of species; for example, mortality and recruitment rate often depend on both conspecific and heterospecific densities. In this study, I examined the spatial variation in temporal variability of community structure and its mechanism by analyzing decadal time series data of rocky intertidal sessile assemblages along the Pacific coast of eastern Hokkaido, Japan.

In chapter 2, I examined how seasonal changes in community structure vary along a vertical gradient. Specific questions were: (i) How does the magnitude of seasonal changes in community structure change vertically? (ii) How does the processes driving seasonal changes in community structure change vertically? I found that the magnitude of seasonal changes in community structure was the largest at mid shore, although seasonal fluctuation in physical environment increased with elevation. I also found that the major processes driving seasonal changes in community structure changed vertically, reflecting the indirect influence of vertical distributions of species.

In chapter 3, I examined the underlying mechanisms of compositional dynamics and its spatial variation by parameterizing a discrete Lotka-Volterra model. First, to evaluate how the species compositions were regulated, I examined the strength of correlation between the compositional turnover and the temporal compositional variance, and the relative strengths of intra- versus interspecific density dependence. Then, I tested the hypothesis that compositional turnover of a community should strongly depend on the magnitude of community-wide endogenous population fluctuations. Lastly, to reveal the cause of spatial variation in the underlying mechanism of compositional dynamics of communities, I examined the relative contribution of demographic and environmental stochasticities in determining the magnitude of endogenous population fluctuations. Then how those two stochasticities varied among species and sites. I found that compositional dynamics was under strong density-dependent processes. I also found that the spatial variation in compositional dynamics largely depended on community-wide magnitude of endogenous population fluctuation, where most part is environmental stochasticity.

In this chapter, I synthesize these results and provide future prospects for research in community ecology. Particularly, I will focus on two topics: temporal scale dependency in pattern of community dynamics and its underlying processes, and the importance of a population's response to the physical environment.

4.1 Temporal scale dependency in pattern of community dynamics and its underlying processes

Examining the major patterns of community dynamics at multiple temporal scales is of great importance because it helps us to mechanistically understand how community composition changes at larger temporal scales (Soininen 2010). Although many studies have been tried, how temporal variability of community structure in sessile assemblages are driven at various scales, such as season and year-to-year scales in intertidal habitats (e.g. Lawson 1957; Castenholz 1961; Lawson 1966; Haven 1973; Lubchenco & Cubit 1980; Underwood & Jernakoff 1984; Jernakoff 1985; Menge et al. 1997; Jenkins et al. 2001; Delany et al. 2003; Noda et al. 2003; Prathep 2005; Titlyanov et al. 2014; Bertocci et al. 2012; Southward & Crisp 1954; Southward & Crisp 1956; Barry et al. 1995; Sagarin et al. 1999; Roos et al. 2003; Oliveira & Qi 2003; Robinson et al. 2007; Branch et al. 2008), none of these studies simultaneously quantified both seasonal and year-to-year dynamics changes with spatially varying environments within a community. In this thesis, I quantified the effects of spatially varying environments on both seasonal and year-to-year dynamics, although vertical patterns of seasonal community dynamics seemed to be mainly caused by the vertical distribution of species which reflected the tidal excursion gradient, not by the vertical difference in magnitude of seasonal fluctuation of the physical environment (Fig. 1b), horizontal variation in year-to-year community dynamics seemed to be mainly caused by environmental stochasticity. Although community dynamics was under the control of strong intraspecific density dependence (Fig. 1c). These findings suggest that the paths of the causal relationship from abiotic environment to community dynamics were different among time scales in rocky intertidal sessile assemblages. This temporal scale dependence of the effect of abiotic environments on community dynamics may relate to the relationship between generation time and time scales of fluctuations in the abiotic environment. In general, the range of physical tolerance such as desiccation and freezing were much wider than seasonal fluctuations of the physical environment in natural systems (Baker 1909; Biebl 1952; Oliveira & Fletcher 1977; Newell 1979; Dring & Brown 1982; Davison et al. 1989; Luning 1990; Norton 1991; Beer & Kautsky 1992) because they cannot spatially refuge from harsh environments through mobility and therefore relatively easily evolve physiological tolerance to harsh environments occurring within their generation time (Menge & Sutherland 1987). Such physiological adaptation, however, will be difficult for extreme climate events which occur every few years. Thus, community dynamics of sessile organisms should be significantly affected by harsh environmental changes occurring every few years but within generation time. Indeed, difference in the effect of the abiotic environment on community dynamics among time scales was reported in a previous study. A recent meta-analysis focusing on aquatic organisms such as macro benthos, zoo plankton, seaweed, and fish, found that seasonal-compositional turnover increased toward high latitude and interannual compositional turnover decrease toward high latitude, although the physical environment largely fluctuate seasonally and interannually at high latitudes (Korhonen et al. 2010).

4.2 The importance of the population response to physical environment

For rocky intertidal sessile assemblages, population dynamics represented spatial variation at two temporal scales: the magnitude of seasonal dynamics for each ecological state tended to be different among tidal levels (chapter 2), and the magnitude of environmental stochasticity of each species tended to be difference among sites (chapter 3). These results suggest that our knowledge about spatial variation in community dynamics will be greatly improved by elucidation of the population response to the physical environment and it can be analyzed by a discrete Lotka-Volterra model as follows:

$$\ln N_{i,t+1,k} - \ln N_{i,t,k} = \alpha_{i,k} - \beta_{i,k} N_{i,t,k} - \gamma_{i,k} M_{i,t,k} + \epsilon_{i,t,k}.$$

$N_{i,t,k}$ and $M_{t,k}$ are coverage of species i and of other species in plot k at year t, respectively. $\alpha_{i,k}$, $\beta_{i,k}$ and $\gamma_{i,k}$ are intrinsic growth rate, strengths of intra- and interspecific density dependence of species i at plot k, respectively. $\epsilon_{i,t,k}$ is a random variable characterized by normal distribution with zero mean and variance $\sigma^2_{i,k}$. $\epsilon_{i,t,k}$ represents the variation which was affected by effects other than intra- and interspecific density dependence of species i at plot k. Therefore, we can elucidate the features of the population response to the physical environment and its spatial variation by analyzing the difference in the properties of temporal variabilities of $\epsilon_{i,t,k}$ (e.g. the magnitude and variability) among species and sites.

4.3 Conclusion

In this study, I examined the spatial variation in the temporal variability of community structure and its mechanisms by analyzing decadal time series data of rocky intertidal sessile assemblages along the Pacific coast of eastern Hokkaido, Japan. I found that vertical patterns of seasonal community dynamics and its major driving processes reflected the indirect influence of the vertical distribution of species (chapter 2). I also found that horizontal variation in year-to-year community dynamics largely depended on environmental stochasticity, although community dynamics were under control of strong intraspecific density dependence (chapter 3). The implications of this study are twofold. First, the paths of the causal relationships from the abiotic environment to community dynamics were different among time scales in rocky intertidal sessile assemblages. Second, our knowledge about spatial variation in community dynamics will be greatly improved by elucidation of the population response to the physical environment.

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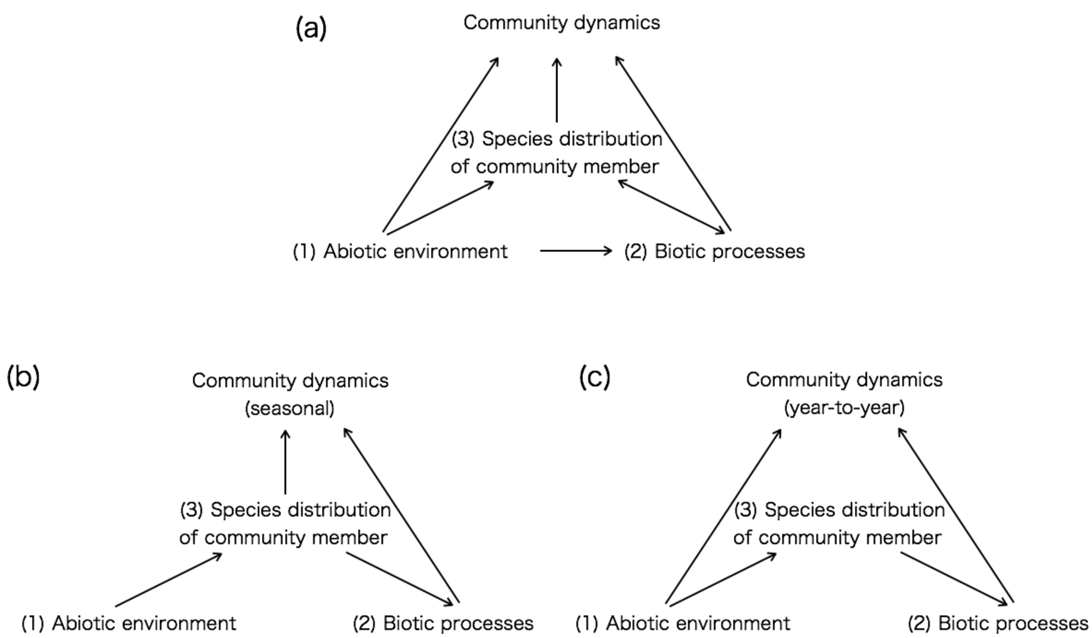

Fig. 1: A schematic diagram shows the factors of community dynamics and its spatial variation