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Diversity patterns and their mechanisms in stream invertebrate assemblages: focusing on effects of disturbance through community-level density dependence

Thesis

In partial fulfillment of the requirements

for the degree of Doctor of Environmental Science

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Chapter I

General Introduction

Species diversity varying with latitude

The latitudinal gradient in species diversity that peaks in the tropics and declines toward the poles is one of the oldest and most fundamental spatial patterns described in ecology (Pianka 1966; Rosenzweig 1995; Willig et al. 2003). Ecologists have been fascinated by the latitudinal gradient since Willdenow (1805), von Humboldt (1808), Darwin (1859), and Wallace (1878) discovered the gradient in nineteenth century. Regardless of the biota's taxonomic affiliation (e.g., mammals, fishes, insects, and plants), geographic context (e.g., continents and oceans), or time domain (e.g., recent and 70Mya), this latitudinal pattern has been reported (Rosenzweig 1995; Willig et al. 2003). The explanations for the latitudinal gradient are still insufficient although almost two centuries lapse after the discovery (Clarke 1992; Rohde 1992; Rosenzweig 1995; Lyons & Willig 1999; Waide et al. 1999; Colwell & Lees 2000; Gaston 2000; Willig et al. 2003).

Latitudinal gradients at regional scales

More than 30 hypotheses have been proposed to explain the latitudinal gradient in species diversity (Rohde 2002; Willig et al. 2003). Although these hypotheses focus on various factors (e.g., area, energy, climate and habitat heterogeneity; Rohde 1992; Rosenzweig 1995), the spatial scales at which analyses are formed may be critical because the effects of influential factors should vary with grain and extent size (Willig et al. 2003; Rahbek 2005). Factors that generate latitudinal gradients at broad spatial scales are rarely identified because several candidate factors change simultaneously with latitude (Gotelli & Ellison 2002). In particular, it is difficult to distinguish the influences of abiotic environmental factors from those of historical factors, such as differential speciation and dispersal, at broad spatial scales (Ricklefs & Schluter 1993; Gotelli & Ellison 2002). At the continental and global scales, abiotic environmental factors and historical factors may change concurrently with latitude. In contrast, at regional scales, where assemblages share an historical background, only abiotic environmental factors change with latitude. Therefore, examining latitudinal patterns at regional scales, rather than the global scale (e.g. temperate-tropical gradient) could prove effective for determining the effects of abiotic environmental factors (Gotelli & Ellison 2002).

Effects of trophic interaction on latitudinal gradients

Previous studies, which proposed many hypotheses to account for the latitudinal gradient in species diversity, have focused on external factors such as energy, climate, and habitat heterogeneity (Rohde 1992, Rosenzweig 1995). However, some recent studies have suggested that effects of interactions within assemblages on latitudinal gradients should not be ignored (Buckley et al. 2003; Hillebrand 2004). Buckley et al. (2003) showed that prey species diversity exhibited a latitudinal gradient but predator species diversity not in the entire food webs inhabiting water-filled leaves of pitcher plants. They suggested that trophic interactions may cause differences in latitudinal patterns among trophic levels. Trophic interactions, such as bottom-up and top-down effects, have been recognized to affect species diversity in general (Fretwell 1977; Oksanen et al. 1981; Holzapfel & Mahall 1999; Worm et al. 2002; Lill & Marquis 2003; Borer et al. 2006). If species diversity of predator assemblages exhibits a latitudinal gradient and predator assemblages have positive effects on prey assemblages, prey species diversity would also show a latitudinal gradient through top-down effects. Hence, I should examine not only how external factors influence latitudinal gradients in species diversity, but also how a latitudinal gradient in a guild are influenced by those in other guilds.

Species diversity varying with disturbance

The latitudinal gradient in species diversity have fascinated ecologists for a long time (Pianka 1966; Rosenzweig 1995; Willig et al. 2003), but latitude, in itself, is not really an explanatory variable for variation in species diversity. Essentially, it acts as a surrogate for various environmental factors determining species diversity. Krebs (2001) shows latitudinal gradients in species diversity may be produced by up to eight interrelated causal factors (history, habitat heterogeneity, competition, predation, climate, climatic variability, productivity, and disturbance) although other factors have been hypothesized to influence species diversity (Rahbek 2001, Hawkins et al 2003, Mora et al 2003). Among them, physical disturbance, such as hurricanes, fires, waves, drought, and floods, has been widely believed to be a major determinant of species diversity because that disrupts ecosystem, community, and population structure (Connell 1978, Sousa 1984, Shea et al 2004).

Numerous studies have examined effects of physical disturbance on species diversity, and hump-shaped relationships between species diversity and disturbance, in which diversity peaks at intermediate disturbance, have been receiving much attention (Connell 1978, Hiura 1995, Hacker & Gaines 1997, Townsend et al 1997, Dial & Roughgarden 1998, Buckling et al 2000, Molino & Sabatier 2001, Shea et al 2004) although other diversity-disturbance relationships have been also reported (Mackey & Currie 2001, Hughes et al 2007). Two important hypotheses have been proposed to explain the hump-shaped patterns, intermediate disturbance hypothesis (Connell 1978) and dynamic equilibrium hypothesis (Huston 1994). These hypotheses rest on the assumption that all species exhibit a trade-off in traits; Connell (1978) presumes a trade-off between competitive ability and disturbance tolerance, and Huston (1994) presumes that between competitive ability and growth rate. Under low levels of disturbance, superior competitor exclude competitively inferior species, and then assemblages are dominated by a few superior species. In contrast, under high levels of disturbance, only species that can withstand disturbance or can quickly grow to reach densities sufficient to avoid stochastic extinction after disturbance can persist, and then assemblages are dominated by a few species with high tolerance to disturbance or high growth rate. Then, high diversity is provided by coexistence of species with different traits along a trade-off under intermediate levels of disturbance, and low diversity in low and high disturbance is explained by interspecific competitive exclusion and physical elimination (Connell 1978, Shea et al 2004).

Variation in diversity-disturbance patterns

Many studies have noted the hump-shaped diversity-disturbance relationship, but negative and positive diversity-disturbance relationships have also reported (Mackey & Currie 2001, Hughes et al 2007). Several explanations have been proposed for the variation, including ones based on dependence of spatial scales (Cadotte 2007), interaction with primary production (Kondoh 2001), and neutral model (Kadmon & Benjamini 2006).

Cadotte (2007) focused on spatial scale and indicated that local species richness decreased with disturbance, but regional species richness peaked at intermediate disturbance because differences among patch (i.e., beta diversity) also peaked at intermediate disturbance. On the other hand, Kondoh (2001) and Kadmon & Benjamini (2006) indicated the degree of disturbance that maximizes species richness is influenced by the level of productivity, and then species richness is positively related with disturbance under extreme high productivity but negatively related with that under extreme low productivity. Kondoh (2001) assumed that all species show a clear trade-off in traits between competitive and colonization abilities, whereas Kadmon & Benjamini (2006) assumed that all species show same traits.

As Kondoh (2001) and Kadmon & Benjamini (2006) focused on whether or not assemblages reach the saturation (i.e., presence or absence of competition), variation in diversity-disturbance patterns may depend on strength of competition. The strength of interspecific competition can be dependent on the sum of population densities within a community, community density (Gause 1934, Paine 1966, Wilbur 1997). As community density increases, the community approaches saturation, and interference among species that compete for limited common resources may be elicited (density dependent competition at the community level).

Stream invertebrates in Hokkaido Island to understand latitudinal gradients

Stream invertebrate assemblages in Hokkaido Island are a good model system to understand latitudinal patterns and their mechanisms. The latitudinal gradients in stream invertebrate assemblages are correlated with temperature (Jacobsen et al. 1997; Castella et al. 2001) and precipitation (Beauchard et al. 2003; Vinson & Hawkins 2003) at broad spatial scales. However, because these meteorological factors vary simultaneously with changes in historical factors at broad spatial scales, studies focusing on these factors have been criticized for not distinguishing the effects of meteorological factors from those of other factors (Heino et al. 2003; Vinson & Hawkins 2003; Bonada et al. 2005). To determine the actual effects of meteorological factors, study areas should be appropriately matched to the scale at which historical factors show little variation but meteorological factors vary considerably.

Since Hokkaido Island spans four degrees of latitude (ca. 400 km), it provides an appropriate spatial scale at which to examine the effects of meteorological factors on latitudinal gradients in stream invertebrate assemblages. Thus, I can achieve a greater understanding of latitudinal gradients by focusing on the regional scale (i.e., Hokkaido Island) to discount historical factors and to extract the effects of environmental factors on latitudinal gradients in diversity.

Trophic habits of stream invertebrate assemblages are relatively well known and their guild structure is simple (Warren & Gaston 1992; Wallace & Webster 1996). Since their feed habits can be categorized into three feeding guilds (detritus feeders, periphyton feeders, and carnivores; Merritt & Cummins 1996; Kawai & Tanida 2005), stream invertebrates are good candidates to study effects of trophic interactions on latitudinal patterns in species diversity.

Stream invertebrate assemblages are effective to test effects of disturbance on species diversity. Various relationships between disturbance and species diversity have reported (Robinson & Minshall 1986, Scarsbrook & Townsend 1993, Death & Winterbourn 1995, Townsend et al. 1997, McCabe & Gotelli 2000, Milner et al. 2001, Miyake & Nakano 2002, Death 2002, Mori et al. in press). These diverse results in diversity-disturbance patterns could be interpreted to be due to differences in strength of competition which altered by disturbance. Stream invertebrates are frequently influenced by unexpected flood disturbance (Hynes 1970, Grossman et al. 1982, Resh et al. 1988), which generally reduces community density by direct elimination and indirect decline in their resources (Robinson & Minshall 1986, McCabe & Gotelli 2000, Death & Zimmermann 2005). Hence, competitive interaction has been considered a minor factor in stream invertebrate assemblages because disturbance may moderate competitive interactions between these species (McAuliffe 1983, Hemphill 1991). However, evidences of competitive interactions affecting community structure have recently been accumulated (Kohler 1992, Kohler & Wiley 1997, Kuhara et al. 1999, Cross & Benke 2002). Therefore, by asking whether or not assemblages are influenced by competitive interaction under observed range of disturbance, I could reach better understanding mechanisms generating diversity patterns with physical disturbance in stream invertebrate assemblages.

Objectives of this thesis

In this study, I examined stream invertebrate assemblages in Hokkaido Island to demonstrate two diversity patterns (i.e., latitudinal patterns and diversity-disturbance patterns) and their mechanisms. In Chapter II, I showed a latitudinal gradient in taxonomic richness of entire stream invertebrate assemblages at a regional scale in Hokkaido Island. Then, I demonstrated that variation in flood disturbance, which affected by precipitation with latitude, determined the community density and local extinction rates of rare species, and consequently produced latitudinal gradient in taxonomic richness in entire stream invertebrate assemblages. In Chapter III, I showed detritus feeders and carnivores exhibited latitudinal gradients, but periphyton feeders did not. Then, I demonstrated that the latitudinal gradient in taxonomic richness of carnivores was generated by both qualitative (i.e., taxonomic richness) and quantitative (i.e., individuals) trophic interaction with detritus feeders. In Chapter IV, I showed that taxonomic richness of periphyton feeders peaked at intermediate disturbance, whereas that of detritus feeders was negatively related with disturbance. This differences in diversity-disturbance patterns between the guilds can be better explained by density dependent competition at the community level which altered by disturbance. The hypotheses for variation in diversity –disturbance patterns which proposed by Kondoh (2001), Kadmon and Benjamini (2006), and Cadotte (2007) cannot perfectly explain my results. However, I can explain observed variation in diversity-disturbance pattern by taking differences in efficacy of density dependent competition between dominant core taxa and rare satellite taxa into account. Finally, in Chapter V, I summarized the present studies and discussed diversity patterns and their mechanisms in stream invertebrate assemblages. In addition, I described generality of the present studies and future direction.

Chapter II

Latitudinal gradients in stream invertebrate assemblages at a regional scale on Hokkaido Island, Japan

Introduction

The latitudinal gradient in species diversity that peaks in the tropics and declines toward the poles is one of the oldest and most fundamental spatial patterns described in community ecology (Pianka, 1966; Rosenzweig, 1995; Willig, Kaufman & Stevens, 2003). This latitudinal pattern has been reported for various terrestrial and marine taxa (Rosenzweig, 1995; Hillebrand, 2004). However, latitudinal patterns in species diversity reported for some invertebrates differ from the standard pattern, with peaks in temperate regions (Price *et al.*, 1998; Kouki, Niemelä & Viitasaari, 1994; Janzen, 1981) or reverse latitudinal gradients (Kouki, Niemelä & Viitasaari, 1994; Buckley *et al.*, 2003). Contradictory results have also been reported for stream invertebrate assemblages (Allan & Flecker, 1993; Vinson & Hawkins, 1998). The standard latitudinal gradient is found in Western Europe (Castella *et al.*, 2001), the northern half of Western Australia (Kay *et al.*, 1999) and Sweden (Sandin & Johnson, 2004); an inverse pattern has been reported in Fennoscandia (Heino, 2001, 2002); and no latitudinal patterns have been identified in the Iberian Peninsula (Bonada *et al.*, 2005) and Finland (Heino *et al.*, 2002). In addition, stream invertebrate assemblages show large variation in species diversity, even within similar latitudinal ranges (Vinson & Hawkins, 2003). To date, the causes of these diverse latitudinal patterns in species diversity of stream invertebrates remain unknown (Allan & Castillo, 2007). Hence there is a need to identify factors that influence species diversity and to analyze latitudinal variation in those factors to understand better the diverse latitudinal patterns.

More than 30 hypotheses have been proposed to explain the standard latitudinal gradient in species diversity (Willig, Kaufman & Stevens, 2003). Although these hypotheses focus on various factors (e.g. area, energy, climate and habitat heterogeneity; Rohde, 1992; Rosenzweig, 1995), the spatial scales at which analyses are formed may be critical because the effects of influential factors should vary with grain and extent size (Willig, Kaufman & Stevens, 2003; Rahbek, 2005). Factors that generate latitudinal gradients at broad spatial scales are rarely identified because several candidate factors change simultaneously with latitude (Gotelli & Ellison, 2002). In particular, it is difficult to distinguish the influences of abiotic environmental factors from those of historical factors, such as differential speciation and dispersal, at broad spatial scales (Ricklefs & Schluter, 1993; Gotelli & Ellison, 2002). At the continental and global scales, abiotic environmental factors and historical factors may change concurrently with latitude. In contrast, at regional scales, where assemblages share an historical background, only abiotic environmental factors change with latitude. Therefore, examining latitudinal patterns at regional scales, rather than the global scale (e.g. temperate-tropical gradient) could prove effective for determining the effects of abiotic environmental factors (Gotelli & Ellison, 2002).

The latitudinal gradients observed in stream invertebrate assemblages are correlated with variation in abiotic environmental factors that vary with latitude (Jacobsen, Schltz & Encalada, 1997; Vinson & Hawkins, 2003). Stream invertebrate assemblages vary with temperature (Jacobsen, Schltz & Encalada, 1997; Castella *et al.*, 2001) or precipitation (Beauchard, Gagneur & Brosse, 2003; Vinson & Hawkins, 2003) at broad spatial scales. Temperature is related to primary productivity, metabolic rates and organism distributions (Vannote & Sweeney, 1980; Ward & Stanford, 1982), and precipitation can be used as a proxy for flood disturbance (Hughes & James, 1989; Poff, Tokar & Johnson, 1996). However, because these meteorological factors vary simultaneously with changes in historical factors at broad spatial scales, studies focusing on these factors have been criticized for not distinguishing the effects of meteorological factors from those of other factors (Heino *et al.*, 2003; Vinson & Hawkins, 2003; Bonada *et al.*, 2005). To determine the actual effects of meteorological factors, study areas should be appropriately matched to the scale at which historical factors show little variation but meteorological factors vary considerably. In this study, I examined stream invertebrate assemblages in Hokkaido Island, Japan. Since Hokkaido Island spans four degrees of latitude (ca. 400 km), it provides an appropriate spatial scale at which to examine the effects of meteorological factors on latitudinal gradients in stream invertebrate assemblages.

In addition to resolving problems with the spatial scales of analyses, indices used to capture the multiple facets of diversity should be standardized. Although species richness has been used as a surrogate for diversity in many studies (e.g. Loreau *et al.*, 2002), diversity indices based on relative abundance (such as the Shannon index), as well as species richness, are important for capturing the full complexity of diversity. Because species richness is influenced by abundance, it can be a misleading indicator of biological diversity (Wilsey *et al.*, 2005). Therefore, I used two indices (the Shannon index and taxon richness) to describe latitudinal patterns in diversity of stream invertebrate assemblages. In addition, evenness and abundance were quantified to examine processes creating latitudinal patterns in diversity. Diversity indices, such as the Shannon index, combine the number of taxa and their evenness across sites (Magurran, 2004). On the other hand, taxon richness (the number of taxa per unit area) depends on both evenness and abundance (Gotelli & Colwell, 2001). Therefore, I can achieve a greater understanding of latitudinal gradients in diversity by examining the contributions of taxon richness and evenness to taxon diversity, and those of evenness and abundance to taxon richness.

I addressed three questions to help understand latitudinal patterns. (1) Are there latitudinal gradients in taxon diversity and taxon richness of stream invertebrate assemblages in Hokkaido Island irrespective of historical factors? (2) What primary processes create these latitudinal gradients in taxon diversity and taxon richness? Separate analyses of taxon diversity, taxon richness, evenness, and abundance help to determine how latitudinal gradients in taxon diversity and taxon richness are formed. (3) What environmental factors are linked to processes that contribute to latitudinal gradients in taxon diversity and taxon richness? I examined the effects of meteorological factors (temperature and precipitation), catchment factors (area, slope, and altitude), physical factors (poor/riffle and substrate), and water quality (nitrogen and phosphorus) on stream invertebrate assemblages and their latitudinal patterns.

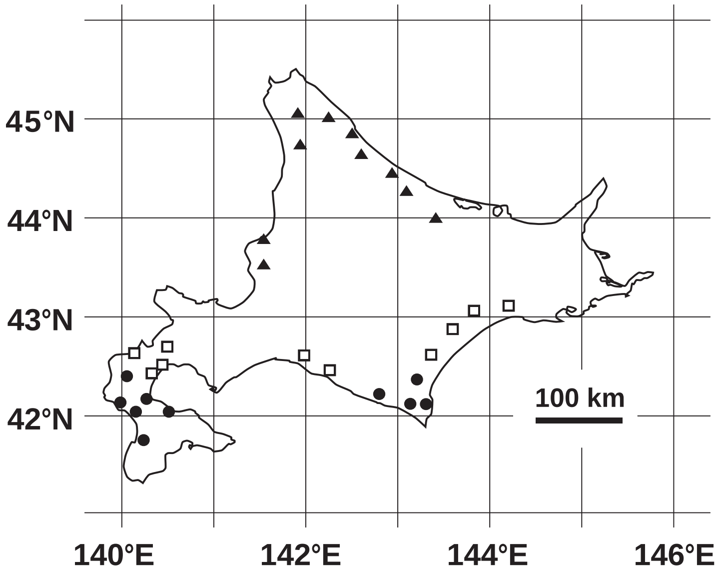

Fig. 2-1 Locations of 30 study streams in Hokkaido Island, Japan. Symbols indicate northern (triangles), middle (squares) and southern (circles) groups when the 30 sites were evenly divided into three groups based on latitude.

Table 2-1 Means, standard deviations (SD) and ranges for nine environmental variables measured in the 30 mountain streams.

Environmental variable	Mean	SD	Range	
			Min	Max
Temperature (°C)	13.4	1.2	9.3	15.0
Precipitation (mm)	100.4	64.4	21.0	304.0
Catchment area (km^2)	7.3	4.2	1.7	13.4
Catchment slope (%)	17.5	5.4	8.1	26.5
Altitude (m)	104.5	69.9	28.0	318.0
Froude number	0.35	0.11	0.23	0.72
Substrate heterogeneity	0.91	0.34	0.41	1.62
Total dissolved nitrogen (mg L^{-1})	0.17	0.15	0.01	0.51
Total dissolved phosphorus (mg L^{-1})	0.021	0.013	0.007	0.055

Materials and methods

Study sites

In June 2004 data were collected from 30 mountain streams in Hokkaido Island (see Plate 2-1), which encompasses ca. 79,500 km^2 and is the northernmost island of Japan (latitude 41°24’N–45°31’N, longitude 139°46’E–145°49’E; Fig. 2-1). The intensity of flood disturbances was monitored from June to November 2005 in 12 mountain streams randomly selected from the 30 study streams. According to the Köppen-Geiger climate classification, the climate of Hokkaido Island is classified as “Df”; the highest mean monthly temperature is above 10°C, the lowest mean monthly temperature is below –3°C, and significant precipitation can be measured in all seasons (Kottek *et al.*, 2006). The study streams were located in different drainage basins and were separated by at least 30 km. Spring-fed, lake-outlet, polluted, and acid streams were excluded. Approximate channel slopes in this study reach, which were obtained from a 1:250,000 map, ranged from 2 to 5%. The pH values ranged from 6.4 to 7.3, and conductivity was 26 to 103 μS cm^{-1}. Other stream characteristics are shown in Table 2-1. Vegetation in the catchment areas was primarily mixed forests with deciduous broad-leaved and coniferous trees.

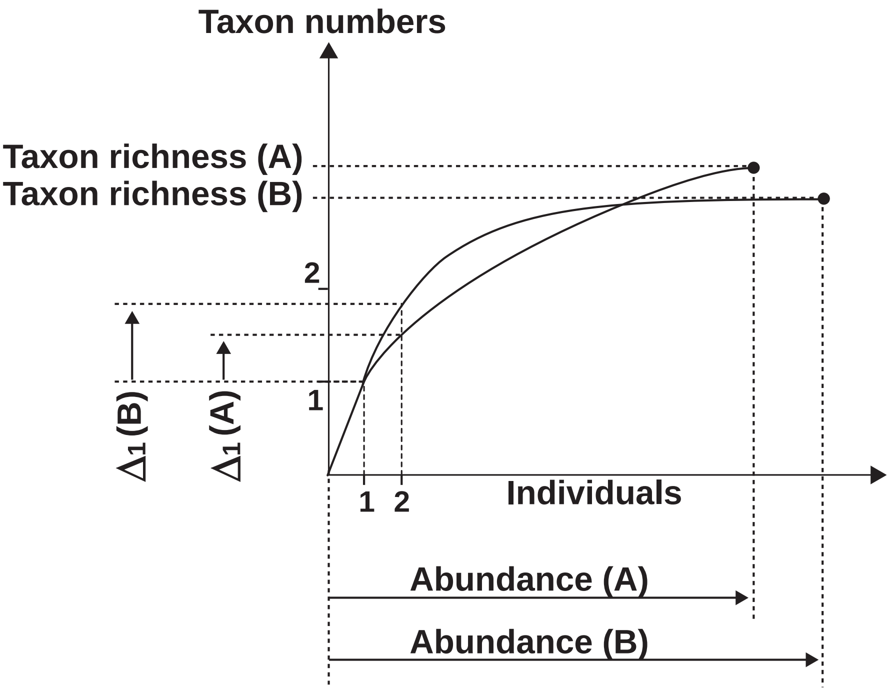

Fig. 2-2 Rarefaction curves for two hypothetical assemblages from different samples (A and B). Taxon richness is represented by taxon number at the endpoint of the rarefaction curve. Abundance corresponds to the wire length of the rarefaction curve toward the *x*-axis. Evenness index (Δ_1) is approximated by the initial rise of the rarefaction curve toward the *y*-axis. Therefore, taxon richness is determined by a balance between abundance and evenness.

Field procedures

A 20-m riffle in each stream was selected as a study reach. Each study reach was evenly divided into three sections, and benthic invertebrates were sampled from each section using a Surber sampler (0.25 × 0.25-m area, 250-µm mesh). Collected samples were vigorously rinsed in a tray and sieved through a 250-µm mesh to isolate invertebrates from particulate organic matter; adherent invertebrates were picked up with forceps (Miyake & Nakano, 2002; Miyake, Hiura & Nakano, 2005). Both invertebrates and detritus were preserved in a 5% buffered formalin solution until they were analyzed. Within each study reach, five evenly-spaced transects with three evenly-spaced measuring points were established. Water velocity and depth were measured at each point after stream invertebrates were sampled. Water velocity was measured with a portable current meter (Model CR-7WP; Cosmo-Riken Co. Ltd., Kashihara, Japan). Substrate type at each point was measured and classified as bedrock, sand (dominant particle size <2 mm), gravel (2–16 mm), pebble (17–64 mm), cobble (65–256 mm), or boulder (>256 mm). Samples for water chemistry were taken directly from each study reach using polyethylene bottles. Particles taken from the area adjacent to each study reach and corresponding to the 50th, 75th, and 90th percentiles of the substratum size distribution (excluding bedrock) were painted and arranged on the surface of the streambed in regular arrays (five rows consisting of three different particle size classes, randomly assigned to transects and placed 1 m apart). Subsequently, the movement of these particles was monitored twice a month (12 occasions). On each occasion, particles that had moved were noted and replaced.

Laboratory procedures and data treatment

In the laboratory, invertebrates were sorted from each Surber sample and identified to the lowest possible taxonomic level, usually genus or species, using the taxonomic keys in Merritt & Cummins (1996) and Kawai & Tanida (2005). Otherwise, specimens were identified to family and subfamily. Taxon diversity and taxon richness were quantified for the three sections from each study reach. The Shannon index was calculated as a measurement of taxon diversity (hereafter, "taxon diversity"; Magurran, 2004). Taxon richness was defined as the observed number of taxa per unit area. To examine processes affecting the development of taxon diversity and taxon richness, abundance (the observed number of individuals per unit area) and Δ_1 were quantified. Values of Δ_1, which is not biased by sample size or species richness, were calculated as a measure of evenness (hereafter, “evenness”; Olszewski, 2004). This index of evenness can be readily interpreted as the probability that the second individual randomly selected from a sample (without replacement of the first specimen) will be of the same species as the first individual (Olszewski, 2004). The Shannon index, as a measure of taxon diversity, combines the number of taxa (i.e. taxon richness) and their evenness as components of biological diversity (Magurran, 2004). Taxon richness is influenced by evenness and abundance (Gotelli & Colwell, 2001). In individual-based species accumulation curves (i.e. rarefaction curves), taxon richness is represented by the number of taxa at the endpoints of the curves (Fig. 2-2). Abundance corresponds to the wire lengths of rarefaction curves toward the x-axis. Because Δ_1 is defined by the difference between the expected richness for the first individual (= 1) and for the second individual in rarefaction curves, it is roughly represented by the initial rise in a rarefaction curve toward the y-axis (Olszewski, 2004). The steeper and longer a rarefaction curve is, the higher the estimate of taxon richness (Bunge & Fitzpatrick, 1993; McCabe & Gotelli, 2003). Thus, analyses of abundance and Δ_1 could reveal whether higher taxon richness results from the passive accumulation of individuals (high abundance), shifts in evenness, or a combination of the two.

The Froude number, which is a useful descriptor of channel flow (Allan & Castillo, 2007), was calculated from average water depth and average current velocity at each reach according to Gordon *et al.* (2004). Low values of Froude number (generally <0.18) are characteristic of pool habitats, while higher values (>0.41) are typical of riffle habitats (Jowett, 1993). Substrate types were coded in order of coarseness as follows: 1 = bedrock, 2 = sand, 3 = gravel, 4 = pebble, 5 = cobble, 6 = boulder (Bain, Finn & Booke, 1985; Inoue & Nunokawa, 2002). The standard deviations of these coded values, which were measured at each point, were used to express substrate heterogeneity at each reach (Bain, Finn & Booke, 1985; Inoue & Nunokawa, 2002). Total dissolved nitrogen and total dissolved phosphorus were analyzed using an auto analyzer (AACS-4; BL-TEC Co. Ltd., Osaka, Japan) after water chemistry samples were filtered using a 0.45-μm membrane filter. Mean temperature and accumulated precipitation during the month before sampling were calculated from the Japan Meteorological Agency data obtained at meteorological station nearest each study site. Catchment area, catchment slope and altitude were derived from digital elevation maps using geographical information system software (ArcGIS; ESRI Inc., Redland, CA, USA). The intensity of disturbance at a site was measured as the average of the percentage of painted particles of all size classes that had moved in each month (see Townsend, Scarsbrook & Dolédec, 1997).

Statistical analysis

The relationship between distance and similarity in stream invertebrate assemblages was analyzed using a Mantel test (10,000 permutations). If stream invertebrate assemblages in Hokkaido Island share a common historical background, similarity between study sites should show no relationship with distance. Bray-Curtis dissimilarity (Sørensen incidence) was calculated based on qualitative data (presence/absence) from pooled samples from the three sections in each stream. Geographic distance among study sites was calculated using latitude and longitude coordinates.

Latitudinal and longitudinal gradients in taxon diversity, taxon richness, abundance and evenness were analyzed using generalized linear mixed models (GLMMs). Response variables in these models were taxon diversity, taxon richness, abundance, and evenness; explanatory variables were the fixed effects of latitude and longitude. The three replicates from each stream were treated as random effects. The relationships of taxon diversity with taxon richness and evenness were also analyzed. To determine the effects of abundance and evenness on taxon richness, I generated individual-based rarefaction curves and analyzed the relationships of taxon richness with abundance and evenness. A model selection procedure was performed based on the second-order Akaike information criteria corrected for small sample size (AICc) to assess the effects of taxon richness and evenness on taxon diversity and the effects of abundance and evenness on taxon richness. These analyses were performed using GLMMs assuming Gaussian error distributions for taxon diversity and evenness, and assuming Poisson error distributions for taxon richness and abundance. The statistical significance of each model was evaluated through a likelihood ratio test. Rarefaction curves were obtained using Hurlbert's (1971) rarefaction equation using the R environment for statistical computing (R Development Core Team, 2006) with the associated package vegan (Oksanen *et al.*, 2007).

Logistic regression was used to test the relationship between taxon rank and presence/absence in each taxon. I evenly divided the 30 study sites based on latitude, creating three groups of 10 sites each. The 10 northernmost sites and the 10 southernmost sites were the northern and southern group, respectively (Fig. 2-1). The remaining 10 sites were the middle group (Fig. 2-1). In each group, I plotted presence ($y = 1$) or absence ($y = 0$) against taxon sequence (most to least abundant; i.e. taxon rank) and evaluated the 0.5 presence–absence probability for taxon rank in logistic regression. The statistical significance of each model was evaluated through a likelihood ratio test.

The effects of monthly accumulated precipitation on disturbance were analyzed using a GLMM that assumed Gaussian error distribution. The statistical significance of the model was evaluated with a likelihood ratio test. Bed disturbance was included in the model as a response variable, and accumulated precipitation served as an explanatory fixed-effect variable. Month was treated as a random effect because of pseudoreplication.

The effects of environmental factors on stream invertebrate assemblages were modelled using GLMMs. Response variables in the models were taxon diversity, taxon richness, abundance and evenness; explanatory fixed-effects variables were temperature, precipitation, catchment area, catchment slope, altitude, Froude number, substrate heterogeneity, total dissolved nitrogen and total dissolved phosphorus (Table 2-1). The three replicates from each stream were treated as random effects. I constructed all possible models from the nine variables and identified the best model using AICc. The relative importance of variables (RIV) was assessed by summing the Akaike weights for each variable across all models containing that variable (Burnham & Anderson, 2002). Thus, if a given variable was consistently included in models with low AICc, its RIV would be much larger than that of a variable that was not associated with good-fitting models. These analyses were conducted using GLMMs assuming Gaussian error distributions for taxon diversity and evenness and assuming Poisson error distributions for taxon richness and abundance. The statistical significance of each model was evaluated using a likelihood ratio test.

Linear regression analyses were used to assess relationships of latitude with temperature, precipitation, catchment area, catchment slope, altitude, Froude number, substrate heterogeneity, total dissolved nitrogen, and total dissolved phosphorus.

All analyses were performed using the R environment for statistical computing (R Development Core Team, 2006) with the associated packages lme4 (Bates & Sarkar, 2007) and vegan (Oksanen *et al.*, 2007). I considered results to be statistically significant when $P < 0.05$.

Results

A total of 94 taxa and 30,983 individuals were found in samples from the 30 sites. Each Surber sample contained 14 to 37 taxa and 45 to 1,078 individuals. The similarity in stream invertebrate assemblages did not decay with distance (Fig. 2-3). Bray-Curtis dissimilarity between study sites did not show a significant relationship with distance (Mantel test; $r = 0.06$, $P = 0.11$).

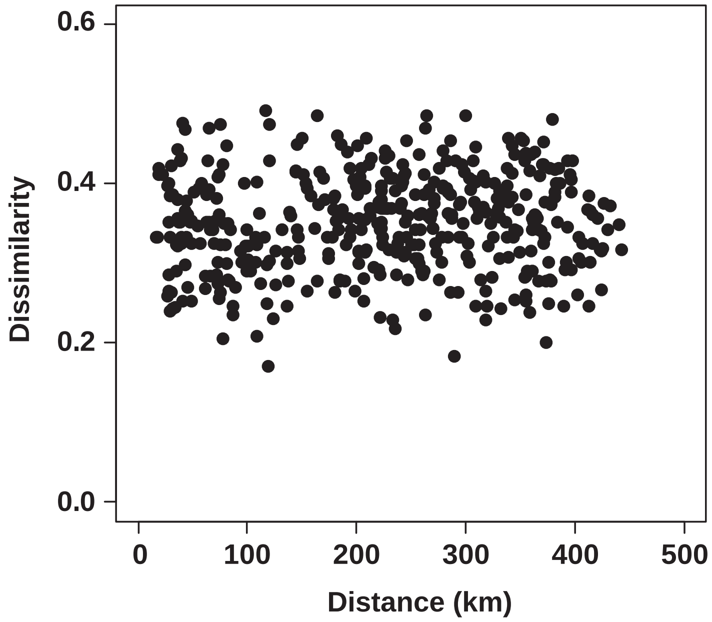

Fig. 2-3 Relationship between geographic distance and Bray-Curtis dissimilarity based on presence/absence data.

Latitudinal and longitudinal gradients

Taxon diversity, taxon richness, and abundance all increased significantly with latitude (likelihood ratio test; taxon diversity: $\chi^2 = 4.42$, $P = 0.03$: taxon richness: $\chi^2 = 7.15$, $P = 0.007$; abundance: $\chi^2 = 16.40$, $P < 0.001$; Fig. 2-4), whereas the relationship between evenness and latitude was not significant ($\chi^2 = 1.95$, $P = 0.16$). There were no significant longitudinal patterns in taxon diversity, taxon richness, abundance, and evenness ($\chi^2 = 0.03$–2.57, $P = 0.11$–0.86; Fig. 2-4).

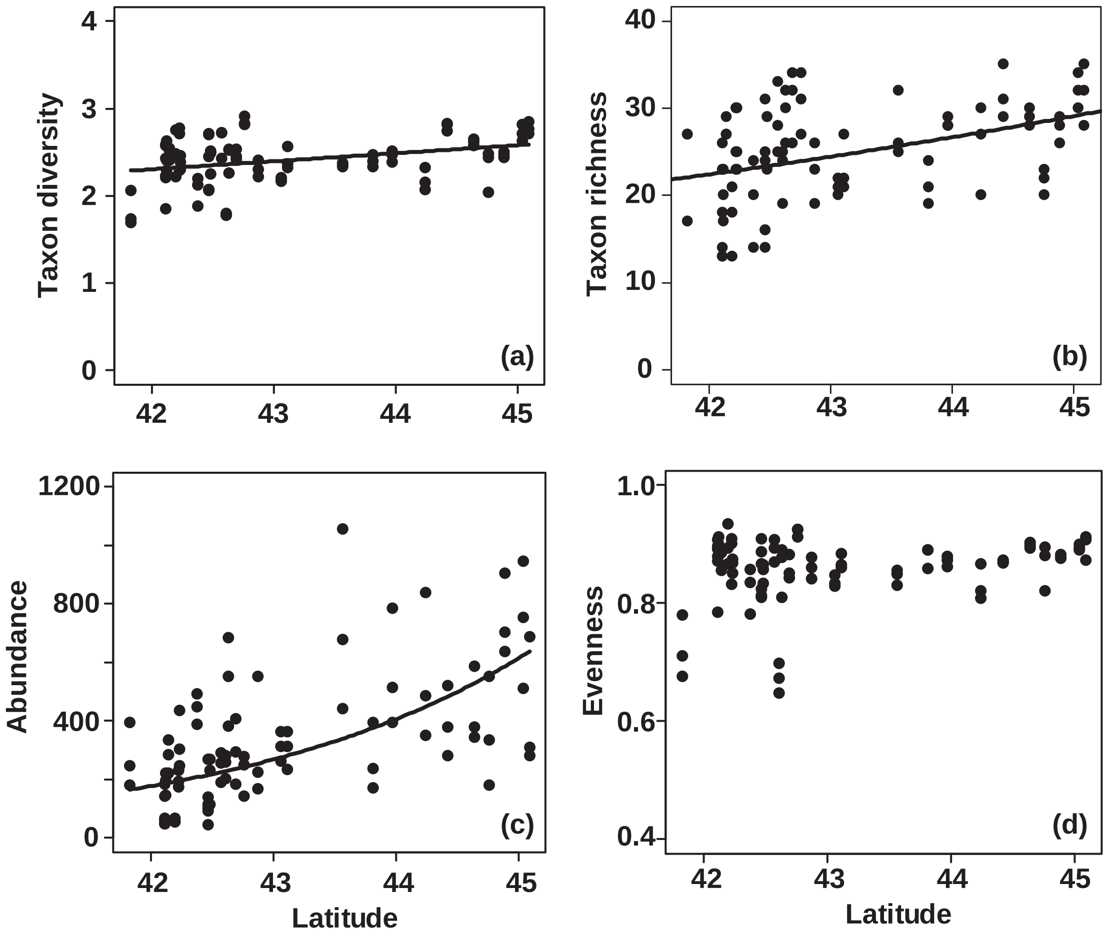

Fig. 2-4 Latitudinal gradients in a) taxon diversity (Shannon index), b) taxon richness (observed number of taxa), c) abundance per Surber sample (0.0625 m^2) and d) evenness (Δ_1). Solid lines represent significant relationships.

Relationships among taxon diversity, taxon richness, abundance, and evenness

Variation in taxon diversity was closely related with taxon richness and evenness (χ^2 = 176.62, $P < 0.001$; Fig. 2-5). The best model for taxon richness included both abundance and evenness (χ^2 = 52.96, $P < 0.001$; Fig. 2-5).

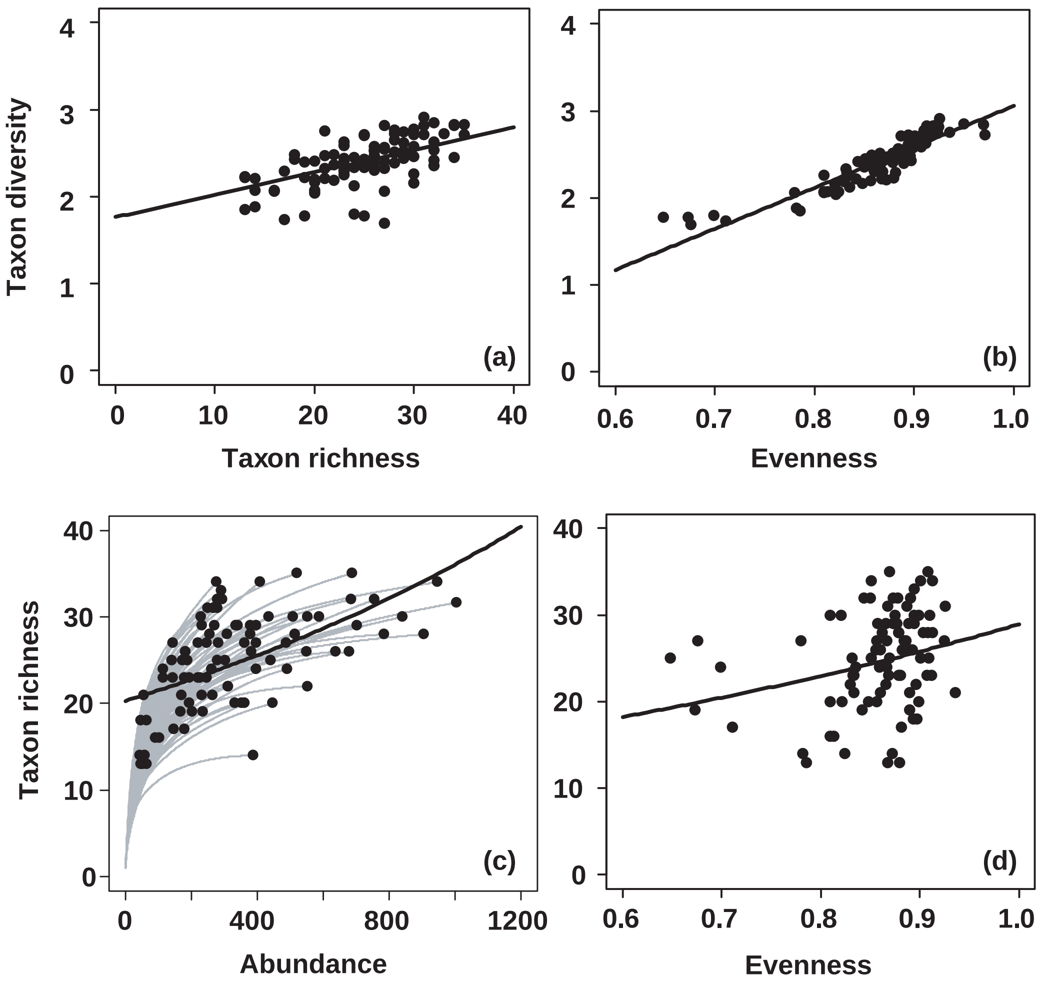

Fig. 2-5 Relationships of taxon diversity (Shannon index) with a) taxon richness (observed taxon number) and b) evenness (Δ_1), and relationships of taxon richness with c) abundance per Surber sample (0.0625 m^2) and d) evenness. Solid lines represent significant relationships and gray lines in (c) represent individual-based rarefaction curves expressing the relationship between expected taxon number and abundance.

Relationships between presence/absence and rank in each taxon

Logistic regression models were significant in all three groups (likelihood ratio tests; northernmost group: $\beta_0 = 4.6$, $\beta_1 = -0.049$, $\chi^2 = 14.31$, $P < 0.001$; middle group: $\beta_0 = 5.9$, $\beta_1 = -0.076$, $\chi^2 = 33.45$, $P < 0.001$; southernmost group: $\beta_0 = 6.0$, $\beta_1 = -0.082$, $\chi^2 = 40.03$, $P < 0.001$).

Taxon rank at the 0.5 presence–absence probability tended to be higher in the south (northernmost group: rank = 95; middle group: rank = 78; southernmost group: rank = 73; Fig. 2-6), suggesting that the high taxon richness in the northernmost group may result from the presence of rare species.

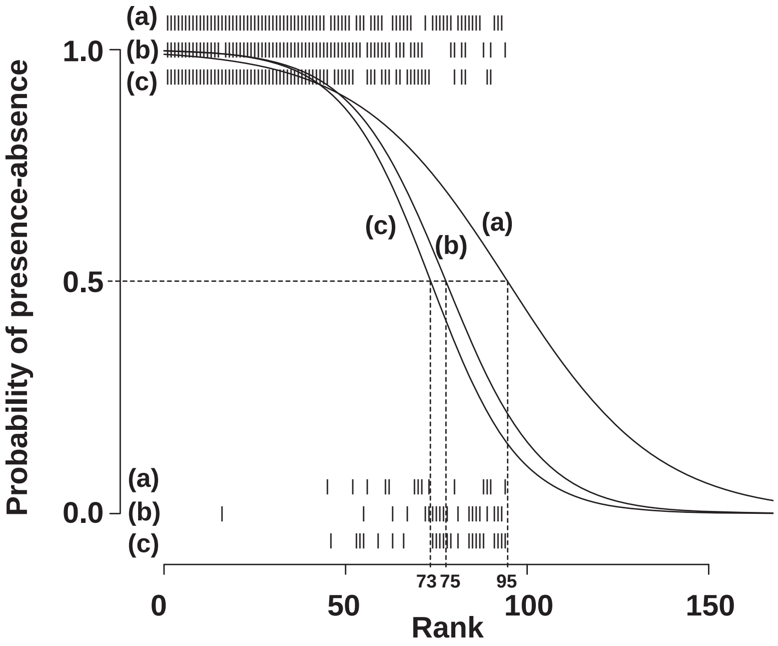

Fig. 2-6 Relationship between the probability of presence–absence and taxon rank in the 30 sites evenly divided into three groups of 10 from north to south: northern (a), middle (b) and southern (c) groups. Dotted lines indicate the 50% presence–absence probability, and vertical bars indicate presence (y = 1) and absence (y =0) for each taxon in the respective groups. Solid lines represent significant relationships.

Table 2-2 Linear regression coefficients and *P*-values for comparisons between latitude and nine environmental variables.

Environmental variable	Coefficient	*P*
Temperature (°C)	0.11	0.56
Precipitation (mm)	–0.70	<0.001
Catchment area (km^2)	0.22	0.25
Catchment slope (%)	–0.36	0.05
Altitude (m)	–0.01	0.96
Froude number	–0.04	0.82
Substrate heterogeneity	–0.34	0.07
Total dissolved nitrogen (mg L^{-1})	–0.07	0.72
Total dissolved phosphorus (mg L^{-1})	–0.14	0.45

Latitudinal gradients in environmental conditions

Precipitation and catchment slope showed clear latitudinal gradients (Table 2-2), decreasing from south to north. The relationship of latitude with substrate heterogeneity was marginally significant. Temperature, catchment area, altitude, Froude number, total dissolved nitrogen, and total dissolved phosphorus did not show clear relationships with latitude.

Factors relating to variation in stream invertebrate assemblages

Disturbance increased significantly with monthly accumulated precipitation (likelihood ratio test, $\chi^2 = 50.59$, $P < 0.001$, disturbance = 0.22 × precipitation – 11.54). High monthly precipitation may cause high discharge events and bed movement (Fig. 2-7), suggesting that monthly precipitation can be used as a proxy for disturbance. Precipitation, catchment area, substrate heterogeneity and total dissolved nitrogen were selected as influential factors that explained variation in stream invertebrate assemblages (Table 2-3). The best model for taxon diversity included precipitation, substrate heterogeneity and catchment area. Taxon diversity was positively influenced by substrate heterogeneity and catchment area but was negatively affected by precipitation. The best models for taxon richness and abundance included precipitation, and these were negatively related to precipitation. Abundance was influenced by total dissolved nitrogen, showing coincident increases. Evenness was positively related with substrate heterogeneity and catchment area. Temperature, catchment slope, altitude, Froude number, and total dissolved phosphorus were not included in the best models. Substrate heterogeneity (RIV = 0.75) and precipitation (0.72) were more important for taxon diversity than catchment area (0.61). Precipitation (RIV = 1.00) was strongly related with abundance, compared to total dissolved nitrogen (0.65). Substrate heterogeneity (RIV = 0.68) was more important for evenness than catchment area (0.59).

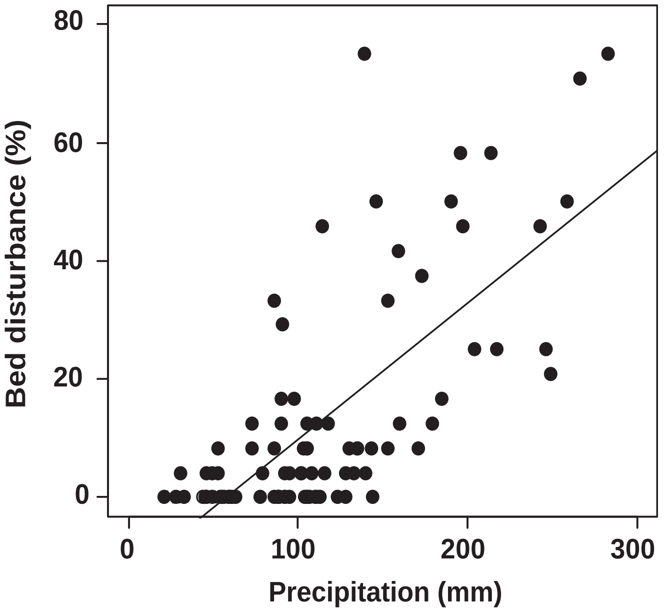

Fig. 2-7 Effects of monthly accumulated precipitation on bed disturbance in mountain streams on Hokkaido Island. Solid line represents significant relationship.

Table 2-3 Best-fit models for explaining patterns in taxon diversity, taxon richness, abundance and evenness. All possible models from combinations of nine environmental variables (temperature, precipitation, catchment area, catchment slope, altitude, Froude number, substrate heterogeneity, total dissolved nitrogen and total dissolved phosphorus) were constructed and model selection was performed using AICc. The relative importance of each variable (RIV) was assessed by summing the Akaike weights for the variable across all models that included the variable; RIV values are given in parenthesis after each environmental factor for each best-fit model. Plus and minus signs indicate the direction of the relationship.

	Best-fit model	*df*	χ^2	*P*
Taxon diversity	+ Substrate heterogeneity (0.75) – precipitation (0.72) + catchment area (0.61)	3	14.33	0.002
Abundance	– Precipitation (1.00) + total dissolved nitrogen (0.65)	2	26.22	<0.001
Evenness	+ Substrate heterogeneity (0.68) + catchment area (0.59)	2	6.29	0.04

Discussion

Similarity in stream invertebrate assemblages

Similarity based on presence/absence data was not related with geographic distance (Fig. 2-3), although distance-decay in similarity among communities has been widely recognized in many ecosystems (Soininen, McDonald & Hillebrand, 2007). The observed lack of decay is probably because Hokkaido Island is on a relatively compact spatial scale and its geological history is relatively simple (Ishigaki & Fukuda, 1994). These findings suggest that communities observed in Hokkaido Island may have been assembled from a common species pool and support my assumption that historical factors have little effect on differences among stream invertebrate assemblages in Hokkaido Island.

Latitudinal gradients

Clear latitudinal gradients in the taxon diversity and taxon richness of stream invertebrates were detected in mountain streams on Hokkaido Island (Fig. 2-4). These gradients show patterns that are reversed from the standard latitudinal gradient observed for various taxa. Vinson & Hawkins (2003) showed that Ephemeroptera, Plecoptera, and Trichoptera, which are generally dominant in mountain streams, do not show simple and monotonic latitudinal gradients in genera richness at a global scale. Heino (2001, 2002) also reported a reverse latitudinal gradient in taxon richness of stoneflies in Fennoscandia and suggested that this opposite latitudinal gradient was generated by both historical and abiotic environmental factors. Factors that might account for reversed latitudinal gradients have not yet been identified (Allan & Castillo, 2007), because it is difficult to distinguish the effects of abiotic environmental factors from those of historical factors. However, the present study concentrated on the effects of environmental factors without being constrained by historical factors.

Processes of latitudinal gradients

The latitudinal pattern in taxon diversity was formed through processes of directional variation in taxon richness. Taxon diversity (the Shannon index) is a metric that combines taxon richness and evenness (Magurran, 2004); these two measurements can both contribute to variation in taxon diversity (Fig. 2-5). The fact that a latitudinal gradient was found in taxon richness but not in evenness (Fig. 2-4) suggests that the latitudinal gradient in taxon diversity resulted from the gradient in taxon richness. Like taxon diversity, taxon richness is positively influenced by two metrics, abundance and evenness (Gotelli & Colwell, 2001), and these

Plate 2-1. A study stream in Hokkaido Island (Japan). Photo credit: T. Mori.

relationships were confirmed in the present study system (Fig. 2-5). The clear latitudinal gradient observed in abundance, coupled with the absence of a similar pattern in evenness (Fig. 2-4), suggests that the latitudinal gradient in taxon richness was driven by that in abundance.

Previous studies have suggested that higher local population densities reduce the local extinction rates of rare species, and that the persistence of rare species results in increases in diversity (Srivastava & Lawton, 1998; Yee & Juliano, 2007). Coddington, Young & Coyle (1996) and Andrew & Hughes (2004) indicated that rare species contribute to latitudinal gradients in species richness. In my study, taxon rank at the 0.5 presence–absence probability tended to increase from north to south (Fig. 2-6), whereas evenness, which is related with the distribution of relative abundance, varied little among study streams (Fig. 2-4). These results suggest that taxon richness may be higher in streams with higher abundance because rare species are more likely to be retained in those sites. Hence, the present latitudinal gradient in taxon richness may be generated by directional variation in abundance (passive accumulation) from south to north, which results in increases in taxon diversity.

Environmental factors affecting latitudinal gradients

Precipitation can be used as a proxy for disturbance in this study system (Fig. 2-7), as shown in other studies (Hughes & James, 1989; Poff, Tokar & Johnson, 1996) and was negatively related to taxon diversity, taxon richness and abundance in this study (Table 2-3). Stream invertebrates are sensitive to flood disturbances from high precipitation (Smith *et al.*, 2001). Disturbances from increased flows reduce taxon diversity, taxon richness and abundance of stream invertebrates by removing animals (Death & Winterbourn, 1995; McCabe & Gotelli, 2000; Miyake & Nakano, 2002). Similarly, the observed latitudinal variation in flood disturbance generated the pattern of taxon richness and resulted in the pattern of taxon diversity. The processes that created variation in taxon richness are consistent with the More Individuals Hypothesis discussed by Srivastava & Lawton (1998). This hypothesis is based on species-energy theory (Wright, 1983) and postulates that greater productivity supports higher population densities, which lower the extinction rates of rare species (Srivastava & Lawton, 1998; Yee & Juliano, 2007). Increases in the persistence of rare species lead to increases in diversity (Srivastava & Lawton, 1998; Yee & Juliano, 2007). Disturbance can play a role similar to that of productivity in the More Individuals Hypothesis. Flood disturbances may interrupt the growth of populations, resulting in decreases in species richness (McCabe & Gotelli, 2000). In the present study precipitation, which was closely related to flood disturbances and varied with latitude, had negative effects on abundance (Tables 2-2 and 2-3), and the directional variation in abundance from south to north could have influenced the local extinction rates of rare species (Fig. 2-6). Therefore, variation in flood disturbance, which affected by precipitation with latitude, determined the abundance and local extinction rates of rare species, and consequently produced latitudinal gradient in taxon richness in my study system.

The availability of nutrients such as nitrogen and phosphorus can regulate the primary production of benthic algae (Hill, Boston & Steinman, 1992; Rosemond, 1993). In addition, nutrient enrichment can enhance the growth of microbes which colonize litter material (Gulis *et al.*, 2004). Many studies have reported increases in the abundance of stream invertebrates with increases in productivity and litter quality (Riseng, Wiley & Stevenson, 2004; Cross *et al.*, 2006). In the present study, total dissolved nitrogen had a positive effect on abundance through increases in food resources. Although taxon richness increased with abundance (Fig. 2-5), total dissolved nitrogen was not included in the best-fit model for taxon richness. Total dissolved nitrogen may have been less important than precipitation for abundance (Table 2-3).

In this study, I was able to detect the effects of an environmental factor (precipitation) on the latitudinal gradients in taxon diversity and taxon richness without interference from historical factors. I also demonstrated processes that produced the latitudinal gradients in the diversity of stream invertebrate assemblages. Flood disturbance varying at large spatial scales may be an important process in the creation of latitudinal patterns. However, flood disturbance would not show monotonic latitudinal gradients at the global or continental scales, and the relationship between flood disturbance and latitude may vary among regions. This between-system variation may be the cause of the diverse latitudinal patterns observed in stream systems. I can better understand latitudinal gradients in diversity by examining relationships between disturbance and stream invertebrate assemblages at the regional scales and beyond. Although I focused here on the effects of abiotic environmental factors on latitudinal patterns in diversity, biotic factors such as competitive interactions should not be ignored (Pianka, 1966). I analyzed entire assemblages, but stream invertebrate assemblages consist of guilds that compete for common resources. Therefore, future studies need to consider guilds and to analyze the effects of abiotic and biotic factors and their interactions on patterns of diversity.

Chapter III

Effects of trophic interactions on latitudinal gradients in species diversity

Introduction

Latitudinal gradients in species diversity which decreases from tropical to poles are one of the striking patterns founded in ecology (Rohde 1992; Gaston 2000; Hillebrand & Azovsky 2001; Willig et al. 2003) and have been well documented for a variety of taxa in both terrestrial and marine ecosystems (Rosenzweig 1995; Brown & Lomolino 1998). Empirical and theoretical development and refinement have been devoted to understand latitudinal gradients (see Pianka 1966; Rohde 1992; Huston 1994). A large number of empirical studies have been done for vertebrates, such as fish (e.g. Oberdorff et al. 1995), birds (e.g., Hawkins et al. 2003), and mammals (e.g. Rosenzweig 1992). Similarly, latitudinal patterns for invertebrates have been documented for a particular taxonomic level, such as order (e.g. Dingle et al. 2000; Heino 2002) and family (e.g. Kerr & Currie 1999; Kaspari et al. 2000). Many hypotheses based on empirical evidence have been proposed to explain latitudinal gradients, and theoretical studies have been performed to validate these hypotheses (Willig et al. 2003). However, nearly all of the theoretical models concern a single guild or trophic level, and thus there is a large gap between empirical and theoretical studies, because most empirical studies have examined latitudinal gradients including some guilds and trophic levels together (Scheiner & Willig 2005).

More than 30 hypotheses have been proposed to account for latitudinal gradients in species diversity (Willig et al. 2003) and have aroused controversy (Clarke 1992; Rohde 1992; Rosenzweig 1995; Lyons & Willig 1999; Waide et al. 1999; Colwell & Lees 2000; Gaston 2000). Although many of the hypotheses focus on effects of external factors on entire assemblages (e.g., area, energy, climate and habitat heterogeneity; Rohde 1992; Rosenzweig 1995), interactions within assemblages should not be ignored (Buckley et al. 2003; Hillebrand 2004). Buckley et al. (2003) showed that prey species diversity exhibited latitudinal gradient but predator species diversity not in the entire food webs inhabiting water-filled leaves of pitcher plants. They suggested that trophic interactions may cause differences in latitudinal patterns among trophic levels. Trophic interactions, such as bottom-up and top-down effects, have been recognized to affect species diversity in general (Fretwell 1977; Oksanen et al. 1981; Holzapfel & Mahall 1999; Worm et al. 2002; Lill & Marquis 2003; Borer et al. 2006). Thus, if species diversity of predator assemblages exhibits a latitudinal gradient and predator assemblages have positive effects on prey assemblages, prey species diversity would also show a latitudinal gradient through top-down effects. Other external factors, such as energy, which have proposed to explain for latitudinal gradients, are unconcerned for the latitudinal pattern in prey species diversity in this case because the pattern is provided by trophic interactions among guilds. Hence, I should examine how a latitudinal gradient in a guild are influenced by those in other guilds.

Stream invertebrates are good candidates to study effects of trophic interactions on latitudinal patterns in species diversity, because their trophic habits are relatively well known and their guild structure is simple (Warren & Gaston 1992; Wallace & Webster 1996). Their feed habits can be categorized into three feeding guilds (detritus feeders, periphyton feeders, and carnivores; Merritt & Cummins 1996; Kawai & Tanida 2005). Previous studies indicated trophic interactions are important for stream invertebrate assemblages (Wallace et al. 1999), and thus a latitudinal pattern in species diversity of a guild may be modified by trophic interactions.

In this study, I examined latitudinal patterns in taxonomic richness of stream invertebrate assemblages in Hokkaido Island, northern Japan, for three different guilds categorized by their feeding habits (detritus feeders, periphyton feeders, and carnivores), and assessed how a latitudinal pattern in a guild was influenced by trophic interaction using Bayesian networks.

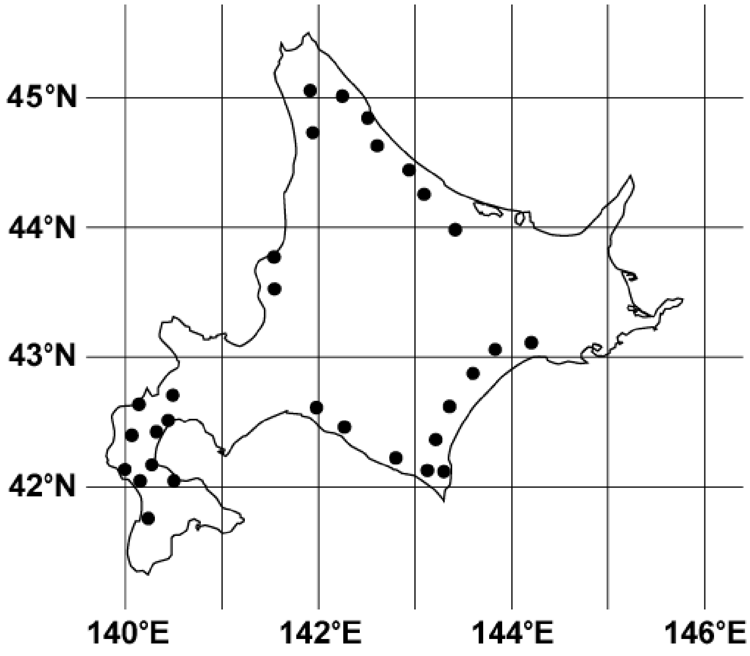

Fig. 3-1 Locations of 30 study streams in Hokkaido Island, Japan.

Materials and methods

Study sites

The study was conducted in June 2004 in 30 mountain streams on Hokkaido Island, which encompasses ca. 79,500 km^2 and is the northernmost island of Japan (latitude 41°24'N - 45°31'N, longitude 139°46'E - 145°49'E; Fig. 3-1). The study streams belong to different stream systems, and are at least 30 km apart from each other. Spring-fed, lake-outlet, polluted or acid streams were excluded. Approximate channel slopes in this study reach, which were obtained from a 1:250,000 map, ranged from 2 to 5%. The pH values ranged from 6.4 to 7.3, and conductivity was 26 to 103 μS cm^{-1}. The catchment vegetation for all streams was primarily mixed forest, with deciduous broad-leaved and coniferous trees.

Field procedures

A 20-m riffle was selected as a study reach in each stream. Each study reach was evenly divided into three sections, and benthic invertebrates were sampled from each section using a Surber sampler (0.25 × 0.25 m area, 250 μm mesh). Samples were rinsed vigorously in a tray and sieved through a 250 μm mesh to isolate invertebrates from particulate organic matter; adherent invertebrates were picked up with forceps (Miyake & Nakano 2002). Invertebrates were preserved in a 5% buffered formalin solution until they were analyzed.

Laboratory procedures and data treatment

In the laboratory, invertebrates were sorted from each Surber sample and identified to the lowest possible taxonomic level, usually genus or species, using the taxonomic keys in Merritt & Cummins (1996) and Kawai & Tanida (2005). Otherwise, specimens were identified to family and subfamily. Subsequently, invertebrates were assigned to feeding guilds (detritus feeders, periphyton feeders, or carnivores), based on Merritt & Cummins (1996) and Kawai & Tanida (2005); detritus feeders, periphyton feeders, and carnivores mainly consume particulate organic matter, periphyton on stream substrate, and other benthic invertebrates, respectively (Wallace & Webster 1996). Observed number of taxa was estimated as taxonomic richness in detritus feeders, periphyton feeders, and carnivores. Taxonomic richness in a guild would be influenced by qualitative (i.e., taxonomic richness) and quantitative (i.e., individuals) factors due to other guilds (Jeffries & Lawton 1985; Warren & Gaston 1992; Wooster 1994; Wallace et al. 1999). Hence, total number of individuals per a sample was also estimated as community density in each guild. Taxonomic richness and community density in each guild were quantified for the three sections from each study reach.

Statistical analyses

Latitudinal gradients in taxonomic richness and community density of detritus feeders, periphyton feeders, and carnivores were analyzed using linear mixed models (LMMs). Response variables in these models were taxonomic richness and community density in detritus feeders, periphyton feeders, and carnivores; explanatory variable was latitude. The three replicates from each stream were treated as random effects.

The statistical significance of each model was evaluated through a likelihood ratio test. All analyses were performed using the R environment for statistical computing (R Development Core Team 2006) with the associated packages lme4 (Bates & Sarkar 2007). I considered results to be statistically significant when $P < 0.05$.

To evaluate how trophic interactions have effects on latitudinal gradients in detritus feeders, periphyton feeders and carnivores, I used Bayesian networks (McMahon 2005; McCarthy 2007), which combine graphical models with multivariate Bayesian statistics. Bayesian networks can determine which variables (i.e., nodes) of a network influence others (McMahon 2005). Bayesian networks are graphical representations of a joint probability distribution of a set of variables of interest, and the joint probability distribution of the variables is then

$$P(x) = \prod_{\upsilon \in V} P(x_\upsilon \mid x_{pa(\upsilon)})$$

where υ denotes a node in V which is the set of nodes; pa(υ) denotes the parents of that node. For continuous nodes, the conditional distributions are given by Gaussian linear models

$$x_{\upsilon \mid pa(\upsilon)} \sim \mathrm{N}(\alpha_{\upsilon \mid pa(\upsilon)} + \beta_{\upsilon \mid pa(\upsilon)} x_{pa(\upsilon)}, \sigma^2_{\upsilon \mid pa(\upsilon)}),$$

where $\alpha_{\upsilon|pa(\upsilon)}$ is a regression intercept, $\beta_{\upsilon|pa(\upsilon)}$ is a regression coefficient, and $\sigma^2_{\upsilon|pa(\upsilon)}$ is the conditional variance.

Variables were represented as nodes in a network and connected by arrows, which are indication of conditional dependence. A link between two nodes represented by an arrow from node A (parent) to node B (child), indicates that A is a causal variable of B. Bayesian networks form a Directed Acyclic Graph, where no directed path leads from a given node to itself. Since latitude is causal for other variables, I did not allow arrows to point from variables to latitude (Fig. 3-2). Taxonomic richness in a guild is affected by its community density (Gotelli & Colwell 2001), but not the other way around. Hence, I did not allow arrows from taxonomic richness to community density in each guild. Many species in detritus feeders differ from those in periphyton feeders in microhabitats (Hynes 1970, Allan & Castillo 2007), and then non-trophic interaction among these may be unimportant in stream invertebrate assemblages. Thus, arrows pointing directly between detritus feeders and periphyton feeders were also banned.

Although there are several algorithms to learn the Bayesian networks from the data (Scutari 2009), the score-based algorithms were employed, and then the different Directed Acyclic Graphs were compared using Bayes' factor. An uninformative prior for the joint probability was used. Then, I used greedy search based on the algorithm to find the Bayesian network with the best score which is proportional to the posterior probability of the Directed Acyclic Graph given the data (Chickering 2002). Bayesian networks were constructed using R environment for statistical computing (R Development Core Team 2009) with the associated package deal (Bottcher & Dethlefsen 2009).

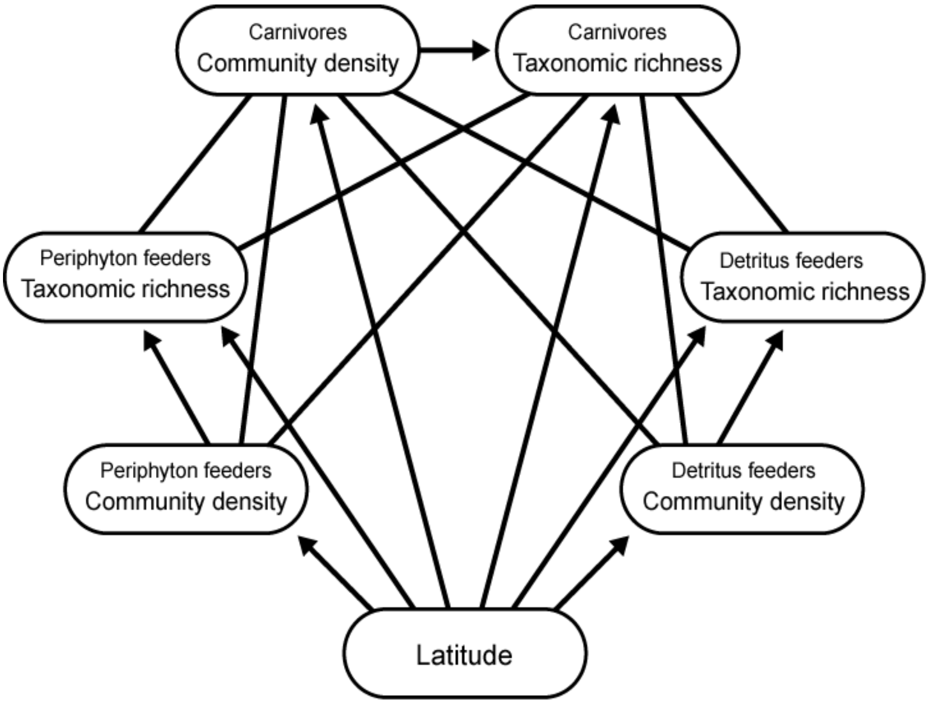

Fig. 3-2 Putative network in the present study. Rounded squares represent variables (i.e., nodes). Arrows indicate that the link from a variable (i.e., node) to other variable is allowed, but not the other way around. Lines indicate that both variables can be causal.

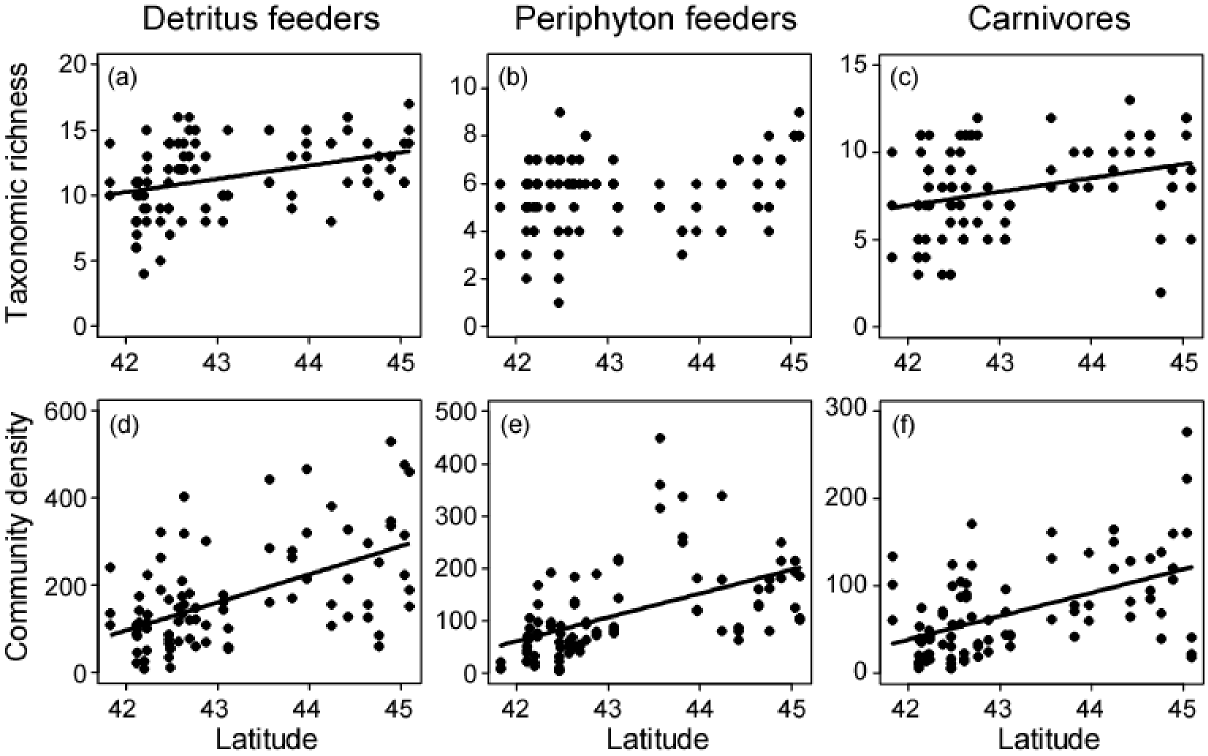

Fig. 3-3 Latitudinal gradients in taxonomic richness and community density of detritus feeders (a, d), periphyton feeders (b, e), and carnivores (c, f). Solid lines represent significant relationships.

Results

A total of 94 taxa and 30,983 individuals were found in samples from the 30 sites. Each Surber sample contained 14 to 37 taxa and 45 to 1,078 individuals. When each taxon was assigned to one of three feeding guilds, the greatest taxonomic richness was found for detritus feeders (45%), followed by carnivores (37%), and periphyton feeders (18%). Similarly, total abundance was numerically dominated by detritus feeders (53%), followed by carnivores (29%), and periphyton feeders (18%).

Latitudinal gradients

Taxonomic richness were positively related with latitude in detritus feeders (likelihood ratio test; $\chi^2 = 7.78$, $P = 0.005$; Fig. 3-3) and carnivores ($\chi^2 = 4.10$, $P = 0.04$; Fig. 3-3), whereas there was no significant latitudinal pattern in taxonomic richness of periphyton feeders ($\chi^2 = 1.50$, $P = 0.22$; Fig. 3-3). On the other hand, community density exhibited positive relationships with latitude in the all three guilds (detritus feeders; $\chi^2 = 17.49$, $P < 0.001$, periphyton feeders; $\chi^2 = 11.67$, $P < 0.001$, carnivores; $\chi^2 = 12.01$, $P < 0.001$; Fig. 3-3).

Bayesian networks

In networks with the highest score, taxonomic richness in each guild was indirectly dependent on latitude (Fig. 3-4). Only community density of periphyton and detritus feeders depended on latitude. Taxonomic richness increased with latitude through its community density in detritus feeders. Although taxonomic richness of carnivores was indirectly affected by latitude, the process of the latitudinal gradient was complex. Community density in carnivores, which exhibited positive effects on taxonomic richness in those, was positively influenced by that in detritus feeders varying with latitude. Similarly, taxonomic richness in carnivores was positively influenced by that in detritus feeders varying with latitude. On the other hand, taxonomic richness of periphyton feeders had no relationship with community density that depended on latitude, and was affected by taxonomic richness in carnivores.

Discussion

Latitudinal gradients in each feeding type

Latitudinal gradients were detected in taxonomic richness in detritus feeders and carnivores, whereas taxonomic richness in periphyton feeders did not show a latitudinal pattern (Fig.3-3). Although the patterns in detritus feeders and carnivores were the reverse of those observed most frequently for various taxa (Rosenzweig 1995), the inverse patterns have been noted for several taxonomic groups, such as parasitic wasps (Janzen 1981), sawflies (Kouki et al. 1994), and invertebrates that inhabit pitcher-plants (Buckley et al. 2003). In stream invertebrates, Heino (2001, 2002) also showed the reverse latitudinal gradient in taxonomic richness of Plecoptera in Fennoscandia and suggested that this pattern may be generated by both ecological and evolutional factors. Factors that might account for the reverse latitudinal gradients, however, have not yet been identified (Allan & Castillo 2007), because it is difficult to distinguish the effects of ecological factors, such as abiotic environmental variables, from those of evolutional factors. Mori et al. (in press) indicated that stream invertebrates observed in Hokkaido Island may have been assembled from a common species pool and suggested that evolutional factors have little effect on the assemblages. They also showed the reverse latitudinal gradient in taxonomic richness of entire stream invertebrate assemblages and demonstrated that the observed gradient was generated by the latitudinal gradient in flood disturbance. Therefore, the present reverse patterns in detritus feeders and carnivores may also be generated by directional variation in ecological factors (i.e., flood disturbance).

Effects of trophic interaction on a latitudinal gradient in a guild

The latitudinal gradient in taxonomic richness of carnivores was influenced through bottom-up effects by detritus feeders. Higher taxonomic richness was provided by higher community density in detritus feeders and carnivores (Fig. 3-4), as shown in many studies (e.g., McCabe & Gotelli 2000, Mori et al in press). Although community density in these guilds varied monotonically with latitude (Fig. 3-3), the latitudinal gradient in community density of carnivores was due to that of detritus feeders (Fig. 3-4). Similarly, taxonomic richness in these guilds exhibited the latitudinal gradients (Fig. 3-3), but the process of the latitudinal gradients was different between detritus feeders and carnivores. The latitudinal gradient in taxonomic

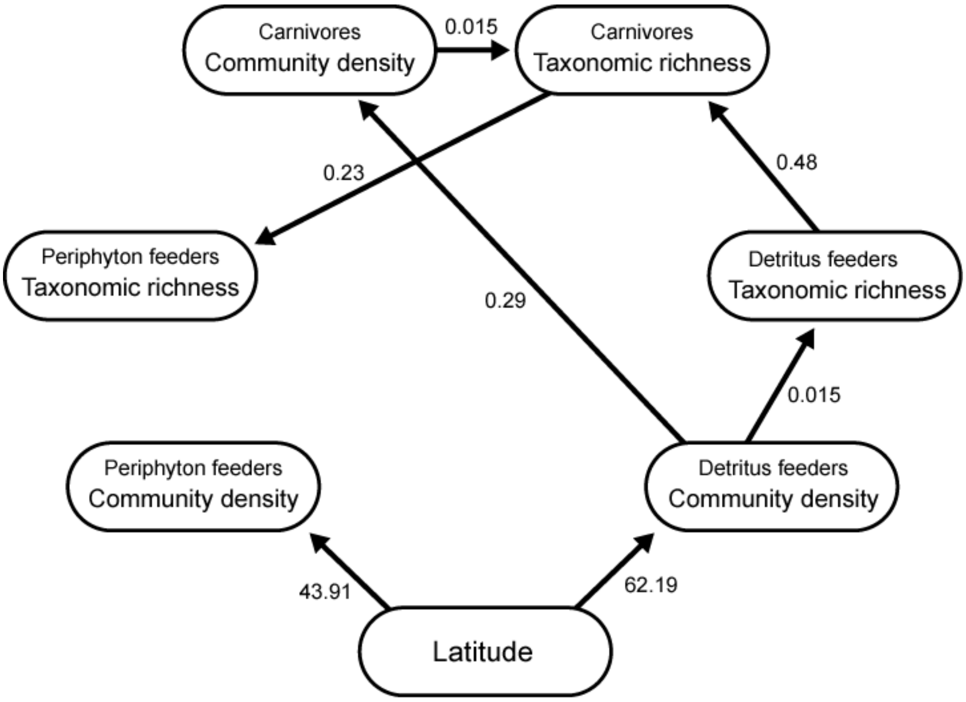

Fig. 3-4 The network with the highest network score. Rounded squares represent variables (i.e., nodes), and arrows represent causal connections between nodes. Numerical values next to arrows show posterior estimates of regression coefficients.

richness of detritus feeders was provided by latitudinal variation in community density of detritus feeders (Fig. 3-4). On the other hand, taxonomic richness of carnivores was indirectly related with latitude through both taxonomic richness and community density of detritus feeders (Fig. 3-4). These results indicate that the latitudinal gradient in taxonomic richness of detritus feeders can be generated without interactions with other guilds, but effects from detritus feeders are essential for forming the latitudinal gradient in taxonomic richness of carnivores.

Taxonomic richness in periphyton feeders was affected through top-down effects by carnivores (Fig. 3-4). However, taxonomic richness in periphyton feeders did not show the latitudinal gradient although that in carnivores did. This is because causal latitudinal variation in taxonomic richness of carnivores was relatively small (i.e., gentle slope with latitude).

Predator-prey ratio, which means that predator species richness and prey species richness are approximately proportional, has been widely recognized in many ecosystems (Jeffries & Lawton 1985; Warren & Gaston1992), and this relationship has also been reported for stream ecosystems (Wooster 1994; Wallace & Webster 1996). Type of prey species, which is a group of prey with similar general characteristics such as body size and habitat use, is a niche dimension for predator species; high prey species richness would provide diverse prey types. Hence, higher prey species richness may result in higher predator species richness (Arnold 1972; Tilman 1986). On the other hand, predator richness may also influence prey richness (Warren & Gaston1992). Although polyphagous predators may remove some species from a community, they may also promote coexistence of potential competitors of prey within a type through reduction of the abundance of prey (Paine 1966; Glasser 1979, 1983). If there are several types of prey within an assemblage, predator richness may increase prey species coexisting in each type. These processes that created predator-prey ratio are qualitative interactions between species richness in the two (Warren & Gaston 1992). Predator-prey ratio is also provided by quantitative interactions between community densities in the two (Krüger & McGavin 2001). Higher community density in prey assemblages may result in higher species richness, as shown in the More Individuals Hypothesis (Srivastava & Lawton 1998; Yee & Juliano, 2007), and higher prey community density may also provide higher predator community density, leading to higher predator species richness (Warren & Gaston1992; Krüger & McGavin 2001).

An alternative explanation for common latitudinal gradient found in the two guilds is that common variables influence both prey and predator species richness without interaction between the two (Warren & Gaston1992). In the present study, detritus feeders was directly affected by latitude, but carnivore feeders not (Fig. 3-4). These results indicate that common variables with latitude did not affect both detritus feeders and carnivores. Since taxonomic richness of carnivores was affected by both taxonomic richness and community density of detritus feeders (Fig. 3-4), taxonomic richness of carnivores may be determined through qualitative and quantitative bottom-up effects by detritus feeders in the present study.

Importance of trophic interactions among guilds on latitudinal gradients has been suggested (Buckley et al 2003; Hillebrand 2004). Although taxonomic richness in a guild is affected by both qualitative and quantitative trophic interactions due to other guilds, processes affecting latitudinal gradient in species diversity through these trophic interaction have not been shown. In the present study, I demonstrated that the latitudinal gradient in taxonomic richness of carnivores was generated by both qualitative and quantitative trophic interaction with detritus feeders.

Chapter IV

Species diversity-disturbance relationships vary with strength of community-level density dependent competition

Introduction

Understanding how species diversity and distribution are determined is one of the fundamental goals of community ecology (Huston 1994, Rosenzweig 1995). Many factors have been hypothesized to influence species diversity (Rahbek 2001, Hawkins et al 2003, Mora et al 2003). Among them, physical disturbance, such as hurricanes, fires, waves, drought, and floods, has been widely believed to be a major determinant of species diversity because that disrupts ecosystem, community, and population structure (Connell 1978, Sousa 1984, Shea et al 2004), and many studies have reported hump-shaped relationships between diversity and disturbance, in which diversity peaks at intermediate disturbance (Connell 1978, Hiura 1995, Hacker and Gaines 1997, Townsend et al 1997, Dial and Roughgarden 1998, Buckling et al 2000, Molino and Sabatier 2001, Shea et al 2004) although other diversity-disturbance relationships have been also reported (Mackey and Currie 2001, Hughes et al 2007) .

Two important hypotheses have been proposed to explain the hump-shaped patterns, intermediate disturbance hypothesis (Connell 1978) and dynamic equilibrium hypothesis (Huston 1994). These hypotheses rest on the assumption that all species exhibit a trade-off in traits; Connell (1978) presumes a trade-off between competitive ability and disturbance tolerance, and Huston (1994) presumes that between competitive ability and growth rate. Under low levels of disturbance, superior competitor exclude competitively inferior species, and then assemblages are dominated by a few superior species. In contrast, under high levels of disturbance, only species that can withstand disturbance or can quickly grow to reach densities sufficient to avoid stochastic extinction after disturbance can persist, and then assemblages are dominated by a few species with high tolerance to disturbance or high growth rate. Then, high diversity is provided by coexistence of species with different traits along a trade-off under intermediate levels of disturbance, and low diversity in low and high disturbance is explained by interspecific competitive exclusion and physical elimination (Connell 1978, Shea et al 2004). According these hypotheses, dominant species is expected to be differentiated with disturbance.

Contrary to the hypotheses, empirical studies have reported that species did not exhibit trade-off in traits assumed by those hypothesis (Lenssen et al 2004, Haddad et al 2008); Lenssen et al (2004) indicated that flood disturbance affected both superior and inferior competitors equally. Haddad et al (2008) also indicated absence of clear trade-off between growth rate and competitive ability. In addition, some studies showed that dominant species did not vary with disturbance although displacement of dominant species is predicted by the hypotheses (Fröder and Sommer 1999, Helfield et al 2007). Hence, hump-shaped relationships may be provided even if species do not exhibit a clear trade-off in traits.

In the hump-shaped patterns, low diversity under low levels of disturbance is expected to be provided by interspecific competition according to the intermediate disturbance hypothesis (Connell 1978) and dynamic equilibrium hypothesis (Huston 1994). The strength of interspecific competition can be dependent on the sum of population densities within a community, community density (Gause 1934, Paine 1966, Wilbur 1997), and then competition does not always occur within an assemblage (e.g. Karban 1989). As community density increases, the community approaches saturation, and interference among species that compete for limited common resources may be elicited (density dependent competition at the community level). Higher disturbance depress both species diversity and community density (McCabe and Gotelli 2000, Death and Zimmermann 2005). On the other hand, lower disturbance allows community density to increase, leading to lower species diversity by higher degree of competition. Thus, the hump-shaped relationships between diversity and disturbance may be detected with expression of community-level density dependent competition, but the negative relationships be detected without that.

Species diversity is a consequence accumulation of species distribution. Patterns of species distribution are closely related with the degree of interspecific competition (Urban 2004), which is expected to change with disturbance (Connell 1978, Wellborn et al 1996). If disturbance determine community composition without competition, species compositions in low diversity leads to be a proper subset of that in high diversity, and as a result the assemblages may be significantly nested distribution patterns (Patterson and Atmar 1986, Urban 2004). On the other hand, competitive exclusion decreases nestedness because that limits community composition (Leibold and Mikkelson 2002). If disturbance determine community composition with competition, co-occurrences of species may be less common than expected by chance (Cody and Diamond 1975, Urban 2004). Therefore, patterns of species distribution are considered to vary through strength of interspecific competition altered by disturbance (Urban 2004, Bloch et al 2007). Patterns of species diversity against disturbance and those of species composition have been examined separately (e.g., McAbendroth et al 2005). However, both patterns should be analyzed together because species diversity is based on species composition. Interspecific competition along community density may work as a bridge between diversity patterns and distribution patterns, but no one has examined simultaneously both patterns by focusing on density dependent competition at the community level.

Stream invertebrate assemblages are good model system to test effects of disturbance on species diversity and distribution patterns. Both hump-shaped and negative relationships between disturbance and species diversity have reported (hump-shaped; Townsend et al 1997, Milner et al 2001, Miyake and Nakano 2002, negative; Robinson and Minshall 1986, Scarsbrook and Townsend 1993, Death and Winterbourn 1995, McCabe and Gotelli 2000, Death 2002, Mori et al in press); different patterns of species distributions also have been described (Heino 2005, Schmera et al 2007, Heino et al 2009). These diverse results in diversity-disturbance patterns and species distribution patterns could be interpreted to be due to differences in strength of density dependent competition at the community level which altered by disturbance. Stream invertebrates are frequently influenced by unexpected flood disturbance (Hynes 1970, Grossman et al 1982, Resh et al 1988), which generally reduces community density by direct elimination and indirect decline in their resources (Robinson and Minshall 1986, McCabe and Gotelli 2000, Death and Zimmermann 2005). Hence, competitive interaction has been considered a minor factor in stream invertebrate assemblages because disturbance may moderate competitive interactions between these species (McAuliffe 1983, Hemphill 1991). However, evidences of competitive interactions affecting community structure have recently been accumulated (Kohler 1992, Kohler and Wiley 1997, Kuhara et al 1999, Cross and Benke 2002). Therefore, by asking whether or not assemblages reach saturation and competition occurs under observed range of disturbance, I could reach better understanding mechanisms generating diversity and distribution patterns in stream invertebrate assemblages.

In this study, I analyzed stream invertebrate assemblages to explore how flood disturbance and food resources have effects on diversity and distribution through community-level density dependent competition. Since species belonging to different ecological guilds may not compete for common resources, I analyzed diversity and distribution patterns within individual guilds. Species richness (the number of taxa per unit area) depends on both evenness and community density (Gotelli and Colwell 2001, Mori et al in press). Therefore, I firstly examined effects of disturbance and food resources on taxonomic richness, community density, and evenness to understand the processes of diversity-disturbance patterns. Secondly, effects of community density on taxonomic richness and evenness were examined on the basis of differences in diversity-disturbance pattern between guilds. Finally, to examine how species composition influences diversity-disturbance patterns, I evaluated whether or not competitive interaction influenced distribution pattern using the C-socre (Stone and Roberts

1990) and the discrepancy index (Brualdi and Sanderson 1999).

Materials and methods

Study sites

The study was conducted in June 2004 in 30 mountain streams on Hokkaido Island, which encompasses ca. 79,500 km^2 and is the northernmost island of Japan (latitude 41°24’N - 45°31’N, longitude 139°46’E - 145°49’E). The study streams were located in different drainage basins and were separated by at least 30 km. Spring-fed, lake-outlet, polluted or acid streams were excluded. The catchment vegetation for all streams was primarily mixed forest, with deciduous broad-leaved and coniferous trees.

Field procedures

A 20-m riffle stretch was selected as a study reach in each stream. Each study reach was evenly divided into three sections, and benthic invertebrates were sampled from each section using a Surber sampler (0.25 × 0.25 m area, 250 µm mesh). Collected samples were rinsed vigorously in a tray and sieved through a 250 µm mesh to isolate invertebrates from particulate organic matter; adherent invertebrates were picked up with forceps (Miyake and Nakano 2002). Both invertebrates and detritus were preserved in 5% buffered formalin solution until they were analyzed. The light condition at each section was measured to estimate primary production by use of hemispherical photography because shade created by an overhanging tree canopy restricts primary production in many streams in undisturbed forests (e.g. Hill et al 1995). Hemispherical photographs were taken on cloudy days or at dawn and dusk (Rich 1990, Fournier et al 1996), using a digital camera (Coolpix 990, Nikon Corporation, Tokyo, Japan) with an exclusive fish-eye lens (Fish-eye converter FC-E8, Nikon Corporation, Tokyo, Japan). The camera was placed on a tripod at a height of 1.0 m above the water surface and leveled with a bubble level (Inoue et al 2004).

Laboratory procedures and data treatment

In the laboratory, invertebrates were sorted from each Surber sample, identified to the lowest possible taxonomic level, usually genus or species, using the taxonomic keys in Merritt and Cummins (1996) and Kawai and Tanida (2005). Otherwise, specimens were identified to family and subfamily. To assess effects of competition between species that compete for common resources, invertebrates were assigned to feeding guilds (periphyton feeders, detritus feeders, or carnivores), based on Merritt and Cummins (1996) and Kawai and Tanida (2005); periphyton feeders graze periphyton including algae, fungi and bacteria, detritus feeders mainly feed on particulate organic matters, and carnivores on other invertebrates. Taxon richness was defined as the observed number of taxa per unit area. To examine processes affecting the development of taxon richness, community density and evenness (Δ_1) were quantified. Values of Δ_1, which is not biased by sample size or species richness, were calculated as a measure of evenness (hereafter, “evenness”; Olszewski, 2004). In mountain streams, primary productivity of periphyton is restricted by light intensity (e.g. Hill et al 1995), and then I measured relative photosynthetically active radiation (rPAR) to estimate food availavility for periphyton feeders. Although the wavelengths of solar radiation range from < 300 to > 5000 nm, those from 400 to 700 nm are referred to as photosynthetically active radiation (PAR).PAR was computed from the hemispherical photographs with an image-processing program, LIA for Win32 (Yamamoto 2003, Inoue et al 2004), and relative PAR (rPAR) was calculated by dividing PAR in each section by that for an unobstructed section. To quantify food resources for detritus feeders, the standing crop of particulate organic matter (POM) contained in each sample was measured as ash-free dry mass (AFDM g m^{-2}). After removal of invertebrates, remains were oven-dried at 80°C for 1 day and weighed, then ashed at 550°C for 4 h and reweighed to determine AFDM. Prey density, which is the sum of community density in periphyton feeders and detritus feeders in each sample, was measured to evaluate food resources for carnivores (Wallace et al 1999). Since bed movement by high discharge events increased monotonically with monthly precipitation in this study system, monthly precipitation can be used as a proxy for disturbance (Mori et al in press). Thus, accumulated precipitation during the month before sampling was calculated from Japan Meteorological Agency data obtained at the nearest meteorological station to each study site.

Statistical analyses

Effects of flood disturbance and food resources on stream invertebrate assemblages were analyzed using generalized linear mixed models (GLMMs). I assumed a Poisson error distribution for taxonomic richness and community density and a Gaussian error distribution for evenness. Taxonomic richness, community density, and evenness were all treated as response variables, and precipitation and food resources as fixed explanatory variables. I evaluated food resources for periphyton feeders, detritus feeders, and carnivores as relative photosynthetically active radiation (rPAR), particulate organic matter (POM), and prey density, respectively. Thus, food resources in models were different by guild. Since disturbance and food resources often have curvilinear effects (Mittelbach et al 2001, Shea et al 2004), both linear and quadratic terms were included for those. I constructed all possible models from the two variables (precipitation and food resources) with both linear and nonlinear terms and identified the best models with the second-order Akaike information criterion corrected for small samples size (AICc). Relationships between precipitation and each food resources were also analyzed using GLMMs. Statistical significance for each model was evaluated by likelihood ratio tests. In addition, the relationship between difference in precipitation between sites and similarity in stream invertebrate assemblages was analyzed using a Mantel test (10,000 permutations) to evaluate change of taxonomic composition. Bray-Curtis dissimilarity was calculated based on qualitative data (presence/absence) from pooled samples from the three sections in each stream.

Effects of community density on taxonomic richness and evenness were analyzed using GLMMs. In addition, effects of evenness on taxonomic richness also were analyzed. A Poisson error distribution was assumed for taxonomic richness, and a Gaussian error distribution for evenness. Both taxonomic richness and evenness were regressed against community density in both a linear and nonlinear (quadratic) models. Similarly, taxonomic richness was regressed against evenness in both models. The three replicates in each stream were treated as a random effect. Statistical significance for each model was evaluated using likelihood ratio tests. If both the linear and nonlinear model revealed significant relationships, they were compared using AICc.

Patterns of taxon co-occurrence in presence–absence matrices of periphyton feeders, detritus feeders, and carnivores were analyzed using the C-score (Stone and Roberts 1990, Gotelli 2000). The C-score measures the average pairwise species co-occurrence (Stone and Roberts 1990). If communities are structured by competitive interactions, there should be more checkerboard species pairs than expected by chance, and the C-score should be significantly larger than expected by chance (Diamond 1975, Gotelli and McCabe 2002, Tello et al 2008). Patterns of nestedness in the matrices of the guilds were analyzed using the discrepancy index (Brualdi and Sanderson 1999, Ulrich et al 2009), which outperform other measures evaluating nestedness and hence recommended its use (Ulrich and Gotelli 2007). The discrepancy index counts of the minimum number of discrepancies for rows and columns that must be erased to produce a perfectly nested matrix (Brualdi and Sanderson 1999), and then the smaller the discrepancy index is, the stronger is the pattern of nestedness. I compared observed C-scores and discrepancy indices to those calculated for 5000 randomly constructed null assemblages. All null model analyses were conducted with EcoSimVersion 6.0 for the C-score (Gotelli and Entsminger 2001) and with R environment for statistical computing (R Development Core Team 2006) with its associated packages, the vegan (Oksanen et al 2007) and the bipartite (Dormann et al 2009). I used fixed sum row and column constraints (Connor and Simberloff 1979) and the sequential swap algorithm for randomization. Gotelli (2000) advocated these constraints because such constructed random matrices seem to be least prone to type I and type II errors. Statistical significance was assessed by comparing the observed index values to the distribution of the values derived from the random matrices (Manly 1995). When hump-shaped relationships between diversity and disturbance would be detected, competition would have minor effects on assemblages under range of disturbance that diversity decreases monotonically with. Hence, I also analyzed patterns of co-occurrence and nestedness using the C-score and the discrepancy index to the extent that taxonomic richness decreases with precipitation.

All analyses using GLMMs were performed in the R environment for statistical computing (R Development Core Team 2006) with its associated package the lme4 (Bates and Sarkar 2007) and vegan (Oksanen et al 2007). I considered results as statistically significant when the *P*-value < 0.05. Logarithmic transformations were conducted for precipitation, particulate organic matter, and prey density before analyses in order to stabilize variances.

Results

A total of 94 taxa and 30,983 individuals were found in samples from the 30 sites. Each Surber sample contained 14 to 37 taxa and 45 to 1,078 individuals. When each taxon was assigned to one of three feeding guilds, the greatest taxonomic richness was found for detritus feeders (45%), followed by carnivores (37%), and periphyton feeders (18%). Similarly, total abundance was numerically dominated by detritus feeders (53%), followed by carnivores (29%), and periphyton feeders (18%).

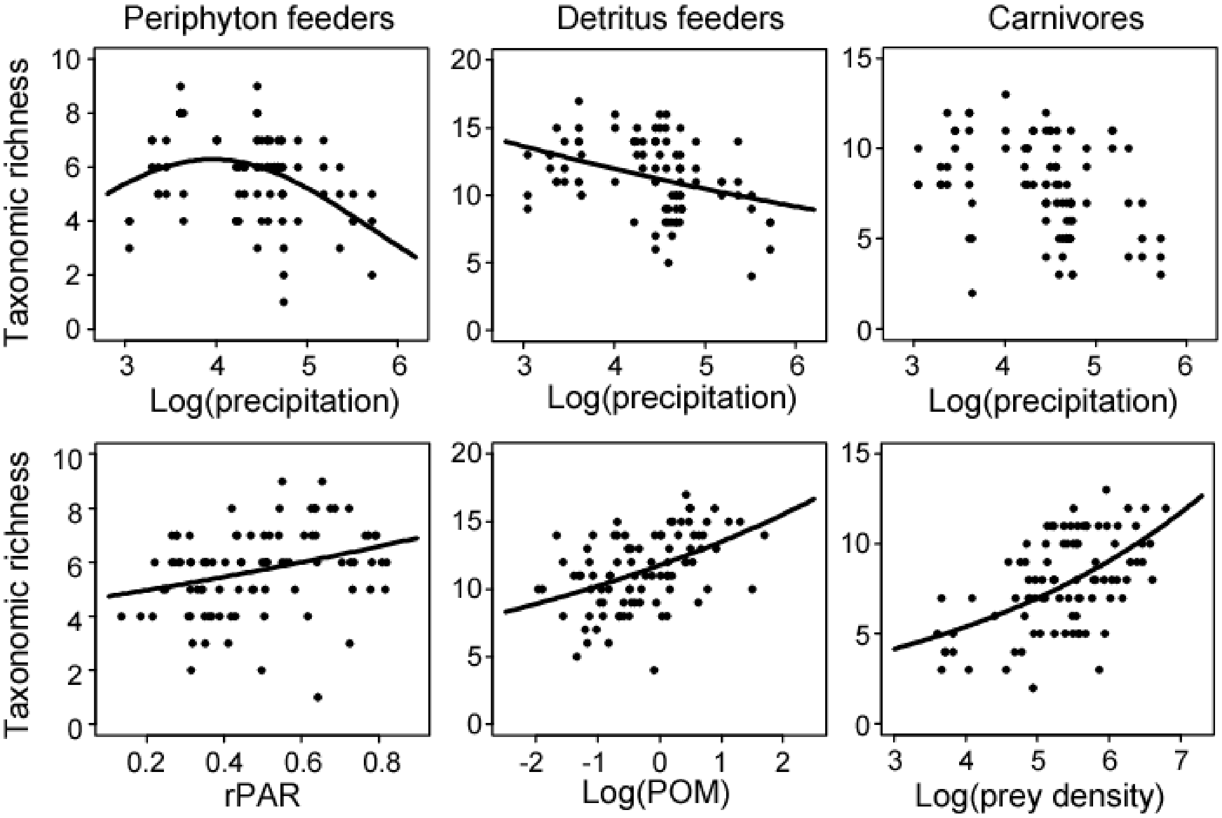

Fig. 4-1. Effects of precipitation and food resources on taxonomic richness in three feeding guilds (periphyton feeders, detritus feeders, and carnivores). Food resources for each feeding guild were evaluated as relative photosynthetically active radiation (rPAR), particulate organic matter (POM), and prey density, respectively. Solid lines represent significant relationships which were selected as results of model selection procedures.

Effects of disturbance and productivity

Effects of precipitation, proxy for flood disturbance, on taxonomic richness differed between feeding guilds (Fig. 4-1). A significant hump-shaped relationship was observed in periphyton feeders, whereas taxonomic richness decreased monotonically with precipitation in detritus feeders (Table 4-1). No clear pattern was found in carnivores. Relative photosynthetically active radiation (rPAR), particulate organic matter (POM), and prey density, proxies for food resources, were positively related to taxonomic richness in periphyton feeders, detritus feeders, and carnivores, respectively (Fig. 4-1). The best models for taxonomic richness in periphyton and detritus feeders included precipitation and their food resources, whereas that for taxonomic richness in carnivores consisted only of prey density (Table 4-1).

Table 4-1 Best-fit models for explaining patterns in taxonomic richness, community density and evenness in periphyton feeders, detritus feeders, and carnivores. All possible models from combinations of two environmental variables with both linear and nonlinear terms (i.e. full model, precipitation + precipitation^2 + food resources + food resources^2) were constructed and model selection was performed using AICc. Plus and minus signs indicate the direction of the relationship.

Community strucutre	Best models	*df*	$\chi 2$	*P*
Periphyton feeders				
Taxonomi richness	- Precipitation^2 + Precipitation + rPAR	3	8.8	0.003
Community density	- Precipitation	1	672.5	<0.001
Evenness	+ Precipitation + rPAR	2	5.1	0.08
Detritus feeders				
Taxonomi richness	- Precipitation + POM	2	15.6	<0.001
Community density	- Precipitation + POM	2	135.3	<0.001
Evenness	-	-	-	-
Carnivores				
Taxonomi richness	+ Prey density	1	17.7	<0.001
Community density	+ Prey density	1	455.7	<0.001
Evenness	-	-	-	-

(POM: particulate organic matter, rPAR: relative photosynthetically active radiation)

Precipitation had negative effects on community density in periphyton feeders and detritus feeders, whereas did not affect community density carnivores (Table 4-1). POM and prey density were positively related to community density in detritus feeders and carnivores, respectively (Table 4-1). The best model for community density in periphyton feeders included only precipitation. Precipitation and POM were selected as influential factors explaining variation in community density in detritus feeders. Prey density was the only variable retained in the best model for community density in carnivores.

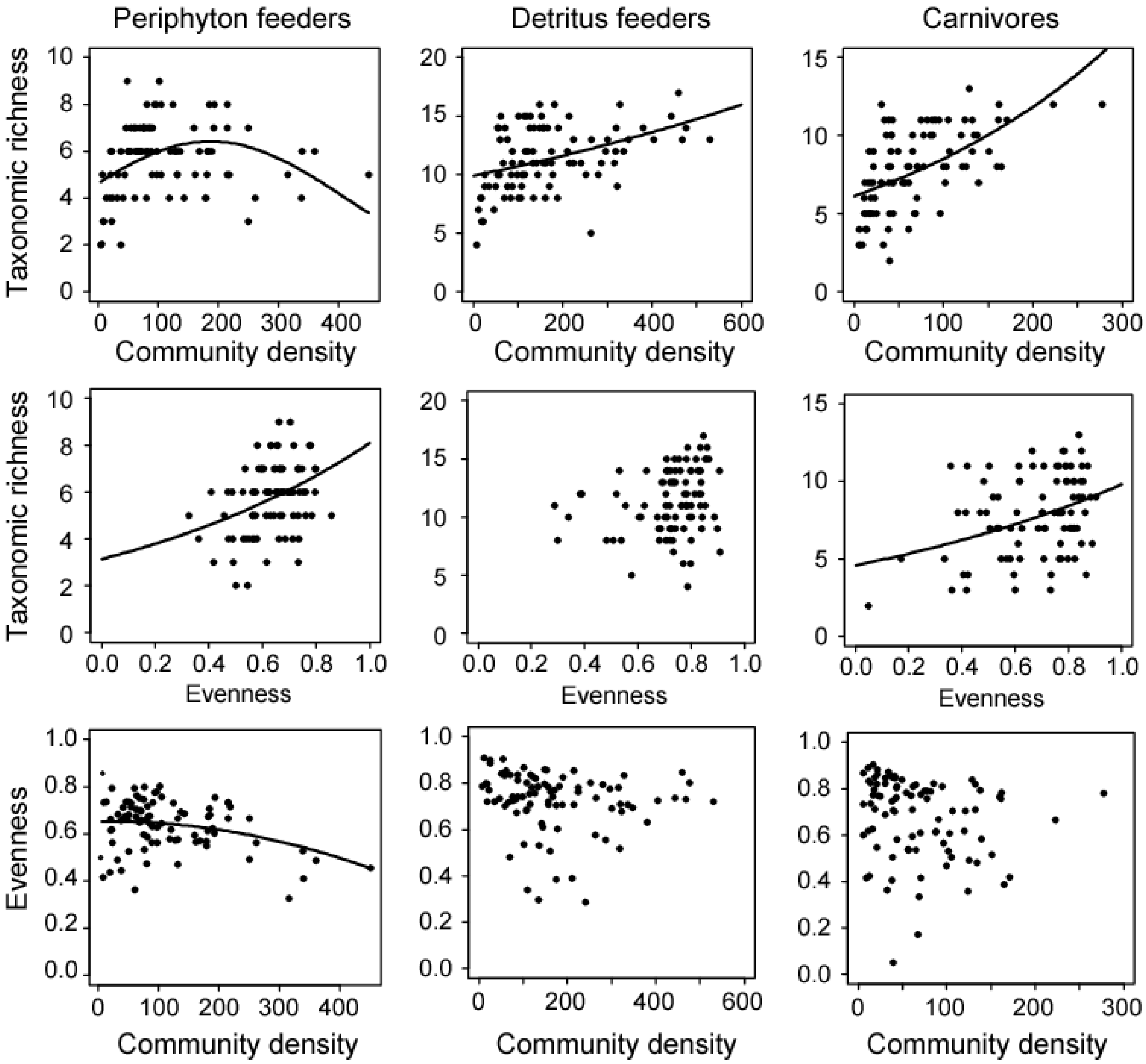

Fig. 4-2. Relationships between taxonomic richness, community density, and evenness in periphyton feeders, detritus feeders, and carnivores. Solid lines represent significant relationships.

Evenness in periphyton feeders increased with precipitation, whereas those in detritus feeders and carnivores did not show clear relationships (Table 4-1). Similarly, evenness in periphyton feeders was positively related with rPAR, whereas that in detritus feeders and carnivores was not related with POM and prey density, respectively. The best model for evenness in periphyton feeders included precipitation and rPAR, but was marginally significant. No variables were selected in the best models for evenness in detritus feeders and carnivores.

Relationships of precipitation with rPAR and POM were insignificant (rPAR; χ^2 = 1.46, P = 0.22, POM; χ^2 = 2.77, P = 0.10), but prey density decreased with precipitation (χ^2 = 24.75, $P < 0.001$). Bray-Curtis dissimilarity between study sites in each guild exhibited significant relationships with differences in precipitation (Mantel test; periphyton feeders; r = 0.32, P = 0.006, detritus feeders; r = 0.26, $P < 0.001$, carnivores; r = 0.15, P = 0.04).

Community density dependent effects

Taxonomic richness exhibited a hump-shaped pattern against community density in periphyton feeders (Fig. 4-2). This relationship was better described as a nonlinear (quadratic) model (likelihood ratio test, χ^2 = 5.29, P = 0.02, AICc = 44.92) compared to a linear model (χ^2 = 0.34, P = 0.56, AICc = 47.87). In contrast, taxonomic richness increased monotonically with community density in detritus feeders and carnivores (Fig. 4-2). A linear model better described the relationship between taxonomic richness and community density in detritus feeders (linear model; χ^2 = 9.46, P = 0.002, AICc = 58.91, nonlinear; χ^2 = 11.2, $P < 0.001$, AICc = 59.16) and carnivores (linear model; χ^2 = 17.03, $P < 0.001$, AICc = 61.99, nonlinear; χ^2 = 20.14, $P < 0.001$, AICc = 63.11).

Taxonomic richness increased with evenness in periphyton feeders and carnivores, whereas not in detritus feeders (Fig. 4-2). The relationships between taxonomic richness and evenness in periphyton feeders and carnivores was better explained by a linear model (periphyton feeders; χ^2 = 10.60, P = 0.001, AICc = 34.61, carnivores; χ^2 = 7.01, P = 0.008, AICc = 70.13) compared to a nonlinear model (periphyton feeders; χ^2 = 11.18, P = 0.003, AICc = 35.02 carnivores; χ^2 = 7.88, P = 0.02, AICc = 70.25). On the other hand, taxonomic richness in detritus feeders did not show significant relationship with evenness (linear model; χ^2 = 3.16, P = 0.07, AICc = 62.20, nonlinear; χ^2 = 3.43, P = 0.18, AICc = 62.93).

Evenness in periphyton feeders exhibited a significant hump-backed relationship with community density, whereas that in detritus feeders and carnivores did not show significant pattern against community density (Fig. 4-2). The relationship between evenness and community density in periphyton feeders was better explained by a nonlinear model (χ^2 = 9.01, P = 0.002, AICc = -174.10) than a linear model (χ^2 = 8.88, P = 0.003, AICc = -173.89). Community density did not significantly influence evenness in detritus feeders (linear model; χ^2 = 0.06, P = 0.80, nonlinear; χ^2 = 2.06, P = 0.36) and carnivores (linear model; χ^2 = 0.21, P = 0.64, nonlinear; χ^2 = 0.62, P = 0.73).

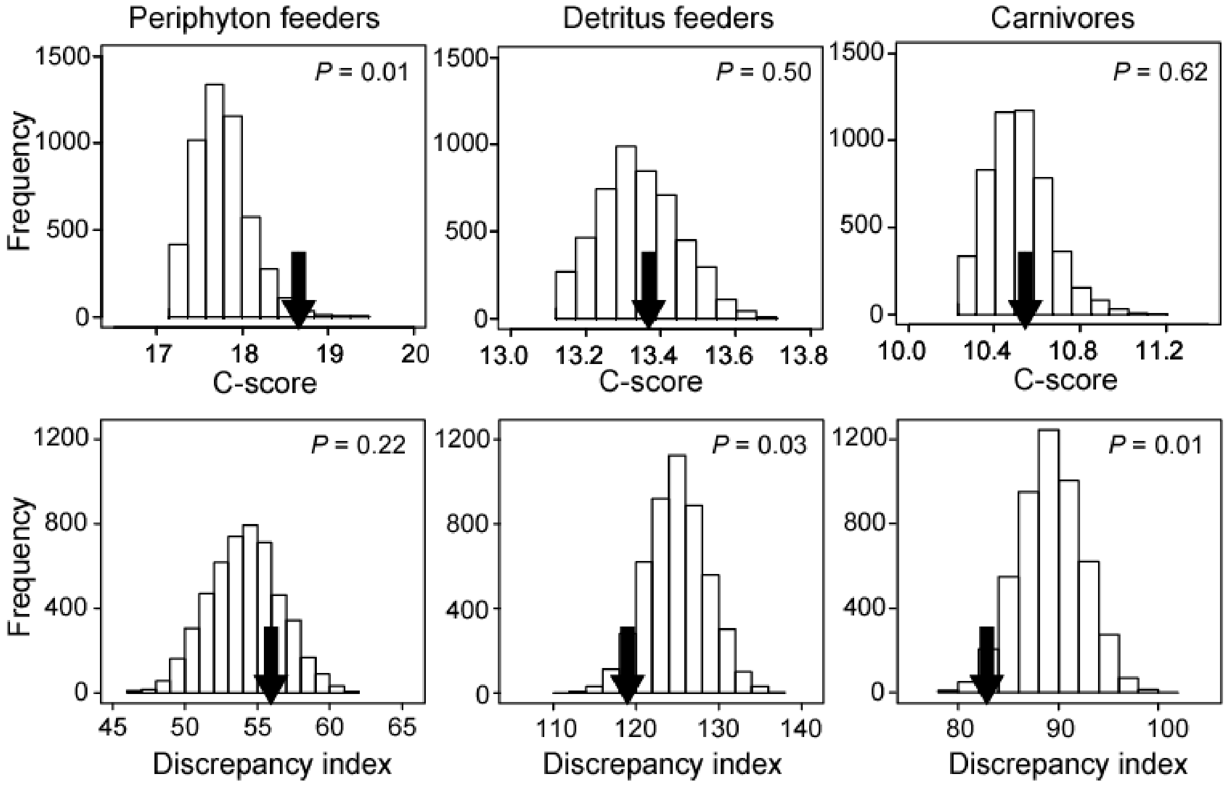

Fig. 4-3. Patterns of taxon co-occurrence and nestedness in periphyton feeders, detritus feeders, and carnivores. Each histogram shows observed C-score and discrepancy index (an arrow) and the distribution of C-scores and discrepancy indices from 5,000 simulated assemblages. Communities structured by interspecific competition tend to show unusually large C-scores (less species co-occurrence than expected by chance). When species composition in low diversity is proper subsets of that in high diversity, the discrepancy index tend to be small P-values indicate associated tail probabilities.

Patterns of taxon distribution

Patterns of taxon co-occurrence and nestedness differed between the guilds (Fig. 4-3). Periphyton feeders had significantly less co-occurrence than expected by chance (P = 0.01), which was evidenced by the larger C-score. In contrast, patterns of taxon co-occurrence in detritus feeders and carnivores did not differ significantly from those in randomly structured assemblages (detritus feeders; P = 0.50, carnivores; P = 0.62). Periphyton feeders did not exhibit a significantly nested pattern (P = 0.22; Fig. 4-3), whereas distribution patterns of detritus feeders and carnivores were significantly nested; the observed discrepancy index in detritus feeders and carnivores were significantly different from the values generated by randomly structured assemblages (detritus feeders; P = 0.03, carnivores; P = 0.01; Fig. 4-3).

Although periphyton feeders showed the significant checkerboard distribution attern in the full range of precipitation, they did not show a checkerboard distribution pattern but did a nested distribution pattern under the range of high precipitation (i.e., from four to six in log (precipitation) in Fig. 4-1) where diversity decreased monotonically with (taxon co-occurrence; P = 0.10, nestedness; P = 0.01).

Epeorus latifolium (Ephemeroptera: Heptageniidae), *Baetis* spp. (Ephemeroptera: Baetidae), *Glossosoma* spp. (Trichoptera: Glossosomatidae), and *Rhithrogena japonica* (Ephemeroptera: Heptageniidae) were distributed in most study streams (i.e., core taxa; Table 4-2), and these four taxa were dominant in each stream (i.e., dominant taxa). *Cinygmula* spp. (Ephemeroptera: Heptageniidae, see Plate 4-2), *Epeorus aesculus* (Ephemeroptera: Heptageniidae), *Epeorus curvatulus* (Ephemeroptera: Heptageniidae), and *Hydroptila* spp. (Trichoptera: Hydroptilidae) were observed in only streams with intermediate to high precipitation (i.e., satellite taxa), whereas *Baetiella japonica* (Ephemeroptera: Baetidae), *Apatania* spp. (Trichoptera: Apataniidae), *Dicosmoecus jozankaeanus* (Trichoptera: Limnephilidae, see Plate 4-1), and *Goera japonica* (Trichoptera: Goeridae) were observed in only streams with from low to intermediate precipitation (i.e., satellite taxa; Table 4-2).

Table 4-2 Periphyton feeders identified in the present study, showing that observed number of sites, sum of individuals detected in 30 study streams, mean relative individuals in observed streams (as mean percentage of individuals of each taxon to community density) and standard error (SE), and range of precipitation which the taxa was detected in the streams with.

Taxon	No. of sites	Sum of individuals	Mean relative individuals ± SE	Log(Precipitation)	
				Max	Min
Epeorus latifolium	30	2988	30.68 ±3.53	5.72	3.30
Baetis spp.	29	3712	34.23 ±3.85	5.72	3.30
Glossosoma spp.	25	1015	9.42 ±1.9	5.19	3.30
Rhithrogena japonica	25	1218	13.47 ±2.72	5.72	3.30
Neophylax spp.	22	151	2.84 ±0.65	5.51	3.45
Ecdyonurus viridis	18	180	2.56 ±0.51	5.72	3.30
Cinygmula spp.	13	212	6.34 ±2.52	5.72	4.45
Acentrella spp.	10	130	5.39 ±4.19	5.36	3.30
Baetiella japonica	9	34	1.58 ±0.6	4.74	3.30
Agapetus spp.	8	115	9.19 ±3.67	5.51	3.62
Agathon kawamurai ezoensin	8	46	2.19 ±1.6	5.19	3.45
Apatania spp.	7	222	13.51 ±3.03	4.95	3.62
Dicosmoecus jozankeanus	6	15	0.64 ±0.22	4.73	3.30
Goera japonica	5	7	0.42 ±0.1	4.73	3.62
Epeorus aesculus	3	7	1.47 ±1.01	4.95	4.45
Epeorus curvatulus	3	23	2.28 ±1.7	5.19	4.45
Hydroptila spp.	2	18	22.13 ±21.46	5.36	4.57

Discussion

Diversity-disturbance patterns by density-dependent competition at the community level

Relationships of taxonomic richness with precipitation, which cause flood disturbance (Mori et al in press), differed between feeding guilds of stream invertebrate assemblages (Fig. 4-1). Contradictory results have been reported in relationships between species diversity and physical disturbance (Mackey and Currie 2001, Hughes et al 2007), and several explanations have been proposed for the inconsistcy, including ones based on interaction with primary production (Kondoh 2001), dependence of spatial scales (Cadotte 2007), and neutral model (Kadmon and Benjamini 2006). However, the observed differences in diversity-disturbance patterns between the guilds can be better explained by density dependent competition at the community level which altered by disturbance, as hereinafter described.

Taxonomic richness in periphyton feeders peaked at intermediate precipitation and community density (Fig. 4-1 and 4-2), and community density decreased with precipitation (Table 4-1). Taxonomic richness increased with community density in the range from high to intermediate precipitation but decreased with that in the range from intermediate to low precipitation. Since the strength of interspecific competition may increase with community density (Gause 1934, Paine 1966, Wilbur 1997), the observed low diversity in streams with low precipitation may be generated by competitive exclusion due to high community density.

Periphyton feeders showed a checkerboard distribution pattern in the observed full range from low to high precipitation (Fig. 4-3), whereas those did not in the range of high to intermediate precipitation. Since checkerboard distribution patterns have usually been interpreted as an indication of competition structuring communities (e.g., Diamond 1975, Tello et al 2008), periphyton feeders may be structured by competitive interaction in the streams with low precipitation but not in the streams with high precipitation. Community density was positively related with precipitation in periphyton feeders (Table 4-1), suggesting that competitive interaction may be reinforced as community density increase. Taxonomic richness increased monotonically with community density in the streams with high to intermediate precipitation (Fig. 4-2). The observed low diversity in streams with high precipitation may be generated by disturbance-induced removal.

The processes that created variation in taxonomic richness of the periphyton feeders in streams with from high to intermediated precipitation, are consistent with the More Individuals Hypothesis that higher local population densities reduce local extinction of rare species, and species diversity lead to be high (Srivastava and Lawton, 1998; Yee and Juliano, 2007). This hypothesis, according to the species-energy theory (Wright 1983), postulates that greater productivity supports higher population densities, and flood disturbance can play a similar role to productivity in the More Individuals Hypothesis (see Mori et al in press). Since taxonomic richness increased monotonically with community density in periphyton feeders without competitive interaction in streams with high to intermediate precipitation, the More Individuals hypothesis can also apply to periphyton feeders in these streams.

Relative photosynthetically active radiation (rPAR), which is a proxy for primary productivity (Hill et al 1995), was positively related with taxonomic richness and evenness in periphyton feeders (Fig. 4-1, Table 4-1). Competitive interactions among periphyton feeders may be intensive in habitats with low light intensity compared to those with high light intensity (Hill et al 1995). In the present study, high rPAR, which enhances primary productivity, may modify density dependent competition. Thus, many taxa can coexist in streams with high rPAR, compared to those with low rPAR. Hence, rPAR could positively influence evenness by reducing competitive exclusion, leading to increase in taxonomic richness.

Decline in taxonomic richness by community-level density dependent competition was not detected in detritus feeders and carnivores. Taxonomic richness of detritus feeders and carnivores increased monotonically with community density (Fig. 4-2), and these guilds did not show a checkerboard distribution pattern but did show significantly nested distribution pattern (Fig. 4-3). Thus, competitive interaction may not occur almost in detritus feeders and carnivores. The pattern that higher community density provided higher diversity has also observed in other studies (e.g., McCabe and Gotelli 2000, Yee and Juliano 2007).

The negative diversity-disturbance pattern in detritus feeders could be simply interpreted by physical elimination through variation in community density, because density dependent competition may be unimportant. Both taxonomic richness and community density in detritus feeders decreased with precipitation and increased with POM (Fig. 4-1, Table 4-1). This is because high flood disturbance directly remove individuals, whereas high food resources can contain many individuals in an area. Hence, both flood disturbance and food resources may determine community density in detritus feeders, and as a result generate variation in taxonomic richness the assemblages.

Taxonomic richness of carnivores may be indirectly affected by flood disturbance through detritus feeders. Prey density was selected in the best model explaining variation in community density of carnivores, whereas precipitation was not in the best model (Table 4-1). Prey density was the sum of community densities of periphyton and detritus feeders, and both community densities were strongly influenced by precipitation (Table 4-1). Therefore, although precipitation was not included in the best models for community density in carnivores (Table 4-1), precipitation may indirectly affect community density in carnivores through prey density. Wallace et al (1999) also indicated bottom-up effects in stream invertebrate assemblages that higher community density of detritus feeders enhanced community densities of carnivores. Like detritus feeders, density dependent competition may be minor in carnivores, and thus taxonomic richness in carnivores increased monotonically with community density (Fig. 4-2). Therefore, prey density, which affected by precipitation, may influence taxonomic richness in carnivores through variation in community density of the assemblages.

The processes that created variation in taxonomic richness in detritus feeders and carnivores in the present study can be explained by the More Individuals Hypothesis, like taxonomic richness of periphyton feeders in streams with high to intermediate precipitation. In other words, I observed taxonomic richness in detritus feeders and carnivores in the range of community density that did not reach the saturation. If community density in detritus feeders and carnivores exceeded a certain level above which interspecific competition is elicited, detritus feeders and carnivores may also show a hump-shaped relationship with disturbance like periphyton feeders.

Diversity-disturbance patterns varied depending on the degree of density dependent competition at the community level in the present study. The hump-shaped relationship between taxonomic richness and precipitation in periphyton feeders can be explained by emergence of density dependent competition at the community level, and the negative relationships in detritus feeders can be explained by absence of that (i.e., the More Individuals Hypothesis). Flood disturbance has negative effects on community density in stream ecosystem through physical removal of individuals (e.g., McCabe and Gotelli 2000). In the range of precipitation where competitive interaction does not occur because of non-saturation of community (i.e., low community density), taxonomic richness may increase with community density. Thus, the negative diversity-disturbance pattern would be observed, as shown by detritus feeders. Taxonomic richness may increase with community density under high to intermediate disturbance before saturation of community (i.e., low community density) but ma decrease with that under intermediate to low disturbance after the saturation (i.e., high community density). Thus, the hump-shaped relationship between disturbance and taxonomic richness will be detected, as shown by the periphyton feeders. If competitive interaction does occur under the full range from low to high disturbance, taxonomic richness would decrease with community density. Thus, the positive diversity-disturbance pattern would be observed although this pattern was not detected in this study.

Variation in diversity-disturbance patterns has been explained by Kondoh (2001), Cadotte (2007), and Kadmon and Benjamini (2006). Kondoh (2001) indicated that the degree of disturbance that maximizes species richness is influenced by the level of productivity, and then species richness is positively related with disturbance under extreme high productivity but negatively related with that under extreme low productivity. Cadotte (2007) focused on spatial scale and indicated that local species richness decreased with disturbance, but regional species richness peaked at intermediate disturbance because differences among patch (i.e., beta diversity) also peaked at intermediate disturbance. These explanations by Kondoh (2001) and Cadotte (2007) can be interpreted as a case that whether or not assemblages attain to saturation community density at a scale and at a level of productivity. However, these explanations can only applicable when all species have trade-off in traits, such as that between competitive ability and disturbance tolerance, like the intermediate disturbance hypothesis (Connell 1978) and dynamic equilibrium hypothesis (Huston 1994). If species show a clear trade-off in traits, assemblages would exhibit hump-shaped diversity-disturbance relationships and show a checkerboard distribution pattern (Urban 2004). In this case, dominant species is expected to be differentiated with disturbance (Kondoh 2001). In the present study, however, periphyton feeders showed the checkerboard distribution pattern, but dominant taxa did not change with disturbance (Table 4-2, Appendix A).

On the other hand, Kadmon and Benjamini (2006) showed that neutral dynamics, in which a trade-off between competitive and colonization abilities was not assumed, can generate negative, hump-shaped, and positive disturbance-diversity patterns. They explained those patterns by balance in two processes, the More Individuals Hypothesis and dilution effects. Dilution effects represent that the increase in the number of locally produced individuals “dilutes” (i.e., decrease) the probability of immigration from the pool of potential colonizers and thus decreases the likelihood that new species will be added. Like Kondoh (2001), they also focused on whether or not assemblages reach the saturation and showed diversity-disturbance patterns depend on productivity. According to the explanation by Kadmon and Benjamini (2006), assemblages should show a nested distribution pattern, and community composition should not differ between that in contrasting ends of disturbance gradients. Dominant taxa of periphyton feeders did not change with disturbance in the present study (Appendix A), but competition of satellite species differed between high and low disturbance, and thus they did not show a nested but checkerboard distribution pattern (Fig. 4-2).

The preceding hypotheses for variation in diversity-disturbance pattern cannot perfectly explain my results. Since diversity-disturbance patterns depend on degrees of density dependent competition, I should consider how density dependent competition influences dominant and satellite taxa to clearly explain variation in diversity-disturbance patterns.

Differences in traits between dominant and rare taxa

Two mayfly taxa (*Epeorus latifolium* and *Baetis* spp.) were dominant in most study streams (i.e., core taxa; Table 4-2, Appendix A). Both taxa have high mobile ability (Hynes 1970, Mackay 1992) and tend to be dominant in mountain streams like my study streams (e.g., Nakano et al 1999, Miyake et al 2003). Semi-dominant taxa in the present study, *Glossosoma* spp. (Trichoptera) and *Rhithrogena japonica* (Ephemeroptera), also broadly inhabited (i.e., core taxa; Table 4-2, Appendix A). Satellite taxa in streams with low to intermediate precipitation differed from those in streams with intermediate to high precipitation (Table 4-2). One mayfly (*Baetiella japonica*) and three caddisfly taxa (*Apatania* spp., *Dicosmoecus jozankeamus*, and *Goera japonica*) were distributed in streams with from low to intermediate precipitation. These satellite caddisfly taxa have a stone–case (Hynes 1970, Merritt and Cummins 1996), and caddisflies with stone-case (see Plate 4-1) are generally vulnerable to flood disturbance (Hynes 1970). Hence, three satellite caddisfly taxa are likely to be locally extinct in stream with high precipitation by disturbance-induced removal. On the other hand, they may be able to coexist with the dominant taxa in streams with low precipitation because microhabitat use of cased caddisfly differs from that of mayfly (e.g. Jowett and Richardson 1990, Subramanian and Sivaramakrishnan 2005). Although three mayfly taxa (*Epeorus latifolium*, *Baetis* spp., and *Rhithrogena japonica*) were highly dominant in the present systems, competitive interaction between dominant mayfly and satellite caddisfly taxa may be minor due to differences of microhabitat use.

Three mayfly (*Cinygmula* spp., *Epeorus aesculus*, *Epeorus curvatulus*) and one caddisfly (*Hydroptila* spp.) were distributed in streams with intermediate to high precipitation (Table 4-2). The satellite and dominant mayfly taxa (i.e., *Epeorus latifolium* and *Rhithrogena japonica*) belong to same family (i.e., Heptageniidae), and these satellite mayfly taxa may be competitively excluded by the dominant mayfly in the case that community attain to saturate (i.e., streams with low precipitation). On the other hand, these satellite mayfly have

Plate 4-1. *Dicosmoecus jozankaeanus* (Trichoptera: Limnephilidae), which were observed in only streams with from low to intermediate precipitation (i.e., satellite taxa) in the present study. Photo credit: N. Kuhara.

streamlined-flattened body shapes (see Plate 4-2), and then can resist high current velocities (i.e., high tolerance against disturbance-induced removal, Hynes 1970). Therefore, *Cinygmula* spp., *Epeorus aesculus*, and *Epeorus curvatulus* may be able to exist in stream with intermediate to high precipitation because of their morphology.

The hump-shaped relationship between taxonomic richness and precipitation in periphyton feeders was generated by displacement of rare taxa. Satellite taxa observed in streams with low to intermediate or those with intermediate to high were relatively low abundance in those streams (i.e., rare taxa). Competitive interaction may not be elicited due to low community density in streams with high precipitation. Thus, the rare taxa with traits of disturbance tolerance (*Cinygmula* spp., *Epeorus aesculus*, *Epeorus curvatulus*) can survive in the streams, whereas those without traits of disturbance tolerance (*Apatania* spp., *Dicosmoecus*

Plate 4-2. *Cinygmula* spp. (Ephemeroptera: Heptageniidae), which were observed in only streams with with intermediate to high precipitation (i.e., satellite taxa) in the present study. Photo credit: N. Kuhara.

jozankeamus, and *Goera japonica*) would be locally extinct by disturbance-induced removal. In contrast, competitive interaction may be elicited due to high community density in streams with low precipitation. Thus, the rare taxa (i.e., *Apatania* spp., *Dicosmoecus jozankeamus*, and *Goera japonica*) can coexist with dominant taxa because of microhabitat differences in the streams, whereas those which may compete with dominant taxa (*Cinygmula* spp., *Epeorus aesculus*, *Epeorus curvatulus*) would be locally excluded due to competition. Therefore, displacement of rare taxa may occur along disturbance. Since the force of removal for rare taxa is relatively weak in streams with intermediate precipitation (Fig. 4-4), the hump-shaped pattern in periphyton feeders may be detected (Fig. 4-4).

Dominant taxa may regulate the strength of density dependent competition. Although periphyton feeders showed the significant checkerboard pattern under the observed full range of precipitation (Fig. 4-3), taxonomic composition of periphyton feeders in streams with high precipitation was nested in those in streams with intermediate precipitation. These results suggest that assemblages were structured without competitive interaction in the range from high to intermediate precipitation, where community density may not reach saturation yet (Fig. 4-4). Since the disturbance tolerant but competitively inferior rare taxa may be replaced with the disturbance vulnerable but non-competitive rare taxa along disturbance (Fig. 4-4), the assemblages would show checkerboard distribution patterns by competitive exclusion after community saturation (Fig. 4-4).

Dominant taxa, such as *Epeorus latifolium* and *Baetis* spp., are considered to not have trade-off in traits. Their abundance was negatively affected by the strength of disturbance and they built up high community densities in the streams with low precipitation, which have caused the removal of rare taxa through competition (Fig. 4-4). Thus, relative abundance of dominant taxa within an assemblage may increase with community density (Fig. 4-4). The present results that evenness in periphyton feeders decreased monotonically with community density and precipitation (Fig. 4-1, Table 4-1) can be interpreted as evidence of this process (Fig. 4-4). Therefore, assemblages in periphyton feeders may be determined through processes of community-level density dependent competition due to dominant taxa against rare taxa.

Since displacement of dominant taxa of periphyton feeders did not occur in the present system, explanations by Kondoh (2001) and Caddote (2007) cannot completely explain my results. Since periphyton feeders did not show a nested distribution pattern, explanation by Kadmon and Benjamini (2006) cannot also apply to them. The present results that periphyton feeders showed checkerboard distribution pattern without displacement of dominant taxa can be explained by density-dependent competition at the community level and displacement of rare taxa with different traits (Fig. 4-4).

Why density dependent competition at the community level was detected in only periphyton feeders? Community density of periphyton feeders was lower compared to those of detritus feeders and carnivores. Detritus and prey organisms may be relatively rich food resources in stream ecosystems, but periphyton in upper stream beds is prone to be lost quickly due to disturbance and feeding (Death and Zimmermann 2005). Therefore, periphyton feeders may be more sensitive to food limitation (Hart 1987, Hart and Robinson 1990, Kohler 1992), and thus more likely to saturate than detritus feeders and carnivores.

The effects of competition on community structure of stream invertebrates have been controversial (Vinson and Hawkins 1998, Allan and Castillo 2007). Some studies have indicated that competition is unimportant for stream invertebrate assemblages because they inhabit unstable environments (Hynes 1970, Resh et al 1988), whereas others have indicated that competition has effects on the distribution and density of stream invertebrates (McAuliffe 1983, Hemphill 1991, Kuhara et al 1999). These contradictory results may be explained by whether or not community density of the assemblage is close to saturation. Therefore, I can reach better understanding of competition and diversity-disturbance relationships by examining not only species numbers and evenness, but also community density.

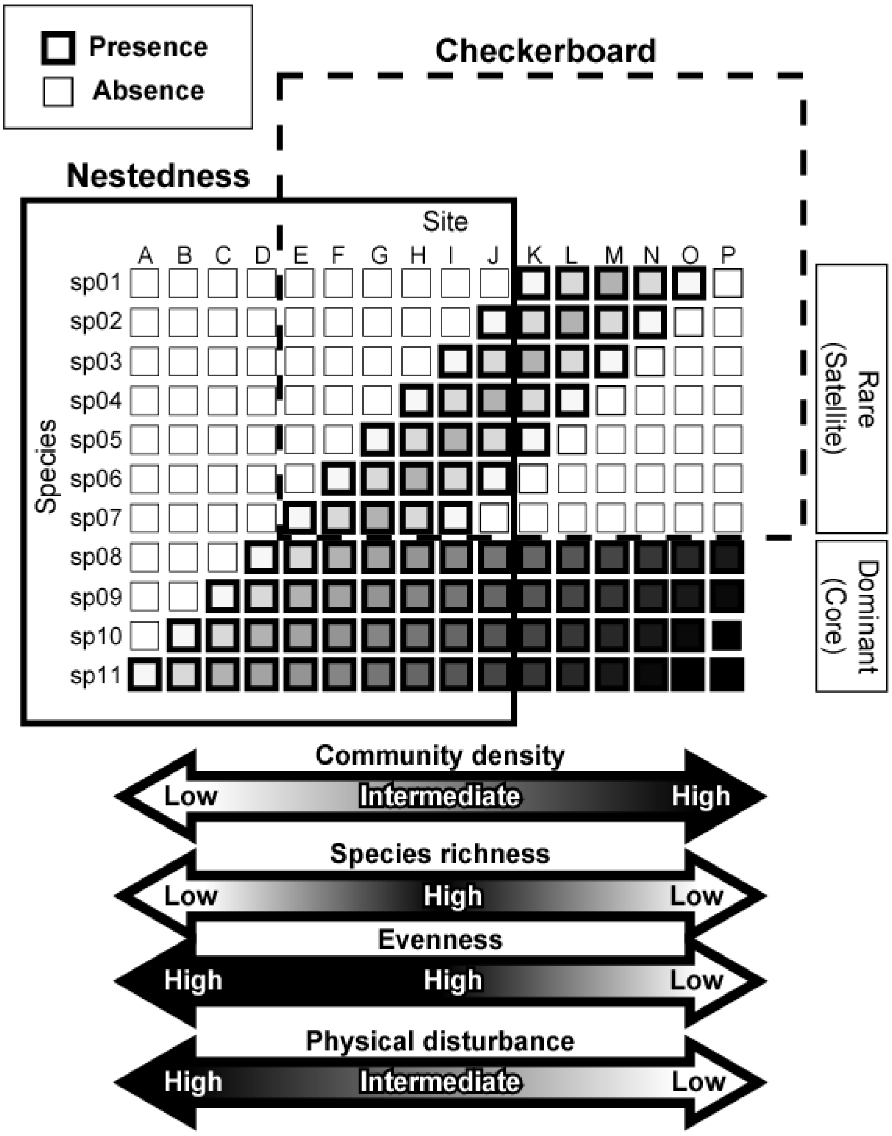

Fig. 4-4. Matrix representing effects of physical disturbance on community density, species richness, evenness, occurrence and density of each species, and distribution patterns through community-level density dependent competition in hypothetical assemblages. Squares with bold and thin edges indicate presence and absence of each species, respectively. Density of each species is represented as a monochrome color gradient from white to black, which is corresponding to from low to high densities. Rows represent species, and columns represent study sites. A range from low to intermediate community density in parallel with from high to intermediate physical disturbance, assemblages may not reach saturation. Since competition at these densities has little effect on assemblages, species richness increases with community density, and evenness is relatively high and constant. In the range of physical disturbance, a negative diversity-disturbance pattern and nested distribution pattern are detected. The other range from intermediate to high community density in parallel with from intermediate to low physical disturbance, assemblages approach saturation. Since competition has negative effects on rare species but not on dominant species, species richness decreases with community density due to local extinction of rare species. In the range of physical disturbance, a hump-shaped diversity-disturbance pattern and checkerboard distribution pattern are detected. The number of individuals of dominant and core species increase monotonically from high to low physical disturbance, whereas rare and satellite species are replaced with other rare species by community-level density dependent competition.

Appendix A. Dominant taxa of periphyton feeders in streams with low, intermediate, and high precipitation. Streams were grouped into three based on degrees of precipitation, although number of streams with each precipitation (*N*) is different. The percentage of individuals of each taxon in each precipitation class is shown in parentheses.

Log (precipitation)	*N*	Dominant taxa in herbivore assemblages				
Low (3.045 - 3.935)	21	*Baetis* spp. (39.3)	*Epeorus latifolium* (25.1)	*Rhithrogena japonica* (18.0)	*Glossosoma spp.* (9.3)	*Ecdyonurus viridis* (2.5)
Intermediate (3.935 - 4.826)	54	*Epeorus latifolium* (34.6)	*Baetis* spp. (29.9)	*Glossosoma* spp. (11.0)	*Rhithrogena japonica* (10.4)	*Cinygmula* spp. (3.4)
High (4.826 - 5.717)	15	*Baetis* spp. (39.3)	*Epeorus latifolium* (32.2)	*Cinygmula* spp. (6.2)	*Apatania* spp. (4.3)	*Agapetus* spp. (3.4)

Chapter V

General discussion

The present study analyzed stream invertebrate assemblages in Hokkaido Island to reveal two related diversity patterns (i.e., latitudinal patterns and diversity-disturbance patterns) and their mechanisms. In Chapter II and III, I showed latitudinal patterns in taxonomic richness of stream invertebrate assemblages and revealed the process creating the patterns. In Chapter IV, I showed diversity-disturbance patterns and demonstrated mechanisms generating variation in the patterns. Here, I summarize the present studies and discuss diversity patterns and their mechanisms in stream invertebrate assemblages. Finally, I describe generality of the present studies and future direction.

Latitudinal gradient in stream invertebrate assemblages in Hokkaido Island.

A clear latitudinal pattern in taxonomic richness of entire stream invertebrate assemblages was detected in mountain streams on Hokkaido Island, and this pattern was generated by flood disturbance, which affected by precipitation decreasing with latitude, through directional variation in community density (Chapter II). This process creating the latitudinal pattern was consistent with the More Individuals Hypothesis (Srivastava & Lawton 1998; Yee and Juliano, 2007).

Factors that generate latitudinal gradients at broad spatial scales are rarely identified because several candidate factors change simultaneously with latitude (Gotelli & Ellison, 2002). In particular, it is difficult to distinguish the influences of abiotic environmental factors from those of historical factors, such as differential speciation and dispersal, at broad spatial scales (Ricklefs & Schluter, 1993; Gotelli & Ellison, 2002). By focusing on the regional scale (i.e., Hokkaido Island) to discount historical factors and to extract the effects of environmental factors on latitudinal gradients in taxonomic richness, I was able to detect processes that an environmental factor (precipitation) produced the latitudinal gradient in taxonomic richness without inference from historical factors (Chapter II).

Stream invertebrate assemblages can be categorized into three feeding guilds based on their feeding habits (detritus feeders, periphyton feeders, and carnivores; Merritt & Cummins 1996; Kawai & Tanida 2005). Detritus feeders and carnivores showed latitudinal gradients in taxonomic richness like entire stream invertebrate assemblages, whereas periphyton feeders did not. Although both detritus feeders and carnivores exhibited latitudinal gradients, processes creating latitudinal gradients differed between the two guilds. The latitudinal gradient in taxonomic richness of detritus feeders was provided by latitudinal variation in community density of detritus feeders, whereas that in taxonomic richness of carnivores was provided by trophic interaction with detritus feeders. Hence, latitudinal gradient in taxonomic richness of detritus feeders can be generated without interactions with other guilds, but effects from detritus feeders are essential for forming the latitudinal gradient in taxonomic richness of carnivores (Chapter III).

Importance of trophic interactions among guilds on latitudinal gradients has been suggested (Buckley et al 2003; Hillebrand 2004), but processes affecting latitudinal gradient in species diversity through trophic interaction have not been shown. In Chapter III, I revealed that the latitudinal gradient in taxonomic richness of carnivores was generated by trophic interaction with detritus feeders (Chapter III).

The results obtained in Chapter II and III indicate that latitudinal patterns in taxonomic richness varied depending on guilds although entire stream invertebrate assemblages exhibited the latitudinal pattern. In other words, since detritus feeders showed latitudinal patterns in taxonomic richness and carnivores also showed that by trophic interaction (Chapter III), entire stream invertebrate assemblages would exhibit that in taxonomic richness though taxonomic richness in periphyton feeders did not change with latitude.

Diversity-disturbance relationships in stream invertebrate assemblages

The latitudinal pattern in species diversity has been observed for various taxa (Rosenzweig 1995; Hillebrand 2004), but latitude, in itself, is not a real explanatory variable for variation in species diversity (Symonds et al 2006). Latitude acts as a surrogate for various environmental factors determining species diversity (Symonds et al 2006). As Krebs (2001) suggests that disturbance is one of the causal factors for latitudinal gradient, physical disturbance (i.e., flood disturbance generated by high precipitation) was important for the latitudinal gradient in taxonomic richness of stream invertebrate assemblages (Chapter II).

Flood disturbance, which affected by precipitation with latitude, had effects on taxonomic richness in detritus feeders, carnivores, and periphyton feeders, but relationships of taxonomic richness with precipitation differed between feeding guilds (Chapter IV). A negative diversity-disturbance pattern in detritus feeders that taxonomic richness decreased with precipitation was explained by the More Individuals Hypothesis because detritus feeders may not attain to saturate in community density. On the other hand, a hump-shaped diversity-disturbance pattern in periphyton feeders that taxonomic richness peaked at intermediate precipitation was structured by density dependent competition at the community level. In streams with high to intermediate precipitation, community density was low and the assemblages may not attain to saturation, and thus periphyton feeders were structured by process of the More Individuals Hypothesis, like detritus feeders. In contrast, periphyton feeders affected by competitive interaction in streams with intermediate to low precipitation because community density was high and the assemblages may attain to saturation. Hence, variation in taxonomic richness of periphyton feeders was determined by expression of density dependent competition at the community level although that was explained by the More Individuals Hypothesis in streams with high to intermediate precipitation.

In the present study, I was able to explain differences in diversity-disturbance relationships between feeding guilds by asking whether or not assemblages reach saturation and then density-dependent competition occur under observed range of disturbance. Variation in diversity-disturbance patterns has been explained by Kondoh (2001), Cadotte (2007), and Kadmon and Benjamini (2006). However, these explanations cannot perfectly explain the present results (Chapter IV). Displacement of dominant taxa that is assumed by Kondoh (2001) and Caddote (2007) did not occur in periphyton feeders. Furthermore, since periphyton feeders showed a checkerboard distribution pattern, explanation by Kadmon and Benjamini (2006) cannot also apply to them. The present results that periphyton feeders showed checkerboard distribution pattern without displacement of dominant taxa can be explained by taking both density-dependent competition at the community level and displacement of rare taxa with different traits into consideration (Chapter IV).

The present study is the first empirical study to reveal importance of density dependent competition at the community level for diversity-disturbance patterns. My explanation for variation in diversity-disturbance relationships is based on the hypothesis proposed by Kondoh (2001). Kondoh (2001) presumes that all species have trade-off in traits between competitive ability and disturbance tolerance, and my explanation is formed by the addition of idea that dominant core taxa did not show trade-off in traits but rare satellite taxa did show trade-off in traits to the hypothesis by Kondoh (2001). Dominant taxa have high community density and then may regulate the strength of density dependent competition. Thus, the idea that adds dominant core taxa to hypothesis by Kondoh (2001) may serve a key role to explain variation in diversity-disturbance patterns.

Relationships between latitudinal patterns and diversity-disturbance patterns

In the present study, precipitation, which cause flood disturbance, negatively affected community density (Chapter II and IV), and relationships between taxonomic richness and community density differed between the guilds due to strength of density dependent competition at the community level (Chapter IV). Precipitation varied with latitude in Hokkaido Island (Chapter II). Taxonomic richness in periphyton feeders did not monotonically change with precipitation by emergence of density dependent competition at the community level (Chapter IV), and hence the richness did not show a latitudinal gradient (Chapter III). In contrast, taxonomic richness in detritus feeders did monotonically change with precipitation by absence of density dependent competition at the community level (Chapter IV), and hence the richness did show a latitudinal gradient (Chapter III). Therefore, strength of density dependent competition at the community level determined diversity-disturbance patterns, and as a result that also determined relationships between taxonomic richness and latitude (i.e., latitudinal gradient).

Conclusions

The present study demonstrates that (1) the latitudinal gradient in taxonomic richness was provided by an environmental factor (i.e., precipitation which cause flood disturbance) without interference by historical factors; (2) the latitudinal pattern in a guild (i.e., carnivores) was generated by both qualitative and quantitative trophic interaction with an other guild (i.e., detritus feeders); and (3) variation in diversity-disturbance relationships was explained by taking both density-dependent competition at the community level and differences in trade-off in traits of rare satellite taxa into consideration.

Some studies indicated that species did not show clear trade-off in traits (Lenssen et al 2004; Haddad et al 2008) and that dominant species did not vary with disturbance (Fröder and Sommer 1999, Helfield et al 2007). Those studies cannot apply to explanations that assume clear trade-off in traits (e.g., Kondoh 2001) and assume no differences in traits (e.g. Kadomon & Benjamin 2006), and this may be because effects of competitive interaction, which vary with environmental factors through community density, differ between dominant core and rare satellite species, as shown in the present study. Hence, future studies need to separate assemblages into dominant core and rare satellite species and to examine how abiotic and biotic factors have effects on dominant core and rare satellite species. Although biological traits of rare satellite species remain poorly understood compared to those of dominant core species (Poff et al 2006), I will be able to reach better understanding of diversity patterns and their mechanisms by examining biological traits of both dominant core and rare satellite species.

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Summary

Chapter I

The latitudinal gradient in species diversity that peaks in the tropics and declines toward the poles is one of the oldest and most fundamental spatial patterns described in ecology, but the explanations for the latitudinal gradient are still insufficient although almost two centuries lapse after the discovery. It is difficult to distinguish the influences of abiotic environmental factors from those of historical factors, such as differential speciation and dispersal, at broad spatial scales. Therefore, examining latitudinal patterns at regional scales, rather than the global scale (e.g. temperate-tropical gradient) could prove effective for determining the effects of abiotic environmental factors.

Previous studies, which proposed many hypotheses to account for the latitudinal gradient in species diversity, have focused on external factors such as energy, climate, and habitat heterogeneity. However, some recent studies have suggested that effects of interactions within assemblages on latitudinal gradients should not be ignored. Hence, I should examine not only how external factors influence latitudinal gradients in species diversity, but also how a latitudinal gradient in a guild are influenced by those in other guilds.

The latitudinal gradient in species diversity have fascinated ecologists for a long time, but it acts as a surrogate for various environmental factors determining species diversity. Although Krebs (2001) shows latitudinal gradients in species diversity may be produced by up to eight interrelated causal factors, physical disturbance, such as hurricanes, fires, waves, drought, and floods, has been widely believed to be a major determinant of species diversity because that disrupts ecosystem, community, and population structure. Many studies have noted the hump-shaped diversity-disturbance relationship, but negative and positive diversity-disturbance relationships have also reported. Several explanations have been proposed for the variation, but no empirical study has examined these explanations.

Since Hokkaido Island spans four degrees of latitude (ca. 400 km), it provides an appropriate spatial scale at which to examine the effects of meteorological factors on latitudinal gradients in stream invertebrate assemblages. Trophic habits of stream invertebrate assemblages are relatively well known and their guild structure is simple. Thus, I could reach better understanding mechanisms generating two related diversity patterns (latitudinal gradients and diversity-disturbance patterns) using advantage of spatial scale of Hokkaido Island and character of stream invertebrate assemblages.

Chapter II

A clear latitudinal pattern in taxonomic richness of entire stream invertebrate assemblages was detected in mountain streams on Hokkaido Island, and this pattern was generated by flood disturbance, which affected by precipitation decreasing with latitude, through directional variation in community density. This process creating the latitudinal pattern was consistent with the More Individuals Hypothesis.

Factors that generate latitudinal gradients at broad spatial scales are rarely identified because several candidate factors change simultaneously with latitude. In particular, it is difficult to distinguish the influences of abiotic environmental factors from those of historical factors, such as differential speciation and dispersal, at broad spatial scales. By focusing on the regional scale (i.e., Hokkaido Island) to discount historical factors and to extract the effects of environmental factors on latitudinal gradients in taxonomic richness, I was able to detect processes that an environmental factor (precipitation) produced the latitudinal gradient in taxonomic richness without inference from historical factors.

Chapter III

Stream invertebrate assemblages can be categorized into three feeding guilds based on their feeding habits (detritus feeders, periphyton feeders, and carnivores). Detritus feeders and carnivores showed latitudinal gradients in taxonomic richness like entire stream invertebrate assemblages, whereas periphyton feeders did not. Although both detritus feeders and carnivores exhibited latitudinal gradients, processes creating latitudinal gradients differed between the two guilds. The latitudinal gradient in taxonomic richness of detritus feeders was provided by latitudinal variation in community density of detritus feeders, whereas that in taxonomic richness of carnivores was provided by trophic interaction with detritus feeders. Hence, latitudinal gradient in taxonomic richness of detritus feeders can be generated without interactions with other guilds, but effects from detritus feeders are essential for forming the latitudinal gradient in taxonomic richness of carnivores.

Importance of trophic interactions among guilds on latitudinal gradients has been suggested, but processes affecting latitudinal gradient in species diversity through trophic interaction have not been shown. I revealed that the latitudinal gradient in taxonomic richness of carnivores was generated by trophic interaction with detritus feeders.

Chapter IV

Flood disturbance, which affected by precipitation with latitude, had effects on taxonomic richness in detritus feeders, carnivores, and periphyton feeders, but relationships of taxonomic richness with precipitation differed between feeding guilds. A negative diversity-disturbance pattern in detritus feeders that taxonomic richness decreased with precipitation was explained by the More Individuals Hypothesis because detritus feeders may not attain to saturate in community density. On the other hand, a hump-shaped diversity-disturbance pattern in periphyton feeders that taxonomic richness peaked at intermediate precipitation was structured by density dependent competition at the community level. In streams with high to intermediate precipitation, community density was low and the assemblages may not attain to saturation, and thus periphyton feeders were structured by process of the More Individuals Hypothesis, like detritus feeders. In contrast, periphyton feeders affected by competitive interaction in streams with intermediate to low precipitation because community density was high and the assemblages may attain to saturation. Hence, variation in taxonomic richness of periphyton feeders was determined by expression of density dependent competition at the community level although that was explained by the More Individuals Hypothesis in streams with high to intermediate precipitation.

In the present study, I was able to explain differences in diversity-disturbance relationships between feeding guilds by asking whether or not assemblages reach saturation and then density-dependent competition occur under observed range of disturbance. Variation in diversity-disturbance patterns has been explained by Kondoh (2001), Cadotte (2007), and Kadmon and Benjamini (2006). However, these explanations cannot perfectly explain the present results. Displacement of dominant taxa that is assumed by Kondoh (2001) and Caddote (2007) did not occur in periphyton feeders. Furthermore, since periphyton feeders showed a checkerboard distribution pattern, explanation by Kadmon and Benjamini (2006) cannot also apply to them. The present results that periphyton feeders showed checkerboard distribution pattern without displacement of dominant taxa can be explained by taking both density-dependent competition at the community level and displacement of rare taxa with different traits into consideration.

The present study is the first empirical study to reveal importance of density dependent competition at the community level for diversity-disturbance patterns. My explanation for variation in diversity-disturbance relationships is based on the hypothesis proposed by Kondoh (2001). Kondoh (2001) presumes that all species have trade-off in traits between competitive ability and disturbance tolerance, and my explanation is formed by the addition of idea that dominant core taxa did not show trade-off in traits but rare satellite taxa did show trade-off in traits to the hypothesis by Kondoh (2001). Dominant taxa have high community density and then may regulate the strength of density dependent competition. Thus, the idea that adds dominant core taxa to hypothesis by Kondoh (2001) may serve a key role to explain variation in diversity-disturbance patterns.

Chapter IV

The present study demonstrates that (1) the latitudinal gradient in taxonomic richness was provided by an environmental factor (i.e., precipitation which cause flood disturbance) without interference by historical factors; (2) the latitudinal pattern in a guild (i.e., carnivores) was generated by both qualitative and quantitative trophic interaction with an other guild (i.e., detritus feeders); and (3) variation in diversity-disturbance relationships was explained by taking both density-dependent competition at the community level and differences in trade-off in traits of rare satellite taxa into consideration.

Some studies indicated that species did not show clear trade-off in traits and that dominant species did not vary with disturbance. Those studies cannot apply to explanations that assume clear trade-off in traits and assume no differences in traits, and this may be because effects of competitive interaction, which vary with environmental factors through community density, differ between dominant core and rare satellite species, as shown in the present study. Hence, future studies need to separate assemblages into dominant core and rare satellite species and to examine how abiotic and biotic factors have effects on dominant core and rare satellite species. Although biological traits of rare satellite species remain poorly understood compared to those of dominant core species, I will be able to reach better understanding of diversity patterns and their mechanisms by examining biological traits of both dominant core and rare satellite species.