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

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Summary

1. Although a latitudinal gradient in species diversity has been observed for various taxa, the factors generating the latitudinal gradient at broad spatial scales are difficult to identify because several candidate factors change simultaneously with latitude. We investigated latitudinal gradients in stream invertebrate assemblages in 30 headwater streams in Hokkaido Island, Japan, focusing on the regional scale to discount historical factors and to extract the effects of environmental factors on latitudinal gradients in diversity.
2. Taxon diversity (Shannon index) and taxon richness (number of taxa per unit area) increased with latitude. Abundance showed a similar latitudinal gradient, whereas evenness (Δ_1) did not. Hence, we conclude that the observed latitudinal gradient in taxon richness was generated by directional variation in abundance (passive accumulation), leading to that in taxon diversity.
3. Precipitation, which is strongly related to flood disturbances, decreased with latitude and was an important factor explaining variation in taxon diversity, taxon richness, and abundance. The probability of a taxon being present tended to increase from south to north, suggesting that the higher taxon richness observed in northern sites may be due to the presence of rare species. These findings indicate that flood disturbance varying with latitude may influence abundance and local extinction rates of rare species, consequently affecting taxon richness and taxon diversity.
4. By detecting the effects of an environmental factor (precipitation) on the latitudinal gradients in taxon diversity and taxon richness without interference by historical factors, this study demonstrates processes that can produce latitudinal gradients in the diversity of stream invertebrate assemblages.

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, we 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, we 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, we 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.

We 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? We 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.

Materials and methods

Study sites

In June 2004 data were collected from 30 mountain streams in 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. 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 1. Vegetation in the catchment areas was primarily mixed forests with deciduous broad-leaved and coniferous trees.

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). 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, we 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. We 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. 1). The remaining 10 sites were the middle group (Fig. 1). In each group, we 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 1). The three replicates from each stream were treated as random effects. We 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). We 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. 3). Bray-Curtis dissimilarity between study sites did not show a significant relationship with distance (Mantel test; $r = 0.06$, $P = 0.11$).

Latitudinal and longitudinal gradients

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

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. 5). The best model for taxon richness included both abundance and evenness (χ^2 = 52.96, P < 0.001; Fig. 5).

Relationships between presence/absence and rank in each taxon

Logistic regression models were significant in all three groups (likelihood ratio tests; northernmost group: β_0 = 4.6, β_1 = –0.049, χ^2 = 14.31, P < 0.001; middle group: β_0 = 5.9, β_1 = –0.076, χ^2 = 33.45, P < 0.001; southernmost group: β_0 = 6.0, β_1 = –0.082, χ^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. 6), suggesting that the high taxon richness in the northernmost group may result from the presence of rare species.

Latitudinal gradients in environmental conditions

Precipitation and catchment slope showed clear latitudinal gradients (Table 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, χ^2 = 50.59, P < 0.001, disturbance = 0.22 × precipitation – 11.54). High monthly precipitation may cause high discharge events and bed movement (Fig. 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 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).

Discussion

Similarity in stream invertebrate assemblages

Similarity based on presence/absence data was not related with geographic distance (Fig. 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 our 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. 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. 5). The fact that a latitudinal gradient was found in taxon richness but not in evenness (Fig. 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 relationships were confirmed in the present study system (Fig. 5). The clear latitudinal gradient observed in abundance, coupled with the absence of a similar pattern in evenness (Fig. 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 our study, taxon rank at the 0.5 presence–absence probability tended to increase from north to south (Fig. 6), whereas evenness, which is related with the distribution of relative abundance, varied little among study streams (Fig. 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. 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 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 and 3), and the directional variation in abundance from south to north could have influenced the local extinction rates of rare species (Fig. 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 our 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. 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 3).

In this study, we were 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. We 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. We can better understand latitudinal gradients in diversity by examining relationships between disturbance and stream invertebrate assemblages at the regional scales and beyond. Although we 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). We 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.

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Table 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

Table 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

Table 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
Taxon richness	– Precipitation (0.99)	1	11.37	<0.001
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

Figure legends

Fig. 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.

Fig. 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.

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

Fig. 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.

Fig. 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.

Fig. 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.

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

Fig. 1.

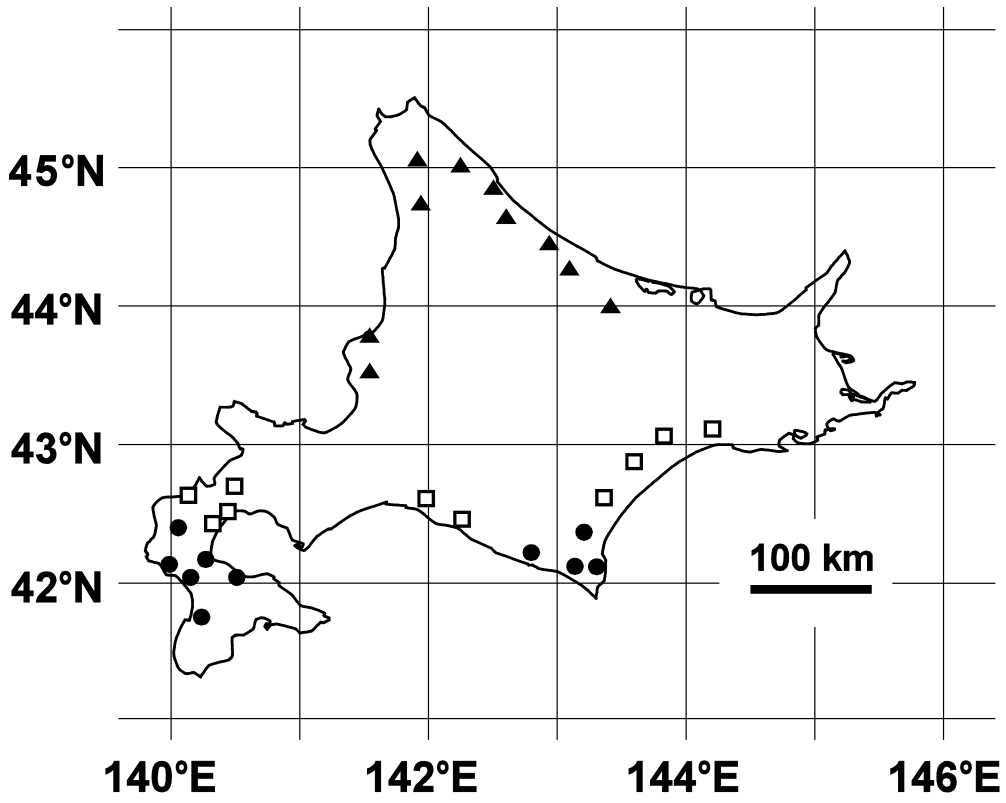

Fig. 2.

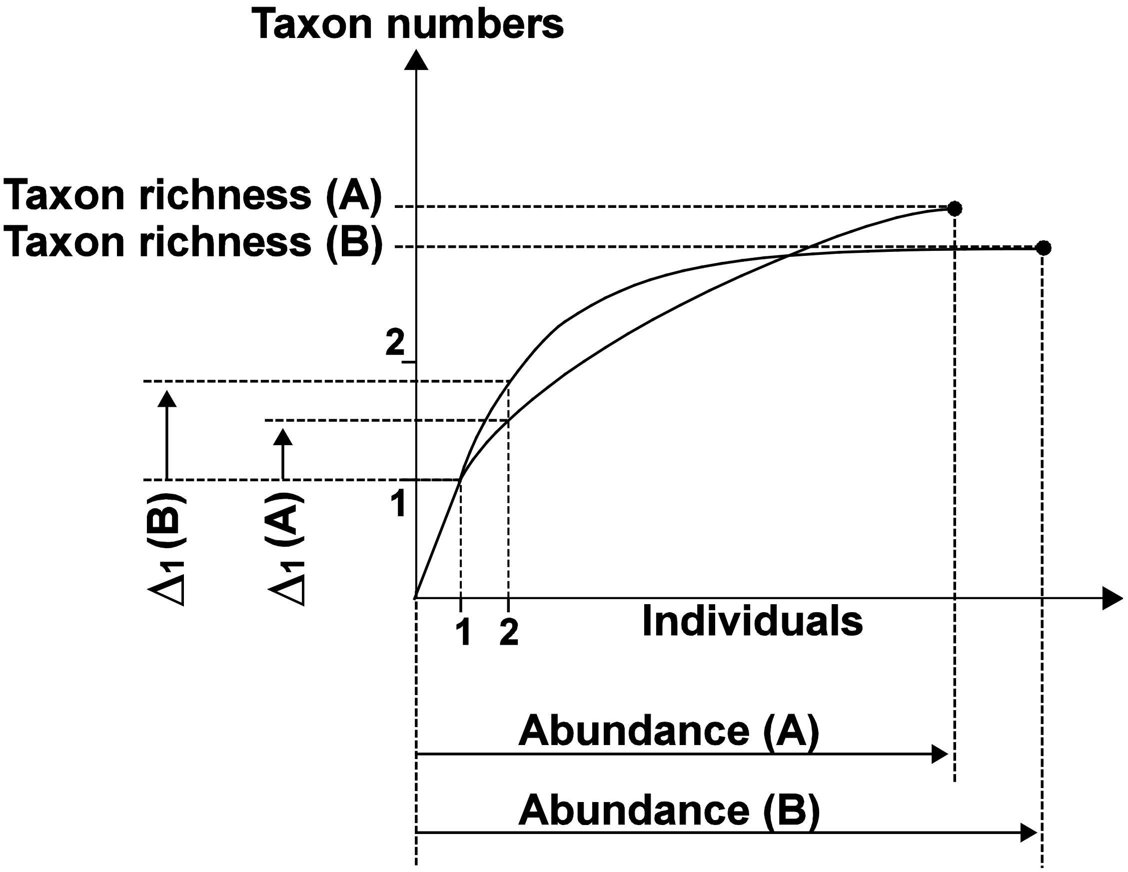
Taxon numbers
Taxon richness (A)
Taxon richness (B)
2
1
Δ1 (B)
Δ1 (A)
1
2
Individuals
Abundance (A)
Abundance (B)

Fig. 3.

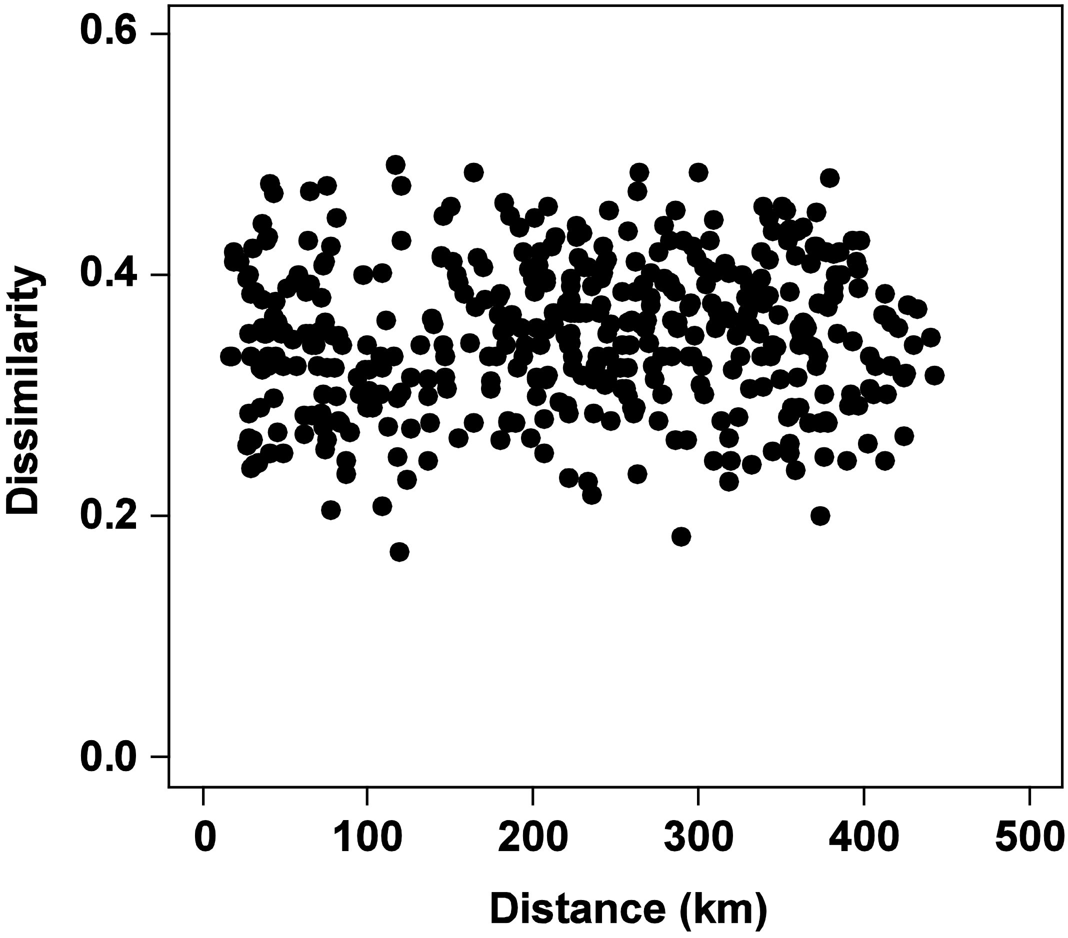

Fig. 4.

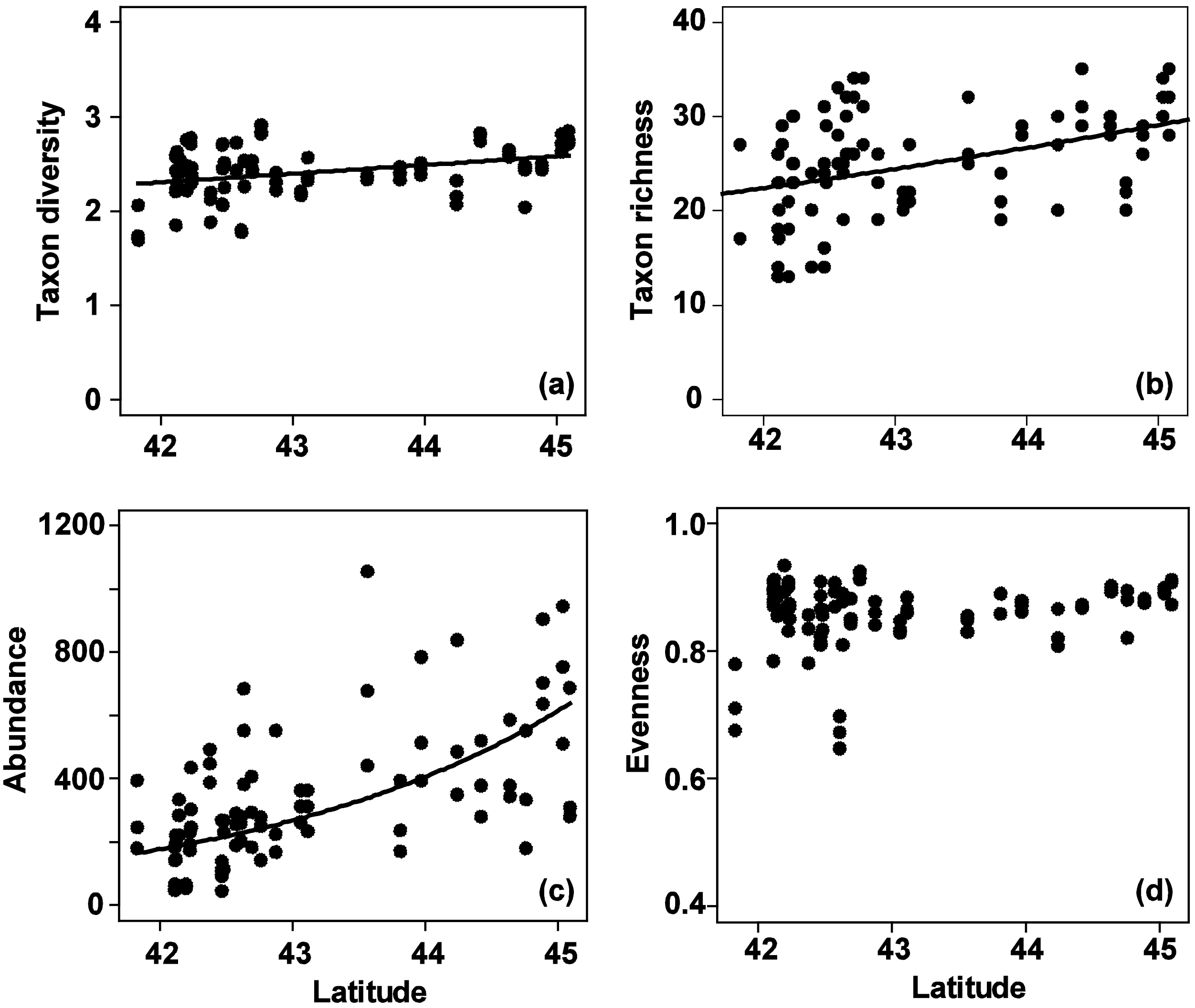
Taxon diversity
4
3
2
1
0
(a)
42
43
44
45
Taxon richness
40
30
20
10
0
(b)
42
43
44
45
Abundance
1200
800
400
0
(c)
42
43
44
45
Latitude
Evenness
1.0
0.8
0.6
0.4
(d)
42
43
44
45
Latitude

Fig. 5.

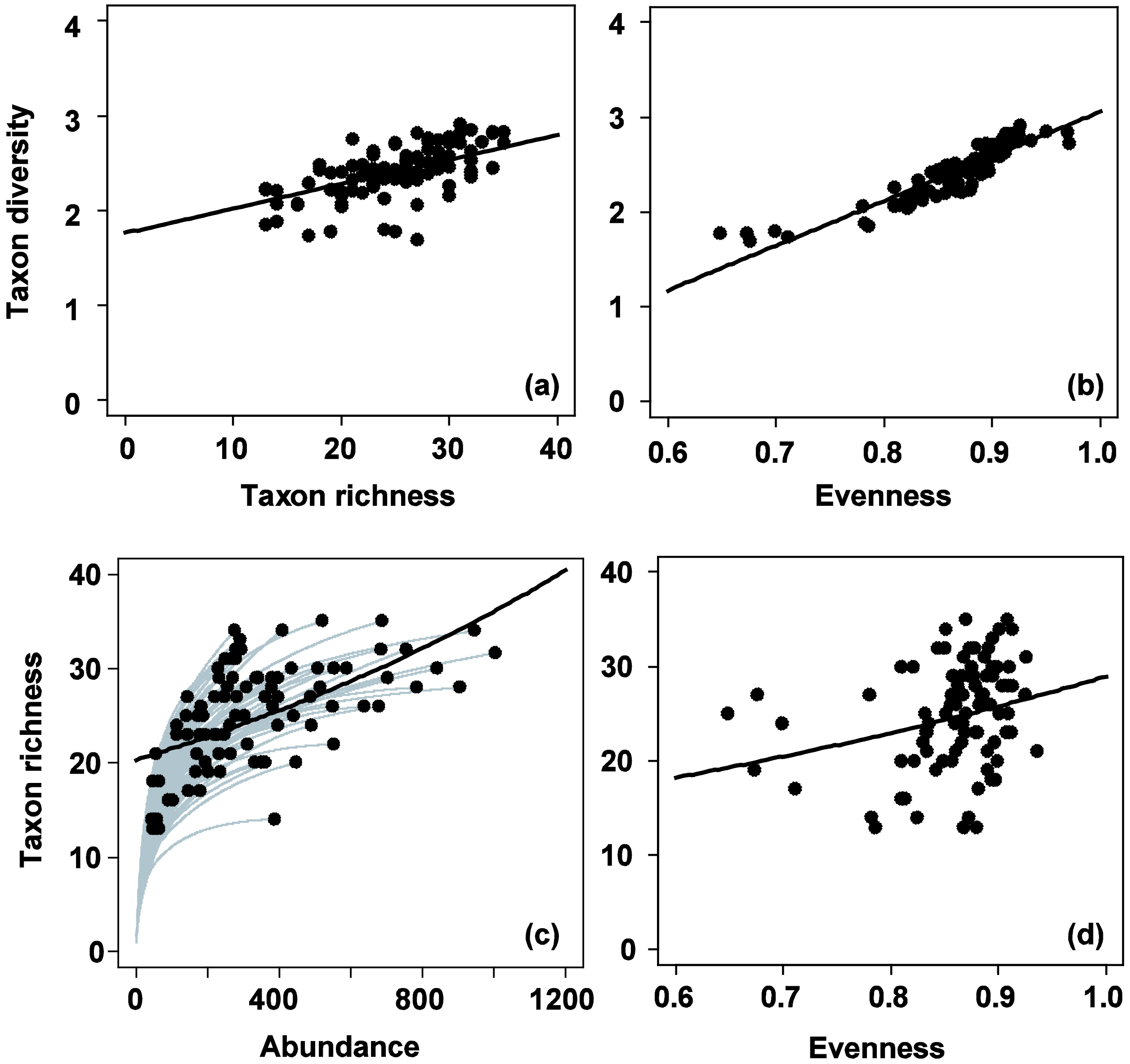
Taxon diversity
4
3
2
1
0
(a)
0
10
20
30
40
Taxon richness
4
3
2
1
0
(b)
0.6
0.7
0.8
0.9
1.0
Evenness
Taxon richness
40
30
20
10
0
(c)
0
400
800
1200
Abundance
40
30
20
10
0
(d)
0.6
0.7
0.8
0.9
1.0
Evenness

Fig. 6.

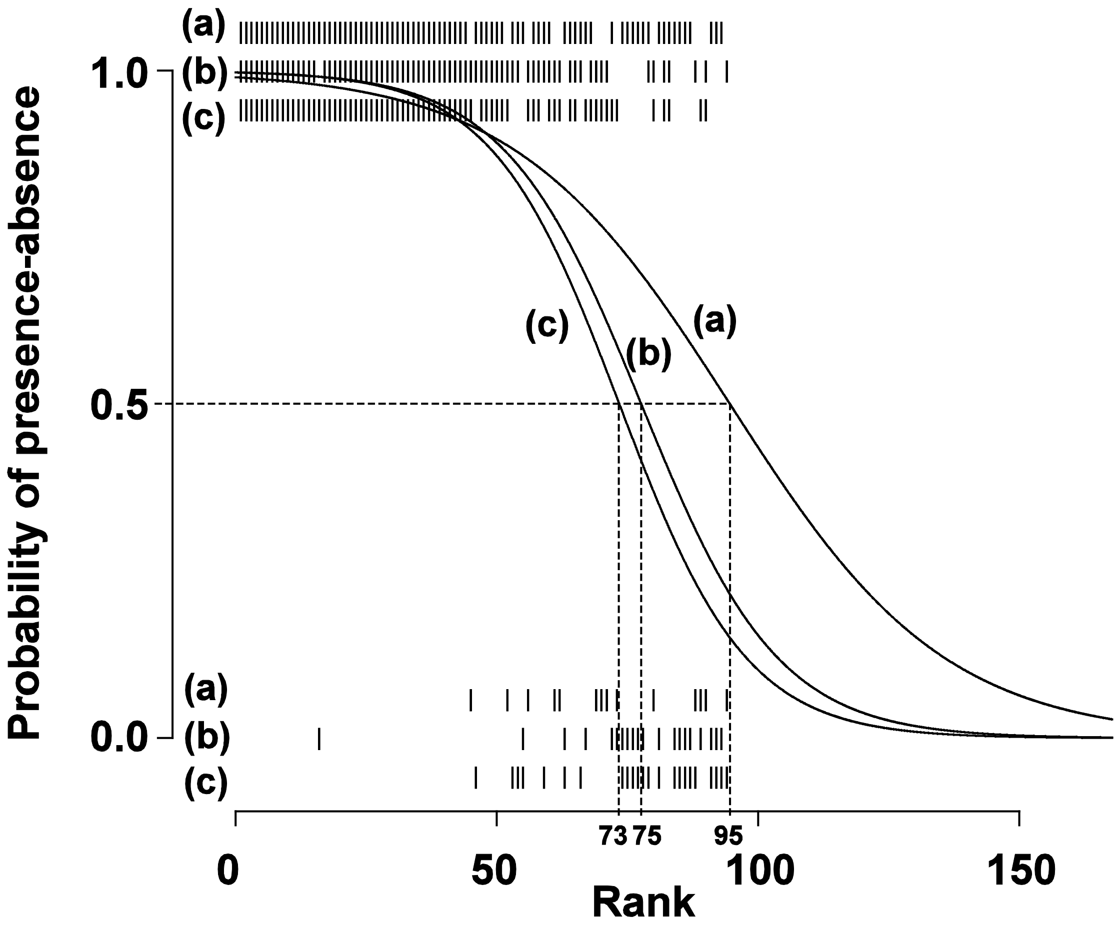
Probability of presence-absence
1.0
0.5
0.0
(a)
(b)
(c)
(a)
(b)
(c)
(c)
(b)
(a)
73
75
95
0
50
100
150
Rank

Fig. 7