

Patterns of functional biodiversity and function–environment relationships in lake littoral macroinvertebrates

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Abstract

I examined variability in the abundances of functional groups, functional diversity measures, and functional structure of littoral macroinvertebrate communities in relation to the environmental features of boreal lakes. The most important environmental variables shaping variation in the abundances of functional groups and functional structure were lake surface area, macrophyte cover, total phosphorous, and water hardness. The same environmental variables (i.e., lake surface area, macrophyte cover) accounted for variability in functional richness and functional diversity, while functional evenness was related to different environmental variables (i.e., hardness, color). Lake surface area and macrophyte cover comprised the most important axes of habitat templates shaping the functional trait structure and biodiversity in boreal lakes: lake area mirrors habitat differences between smaller and larger lakes, and macrophyte cover portrays the effects of habitat structural complexity on functional biodiversity. Functional biodiversity measures were also strongly correlated to species-level measures, and the correlation between similarity in functional and taxonomic structure was strong. Functional and taxonomic measures of macroinvertebrate communities thus provide rather similar information about littoral communities and ecosystem functioning.

Ecological communities can be characterized following two major approaches. The traditional approach is based on taxonomic structure, whereas a more recent one is based on the functional trait characteristics of species in ecological communities. Although the functional trait approach has a long history in ecological research (Statzner et al. 2001), it has experienced a recent revival with increased interest in the connections between ecosystem functioning, biodiversity, and environmental degradation in the last two decades (Kinzig et al. 2002). In the last decade, functional characterizations have been utilized in studies of various organism groups, including mammals (e.g., Stevens et al. 2003), birds (e.g., Hausner et al. 2003), fish (e.g., Hoeninghaus et al. 2007), insects (e.g., Ribera et al. 2001), zooplankton (e.g., Barnett et al. 2007), phytoplankton (e.g., Reynolds et al. 2002), and plants in general (e.g., Díaz and Cabido 2001). Particularly, in research on stream benthic macroinvertebrates, the use of various functional traits has attained a key role in the examination of community–environment relationships and anthropogenic degradation of ecosystem conditions (Dolédec et al. 1999; Lamouroux et al. 2004; Finn and Poff 2005). By contrast, the functional approach has not yet attained such a position in studies of lake littoral organisms, and there are only scattered examples of the use of functional

characterizations of lake littoral macroinvertebrate communities (Johnson and Goedkoop 2002; Tolonen et al. 2003). This is unfortunate, given that functional trait characterizations of lake littoral macroinvertebrates would obviously increase our understanding of the community–environment relationships and functioning of lake ecosystems in comparison to purely taxonomic approaches.

Southwood (1977) formulated the theory of habitat templates to incorporate the idea that certain suites of environmental features select species with suitable traits to coexist in a local community. It thus follows that there should be a close correspondence between local habitat conditions and functional trait characteristics of ecological communities. The use of functional traits is also intimately related to the concept of environmental filters, although the original formulation of habitat templates considered primarily local spatial and temporal heterogeneity, whereas the idea of environmental filters generally considers ecological features at multiple scales (Tonn 1990; Poff 1997). However, in the heart of both theories is the fact that the environmental filtering process acts on species traits, and only species possessing suitable traits are able to overcome the challenges presented by environmental conditions. The most influential environmental filters determining the functional characteristics of ecological communities in freshwater ecosystems typically include ecosystem size, habitat structural characteristics, trophic state variables, and biotic interactions (Tonn 1990; Poff 1997). Previous studies have suggested that these filters are also important for the functional trait characteristics of littoral macroinvertebrate communities (Johnson and Goedkoop 2002; Tolonen et al. 2003).

Various species traits have been proposed for freshwater macroinvertebrates, including body size, reproductive characteristics, mobility, and feeding habits (Usseglio-

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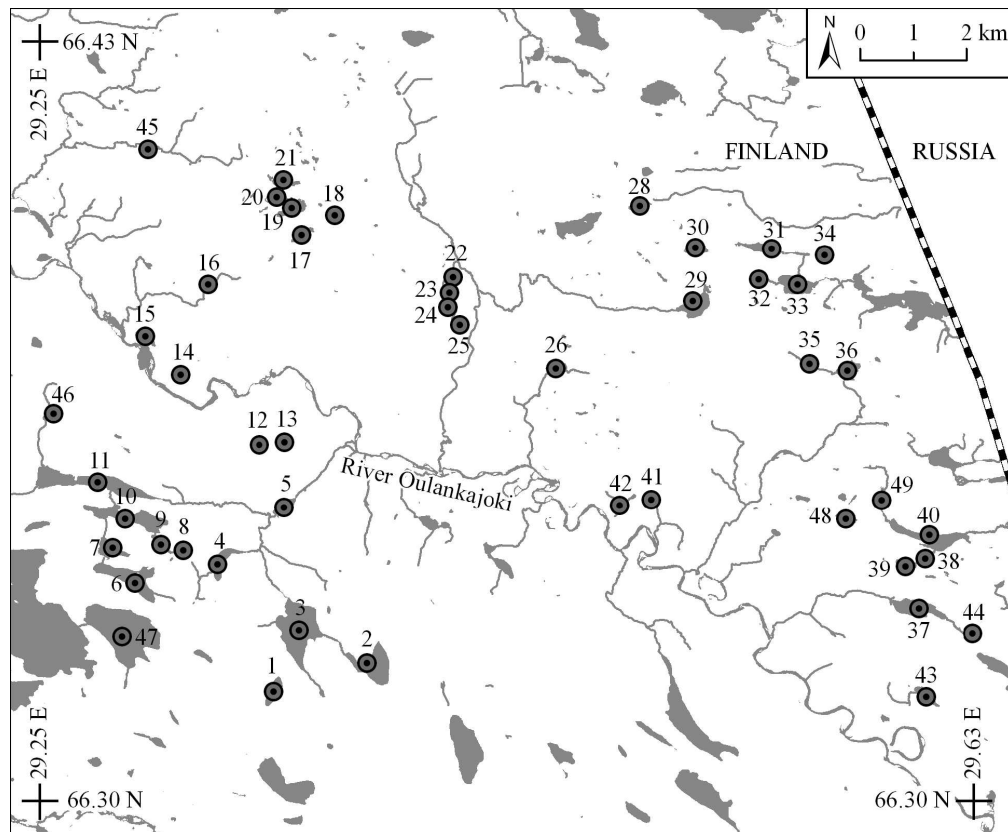


Fig. 1. A map of the study area, showing the distribution of the lakes studied in the Oulankajoki drainage basin.

Polatera et al. 2000). Traits that are likely most important to ecosystem functioning (e.g., detritus processing, animal-microbial interactions, herbivory, and energy transfer to the consumers at higher trophic levels) in freshwater ecosystems include not only functional feeding roles, but also where and how the food resources are obtained (Covich et al. 1999). I thus used a combination of functional feeding groups (Cummins 1973) and habit trait groups (Merritt and Cummins 1996) as the basis for the analysis of the functional biodiversity of littoral macroinvertebrates in boreal lakes.

I specifically examined the responses of single functional groups, functional structure, and measures of functional diversity to the environmental features of lakes. The measures of functional diversity were simple indices of functional richness, functional diversity, and functional evenness. Based on the findings of a few earlier littoral studies, I hypothesized that functional biodiversity should increase with lake size and habitat complexity, given that both of these features generally correlate with more niche opportunities for organisms (Eadie and Keast 1984; Huston 1994). Lake size should also correlate with variation in the abundances of many functional groups as habitat conditions differ between small and large lakes (Tonn and Magnuson 1982; Rahel 1984). I further expected that habitat structural characteristics, including macrophyte cover, would be strongly related to actively swimming and predaceous functional groups because a more complex habitat provides refugia for such sensitive

organisms against fish predators (Nilsson and Söderberg 1996; Tolonen et al. 2003). Habitat structural characteristics should also be related to the abundances of various other functional groups, which prefer certain conditions for feeding and which have habit traits suitable to particular habitats. Finally, I tested for the relationships between functional and taxonomic biodiversity of littoral macroinvertebrates communities, because findings from stream ecosystems have shown that these two characterizations may or may not be strongly related (Heino et al. 2007; Hoenighaus et al. 2007).

Methods

Study area and lake selection—The study landscape is located in the River Oulankajoki drainage basin in northeastern Finland (centered on 66°22'N, 29°25'E; area extent encompassing the sampled lakes was 170 km²; Fig. 1). The bedrock of the study area is highly variable, with extensive, yet scattered occurrence of calcareous rocks. Accompanied by considerable relative altitudinal differences, this geological variability is mirrored in highly variable vegetation, ranging from old-growth coniferous forests to mixed-deciduous riparian woodlots, and from nutrient-poor bogs to fertile fens. These factors also provide the basis for a high variability of freshwater ecosystems in the region. There are various types of lakes in the region, ranging from small calcareous lakes with high hardness and pH to peatland-bordered lakes with lower hardness and

pH. There are also various kinds of larger, predominantly forest-bordered lakes with intermediate water chemistry characteristics. Most lakes more than one than 0.01 km² in area harbor fish, with European perch (*Perca fluviatilis* L.) being the most common species in terms of frequency and abundance (J. Heino, pers. obs.). Other native fish species in the region include northern pike (*Esox lucius* L.), whitefish (*Coregonus lavaretus* s.l.), roach (*Rutilus rutilus* L.), European minnow (*Phoxinus phoxinus* L.), burbot (*Lota lota* L.), and nine-spine stickleback (*Pungitius pungitius* L.).

Forty-eight lakes were selected from those available in the River Oulankajoki basin based on two major criteria. First, they had to be located within two-kilometers distance from the nearest road to facilitate sampling. Second, they could not show any notable anthropogenic degradation of water chemistry and habitat structure to guarantee that only near-pristine lakes were sampled. In practice, the majority of the lakes were not affected by any considerable anthropogenic pressure, and their catchments have been historically, and are currently, subject to modest forestry practices. However, game fish have been stocked in some of the lakes, although they also harbored fish naturally. The sampling was concentrated on small lakes less than 0.10 km² in area because they are typically most numerous both globally (Downing et al. 2006) and in the Oulanka region (J. Heino, pers. obs.). Thus, the present lake survey should be representative of most lakes in the study area without the typical bias of lake surveys towards large lakes. However, there was considerable variation in lake size and other environmental features (Table 1).

Environmental variables—Twenty supra-lake, water chemistry, morphometry, and habitat variables were measured for each lake. Supra-lake variables were (1) % area of peatland in the catchment (determined using GIS based on CORINE land-cover raster data bases from the Finnish Environment Institute), (2) % peatland of the shoreline, (3) % forest of the shoreline, (4) % deciduous trees in the riparian zone, and (5) % coniferous trees in the riparian zone (determined in the field). Water chemistry parameters were (6) pH, (7) hardness (dH), (8) conductivity (mS m⁻¹), (9) color (mg pt L⁻¹), (10) total phosphorus (µg L⁻¹), and (11) chlorophyll *a* (mg L⁻¹). Water chemistry samples were taken simultaneously with the field work in September 2005. Water chemistry parameters were determined in the laboratory based on Finnish national standards. Lake morphometry variables were measured using GIS and comprised (12) lake surface area (m²), (13) shoreline length (m), and (14) shoreline development factor:

$$D_L = L / \left[2 \times \sqrt{(\pi \times A)} \right] \quad (1)$$

where *L* is shoreline length and *A* is lake area. Habitat variables were measured 1 m from the shoreline and included (15) near-shore depth (cm), (16) cover of macrophytes (%), (17) cover of bryophytes (%), and (18) cover of algae (%). Furthermore, substratum particle size and organic material were divided into nine classes, the

Table 1. Variation in selected environmental variables of the study lakes.

Variable	Mean	SD	Minimum	Maximum
Deciduous trees (%)	32.85	24.24	2	90
Hardness (dH)	2.44	1.69	0.3	7.0
Color (mg pt L ⁻¹)	47.71	31.97	5	150
Total phosphorous (µg L ⁻¹)	7.28	5.99	1.7	34.3
Chlorophyll <i>a</i> (mg L ⁻¹)	1.63	1.73	0	7.6
Surface area (km ²)	0.113	0.173	0.008	0.925
Shoreline development factor	1.55	0.43	1.0	3.1
Near-shore depth (cm)	45.17	20.47	22.0	104.2
Macrophyte cover (%)	11.08	13.78	0	53
Moss cover (%)	2.72	8.10	0	38

relative cover (%) of which were estimated at each sampling point: wood, other coarse organic matter, fine organic matter, sand (0.25–2 mm), gravel (2–16 mm), pebble (16–64 mm), cobble (64–256 mm), small boulder (256–512 mm), and large boulder (>512 mm). The mean values of the nine substratum variables were subjected to principal components analysis to derive two uncorrelated composite variables: (19) PC1 (inorganic bottom: high negative loading for fine organic matter, and high positive ones for sand, gravel, pebble, cobble, and boulders; variance explained 45.8%) and (20) PC2 (coarse organic matter: high positive loadings for wood and other coarse organic material; variance explained 17.4%). Supra-lake, water chemistry, and lake morphometry variables were based on a single measurement, while habitat variables were based on five measurements, the mean values of which were used in the analyses.

Macroinvertebrate data—Macroinvertebrate sampling was conducted in September 2005. Autumnal samples are representative of the macroinvertebrate communities of boreal lakes because most aquatic insect species are present as larvae and there is little emergence of adults (J. Heino, pers. obs.). The field crew took five samples from each lake, starting from a random point, after which the sampling points were evenly distributed across a 100-m stretch of the littoral zone. This sampling scheme was designed to guarantee that assemblage heterogeneity for each lake was incorporated in samples. Samples were taken ~1 m from the shoreline. A 30-cm × 100-cm sample was taken at each point. The sampling comprised a sweep using a D-net (mesh size 0.5 mm) on soft organic bottoms and vegetation, while a similar-sized plot was kicked to agitate macroinvertebrates using a D-net on stony bottoms. All samples from a lake were pooled. The macroinvertebrates were preserved in 70% alcohol immediately after sampling, and they were subsequently taken to the laboratory for further processing and identification. All macroinvertebrates were separated from associated material and were identified according to species or genus level. This was also the identification level of the dipterans, including chironomid midges (Diptera: Chironomidae).

Table 2. Characterization of functional feeding groups and habit traits of groups of freshwater macroinvertebrates. Modified from Merritt and Cummins (1996) and Heino (2005).

Functional category	Ecological characteristics
Functional feeding group	Feeding characteristics
Gatherers	Feed on fine particulate detritus on lake bottom
Filterers	Filter suspended material from water column and often build nets for capturing their food, including small organisms
Herbivore-piercers	Feed on living vascular hydrophytes and algae by piercing and sucking cell and tissue fluids
Predators	Attack other animals and engulf whole prey or suck body fluids
Scrapers	Feed on periphytic algae and associated material on mineral and organic substrates
Shredders	Feed on living or decomposing vascular plant tissue, coarse particulate organic material, by chewing large pieces
Habit trait group	Mode of existence
Burrowers	Inhabit fine sediments and may construct burrows with protruding tubes or ingest their way through sediments
Climbers	Live on vascular hydrophytes or coarse detrital debris, moving vertically on stem-type surfaces
Clingers	Possess behavioral or morphological adaptations for attachment to surfaces mainly on wave-swept shores
Sprawlers	Inhabit the surfaces of floating leaves of vascular hydrophytes or fine sediments
Swimmers	Adapted for short periods of swimming between benthic objects or swimming by rowing with the specially adapted hind legs

Characterization of functional groups—Macroinvertebrates were categorized into six functional feeding groups and five habit trait groups according to Merritt and Cummins (1996) and expert judgment for aquatic insects, as well as expert judgment for other minor groups of macroinvertebrates. Functional feeding groups included shredders, gatherers, filterers, scrapers, herbivore-piercers, and predators. Habit trait groups included burrowers, climbers, clingers, sprawlers, and swimmers. Divers were not differentiated from swimmers in the present categorization due to difficulties in separating swimming and diving behavior. Functional feeding groups refer to the feeding mode and approximate food type of macroinvertebrates, whereas habit trait groups include information on the relative mobility and where food is obtained (Table 2). Both of these characteristics should be important with regard to the functional roles of macroinvertebrates in the lake littoral zone. Combinations of functional feeding groups and habit trait groups were used, and the 24 observed combinations were termed subsequently as functional groups (Table 3).

Nonchironomid macroinvertebrates could have been characterized by several other traits as well (Usseglio-Polatera et al. 2000; Poff et al. 2006), but the two traits used in this study are perhaps most directly related to ecosystem functioning in freshwater ecosystems. A further reason for limiting the analysis to the combination of functional feeding groups and habit trait groups was that no comprehensive literature on other traits was found for chironomids, which comprised a major portion of macroinvertebrate taxa and abundance found in the lake survey (J. Heino, J. Kotanen, and L. Paasivirta, unpubl. data). I thus assumed that although the array of traits that could be utilized was limited, omitting chironomids from the analyses could lead to patterns that were not fully representative of lake littoral ecosystems.

There is evidence that the feeding roles of freshwater macroinvertebrates may vary with larval stage, as well as temporally and geographically, and many taxa may be rather omnivorous and highly flexible in their feeding habits (Mihuc 1997; Dangles 2002). These problems were exemplified by two groups of aquatic insects. First, a few net-building species of caddisflies (Trichoptera: Polycentropodidae) were assigned to either filterer or predator category (both types were represented in the data), although they are likely to use both feeding modes. Second, similarly problematic were some waterboatmen (Heteroptera: Corixidae) that could have been classified as herbivores or predators (both types were represented in the data), although most of these species are supposedly highly omnivorous. However, it did not make a strong difference to the results whether species in the two above groups were assigned to either of the mentioned categories. There are some classification systems which take flexibility in feeding habits into account by a point-scoring system (Schmedtje and Colling 1996; Moog 2002), whereby a score is assigned to each taxa with regard to the functional feeding groups it represents (e.g., eight points for shredder and two points for gatherer). However, these more-defined approaches for functional feeding group categorization were not possible in the context of this study, because the aim was to use the combined, categorical functional groups, incorporating both functional feeding modes and habit traits.

Measures of functional diversity and functional structure—There has recently been increased interest in developing continuous measures of functional diversity (Petchey and Gaston 2002; Petchey et al. 2007). Although such measures are surely preferable over discontinuous ones, I had to rely on the latter types of measures because the lack of comprehensive trait data on chironomid genera again

Table 3. Frequency of occurrence (number of lakes) and minimum, maximum, and mean abundance (at occupied lakes) of each functional group in the study lakes. Functional groups were based on the combination of functional feeding groups and habit trait groups. Also shown are common example genera for each functional group. A key to orders of the listed genera: A = Amphipoda; B = Basommatophora; C = Coleoptera; D = Diptera; E = Ephemeroptera; H = Heteroptera; I = Isopoda; M = Megaloptera; O = Odonata; P = Plecoptera; T = Trichoptera; V = Veneroida.

Functional group	Frequency	Mean	Min	Max	Common genera
Filterer-climbers	16	33	0	275	<i>Tanytarsus</i> (D)
Filterer-clingers	40	30	0	304	<i>Polycentropus</i> (T), <i>Microtendipes</i> (D)
Filterer-burrowers	45	33	0	241	<i>Pisidium</i> (V), <i>Sphaerium</i> (V)
Gatherer-burrowers	48	78	3	1484	<i>Ephemera</i> (E), <i>Dicortendipes</i> (D), <i>Cladotanytarsus</i> (D)
Gatherer-climbers	8	6	0	22	<i>Lauterborniella</i> (D)
Gatherer-sprawlers	48	123	3	507	<i>Caenis</i> (E), <i>Mystacides</i> (T), <i>Psectrocladius</i> (D)
Gatherer-swimmers	47	67	0	308	<i>Cloeon</i> (E), <i>Leptophlebia</i> (E)
Herbivore-climbers	10	6	0	30	<i>Haliplus</i> (C), <i>Laccobius</i> (C)
Herbivore-clingers	2	2	0	2	<i>Hydroptila</i> (T)
Herbivore-swimmers	20	16	0	190	<i>Sigara</i> (H)
Predator-burrowers	47	40	0	371	<i>Sialis</i> (M), <i>Culicoides</i> (D), <i>Clinotanypus</i> (D)
Predator-climbers	40	11	0	116	<i>Coenagrion</i> (O), <i>Aeshna</i> (O)
Predator-clingers	1	2	0	2	<i>Oecetis</i> (T)
Predator-sprawlers	48	112	4	427	<i>Somatochlora</i> (O), <i>Chrysops</i> (D), <i>Procladius</i> (D)
Predator-swimmers	25	2	0	8	<i>Callicorixa</i> (H), <i>Hygrotus</i> (C), <i>Nebrioporus</i> (C)
Scraper-climbers	42	12	0	53	<i>Gyraulus</i> (B), <i>Bathynomphalus</i> (B), <i>Lymnaea</i> (B)
Scraper-clingers	15	25	0	98	<i>Heptagenia</i> (E), <i>Oulimnius</i> (C), <i>Tinodes</i> (T)
Scraper-sprawlers	12	3	0	12	<i>Molanna</i> (T)
Scraper-swimmers	1	1	0	1	<i>Baetis</i> (E)
Shredder-burrowers	20	25	0	363	<i>Glyptotendipes</i> (D)
Shredder-climbers	41	9	0	41	<i>Agrypnia</i> (T), <i>Phryganea</i> (T), <i>Polypedilum</i> (D)
Shredder-clingers	33	22	0	202	<i>Cricotopus</i> (D)
Shredder-sprawlers	26	119	0	398	<i>Asellus</i> (I), <i>Nemoura</i> (P), <i>Limnephilus</i> (T)
Shredder-swimmers	12	125	0	561	<i>Gammarus</i> (A)

prevented me from using more sophisticated measures. Three simple measures of functional diversity were thus calculated for each lake: (1) functional richness (FR) or the number of functional groups; (2) functional diversity (FD) based on Shannon's index, describing both the number of functional groups and the division of individuals among the functional groups:

$$H' = - \sum_i^s p_i \log p_i \quad (2)$$

where p_i is the proportion of functional group i ; and (3) functional evenness (FE) based on Pielou's formula:

$$J' = H' / \log FR \quad (3)$$

where H' is Shannon's index value and FR is the number of functional groups. Finally, functional structure (FS) refers to the composition and abundance of functional groups in each lake. Species diversity and species evenness were also calculated based on Shannon's and Pielou's indices, respectively.

Statistical analyses—To normalize distributions, environmental variables were transformed using appropriate transformations (logarithmic, arcsine, or square-root) when necessary. Cross-correlations between the 20 environmental variables were then calculated using the Pearson correlation, and variables that were strongly correlated ($r > 0.6$) to other variables were excluded from regression and con-

strained ordination analyses to diminish the chance of spurious correlations. There were 12 weakly correlated explanatory variables that were used in the following analyses.

I first examined the relationships between environmental variables and the abundances of major functional groups (i.e., those that occurred in more than one-third of the lakes) using multiple regression analysis with forward stepwise selection of the explanatory variables ($\alpha = 0.05$). I similarly used multiple regression with forward stepwise selection to examine the relationships between environmental variables and the three indices describing functional diversity. Highly similar regression models were obtained for both abundances and diversity indices, when the inclusion of explanatory variables in the model was based on forward stepwise selection with Akaike information criterion (e.g., Johnson and Omland 2004). However, I decided to present only the models based on probability value ($\alpha = 0.05$) due to the facts that (1) they were more parsimonious in terms of the number of included explanatory variables, and (2) there was much redundancy between the two types of analyses in terms of the identity of the explanatory variables.

I used constrained ordination methods on log-transformed abundance data of functional groups to examine the relationships between environmental variables and functional structure (e.g., Legendre and Legendre 1998). In practice, both redundancy analysis (RDA) and canonical correspondence analysis (CCA) provided similar

insights into the relationships between environmental variables and functional structure, and thus only the results of the former method are shown. Furthermore, preliminary detrended correspondence analysis (DCA) showed that the gradients in functional structure were rather short (DCA axis 1: 1.521; DCA axis 2: 1.168), implying linear responses and supporting the use of RDA. The inclusion of explanatory variables in the RDA model was based on forward stepwise selection ($\alpha = 0.05$), with the significance of the variables being assessed by Monte Carlo randomizations (1,000 runs).

Finally, I used two correlative methods to examine the relationships between functional and taxonomic data. Spearman's rank correlation was used to test for correlations between functional and taxonomic data in richness, diversity, and evenness. A nonparametric Mantel test based on Bray-Curtis similarities, Spearman's rank correlation coefficient, and a permutation test (1,000 runs) for significance testing were used to examine community patterns between functional data (log-abundances of 24 functional groups) and taxonomic data (log-abundances of 155 taxa).

All explanatory, correlation, and regression analyses were run using SPSS version 11.5 (SPSS) while analyses with Akaike information criterion and constrained ordination were conducted using Brodgar version 2.5 (Highland Statistics), and non-parametric Mantel test with PRIMER version 6.0 (Clarke and Gorley 2006).

Results

The dominant functional groups in terms of frequency of occurrence and mean abundance at occupied sites were gatherer-burrowers, gatherer-sprawlers, gatherer-swimmers, predator-burrowers, and predator-sprawlers, representing macroinvertebrate genera typical of boreal lakes (Table 3). The most uncommon functional groups were herbivore-clingers, predator-clingers, and scraper-swimmers, representing genera that are more typical of running waters (Table 3). There were some significant relationships between the abundances of the major functional groups and environmental variables, although the strength of these relationships varied considerably among groups (Table 4). In general, gathering functional groups showed significant relationships to total phosphorus; herbivore-swimmers, predator-climbers, and predator-swimmers mainly to macrophytes; predator-sprawlers to color, area, and total phosphorus; scraping functional groups to mainly riparian deciduous trees; shredder-burrowers to coarse organic material and total phosphorus; shredder-sprawlers to area, macrophytes, and hardness; and shredder-clingers to peatland area (Table 4). Thus, although some of the relationships were ecologically reasonable, some relationships did not seem to have a direct ecological background.

Variation in the three measures of functional diversity was related to partly different environmental features of lakes (Table 4). Functional richness was best explained by a model including macrophytes, area, and PC2; functional diversity by macrophytes, area, hardness, and total phosphorus; and functional evenness by hardness, color,

macrophytes, and total phosphorus. In general, area and macrophytes were positively related to functional biodiversity, while hardness and total phosphorus were negatively related to the dependent variables (Table 4).

Functional structure of littoral macroinvertebrate communities was significantly related to the same variables as functional biodiversity indices. Forward selection in the RDA showed that lake surface area (conditional effect: 0.08), macrophytes (conditional effect: 0.07), total phosphorus (conditional effect: 0.04), and hardness (conditional effect: 0.03) primarily determined variation in functional structure (Table 5, Fig. 2a). However, these variables accounted for only a minor proportion of the variability in functional structure ($R^2 = 0.22$). In the RDA biplot, the functional groups showing the strongest relationships to the environmental variables were herbivores-clingers and scrapers-clingers to area; gatherers-swimmers and filterers-clingers to total phosphorus; and herbivores-swimmers to macrophytes (Fig. 2b). Other functional groups were not strongly related to any single environmental variable, whereas some were rather indifferent in their environmental responses.

Functional richness was strongly correlated with species richness ($r_s = 0.833$, $p < 0.001$; Fig. 3a). Functional diversity and species diversity ($r_s = 0.795$, $p < 0.001$; Fig. 3b), as well as functional evenness and species evenness ($r_s = 0.767$, $p < 0.001$; Fig. 3c) were also significantly correlated. Finally, community patterns between functional and taxonomic data were relatively similar, and the relationship was highly significant in the Mantel test ($r_s = 0.723$, $p < 0.001$).

Discussion

Examination of functional biodiversity has recently been regarded as an important part of studies on ecosystem functioning (e.g., Kinzig et al. 2002), biodiversity-environment relationships (e.g., Stevens et al. 2003), and environmental assessment (e.g., Dolédec et al. 1999). Although there is no single, standardized measure of functional biodiversity (Díaz and Cabido 2001), it could be considered to include variation in diversity within single functional groups, functional structure, and functional diversity in ecosystems. Thus, I considered these aspects of the functional biodiversity of lake littoral macroinvertebrates, and their responses to major environmental gradients. The present findings should shed light into community-environment relationships and ecosystem functioning, and to complete existing knowledge provided by primarily taxonomic approaches on the variability of littoral macroinvertebrate communities (Hoffman et al. 1996; Brodersen et al. 1998; Brauns et al. 2007). For example, information on functional trait characteristics may aid in predicting how communities will change in response to environmental changes, and thus facilitate understanding the importance of biodiversity in general (e.g., Norberg 2004). The following discussion should thus be important in providing foundations for future research on the importance of functional biodiversity in ecosystem functioning and assessment of environmental degradation.

Table 4. Results of regression analyses for the environmental relationships of the abundances of functional groups and functional diversity measures. Only significant models for the functional groups occurring in more than one-third of the lakes are shown. Abbreviations: B = bryophytes; C = color; D = depth; H = hardness; M = macrophytes; PL = peatland; RD = riparian deciduous trees; SA = lake surface area; TP = total phosphorus; PC2 = second principal component of substratum characteristics.

Dependent variable	Model	R^2	F	p
Filterer-clingers	$y = 1.270 + 1.103(M)$	0.161	8.797	0.005
Gatherer-burrowers	$y = 4.927 + 2.059(TP) - 2.064(D)$	0.201	5.675	0.006
Gatherer-swimmers	$y = 0.596 + 2.728(TP) + 0.830(M)$	0.404	15.256	<0.001
Herbivore-swimmers	$y = 0.192 + 0.723(M)$	0.119	6.195	0.016
Predator-climbers	$y = 1.131 + 0.627(M) + 0.041(B) + 0.321(PC2)$	0.397	9.671	<0.001
Predator-sprawlers	$y = 2.092 + 0.955(C) - 0.978(SA) + 1.826(TP)$	0.513	15.424	<0.001
Scraper-swimmers	$y = 0.287 + 0.362(M)$	0.095	4.844	0.033
Scraper-climbers	$y = 1.115 + 0.020(RD)$	0.175	9.758	0.003
Scraper-sprawlers	$y = -0.790 + 0.008(RD) + 0.562(SA) + 0.977(H)$	0.344	7.690	<0.001
Shredder-burrowers	$y = -1.319 + 0.544(PC2) + 2.508(TP)$	0.416	16.015	<0.001
Shredder-sprawlers	$y = -3.283 + 3.104(SA) + 1.661(M) + 3.295(H)$	0.493	14.242	<0.001
Shredder-clingers	$y = -2.600 + 0.795(PL)$	0.116	6.052	0.018
Functional richness	$y = 9.068 + 2.735(M) + 2.837(SA) + 0.523(PC2)$	0.617	23.637	<0.001
Functional diversity	$y = 0.849 + 0.139(M) + 0.120(SA) - 0.205(H) - 0.200(TP)$	0.422	7.859	<0.001
Functional evenness	$y = 1.052 - 0.277(H) - 0.098(C) + 0.066(M) - 0.132(TP)$	0.402	7.215	<0.001

The major functional groups showed varying responses to the environmental features of lakes. As a generalization, abundances of the functional groups dependent either directly or indirectly on habitat structural complexity were significantly related to macrophyte cover. These groups included herbivore-swimmers, predator-climbers, and predator-swimmers. These groups may prefer macrophytes, because macrophytes provide refugia against fish predation. For example, the actively swimming functional groups included mainly waterboatmen (Heteroptera: Corixidae) and diving beetles (Coleoptera: Dytiscidae), which have been shown previously to have preference for macrophytes, perhaps in response to the cover macrophytes confer against fish predators (Nilsson and Söderberg 1996; Tolonen et al. 2003). Although also predator-climbers, consisting of mainly dragonfly larvae (Odonata: Coenagrionidae, Aeshnidae), may benefit from such refugia against fish predators, the increase of their abundance with macrophyte and bryophyte cover may also be related to their own foraging demands in terms of perches provided by aquatic plants. Furthermore, the responses of the predaceous functional groups to macrophytes may also mirror the fact that the total abundance and species richness of littoral invertebrates are typically strongly related to macrophyte cover (Carpenter and Lodge 1986; Brown et al. 1988), thereby providing more prey for the invertebrate predators. This reasoning was also supported by the finding that 6 of the 12 functional groups showing significant responses to the environment had macrophytes in their regression model. By contrast, the gathering functional groups showed increases in abundance mainly with total phosphorus, which may have been related to higher nutrient concentrations of fine organic material in more nutrient-rich lakes. Shredders-burrowers were positively associated with coarse organic matter, which was also likely a direct response to food availability and quality (e.g., allochthonous organic material; France 1995). By contrast, the environmental relationships of the remaining

functional groups were either more complex, or could perhaps be better explained by some unmeasured environmental factors.

It was not surprising that functional richness and functional diversity were moderately to strongly related to macrophyte cover and lake area. Wider habitat variability in larger lakes may provide more niche opportunities to species (Tonn and Magnuson 1982; Eadie and Keast 1984). For example, larger forest lakes typically have both stony erosional and non-stony depositional habitats, which offer differing conditions for the organisms, whereas smaller bog lakes typically have only depositional habitats with high loads of fine particulate organic matter. The structural complexity provided by aquatic plants may, in turn, increase vertical heterogeneity, leading to a high variability of niche opportunities. Both of these sources of heterogeneity may also determine trait variability, functional richness, and functional diversity of littoral communities. By contrast, functional evenness showed negative relationships to hardness, color, and total phosphorus, and a positive relationship to macrophytes, implying that the communities in hard water lakes with high nutrient concentrations and low macrophyte cover supported some dominating functional groups and thus had low evenness. Overall, the above findings were expected, given that functional richness was strongly correlated with species richness, the latter of which has typically been connected to variation in habitat heterogeneity (Eadie and Keast 1984; Huston 1994). Furthermore, functional diversity and functional evenness were significantly correlated with species diversity and species evenness, respectively. This finding was not surprising, because both functional and taxonomic components of biodiversity can be related to the same environmental factors along extensive gradients.

The functional structure of littoral macroinvertebrate communities was generally determined by the same environmental features as functional richness and functional diversity. Thus, lake surface area, macrophyte cover,

Table 5. Summary of redundancy analysis (RDA), showing eigenvalues and percentage variance explained by the first two axes, as well as the correlations between environmental variables and the axes.

Variable	Axis 1	Axis 2
Eigenvalue	0.114	0.061
% variance	11.420	6.122
Correlations		
Area	0.62	0.76
Macrophytes	0.56	-0.64
Total phosphorus	0.67	-0.43
Hardness	0.25	-0.24

total phosphorus, and hardness were the most important environmental variables shaping the functional structure of communities. It is notable that the same environmental variables have also been identified as the most influential determinants of the taxonomic structure of littoral macroinvertebrate communities (Brodersen et al. 1998; Brauns et al. 2007). Furthermore, the constrained ordination models explaining variation in functional and taxonomic structure could be expected to be stronger for the former characterization of communities (e.g., Heino et al. 2007). This was not the case, however, and the explanatory power of the constrained ordination models of functional and taxonomic structure was highly similar (J. Heino, J. Kotanen and L. Paasivirta, unpubl.). Thus, these findings suggest that functional and taxonomic approaches may be rather redundant in terms of providing similar information about communities. This reasoning was also supported by the rather high Mantel correlation between functional and taxonomic resemblance matrices. This was surprising because the number of functional groups was naturally much lower than the number of taxa, and thus these differing characterizations of communities might have shown differing patterns (e.g., Hoeninghaus et al. 2007). It has been suggested that functional trait structure is rather invariant along natural ecological gradients, and their patterns should thus deviate from those shown by taxonomic structure across large geographical extents (e.g., Charvet et al. 2000), whereas the patterns shown by functional and taxonomic structure may be more similar within smaller regions (e.g., Heino et al. 2007). Thus, analyzing data beyond a single drainage basin might lead to different patterns between the functional and taxonomic structure of littoral macroinvertebrate communities.

Because functional biodiversity showed discernible changes along environmental gradients, it would be important to understand whether these changes are related to corresponding variation in ecosystem functioning, or whether functional characteristics mainly follow the action of the filtering process (e.g., Heino 2005). Disentangling these two aspects may be difficult because they are intimately intertwined. Because the taxonomic diversity and structure of littoral macroinvertebrate communities typically responds to the same environmental gradients as was found here for functional characteristics, it appears that the filtering process provides a more likely scenario.

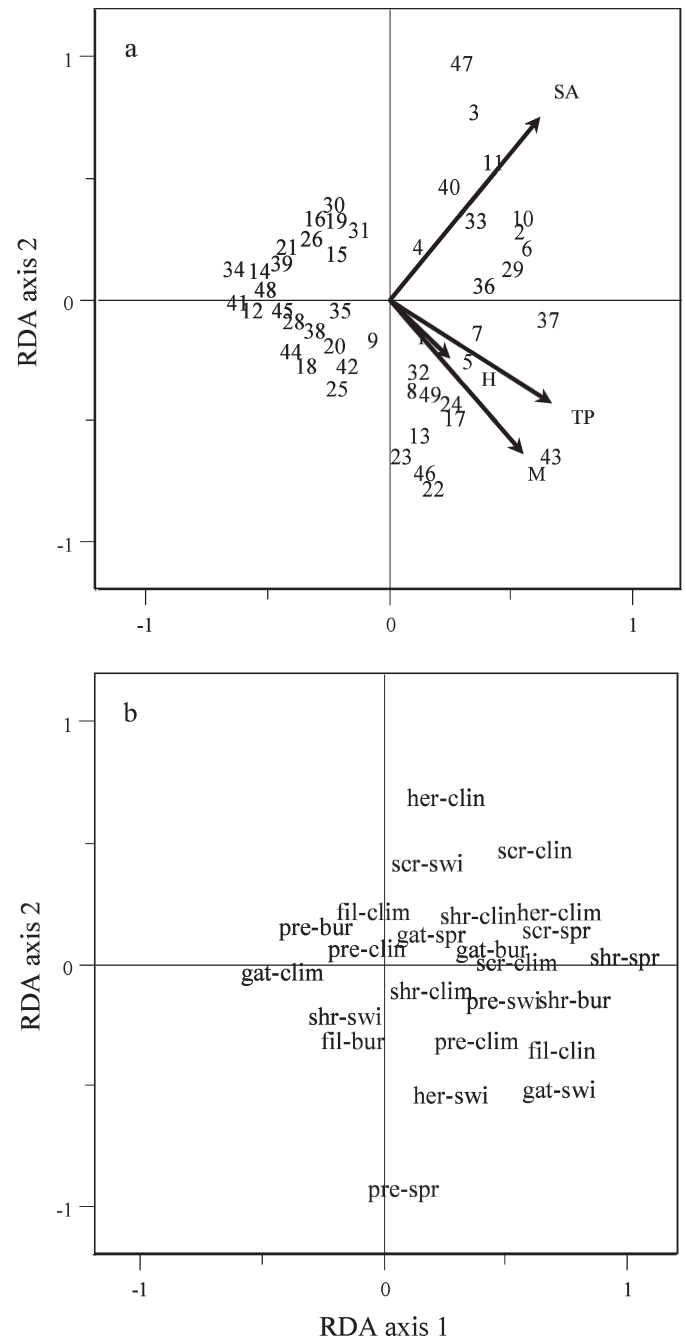


Fig. 2. Biplots from redundancy analysis (RDA), showing the relationships between (a) significant environmental variables and functional communities, and (b) the distributions of functional groups along the first two RDA axes. Abbreviations of environmental variables: H = hardness; M = macrophytes; SA = lake surface area; TP = total phosphorus. Abbreviations of functional groups refer to the first three letters of the functional feeding groups and the habit trait groups.

Thus, environmental variables filter species with suitable traits to facilitate occurrence in prevailing conditions (Tonn 1990; Poff 1997), and this filtering process is then mirrored in the functional characteristics of lake littoral communities. The relationships I found between functional biodiversity, macrophyte cover, and lake area may indeed refer

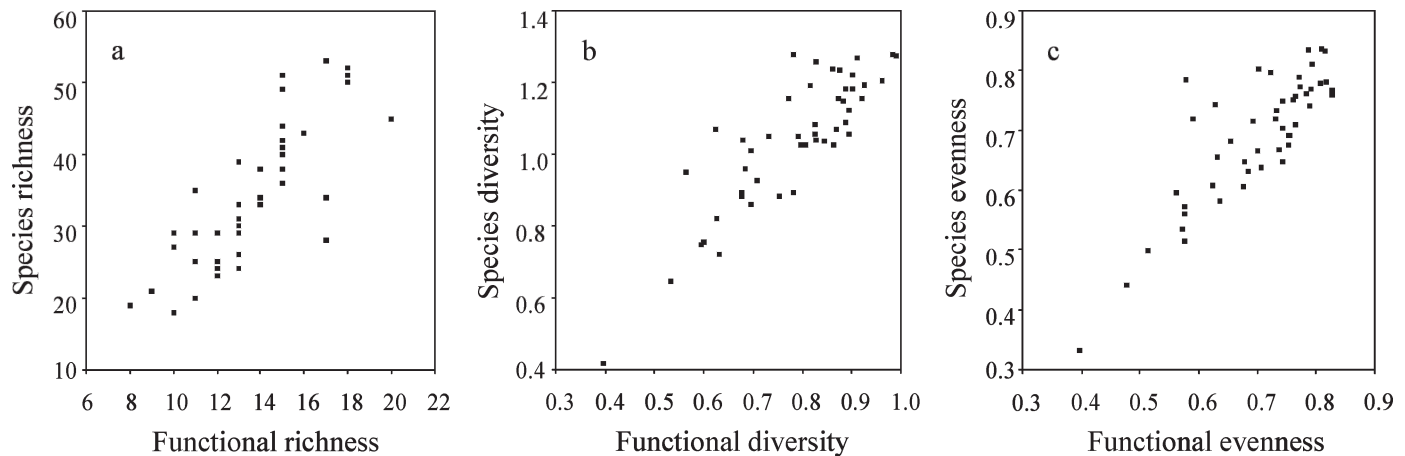


Fig. 3. Relationships between (a) species richness and functional richness, (b) species diversity and functional diversity, and (c) species evenness and functional evenness.

to such a filtering process. It is also important to note that such relationships to habitat characteristics are likely to be more pronounced if combinations of functional feeding groups (Cummins 1973) and habit trait groups (Merritt and Cummins 1996) are used. This is because habitat characteristics do affect whether gatherer-burrowers or gatherer-swimmers, for example, are dominant in the littoral zone, and these differences have possible influences on ecosystem processes (e.g., processing of fine organic material within sediments vs. on sediments). It thus follows that, when present, species of different functional groups contribute to ecosystem functioning.

Further studies on lake littoral macroinvertebrates should aim at linking directly functional biodiversity and ecosystem functions, including detritus processing, animal-microbial interactions, and biomass production. These studies should consider diversity both within (e.g., the number of shredder species) and between functional groups (i.e., the number of functional groups), which obviously are related to different ecosystem functions (e.g., detritus processing vs. biomass production of whole macroinvertebrate communities). Although these aspects of functional biodiversity have been given considerable attention by stream ecologists (e.g., Dangles and Malmqvist 2004), researchers have largely ignored the contributions to ecosystem processes by littoral macroinvertebrates until recently (e.g., Bjelke and Hermann 2005). Furthermore, future studies should not only address patterns in functional biodiversity and ecosystem functioning along natural environmental gradients, but they should also examine how various functional characteristics of littoral macroinvertebrate communities respond to anthropogenic effects, including alteration of the riparian zone, habitat structural changes, and eutrophication. Research conducted on stream macroinvertebrate communities suggests that functional traits have desirable qualities in the assessment of anthropogenic effects over purely taxonomy-based approaches, including weaker responses to natural environmental features and geographical location, whereas they typically clearly portray anthropogenic degradation (e.g.,

Statzner et al. 2004). However, the present finding that functional biodiversity showed considerable variability across near-pristine lakes strongly suggests that natural environmental gradients are important filters of the functional traits of littoral macroinvertebrate communities, and these gradients should be accounted for prior to the examination of anthropogenic effects on lake ecosystems.

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