# Describing lake fish communities: Do presence–absence and biomass data show similar spatial and environmental relationships?

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We examined if community–environment and community–geographical-location relationships differ between presence–absence and biomass data of lake fishes. Our study lakes ranged across very long gradients of the features of boreal lakes in the ecoregions of Finland, providing an excellent opportunity to examine patterns in lake fish communities. Fish community structure responded to multiple environmental gradients, yet there was a clear pattern of succession from salmonids in oligotrophic lakes through European perch in mesotrophic lakes to cyprinids in eutrophic lakes. Such patterns prevailed especially in the biomass data. Partitioning of variation in the species matrix between environmental and spatial variables did not reveal clear differences between presence-absence and biomass data. Although slightly different combinations of environmental factors were included in the constrained ordination models, the relatively similar variation in presence–absence and biomass data along environmental and spatial gradients suggests that they may be used interchangeably to describe community–environment relationships at large geographical extents.

## Introduction

Characterising community–environment relationships is an important step in the inquiry on factors structuring local communities. Prevailing paradigms state that local communities are structured by environmental features at multiple spatial scales, and thus community structure follows the action of various environmental filters that contribute to community assembly (Tonn 1990, Tonn *et al.* 1990, Keddy 1992, Poff 1997). Freshwater fish communities have been particularly suitable study objects of community–environment relationships at within-region scales (Jackson *et al.* 2001). Factors structuring lake fish communities have been examined in a number of studies from

boreal, temperate, and tropical regions (Eadie and Keast 1984, Jackson and Harvey 1989, Robinson and Tonn 1989, Rodriquez and Lewis 1997, Mehner *et al.* 2007). A general finding of these studies has been that a small suite of environmental factors often accounts for a considerable part of variability in the fish community structure. These factors include lake size, water chemistry in terms of acidity, nutrients, and turbidity, as well as biotic factors such as predation and competition. Despite that a single dominant gradient, such as lake size, may be utilised well in understanding variation in fish community structure, it is the interplay of various abiotic and biotic factors that is responsible for generating variation in community structure. For example, lake size and depth may be associated with anoxic winter-kill conditions in boreal lakes, and such conditions may indirectly mediate predatory and competitive interactions among lake fish (Tonn and Magnuson 1982, Rahel 1984, Öhman *et al.* 2006). Our understanding of the degree to which the same suite of abiotic and biotic factors has general effects on lake fish communities would benefit from descriptive studies of community–environment relationships in geographically separate regions.

It can be easily envisaged that different characterisations of communities may lead to differing insights into community–environment relationships at various spatial scales (Allen and Hoekstra 1991). For example, local communities may differ between ecoregions (Heino *et al.* 2007), and thus also community–environment relationships may vary among such ecologically-defined regions (Mykrä *et al.* 2007). Furthermore, how local communities are described may also affect community–environment relationships. Many studies unravelling the determinants of fish community structure have been based on presence–absence data (Tonn and Magnuson 1982, Rahel 1984, Tonn *et al.* 1990, Olden *et al.* 2001). Although studies using such qualitative data have undoubtedly provided important information about the patterns in fish community structure, alternative data types should also be considered in community studies. Among these are quantitative abundance (Mehner *et al.* 2005, Diekmann *et al.* 2005) and biomass data (Garcia *et al.* 2006, Massol *et al.* 2007).

Although acquiring such data is more difficult, costly, and requires more effort in the field (Jackson and Harvey 1997), quantitative data are important when the goal is to understand effects of environmental gradients on dominance patterns in ecological communities, as well as how community structure may contribute to food web interactions and ecosystem functioning (Persson 1991, Saint-Germain *et al.* 2007). It can be hypothesised, for example, that fish biomass data reflect the effects of environmental variables on community structure, whereas presence–absence data may portray environmental factors less efficiently. By contrast, presence–absence data may also reflect spatial gradients in community structure that may be under regional control, including biogeographic history, climatic factors, and dispersal processes (Lehtonen *et al.* 2008).

Our objective in this study was to compare patterns of fish community structure given by presence–absence and biomass data originating from surveys of boreal lakes in Finland. First, we hypothesised that presence–absence data would reflect both geographical location and environmental factors, whereas biomass data should show primarily the action of environmental factors. Second, the environmental factors most closely associated with variation in fish community structure should also differ between presence–absence and biomass data. Third, we also examined community–environment relationships across four boreal ecoregions and within two of them to determine whether presence–absence and biomass data show differing environmental relationships in different regional settings.

Description of community–environment relationships may also be contingent on the use of particular analytical methods. Our analytical approach followed the general routines of variation partitioning in constrained ordination (Borcard *et al.* 1992, Cushman and McGarical 2002) and, in particular, patterns shown by qualitative and quantitative data based on such analyses (Cushman and McGarical 2004). However, our data differ from those in many similar studies on fish communities, as we considered patterns across relatively large variation in lake size as compared with that in previous studies that have dealt with small lakes in the same region (Tonn *et al.* 1990, Magnuson *et al.* 1998).

# Methods

## Study area

This study was conducted in European freshwater ecoregion number 22 (i.e. Fennoscandian Shield). This large freshwater ecoregion embraces four boreal vegetation zones (i.e. national ecoregions) in Finland. These national ecoregions are hemiboreal, south boreal, middle boreal, and north boreal (Nordic Council of Ministers 1984). We had data for 9, 125, 38 and 12 lakes from the four ecoregions, respectively. Due to small sample size, hemiboreal and north boreal ecoregions were not considered separately. Descriptions of land cover and land use in these ecoregions can be found elsewhere, and they are defined as areas with similar climate, vegetation, and land use (Nordic Council of Ministers 1984). In general, the watersheds of the study lakes are variously affected by anthropogenic land use, including forestry, agriculture, and urban lands. Typical natural characteristic of boreal catchments are extensive coniferous forests and peatlands, which have important influences on the water chemistry of lakes in terms of humic and acidic substances.

## Environmental data

Water chemistry and other environmental variables were obtained from the database of the Finnish Environment Authorities. For water chemistry variables, values measured close to the time of fish sampling were used when available. We had data for 10 such variables, including pH, alkalinity, conductivity, total phosphorus, total nitrogen, colour, chemical oxygen demand, turbidity, chlorophyll *a*, and secchi depth. Measurements of some variables were missing from a number of lakes (less than 15%). In such cases, we used a mean value calculated from the set of all other lakes in our data (Legendre and Legendre 1998). We also had data for four morphometry variables, including lake surface area, maximum depth, shoreline perimeter, and shoreline development factor (Riera *et al*. 2000). The included water chemistry and morphometry variables have been found to be influential in other studies of fish communities (Tonn and Magnuson 1982, Eadie and Keast 1984, Jackson and Harvey 1989, Robinson and Tonn 1989). Prior to constrained ordination analyses, among-variable correlations were calculated to reduce the number of variables to those not strongly correlated with each other ($R^2$ < 0.5). There were eight relatively weakly-correlated environmental variables: lake area, shoreline development factor, maximum depth, pH, colour, conductivity, total phosphorus, and chlorophyll *a* (Table 1). All environmental variables, except pH, were transformed using logarithmic transformation to improve normality prior to constrained ordination analyses.

## Lake fish data

Fish data were taken from the database of the Finnish Game and Fisheries Research Institute, compiled for the fish community monitoring

**Table 1**. Means, standard errors (SE), and minimum and maximum values of the environmental variables used in the CCAs. Values are shown separately for across-ecoregion and within-ecoregion data sets.

| Variable | Across ecoregions | | | | South boreal | | | | Middle boreal | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Mean | SE | Min. | Max | Mean | SE | Min. | Max | Mean | SE | Min. | Max |
| Lake area (ha) | 1224 | 308 | 0.9 | 31540 | 1189 | 358 | 0.9 | 28264 | 608 | 232 | 3.1 | 7784 |
| Shoreline development factor | 2.62 | 0.13 | 1.08 | 13.18 | 2.65 | 0.17 | 1.08 | 13.18 | 2.62 | 0.24 | 1.19 | 8.68 |
| Maximum depth (m) | 13.58 | 0.96 | 2 | 85 | 13.96 | 1.18 | 2 | 85 | 12.56 | 1.81 | 2 | 52 |
| pH | 6.7 | 0.06 | 4.9 | 9.6 | 6.8 | 0.07 | 4.9 | 9.6 | 6.5 | 0.09 | 5.0 | 8.2 |
| Colour (mg Pt l$^{-1}$) | 85 | 6 | 5 | 503 | 86 | 9 | 5 | 503 | 97 | 11 | 10 | 300 |
| Conductivity (mS m$^{-1}$) | 7.68 | 1.06 | 0.5 | 144 | 9.40 | 1.51 | 1.7 | 144 | 2.80 | 0.28 | 0.5 | 7.9 |
| Total phosphorus ($\mu$g l$^{-1}$) | 25.90 | 1.67 | 2 | 130 | 26.42 | 1.99 | 2 | 126 | 23.79 | 2.56 | 4 | 59 |
| Chlorophyll *a* ($\mu$g l$^{-1}$) | 14.64 | 1.09 | 1 | 120 | 15.84 | 1.41 | 1 | 120 | 13.46 | 2.15 | 1 | 57 |

according to the EU Water Framework Directive. Altogether, the data for this study incorporated 184 lakes. The fish community survey was based on test fishing conducted from mid-July to early September 1998–2006 with NORDIC multimesh survey nets (1.5 × 30 m, 12 panels with mesh size 5 to 55 mm from knot to knot, European Standard EN 14757:2005). Stratified random sampling with respect to lake area and depth relations was applied. The number of unit efforts per lake (net nights from ca. 20:00 to 8:00) was 5 to 60 according to size and depth relations of the lakes. Both fish presence–absence and biomass data were obtained from these surveys. Biomass data were given as CPUE, being average total biomass of fish per one net in one night. When using biomass data based on gillnet sampling, it has to be kept in mind that gillnets are selective gear and the CPUE values have to be considered as relative biomass values. Several characteristics of fish species, including swimming activity, schooling behaviour, as well as the size and shape of fish affect their catchability by gillnets (Kurkilahti 1999, Olin and Malinen 2003). Thirty species were caught in the gillnet surveys at the across-ecoregion scale, 26 species in the south-boreal ecoregion, and 16 species in the middle-boreal ecoregion (Table 2).

## Statistical methods

Variability in fish community structure was analysed in relation to two explanatory variable groups: (i) local environmental and (ii) spatial location variables. Spatial variables included the north (N) and east (E) coordinates that were centred on their respective means and standardised:

$$b = (x_{ij} - \bar{x})/s_i$$

where $b$ is the standardised coordinate value, $x$ is the original coordinate value, $\bar{x}$ is the coordinate column mean, and $s_i$ is the standard deviation of coordinate column $i$ (McCune and Grace 2002). Subsequently, a third order spatial polynomial of the form:

$$Z = b_1N + b_2E + b_3N^2 + b_4E^2 + b_5NE + b_6N^2E \\ + b_7NE^2 + b_8N^3 + b_9E^3$$

that describes the spatial location of each lake was constructed separately for the across-ecoregion and within-ecoregion data sets. Using these multiple spatial variables allows one to model more complex spatial patterns in ecological communities than mere north and east coordinates (Borcard *et al.* 1992). Although these spatial variables are efficient in modelling only broad-scale patterns, they were deemed suitable for the present large-scale study, the aim of which was to simply compare the relative contribution of local environmental variables and spatial location to fish communities characterised by qualitative *versus* quantitative data.

All the analyses below were based on both presence–absence and biomass data at the across-ecoregion and within-ecoregion scales. No transformation was used for the biomass data, as transformation would bring biomass data closer to presence–absence data with regard to patterns they show (Heino 2008). A reason for this was that we wanted to examine patterns shown by the characterisations of communities at the opposite ends of the qualitative-quantitative continuum. Our main method of data analysis was constrained ordination (ter Braak 1995, Legendre and Legendre 1998). We first ran a detrended correspondence analysis (DCA) to find out whether fish species showed linear or unimodal responses to the underlying gradients. The gradient length of the first DCA axis was never below 2 SD units at the across-ecoregion and within-ecoregion scales, which implied somewhat unimodal responses of species. Thus, we considered canonical correspondence analysis (CCA) as a suitable method for analysing the data. We ran separate CCAs with forward selection for both spatial variables and environmental variables to obtain a set of reduced variables for the final analyses. Given that a number of explanatory variables affect the amount of variation in the biotic data explained by the variables, we limited our consideration to the five most important spatial and environmental variables. We used these reduced sets of variables for examining the relative importance of environmental and spatial variables in accounting for variability in fish community structure (Borcard *et al.* 1992, Legendre and Legendre 1998). We ran a series of three CCAs for community struc-

ture: species-by-sites matrix (i) constrained by both environmental and spatial variables ($a + b + c$, fractions following Fig. 1), (ii) constrained by environmental variables only ($a + b$), and (iii) constrained by spatial variables only ($b + c$). In the CCA, the sum of canonical eigenvalues divided by the total inertia of species data is equal to the amount of explained variation. Variation in community structure was subsequently partitioned into shared environmental and spatial position [$b = (a + b) + (b + c) - (a + b + c)$], pure environmental [$a = (a + b) - (b)$], pure spatial [$c = (b + c) - (b)$] and unexplained proportions [$d = 1 - (a + b + c)$].

**Table 2**. List of fish species caught in the lake surveys at the across-ecoregions (Finland) and within-ecoregion scales (south-boreal and middle-boreal ecoregions). The total number of lakes was 184, 125, and 38 for Finland, south-boreal ecoregion, and middle-boreal ecoregion, respectively.

| Scientific name | Abbreviation | Common name | Number of lakes species caught | | |
| --- | --- | --- | --- | --- | --- |
| | | | Finland | South boreal | Middle boreal |
| **Esocidae** | | | | | |
| *Esox lucius* | Eso luc | Northern pike | 133 | 94 | 28 |
| **Salmonidae** | | | | | |
| *Salmo trutta* | Sal tru | Brown trout | 5 | 1 | – |
| *Salmo salar** | Sal sal | Atlantic salmon | 1 | – | – |
| *Salvelinus alpinus* | Sal alp | Arctic charr | 2 | 1 | – |
| *Thymallus thymallus* | Thy thy | Grayling | 2 | – | – |
| **Coregonidae** | | | | | |
| *Coregonus lavaretus s.l.* | Cor lav | Whitefish | 56 | 34 | 13 |
| *Coregonus albula* | Cor alb | Vendace | 46 | 29 | 12 |
| *Coregonus peled** | Cor pel | Peled | 3 | 2 | – |
| **Osmeridae** | | | | | |
| *Osmerus eperlanus* | Osm epe | European smelt | 40 | 32 | 7 |
| **Cyprinidae** | | | | | |
| *Rutilus rutilus* | Rut rut | Roach | 156 | 112 | 33 |
| *Leuciscus leuciscus* | Leu leu | Common dace | 13 | 5 | 5 |
| *Leuciscus cephalus* | Leu cep | Chub | 1 | 1 | – |
| *Leuciscus idus* | Leu idu | Ide | 13 | 8 | 4 |
| *Phoxinus phoxinus* | Pho pho | Minnow | 6 | 2 | – |
| *Scardinius erythropthalmus* | Sca ery | Rudd | 18 | 16 | – |
| *Aspius asipus* | Asp asp | Asp | 8 | 7 | – |
| *Tinca tinca* | Tin tin | Tench | 10 | 10 | – |
| *Alburnus alburnus* | Alb alb | Bleak | 88 | 64 | 19 |
| *Blicca bjoerkna* | Bli bjo | White bream | 32 | 29 | 1 |
| *Abramis brama* | Abr bra | Bream | 87 | 76 | 8 |
| *Abramis ballerus* | Abr ball | Blue bream | 12 | 10 | 1 |
| *Carassius carassius* | Car car | Crucian carp | 12 | 8 | 1 |
| **Balitoridae** | | | | | |
| *Barbatula barbatula* | Bar bar | Stone loach | 1 | 1 | – |
| **Lotidae** | | | | | |
| *Lota lota* | Lot lot | Burbot | 24 | 16 | 5 |
| **Gasterosteidae** | | | | | |
| *Pungitius pungitius* | Pun pun | Nine-spined stickleback | 1 | – | – |
| **Cottidae** | | | | | |
| *Cottus gobio* | Cot gob | Bullhead | 5 | 5 | – |
| *Cottus poecilopus* | Cot poe | Alpine bullhead | 2 | – | – |
| **Percidae** | | | | | |
| *Perca fluviatilis* | Per flu | European Perch | 183 | 125 | 38 |
| *Gymnocephalus cernuus* | Gym cer | Ruffe | 136 | 96 | 27 |
| *Sander lucioperca* | San luc | Pikeperch | 55 | 42 | 11 |

* Non-reproducing populations.
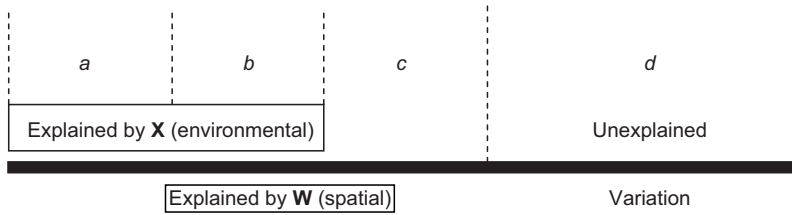
**Fig. 1**. Schematic diagram of the different fractions of variability in community structure. The variation in response matrix **Y** comprising species is partitioned between environmental (matrix **X**) and spatial (matrix **W**) explanatory variables. The horizontal line corresponds to 100% of variation in the matrix **Y** comprising species. Fraction *a* refers to pure environmental effects, *b* to shared environmental and spatial effects, and *c* to pure spatial effects. Figure follows Borcard *et al.* (1992) and Legendre and Legendre (1998).

We also ran similar variation partitioning analyses as above for testing if the presence–absence approach provides results similar to those of the biomass approach, when there are only species-poor *versus* species-rich lakes in the data set. We did this by selecting in separate analyses lakes with ≤ 5 species and compared them with lakes with > 5 species. These analyses were subsequently ran for both presence–absence and biomass data. Given that the main patterns did not deviate from those for all species and lakes included in the analyses, we do not present the results of these trial analyses in this paper.

Finally, we constructed CCA biplots to illustrate relationships between species and environmental variables to see which species contributed most to community patterns. These results were limited to the across-ecoregion scale, where species showed clearer responses to environmental gradients than in either south-boreal or middle-boreal ecoregions. Given that the higher terms of the spatial polynomial do not have such a straightforward explanation as environmental variables, we show only the relationships between species and environmental variables in the CCA biplots. CCAs were run using Brodgar version 2.51 (http://www.brodgar.com/brodgar.htm).

## Results

The most common species in terms of the number of sites occupied were perch, roach, ruffe, and pike (Table 2). These are the core species of lake fish communities in northern and central Europe (Tammi *et al.* 1999, Diekmann

*et al*. 2005). The most uncommon species were chub, stone loach, Arctic charr, grayling, Atlantic salmon, and alpine bullhead. The rarity of these species likely resulted from the fact that they are either more common in northern lakes, of which very few were sampled (e.g. Arctic charr, grayling), or the fact that they were not caught efficiently by multi-mesh gillnets (e.g. stone loach, alpine bullhead). The relationships of the mentioned and other species to environmental features at the across-ecoregion scale revealed a number of general patterns (Fig. 2). Not surprisingly, the common species were situated close to the origin of the two-dimensional CCA biplot, reflecting the fact that they are generalists in their habitat distributions based on both presence-absence and abundance data. These species included perch, roach, ruffe, and pike (for clarity not all shown in Fig. 2). By contrast, rare species were located at the end of the first CCA axis based on both presence–absence and biomass data. These species included Arctic charr, Atlantic salmon, brown trout, grayling, and Alpine bullhead, which were inclined to deep, oligotrophic lakes. By contrast, Crucian carp appeared to have high biomass in shallow lakes.

The most important environmental variables associated with variation in community structure showed some variability with regard to the type of data and geographical setting (Table 3). Total phosphorus was the most important variable in three of the six CCAs with environmental variables as constraining factors. Lake area was the first variable to enter the CCA models in the middle-boreal ecoregion based on both presence–absence and biomass data. Shoreline
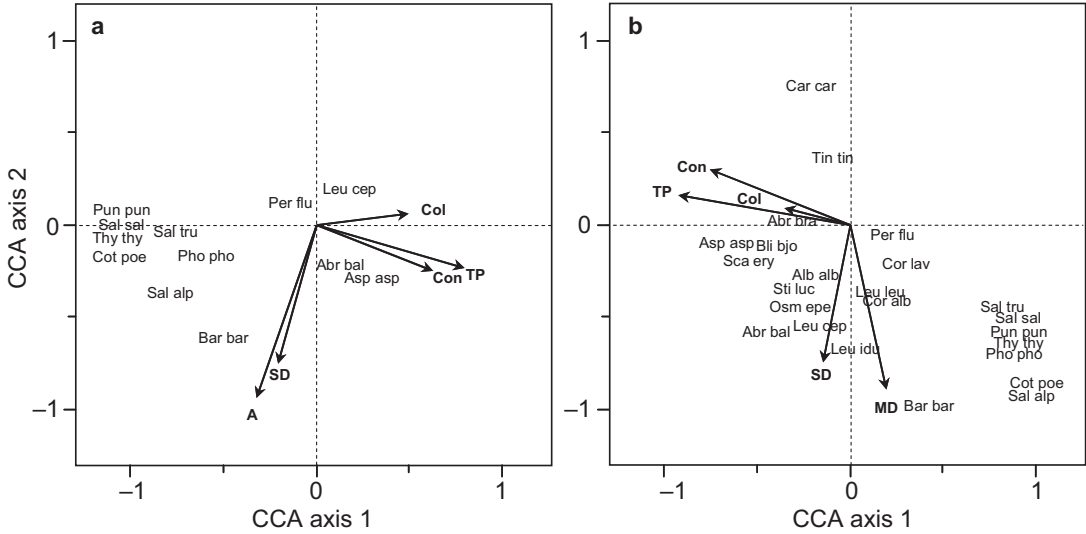
Fig. 2. CCA ordination diagrams showing the relationships between the first two axes, environmental variables, and selected species: (**a**) presence–absence, and (**b**) biomass data at the across-ecoregion scale. Shown are the five most variables in each constrained ordination analysis. Abbreviations of environmental variables: A = lake surface area, Col = colour, Con = Conductivity, MD = maximum depth, SD = shoreline development factor, TP = total phosphorus. Abbreviations for species are shown in Table 2. For clarity, not all core and rare species situated close to the centroid are shown.

Table 3. Summary of the CCAs for presence-absence and biomass data. Shown are the five most influential environmental variables in the forward selection of the CCAs. Contribution refers to increase in the sum of canonical eigenvalues. Sum of canonical eigenvalues (Σ) divided by total inertia equals to explained variation.

| Presence–absence data | | Biomass data | |
|---|---|---|---|
| Variable | Contribution | Variable | Contribution |
| **Across ecoregions** (*n* = 184) | | | |
| Total phosphorus | 0.14 | Total phosphorus | 0.15 |
| Area | 0.11 | Maximum depth | 0.08 |
| Shoreline development | 0.07 | Shoreline development | 0.04 |
| Conductivity | 0.05 | Conductivity | 0.03 |
| Colour | 0.04 | Colour | 0.03 |
| Σ | 0.41 | Σ | 0.33 |
| Total inertia | 2.76 | Total inertia | 2.64 |
| **South boreal** (*n* = 125) | | | |
| Shoreline development | 0.13 | Total phosphorus | 0.13 |
| Total phosphorus | 0.10 | Shoreline development | 0.06 |
| Maximum depth | 0.05 | Colour | 0.04 |
| Colour | 0.04 | Maximum depth | 0.04 |
| Conductivity | 0.03 | pH | 0.04 |
| Σ | 0.35 | Σ | 0.31 |
| Total inertia | 2.02 | Total inertia | 1.76 |
| **Middle boreal** (*n* = 38) | | | |
| Area | 0.16 | Area | 0.15 |
| pH | 0.09 | pH | 0.08 |
| Colour | 0.07 | Conductivity | 0.08 |
| Conductivity | 0.06 | Chlorophyll *a* | 0.05 |
| Chlorophyll *a* | 0.04 | Total phosphorus | 0.10 |
| Σ | 0.42 | Σ | 0.47 |
| Total inertia | 1.70 | Total inertia | 1.39 |

development factor was selected first in one analysis. The first five variables entering the models were significant in forward selection in the across-ecoregion and south-boreal data sets ($P < 0.05$), while a few variables were not significant in the middle-boreal data sets ($P > 0.05$). However, given that the number of explanatory variables affects the amount of explained variation in constrained ordination, we decided to include the five most important variables, whether significant or not, when examining the relative roles of environmental and spatial variables for community structure of different data types and regional settings.

The environmental and spatial variables accounted for only a modest part of variability in community structure (Table 4). Variation partitioning showed that the contributions of environmental and spatial variables to community structure were quite similar in the presence–absence and biomass data, but there were slight regional differences (Fig. 3). For the presence–absence data at the across-ecoregion scale, pure environmental component amounted to 9.1%, pure spatial component to 13.4%, shared environmental and spatial component to 5.8% and unexplained component to 71.7%. For the biomass data, the corresponding figures were 10.6%, 6.5%, 1.5% and 81.4%. For the presence–absence data from the south-boreal ecoregion, pure environmental effects amounted to 12.3%, pure spatial effects to 12.8%, shared environmental and spa-

tial effects to 5% and unexplained fraction to 69.9%. The corresponding figures for biomass data were 15.9%, 7.4%, 1.7% and 75%. For the presence-absence data from the middle-boreal ecoregion, pure environmental effects amounted to 20.0%, pure spatial effects to 15.9%, shared environmental and spatial effects to 4.7% and unexplained fraction to 59.4%. The respective figures for the biomass data were 15.8%, 17.3%, 18.0% and 48.9%.

## Discussion

We found no clear-cut support for our hypotheses regarding structuring of fish communities based on presence–absence *versus* biomass data. First, although we hypothesised that biomass data should exhibit stronger environmental relationships than presence–absence data, pure environmental effects did not appreciably differ between the two characterisations of communities. Second, although we hypothesised that presence–absence data should portray more clearly geographical gradients than biomass data, we found only ambiguous differences between the two characterisations of communities in this respect. Pure spatial effects were slightly more important for presence–absence than biomass data at the across-ecoregion scale and in the south-boreal ecoregion. This latter finding of geographical structuring may be due to some

**Table 4**. Amounts of variability in community structure explained by environmental ($a + b$), spatial ($b + c$), and combined environmental and spatial variables ($a + b + c$). These fractions were used in variation partitioning.
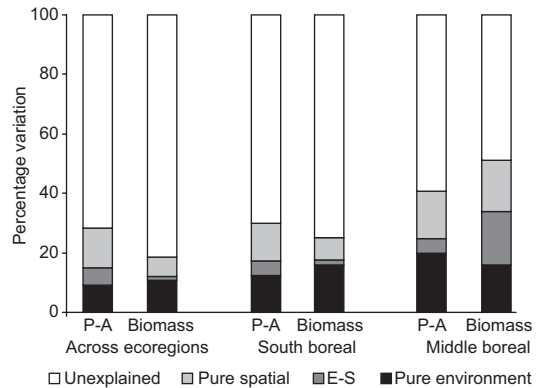
| Presence–absence data | | Biomass data | |
|---|---|---|---|
| Variable group | Variation (%) | Variable group | Variation (%) |
| **Across ecoregions** | | | |
| Environment ($a + b$) | 14.9 | Environment ($a + b$) | 12.1 |
| Spatial ($b + c$) | 19.2 | Spatial ($b + c$) | 8.0 |
| Combined ($a + b + c$) | 28.3 | Combined ($a + b + c$) | 18.6 |
| **South boreal** | | | |
| Environment ($a + b$) | 17.3 | Environment ($a + b$) | 17.6 |
| Spatial ($b + c$) | 17.8 | Spatial ($b + c$) | 9.1 |
| Combined ($a + b + c$) | 30.1 | Combined ($a + b + c$) | 25.0 |
| **Middle boreal** | | | |
| Environment ($a + b$) | 24.7 | Environment ($a + b$) | 33.8 |
| Spatial ($b + c$) | 20.6 | Spatial ($b + c$) | 35.5 |
| Combined ($a + b + c$) | 40.6 | Combined ($a + b + c$) | 51.1 |

important, yet unmeasured, environmental gradients that covary with the geographical location of lakes (Borcard *et al.* 1992). Such effects of confounded environmental and spatial variables were already seen in the biomass data of the middle-boreal ecoregion. Third, we found some support for our hypothesis regarding the roles of different environmental variables in accounting for variability in community structure based on presence–absence and biomass data.

The environmental variables that were selected in the constrained ordination models varied in relative importance with regard to the data type and regional context. This was seen in the fact that the order of entry of environmental variables in the constrained ordination models did not remain the same. However, the environmental factors most important in this study, including total phosphorus, pH, shoreline development factor, and lake area, have also been found influential in previous studies on fish communities utilising mainly presence–absence data (Tonn and Magnuson 1982, Eadie and Keast 1984, Rahel 1984, Jackson and Harvey 1989, Tonn *et al.* 1990). Also, the studies that have been based on quantitative data have often stressed the importance of the same factors for variation in fish community structure (Jeppesen *et al.* 2000, Olin *et al.* 2002, Diekmann *et al.* 2005, Massol *et al.* 2007). However, it is the range in an environmental variable that is likely to be important in determining a variable's importance for variation in community structure. In this respect, the environmental variables we found important for variation in fish community structure showed considerable variation among lakes (Table 1), and thus it was not surprising that they appeared important in this study. For example, total phosphorus varied so much that it portrayed lake conditions from ultraoligotrophic to highly eutrophic. Thus, given the importance of this variable for fish community structure in terms of species composition and dominance patterns, clear community–environment relationships shown by the constrained ordination were expected.

Species distributions along environmental gradients were in agreement with what is known about the succession of fish species along lake productivity and size gradients in north-



**Fig. 3**. Graphs of variation partitioning between pure environmental, shared environmental and spatial, pure spatial, and unexplained fractions for presence-absence and biomass data. Separate analyses were run for across-ecoregion and within-ecoregion data.

ern Europe (Persson *et al.* 1991, Jeppesen *et al.* 2000). In general, species preferring oligotrophic waters were distributed at the low end of the productivity gradient especially based on biomass data in constrained ordination. These species included Arctic charr, Atlantic salmon, brown trout, grayling, Alpine bullhead, and nine-spined stickleback, which were rare but affected equally the ordinations of the presence–absence and biomass data. By contrast, based on the biomass data, some cyprinids were inclined towards moderate productivity, being also distributed according to variation in the shoreline development factor. These relationships suggest that some cyprinids may prefer not only high nutrient conditions, but also lakes with complex habitat in terms of a variable shoreline. By contrast, common generalist species were generally rather indifferent with regard to their responses to environmental factors. These species were perch, roach, ruffe, and pike, which remained generalists with regard to both presence–absence and biomass data. Alternatively, the occurrence of perch and roach near the origin of the constrained ordination biplot may also be related to the fact that these species often attain highest abundances in mesotrophic lakes (Olin *et al.* 2002). These patterns lend some support for the succession of fish communities along a productivity gradient from oligotrophic conditions dominated by salmonids, through mesotrophic

conditions dominated by perch, to eutrophic conditions dominated by cyprinids (Persson *et al.* 1991, Jeppesen *et al.* 2000, De Leeuw *et al.* 2003). However, some studies have provided little support for such gradual successional patterns in lake fish communities (Radke and Eckmann 2001, Diekmann *et al.* 2005, Mehner *et al.* 2005). These differing findings likely result from the facts that (i) the method of analysis (e.g. ordination *versus* cluster analysis) affects the interpretation of community patterns, and that (ii) other environmental gradients (e.g. lake size, habitat heterogeneity, winter oxygen conditions, and biotic interactions) besides productivity contribute to shifts in the dominance of salmonids, percids, and cyprinids (Horppila *et al.* 2000, Helminen *et al.* 2000, Diekmann *et al.* 2005). Thus, understanding variation in fish community structure clearly requires multiple environmental variables.

In general, our findings were rather ambiguous, as they suggested that different characterisations of communities provide either redundant or complementary information. Complementary insights are suggested by slightly differing relationships of the presence–absence and biomass data to environmental variables. Alternatively, given that only a modest proportion variability in community structure was accounted for by the ecological variables, remaining variation in the community structure may have been related to different, yet unmeasured, environmental variables. These unmeasured factors may be related to post-ice age colonisation routes (Heino 2001), present-day dispersal barriers (Spens *et al.* 2007), water course distances between lakes (Olden *et al.* 2001), and the history of stocking activities (Lehtonen *et al.* 2008). It may well be that findings from studies utilising presence-absence data cannot be compared directly with those from studies utilising biomass data (Cushman and McGarical 2004). However, we expected even more drastic differences in community patterns between the two data types in terms of the relative contribution of environmental and spatial variables to community structure. Thus, as the main patterns in community–environment relationships are likely to remain relatively similar between presence–absence and biomass data, these two characterisations provide somewhat

redundant information about lake fish communities at large geographical extents.

From the applied perspective, two main points emerged from our study. First, although the sites were located within the Fennoscandian Shield freshwater ecoregion, there was some variability in both presence–absence and biomass data that was related to the geographical location of the lakes. Furthermore, even within the smaller geographical extents of the national ecoregions, there was some spatially-structured variation in fish communities. Thus, one should not uncritically assume that only local environmental conditions are influential for the biological classification and assessments programs, such as the Water Framework Directive of the European Union. Second, both presence-absence and biomass data were related to largely the same major environmental gradients. The degree to which these two types of fish community characterisations reflect anthropogenic environmental changes similarly remains to be tested in further assessment studies.

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