



Macroinvertebrate species occupancy frequency distribution patterns in eutrophic lakes

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Abstract Metacommunity models describe species occupancy frequency distribution (hereinafter ‘SOFD’). Our goal is to present how the differences in eight macroinvertebrate orders dispersal ability affect SOFD patterns. A total of 293 species from eight macroinvertebrate orders were observed in 14 eutrophic lakes in southern Finland. Species occupancy ranged from 1 to 14. About 30% (89 out of 293) of the species were found in only one lake, yielding a surprisingly high number of rare species. So, there were few widely distributed common species and numerous rare species with a restricted distribution. Combined data from eight macroinvertebrate orders

supported the bimodal truncated SOFD pattern. Similarly, the low dispersal ability orders, watermites and mayflies, fitted the bimodal truncated SOFD pattern. However, bimodal symmetric SOFD pattern also fitted relatively well to the dragonflies and damselflies with high dispersal ability. It seems that differences in dispersal ability among different macroinvertebrate orders may partly explain observed differences. Moreover, our results supported slightly more a niche-based model rather than a metapopulation dynamics model in eutrophic lakes littoral macroinvertebrate metacommunities. Our results highlight that the dispersal ability is important trait for species conservation in patchily distributed habitat.

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Introduction

Species which occurred isolated in patches, like waterbodies, form local communities. At the landscape level, most species either appear at a small number of suitable patches (satellite species; often rare) or at many patches (core species; often common and abundant). Species occupancy frequency distribution (hereinafter SOFD) is a proper method for

characterizing this kind of local communities at regional scales. A SOFD approach offers information on the number or proportion of local communities in which each species occurred. The shape of the SOFD is one of the most studied patterns within community ecology (see reviews by Tokeshi 1992; McGeoch and Gaston 2002; Jenkins 2011; Hui 2012). Reviews (McGeoch and Gaston 2002; Jenkins 2011; Hui 2012) in this topic found that the two most common models which explain variations in the SOFD pattern are: (1), the metapopulation dynamic model (hereafter MPDM; Hanski 1982, 1999) and (2) the niche-based model (hereafter NBM; Brown 1984). These two models are not mutually exclusive. Local communities that share several (core) species and simultaneously have several species, which are occupying only one or few locations (satellite) conform to a bimodal core-satellite pattern, resulting from a MPDM, which is based on local extinction and colonization dynamics (Hanski 1982, 1999). Alternatively, the so-called unimodal-satellite-dominant or niche-based model relies on the idea that local communities have many rare narrow-niche specialist species and few common broad-niche generalist species (Brown 1984).

Previous studies have found that SOFDs generally have a bimodal core-satellite pattern in terrestrial communities (Hanski 1982, 1998, 1999; McGeoch and Gaston 2002; Jenkins 2011; Autio et al. 2013). However, in aquatic communities, the support for bimodal core-satellite pattern is relatively weak and the unimodal-satellite-dominant pattern seems to be more common (Tokeshi 1992; Heino 2008, 2015; Verberk et al. 2010; Korkeamäki et al. 2018; Renner et al. 2020). For example, Jenkins (2011) re-analysed two freshwater macroinvertebrate datasets (Wiberg-Larsen et al. 2000; Oertli et al. 2008) and he found unimodal-satellite SOFD pattern in both cases.

Most previous SOFD studies have, however, focused on single taxonomic group in aquatic macroinvertebrate assemblages, such as chironomids (Diptera: Chironomidae) (Tokeshi 1992), caddisflies (Trichoptera) (Wiberg-Larsen et al. 2000) and damselflies and dragonflies (Odonata) (Korkeamäki et al. 2018; Renner et al. 2020), or combined data several macroinvertebrate taxonomic groups together (Heino 2008, 2015; Verberk et al. 2010; see also Jenkins 2011). Therefore, it was not clear whether several species groups in aquatic invertebrate communities would produce unimodal-satellite SOFD pattern or

whether there is variation between taxonomic groups in the SOFD patterns in a regional scale. The general purpose of our study was to test how dispersal ability modifies SOFD distribution in eight macroinvertebrate orders from 14 eutrophic lakes in southern Finland. Previous study has found that different aquatic insect orders differed in dispersal ability (Sarremejane et al. 2020).

We explored four main research questions. First, are there differences in macroinvertebrate watermite dispersal ability in relation to other aquatic insect orders? We assumed that non-flying water mite had lower dispersal ability than flying aquatic insect orders. Second, are there differences in species richness in relation to regional species' richness between macroinvertebrate orders? We predicted that a proportion of observed species from regional species pool increases with dispersal ability. Third, is unimodal-satellite SOFD pattern fitted the best with combined macroinvertebrate data? We expected that a unimodal-satellite SOFD pattern would occur in eutrophic lakes as this is frequently observed in other aquatic macroinvertebrates orders (Tokeshi 1992; Heino 2008, 2015; Verberk et al. 2010; Jenkins 2011; Korkeamäki et al. 2018; Renner et al. 2020). Fourth, how dispersal ability affects SOFD pattern (organismal scaling hypothesis) (e.g. Collins and Glenn 1997)? Local patchily distributed and geographically isolated communities are linked to each other with species dispersal. Only a species with a high dispersal ability can colonize distant patches. Therefore, species with high dispersal ability will occur in most communities. Alternatively, species with a poor dispersal ability occur only at a few local communities in a region. Thus, we predicted that macroinvertebrate orders with a poor dispersal ability will occur only at a few sites in a region, whereas species with good dispersal ability will be found at most sites, as suggested by Collins and Glenn (1997), and are predicted to exhibit bimodal SOFDs with both equal number of cores (common) and satellite (rare) species. A satellite-dominant unimodal SOFD pattern is predicted to occur in poor dispersal ability macroinvertebrate orders (Collins and Glenn 1997).

Materials and methods

Dispersal ability of macroinvertebrates

There are already published data from aquatic insect dispersal ability (Sarremejane et al. 2020), but not for watermites, so here, to estimate the dispersal ability of local Finnish species belonging to eight different macroinvertebrate orders, we sent a questionnaire to experienced entomologists in Finland. In this study, we used eight macroinvertebrate orders: watermites (Hydracarina), mayflies (Ephemeroptera), dragonflies and damselflies (Odonata), caddisflies (Trichoptera), water bugs (Heteroptera), aquatic dipterans (Diptera, excluded chironomids), chironomids (Chironomidae) and aquatic beetles (Coleoptera). Lepidoptera and Megaloptera (Sialidae) and spiders (Arachne) were excluded from our data.

In the questionnaire, we asked each of them to rank eight macroinvertebrate orders in their dispersal ability. To ensure that all taxonomic groups followed the same methodology and to ensure comparability, we followed the same procedure for all taxonomic groups. In the questionnaire, value 1 indicates that a given taxon has the lowest dispersal ability, while value 8 means that a given taxon has the highest dispersal ability. To obtain the dispersal ability index for each macroinvertebrate order, we calculated the average dispersal ability index from the returned questionnaires ($n = 10$) (Supplementary Table 2).

Study area of field data

Our study was performed in Kanta-Häme and Pirkanmaa regions in southern Finland (61°30' N, 24°20' E) within an area of 50 × 80 km. We sampled 14 lakes (see more details in Suutari et al. 2009). The minimum distance between lakes was 0.8 km. All study sites are eutrophic with rich aquatic macrophyte communities with emergent, floating-leaved and submerged macrophytes, which cover more than half of the studied lakes or bays of large lakes. The surface area of lakes and bays varied greatly from few hectares to more than hundreds of hectares. All studied waterbodies were shallow and the coverage of the bottom was mud.

Macroarthropod samples

We collected macroinvertebrate samples in late May–early June 2000 (sweep samples) and September (traps). We took eight 2-min-sweep samples with a pond net (D-shape, width 35 cm, height 25 cm and mesh size 0.4 mm) from each lake. The samples were taken from the lower littoral zone vegetation (depth 0.5–1.0 m). To obtain a more extensive picture of the species richness in our study locations, we placed three cylinder-like traps covered with nets (mesh size 0.5 mm) (description of traps in Bagge 1999) in each study lake. Traps were left overnight (ca. 17 h) on the bottom vegetation in lower littoral zone. Two traps were provided with fish baits and one with a yellow light stick. Arthropods captured by pond net and traps were conserved in 70% ethanol. L. Paasivirta identified the Diptera and watermite species and J. Salmela identified all specimens from other insect orders to the species level with a microscope. From the collected samples, we were able to identify most of the macroinvertebrate specimens to the species level. Nevertheless, in few cases when species-level identification was impossible, individuals were identified to the higher systematic level such as genus or family level (Supplementary table 1).

Statistical methods

To make sure that our measure of dispersal ability index is reliable, we tested the level of agreement between ten judges agreed on their dispersal rankings of eight different macroinvertebrate species groups we used Kendall's coefficient of concordance W . Kendall's W varied from perfect agreement, $W = 1$, and perfect disagreement $W = 0$. For test differences between macroinvertebrate orders in their dispersal ability, we used a related-samples Friedman's two-way ANOVA because our rankings are ordinal variables. We used Bonferroni corrected P values in comparison between the macroinvertebrates species groups.

In the figures, we used classes of 10% occupancy and the number of species in each 10% class, as suggested by McGeoch and Gaston (2002), to demonstrate the variation in SOFD between eight macroinvertebrate orders and combined data from all macroinvertebrate orders in eutrophic lakes.

We used the recently developed methods to identify different SOFD patterns (Jenkins 2011; Hui 2012) where the multi-model inference approach was applied to regressions of ranked species occupancy curves (RSOCs). For statistical test, we constructed nine binary (presence/absence) species-by-site matrixes (one combined all species data and eight macroinvertebrate orders). In each matrix, species are in rows and 14 eutrophic lakes in columns. Then, we calculated the occupancy frequency of each species as the sum of all the studied lakes where it was found. Each macroinvertebrate species' occupancy frequency was divided by the total number of studied lakes ($n = 14$), and then, these relative occupancy values (O_i) were sorted in decreasing order. Each macroinvertebrate species had its own rank value, R_i , which was inversely correlated with the relative occupancy value. For each dataset, we then performed five regression analyses in which the relative occupancy of a species (O_i) is the dependent variable and R_i is the independent variable. Finally, we evaluated the five most common SOFD patterns: (1) a unimodal-satellite dominant, (2) a bimodal symmetrical, (3) a bimodal asymmetrical, (4) bimodal truncated or (5) a uniform (random) pattern best fitted our macroinvertebrate assemblage in eutrophic lakes in Finland (cf., Jenkins 2011; Hui 2012). As in Jenkins (2011) and Hui (2012), the Levenberg–Marquardt algorithm (with 999 iterations) was used for the nonlinear regressions, estimating the parameters (y_0 , a , b and c) of the following four equations (by means of ordinary least squares (OLS)) to find the best fitting SOFD pattern. The equations are:

- (1) $O_i = y_0 + a \cdot \exp(-bR_i)$ with initial parameters $y_0 = 0.01$, $a = 1.0$, $b = 0.01$: unimodal-satellite mode (exponential concave) pattern.
- (2) $O_i = a / (1 + \exp(-bR_i + c))$ with initial parameters $a = 1.0$, $b = -0.1$, $c = -1.0$: bimodal symmetrical (sigmoidal symmetric) pattern.
- (3) $O_i = a[1 - \exp(-bR_i^c)]$ with initial parameters $a = 1.0$, $b = -1.0$, $c = -1.0$: bimodal asymmetric (sigmoidal asymmetric) pattern.
- (4) $O_i = aR_i^b \exp(-cR_i)$ with initial parameters, $a = 100$, $b = 0.05$, $c = -0.04$: bimodal truncated (power exponential) pattern.
- (5) $O_i = aR_i + b$ with initial parameters $a = 0.01$, $b = 0.01$: uniform (random) pattern.

We also examined the homogeneity of variance, normality of residuals and independent error terms, as well as the tails and shoulders from graphs of regression.

We used the Akaike information criterion for small sample sizes (AICc) to compare the five alternative models where the one with the smallest AICc value would fit the best with data. Alternative models with $\Delta\text{AICc} (= \text{AICc}_{\min} - \text{AICc}_i) < 7$ would be considered as equally supported (Anderson et al. 2000; Burnham and Anderson 2000; Burnham et al. 2011; Jenkins 2011). We used the IBM SPSS statistical package version 26 for all statistical calculations.

Results

Dispersal ability of macroinvertebrate orders

The experts ($n = 10$) agreed with each other in dispersal ability between eight macroinvertebrate orders (Kendall's $W = 0.51$, $\chi^2 = 35.87$, $df = 7$, $P < 0.001$). There were differences between dispersal abilities between macroinvertebrate orders (related-samples Friedman's two-way ANOVA, $\chi^2 = 35.87$, $df = 7$, $P < 0.001$; Table 2). The experts evaluated that dragonflies and damselflies had the highest and watermites the lowest dispersal ability (Bonferroni corrected $P < 0.001$). Odonates also have a higher dispersal ability than mayflies ($P < 0.001$) and chironomids ($P = 0.020$). All other macroinvertebrate species groups did not differ from each other ($P > 0.073$ in every case) (Table 1).

Species richness

We found 293 macroinvertebrate species or higher systematic in the 14 eutrophic lakes (Table 1). Chironomids and aquatic beetles were the most species rich macroinvertebrate orders (Table 1). Both taxonomic groups had more than 60 species. All other macroinvertebrate groups had less than 40 species (Table 1). The lowest dispersal ability insect orders covered only small proportion of regional species pool: caddisflies (14%) and chironomids flies (27%) (Table 2). A high fraction of macroinvertebrate orders, which had high dispersal ability, was observed from national species pool (Table 2). We found that almost half of the waterbug species observed in this study

Table 1 Average dispersal ability of eight macroinvertebrate species groups evaluated by expert entomologist in Finland ($n = 10$)

Taxon	Mean	SD	Min	Max
Watermite, Hydracarina	2.2	2.0	1	6
Mayfly, Ephemeroptera	2.3	0.9	1	4
Dragonfly, Odonata	7.5	1.3	4	8
Caddisfly, Trichoptera	4.8	1.8	2	6
Water bug, Heteroptera	5.4	1.8	2	7
Aquatic fly, Diptera (excl. chironomids)	4.5	1.5	3	7
Chironomids, Diptera Chironomidae	3.8	1.9	1	8
Aquatic beetle, Coleoptera	5.5	2.0	1	8

Scientific names as in table above. Value 1 denotes the lowest dispersal ability, and value 8 denotes the best dispersal ability. See more detail from [Methods](#) section about questionnaire

Table 2 The total species numbers of macroinvertebrate orders in 14 eutrophic lakes in Finland

Taxonomic group	Scientific name	This study	Regional	%R	Finland	%F	Source
Watermite	Hydracarina	36	69	52	139	26	Bagge and Bagge (2009)
Mayfly	Ephemeroptera	14	31	45	55	25	Savolainen (2009)
Dragonfly	Odonata	18	44	41	52	35	Karjalainen (2002)
Caddisfly	Trichoptera	25	177	14	219	11	Salokannel and Mattila (2018)
Water bug	Heteroptera	24	39	62	50	48	Rintala and Rinne (2010)
Aquatic dipterans**	Diptera (excl. chironomids)	24					
Chironomids	Chironomidae	91	530	17	781	12	Paasivirta L. unpublished data
Aquatic beetle	Coleoptera	61			92*	66	Rassi (1993)

The regional species richness in study area and species richness in each macroinvertebrate orders in Finland were collected from the literature (source). Relative proportion (in per cent) of observed species richness from regional species pool (%R) and from species richness in Finland (%F)

*Part of species is terrestrial in Finland

**Difficult to estimate number of species in Finland

have been also recorded in Finland (24 out of 50 species). Furthermore, two-thirds of aquatic beetles observed in Finland were found in this study. Moreover, a high proportion of odonates and mayflies was found in this study from a national species pool (Table 2).

Species occupancy frequencies

The macroinvertebrate species occurrence varied from 1 to 14 lakes. Most species (30% or 89 out of 293 of species) were found only in one lake (Fig. 1). On average, each species occurred in less than one-third (mean = 4.4, SD = 3.7, $n = 293$) of the studied eutrophic lakes. However, each dragonfly and

damsel fly species occurred in almost half (mean 6.8, SD = 4.2, $n = 18$) of the studied lakes. For all other macroinvertebrate groups, one species occurred in about one-third of the studied lakes: waterbugs (Heteroptera, 4.9, SD = 3.5, $n = 24$), chironomids (Chironomidae, 4.8 SD = 3.9, $n = 91$), other aquatic dipterans (Diptera excluded chironomids, 3.5, SD = 3.5), watermites (Hydracarina) (4.3, SD = 3.3), mayflies (Ephemeroptera, 4.2, SD = 4.2, $n = 14$), caddisflies (Trichoptera, 3.9, SD = 4.2, $n = 25$) and water beetles (Coleoptera 3.4, SD = 3.1, $n = 61$).

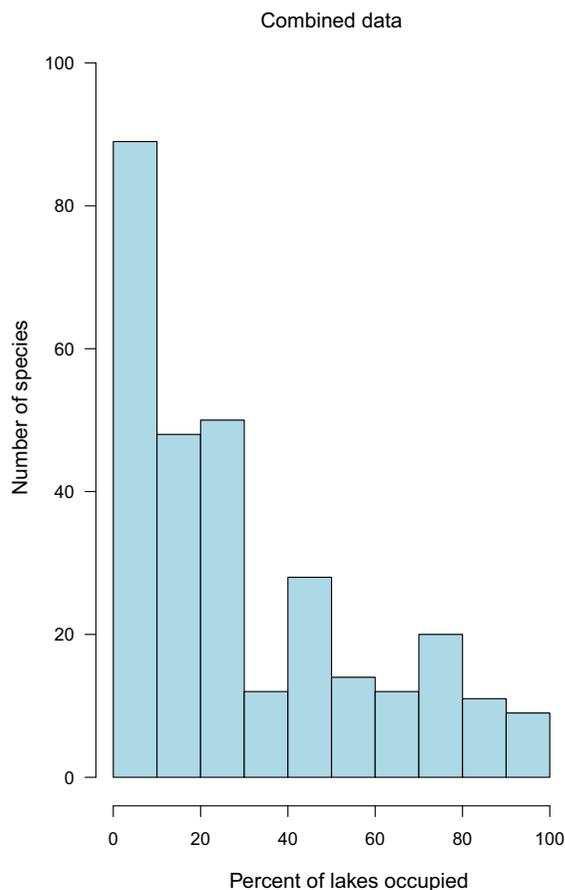


Fig. 1 Number of macroinvertebrate species ($n = 293$ species) in relation to the proportion of occupied eutrophic lakes (%) ($n = 14$ water bodies) in southern Finland

SOFD patterns

The combined macroinvertebrate species data fitted best with the bimodal truncated SOFD pattern (Table 3; Fig. 1). All alternative SOFD pattern models did not conform to combined data ($\Delta AICc > 7$; Table 3). Most of the studied macroinvertebrate orders had the unimodal-satellite or bimodal truncated SOFD pattern (Table 3; Fig. 2). According to $\Delta AICc$ values, both SOFD models fitted most of the macroinvertebrate orders very well (Table 3). The SOFD pattern varied considerably between the studied macroinvertebrate orders as expected by their differences in the dispersal abilities (Table 3; Fig. 2). The lowest dispersal ability macroinvertebrate order fitted with bimodal truncated distribution such as watermites (Fig. 2a) and mayflies (2b). On the other hand,

dragonflies and damselflies, which had the highest dispersal ability, had a bimodal symmetrical SOFD pattern (Table 2; Fig. 2c). Also, in water bugs both bimodal symmetrical and bimodal asymmetrical SOFD patterns fitted equally well (Table 3, Fig. 2d).

Discussion

We found that aquatic insect orders varied in their dispersal ability. The lowest dispersal ability was in wingless watermites. The highest dispersal ability was in dragonflies and damselflies as in Sarremejane et al.'s (2020) study. Also, other aquatic insect orders were ranked similarly in the Sarremejane et al. (2020) study as our one. For example, in our study the lowest dispersal ability in aquatic insect order was found for mayflies (Ephemeroptera), Chironomidae and other aquatic flies (Diptera), as in Sarremejane et al. study (2020).

Our results emphasize the high macroinvertebrate diversity of eutrophic lakes in southern Finland. We found a total of 293 macroinvertebrate species in the 14 studied lakes. In our study, we observed about half of macroinvertebrate species recorded from regional species pool. The only exception was caddisfly (14%) and chironomids fly species (27%), which was observed less in our study than regional species pool. Moreover, a high fraction of several macroinvertebrate orders was observed from national species pool (Table 1). For example, we found about 35% of the 52 odonate species recorded from Finland (Karjalainen 2002). This means that our results contrast with the results of many previous studies where oligotrophic and dystrophic lakes usually harbour a lower number of odonate species in Finland (Korkeamäki 2003; Honkanen et al. 2011; Korkeamäki et al. 2018) and other studies in northern Europe (e.g. Oertli et al. 2002; Flenner and Sahlén 2008; Koch et al. 2014). In the current study, we observed 14 mayfly species which was about 25% from all species (55) recorded in Finland (Savolainen 2009) (Table 1).

We found both unimodal-satellite-dominant and bimodal symmetrical SOFD patterns in different macroinvertebrate orders in eutrophic lakes. Sampling artefacts may partly affect our observed SOFD patterns (see discussion in McGeoch and Gaston 2002). The patterns are affected by the accuracy of the sampling (McGeoch and Gaston 2002; Heatherly et al.

Table 3 Results of species occupancy frequency distributions (SOFD) in the combined data and in eight macroinvertebrate order groups in southern Finland

Macroinvertebrate group	Figure	Species	AICc	Δ AICc
<i>Combined data</i>	1	293		
Bimodal truncated			– 2206.1	0
Unimodal-satellite			– 2186.2	19.9
Bimodal asymmetric			– 1925.3	280.9
Random			– 1345.5	860.6
Bimodal symmetric			– 771.6	1434.7
<i>Watermite (Hydracarina)</i>	2a	36		
Bimodal truncated			– 245.4	0.0
Unimodal-satellite			– 244.4	1.1
Bimodal asymmetric			– 222.7	22.7
Random			– 187.4	58.1
Bimodal symmetric			– 99.3	146.2
<i>Mayfly (Ephemeroptera)</i>	2b	14		
Bimodal truncated			– 67.8	0.0
Unimodal-satellite			– 67.6	0.2
Bimodal symmetric			– 67.0	0.8
Bimodal asymmetric			– 52.9	14.9
Random			– 48.8	19.0
<i>Dragonfly (Odonata)</i>	2c	18		
Bimodal symmetric			– 137.3	0.0
Bimodal truncated			– 113.2	24.1
Unimodal-satellite			– 112.3	25.0
Random			– 111.4	25.9
Bimodal asymmetric			– 59.1	78.2
<i>Water bug (Heteroptera)</i>	2d	24		
Bimodal symmetric			– 142.1	0.0
Bimodal asymmetric			– 142.1	0.0
Unimodal-satellite			– 135.6	6.4
Bimodal truncated			– 135.3	6.8
Random			– 124.3	17.7
<i>Caddisfly (Trichoptera)</i>	2e	25		
Unimodal-satellite			– 159.2	0.0
Bimodal truncated			– 157.7	1.5
Bimodal symmetric			– 156.3	2.9
Bimodal asymmetric			– 101.4	57.8
Random			– 91.3	67.9
<i>Diptera (excluded chironomids)</i>	2f	24		
Unimodal-satellite			– 160.2	0.0
Bimodal truncated			– 158.6	1.6
Bimodal symmetric			– 145.8	14.5
Bimodal asymmetric			– 120.4	39.8
Random			– 92.9	67.3
<i>Chironomidae (Diptera)</i>	2g	91		
Bimodal truncated			– 647.3	0.0

Table 3 continued

Macroinvertebrate group	Figure	Species	AICc	Δ AICc
Unimodal-satellite			– 627.9	19.4
Bimodal asymmetric			– 592.9	54.4
Random			– 439.1	208.2
Bimodal symmetric			– 227.1	420.1
<i>Water beetle (Coleoptera)</i>	2h	61		
Bimodal truncated			– 432.1	0.0
Unimodal-satellite			– 426.1	6.0
Bimodal asymmetric			– 386.9	45.2
Random			– 268.2	163.8
Bimodal symmetric			– 179.1	253.0

The four most likely SOFD patterns (random, unimodal-satellite dominant, bimodal symmetrical and bimodal asymmetrical) were analysed both with combined data and separately for eight macroinvertebrate groups in eutrophic lakes. “Figure” column joins statistical models with data figures. “Species” column shows the number of species in each study macroinvertebrate groups. AICc (Akaike information criterion for small sample sizes) as well as Δ AICc (= $AICc_i - AICc_{min}$) values are presented. The model with the lowest AICc is considered the best of the tested models. The model that best fitted the data is in the first

2007), but our data were gathered using two different methods known to detect the majority of the macroinvertebrate species present at an aquatic vegetation zone of lakes. Our sample size (the number of water bodies) was large enough, 14 lakes, and larger than the minimum, ten sites (McGeoch and Gaston 2002; Hui 2012). Hui (2012) also found that the number of species affects SOFD patterns. If the number of species was less than ten, then bimodal asymmetric pattern occurred more often. In our study, the number of species varied from 14 up to 293 (Table 1) So, it is unlikely that that all observed SOFD patterns are due to sampling artefacts or low number of study sites nor low number of species.

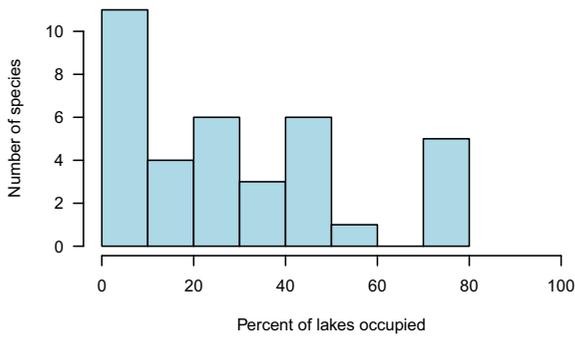
We found unimodal-satellite SOFD pattern in our combined macroinvertebrate data from 14 eutrophic lakes (Table 3; Fig. 1). This result is also in accordance with previously published results for aquatic habitats (e.g. Verberk et al. 2010; Heino 2015; Korkeamäki et al. 2018; Renner et al. 2020). The general theory of species community structure, suggested by e.g. Brown (1984) and discussed by Lennon et al. (2004), coincides well with the pattern observed by us: our studied lakes harbour merely a small number of common species and numerous rare ones. According to the NBM, common species with wider niches and a high tolerance of environmental variation are widely distributed and locally abundant. On the

Fig. 2 Number of species in each eight macroinvertebrate groups in relation to the proportion of occupied eutrophic lakes (%) ($n = 14$ water bodies) in southern Finland. Studied macroinvertebrate groups are: **a** Hydracarina (36 species), **b** Ephemeroptera (14), **c** Odonata (18), **d** Heteroptera (24), **e** Trichoptera (25), **f** Diptera, excluded chironomids (24), **g** Chironomidae (91) and **h** Coleoptera (61)

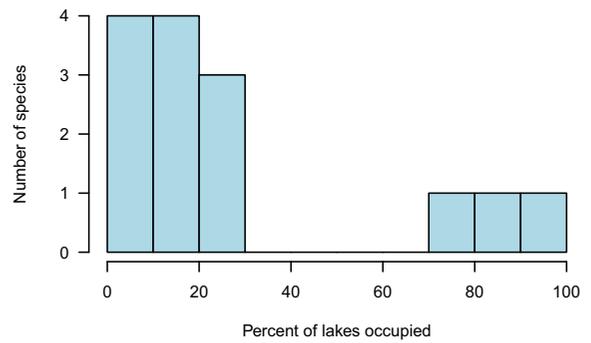
other hand, rare species with narrow niches and a greater sensitivity to environmental variation occur more locally and have a limited regional distribution (Brown 1984). This SOFD pattern may be dependent on both biotic and abiotic factors, as suggested by McGeoch and Gaston (2002) and Jenkins (2011). This will result in a unimodal-satellite SOFD pattern with many satellite species, in particular when data from numerous taxonomically dissimilar species with different niches requirement pooled together from communities (see Heino 2015; Jokimäki et al. 2016; Korkeamäki et al. 2018; Renner et al. 2020). According to our data, few common species occupied a larger proportion of the lakes and numerous rare species occupied only small proportion of lakes, which supports NBM.

According to Hui (2012), two most frequent models were unimodal-satellite-dominant and the bimodal truncated SOFD patterns, particularly in insects and arthropods. We found very similar frequencies in this study. It seems that in most of macroinvertebrates

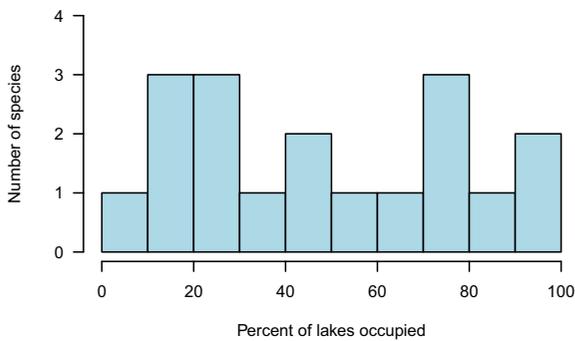
(a) Hydracarina



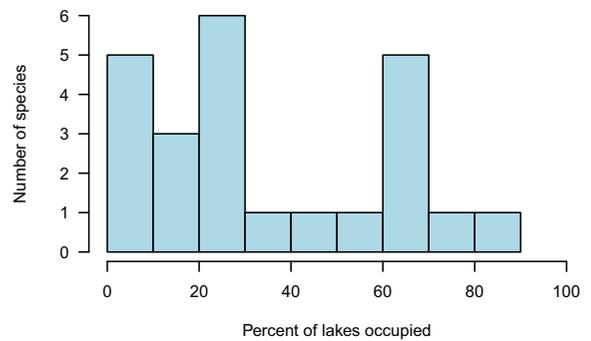
(b) Ephemeroptera



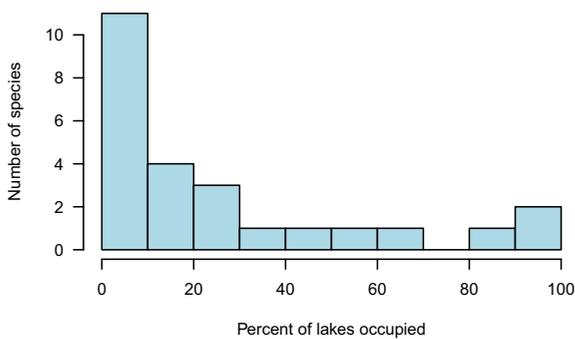
(c) Odonata



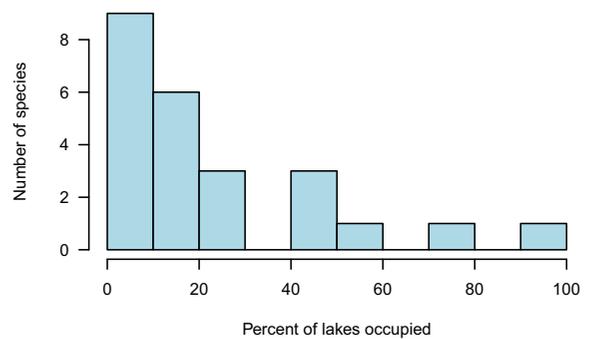
(d) Heteroptera



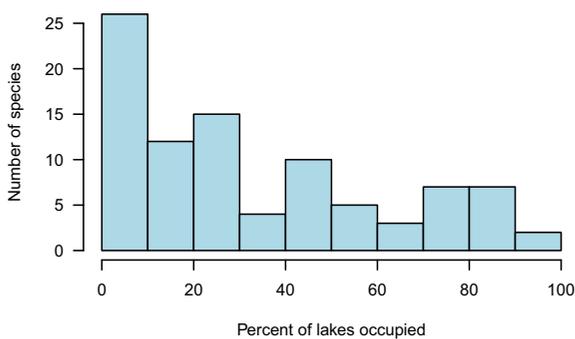
(e) Trichoptera



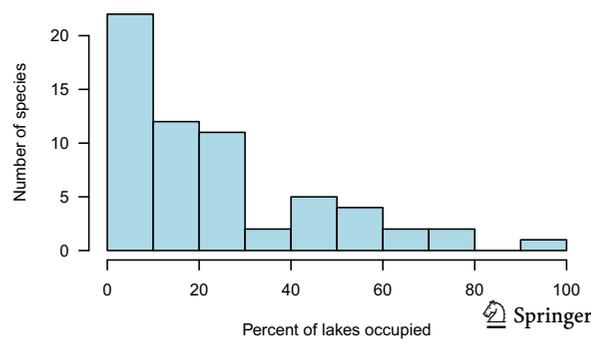
(f) Diptera



(g) Chironomidae



(h) Coleoptera



orders unimodal-satellite-dominant and the bimodal truncated SOFD patterns are the most common patterns (Table 3; Fig. 2). In their reviews, both McGeoch and Gaston (2002) and Hui (2012) estimated that one-fourth of SOFD patterns were bimodal symmetric. Our data support this frequency because we observed two out of nine models were bimodal symmetric.

We found that the SOFD patterns varied between macroinvertebrate orders (Table 3; Fig. 2). A dispersal ability seems to affect SOFD pattern as predicted by organismal scaling hypothesis. This hypothesis predicts a unimodal SOFD pattern dominated by satellite species with poor dispersal ability, such as wingless water mites and mayflies in our study (Collins and Glenn 1997). Macroinvertebrate orders with very good dispersal ability have bimodal symmetric SOFD pattern, as we found in dragonflies and damselflies in our study and in previous studies (Andersen et al. 2016; Suhling et al. 2017; Suhonen et al. 2010b). According to the MPDM (Hanski 1982, 1999), bimodality should result from random colonization and extinction events among the species in the local communities. The rare species with low dispersal ability occupied only part of suitable eutrophic lakes. Moreover, rare species seems to have smaller population size which increases local extinction risk (Korkeamäki and Suhonen 2002; Suhonen et al. 2010a, 2014).

The common species might also be widely distributed due to a low local extinction risk and a high colonization probability due to their high dispersal ability (Hanski and Gyllenberg 1997; Hanski 1998). This may partly explain bimodal symmetric SOFD pattern in odonates and water bugs in our study.

Conclusion

To conclude, our results demonstrate a general SOFD pattern of numerous rare and few common macroinvertebrate species, as in several previous studies in aquatic environments (Tokeshi 1992; Heino 2008, 2015; Verberk et al. 2010; Jenkins 2011; Korkeamäki et al. 2018; Renner et al. 2020). However, high dispersal ability of macroinvertebrate orders fitted relatively well with bimodal symmetric SOFD pattern as predicted by organismal scaling hypothesis (Collins and Glenn 1997). The differences between

our and most of the previous studies were that there was pooled species with different dispersal ability species groups together. Pooling different kinds of species together may shift the results towards unimodal-satellite-dominant SOFD pattern similarly as increasing extent of study area (e.g. McGeoch and Gaston 2002). To achieve a better understanding of the variation in SOFD for an aquatic macroinvertebrate assemblage, more field studies from several macroinvertebrate orders simultaneously collected from several waterbodies within same ecoregion are required. Different macroinvertebrate orders should be analysed separately to understand whether dispersal ability is modified SOFD patterns. Our results provide support for both the NBM (Brown 1984) and the MPDM (Hanski 1982) due to a high variation between macroinvertebrate orders in their dispersal ability (Sarremejane et al. 2020) and predicted by organismal scaling hypothesis (Collins and Glenn 1997). Moreover, we also need studies from different locations to understand geographical variation in SOFD patterns as was found in odonate assemblages in northern Europe (Korkeamäki et al. 2018). Our results highlight that the dispersal ability is important trait for species conservation in a scarce, but patchily distributed habitat.

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Author contributions MJR, JSa and JSu collected the field data. JSu developed both the study concept and analysed the data. LP identified Diptera and watermite samples, and JSa identified all other insect order specimens. ES entered and handled the raw data. All authors wrote the manuscript.

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Declarations

Conflict of interest None declared.

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