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Regional variations in occupancy frequency distribution patterns between odonate assemblages in Fennoscandia

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Abstract. Odonate (damselfly and dragonfly) species richness and species occupancy frequency distributions (SOFDs) were analyzed in relation to geographical location in standing waters (lakes and ponds) in Fennoscandia, from southern Sweden to central Finland. In total, 46 dragonfly and damselfly species were recorded from 292 waterbodies. Species richness decreased to the north and increased with waterbody area in central Finland, but not in southern Finland or in Sweden. Species occupancy ranged from 1 up to 209 lakes and ponds. Over 50% of the species occurred in <10% of the waterbodies, although this proportion decreased to the north. In the southern lakes and ponds, none of the species occurred in all lakes, whereas in the north, many species were present in all of the studied waterbodies. The dispersal ability of the species did not explain the observed species occupancy frequencies, but generalist species with a large geographical range occurred in a higher percentage of the waterbodies. At Fennoscandia scale, we found that the unimodal satellite pattern was predominant. However, at smaller scale, we found geographical variations in odonate species SOFD patterns. The most southern communities followed the unimodal satellite-dominant pattern, whereas in other regions, communities fitted best with the bimodal core–satellite patterns. It seems that the richer species pool in the southern locations, and the larger distribution range of the northern species, skewed the unimodal pattern into a bimodal satellite-dominant pattern.

Key words: core–satellite species patterns; damselfly; dragonfly; freshwater lake; Odonata; pond; species richness.

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Introduction

The shape of the species occupancy frequency distribution (SOFD) is a widely studied area in community ecology (see reviews by McGeoch and Gaston 2002, Jenkins 2011). In natural communities, many species occur either on few sites (satellite species; often rare species) or at many sites (core species; often common species), forming a bimodal core–satellite pattern (Hanski 1982, 1999). Using the core–satellite species pattern will yield more information about community structure than mere species richness. In terrestrial habitats, SOFDs generally have a bimodal core–satellite pattern (Hanski 1982, 1998, 1999, McGeoch and Gaston 2002, Jenkins 2011). By contrast, in aquatic communities only weak support for a bimodal SOFD pattern has been found (Verberk et al. 2010, Heino 2015). It therefore remains unclear whether or not aquatic

animal communities exhibit this general macroecological pattern.

In many cases, SOFD patterns can largely be explained by sampling methods and efficiency. For example, the grain size as well as the extent and intensity of sampling can vary extensively, and a decrease in sample area or number of sites may change the observed SOFD patterns from unimodal to bimodal (McGeoch and Gaston 2002). However, SOFD patterns may also depend on abiotic and biotic factors: (1) habitat disturbance, (2) niche breadth, (3) dispersal ability, (4) sampling site position within geographical range, and (5) geographical range size distribution (McGeoch and Gaston 2002, Jenkins 2011, Jokimäki et al. 2016). First, in stable habitats with low levels of disturbance, communities should follow the bimodal SOFD pattern (Jenkins 2011). Second, generalist species will occur at most sites, whereas specialist species will occur at fewer sites. This accounts for the clear nested species subset pattern observed for dragonfly communities (Sahlén and Ekestubbe 2001, Koch et al. 2014). Moreover, generalist species with broad niches tend to have a wide geographical distribution, whereas specialist species are limited by their narrow niches. Thus, this niche-based hypothesis mainly predicts a right-skewed unimodal SOFD pattern (Brown 1984). Third, dispersal ability varies between species, and in aquatic insects, it depends on body size (Heino 2015). Large species are often good fliers that are capable of dispersing over long distances, whereas smaller species can be expected to have a more restricted dispersal ability (Conrad et al. 1999, McCauley 2006, Wikelski et al. 2006, McCauley et al. 2008, Hassall and Thompson 2012, Troast et al. 2016). Thus, the dispersal-ability hypothesis predicts a satellite-dominant unimodal SOFD pattern (Collins and Glenn 1997). Fourth, it is traditionally thought that species tend to have their highest density/abundance at the center of their geographical distribution (Brown 1984). In addition, occupancy and abundance of species are often positively correlated (Hanski 1982, Brown 1984, Collins and Glenn 1997). Accordingly, as the species pool is richer, the relative number of satellite species can be expected to be higher in the southern than in the northern regions (McGeoch and Gaston 2002). Finally, regions at lower latitudes should have fewer core species and a larger number of satellite species than the regions at higher latitudes (McGeoch and Gaston 2002) because species occurring at lower latitudes have smaller latitudinal ranges than species at higher latitudes (the so-called Rapoport's latitude rule; Gaston et al. 1998, McGeoch and Gaston 2002).

Understanding the variation in the shape of SOFD patterns in aquatic communities needs further investigation. By using a semiaquatic insect group as study organisms, we will establish whether the bimodal SOFD pattern, which is often found in terrestrial taxa, is general also for aquatic communities. Moreover, as conservation efforts in a changing climate should be based on correct assumptions on current and projected community structure, we anticipate that a SOFD pattern analysis could be used as one of the cornerstones to such work.

The specific aim of this study was to determine whether odonate SOFD patterns vary between the lakes and ponds of four geographical regions in Finland and Sweden, and whether the differences in SOFD patterns can be related to the five aforementioned abiotic and biotic factors. First, we predict that species richness increases with lake and pond area, since a larger area will in general allow for more niches (Oertli et al. 2002). Second, we predict that species occupation frequency in the lakes will increase with the geographical range of the species, because species with a wide geographical range are often locally abundant and therefore occur in many patches (Brown 1984). Third, we expect that generalist species occur more frequently in the waterbodies than do specialist species. Fourth, we predict that large-bodied species occur in a larger number of waterbodies than small-bodied ones, due to differences in dispersal ability (McGeoch and Gaston 2002, Heino 2015). Finally, we predict that southern regions have fewer core species and a larger number of satellite species than regions at higher latitudes (McGeoch and Gaston 2002).

Materials and Methods

Description of data, methods, and study areas

We used data from 292 lakes and permanent ponds (waterbodies from now on) in Sweden and Finland (Fig. 1) along a 900-km latitudinal extent. The original data have been gathered

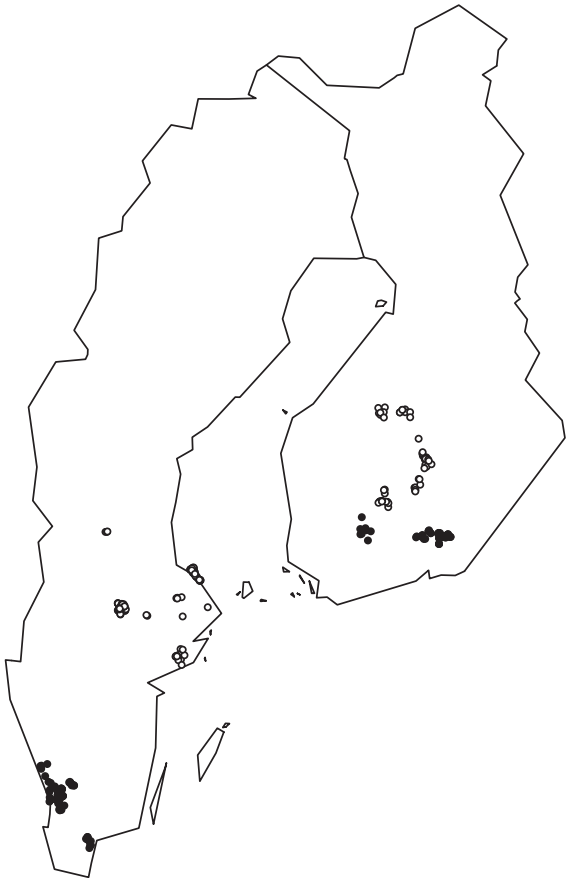

Fig. 1. Location of the 292 studied waterbodies in southern Sweden (filled dot), in central Sweden (open dot), in southern Finland (filled dot), and in central Finland (open dot).

between 1995 and 2016 (Fig. 1) and consist of published studies as well as one previously unpublished survey (Table 1). All data were based on intensive field work (see more details in the original studies from Sahlén and Ekestubbe 2001, Flenner and Sahlén 2008, Honkanen et al. 2011, Suutari et al. 2009, Wittwer et al. 2010, Korkeamäki 2013, Koch et al. 2014, Suhonen et al. 2014, Al Jawaheri and Sahlén 2017). In all studied waterbodies, we aimed at detecting the majority of the species present, missing as few rare ones as possible. There have been publications in recent years discussing the reliability of various methods for estimation of odonate species richness (Raebel et al. 2010, Bried et al. 2012*a*,*b*, Hardersen et al. 2017), and it has been shown that even small samples could produce a fairly reliable species list for any given site, given that the sampling is repeated (Bried et al. 2012*b*). Further, it is well known that the rarest species at any site will always have less chance of being detected (Mao and Colwell 2005).

Although the total latitudinal difference is only 8°, there is a profound climate and vegetation gradient between southern Sweden and central Finland. While oceanic climate and temperate broadleaf and mixed forests appear in southern Sweden, central Finland has continental climate in the mid-Boreal vegetation zone. Yearly mean temperature for the southernmost localities is above 7.0°C (SMHI 2017), while it is around 3.8°C for the northernmost ones (Finnish Meteorological Institute 2017). Further, there is an ecotone between the southern and the northern areas which constitutes the northern limit of a number of thermophilous tree species (Heikkilä and Seppä 2003). All lakes are located in areas with numerous lakes (around one lake per 9 km^2; Henriksen et al. 1998) of which we investigated only a small fraction. Thus, we divided the waterbodies into four groups based on their geographical location: southern Sweden (55°–58° N, $n = 94$), central Sweden (58°–61°20′ N, $n = 91$), southern Finland (60°–61°30′ N, $n = 58$), and central Finland (61°30′–63°30′ N, $n = 49$).

We measured the geographical range of each species as the number of occupied 50 × 50 km squares in the maps by Boudot and Kalkman (2015), which represent an up-to-date compilation of known records in Sweden and Finland (up to 2014). In total, 20 of the species occurring in the study have much larger geographic ranges in Europe, in the Palearctic, or even in the Holarctic area. The species at the edge of their distribution vary between our areas: 7 in southern Sweden, 17 in central Sweden 8 in southern Finland, and 15 in central Finland. It is expected that more species are at their range margin further to the north. However, one species (*Coenagrion johansoni*) is at its southern border in southern Sweden. Note that several species are at their northern borders both in Sweden and in Finland.

We also divided species into groups by their breeding habitat and dispersal ability. In regard to their breeding habitat, we used data from extensive field work in Finland and Sweden (Valle 1952, Korkeamäki and Suhonen 2002,

Table 1. Number of waterbodies (lakes and permanent ponds) studied in Finland and Sweden.

Region	Number of waterbodies	Waterbody area (ha)				Methods	Source
		Mean	SD	Min	Max		
Southern Sweden	94	12.57	32.85	0.02	247.50		
						L	Al Jawaheri and Sahlén (2017)
						L	Wittwer et al. (2010)
						L	Koch et al. (2014)
						L, E, A	G. Sahlén, previously *unpublished data*
Central Sweden	91	3.22	5.86	0.02	41.25		
						L, E, A	G. Sahlén, previously *unpublished data*
						L	Sahlén and Ekestubbe (2001)
						L	Flenner and Sahlén (2008)
Southern Finland	58	6.87	19.96	0.02	140.90		
						L	Suutari et al. (2009)
						E, A	Korkeamäki (2013)
Central Finland	49	10.44	25.86	0.04	147.60		
						E, A	Suhonen et al. (2014)
						L, E	Honkanen et al. (2011)
Combined	292	8.06	23.46	0.02	247.50	L, E, A	

Notes: The mean, standard deviation (SD), minimum (min), and maximum (max) are given for each of the four geographical regions. Methods indicate how the odonate species were sampled: L is larvae, E is exuviae, and A is adults.

Suhonen et al. 2010, 2014, Sahlén, *unpublished data*) to classify the species into three groups: generalists (14 species) breeding in both standing and running water (at least in Finland or Sweden), specialists (28 species) breeding mainly in standing water, and tourist species (five species) mainly breeding in running water but sometimes encountered in standing water (Table 2).

The Odonata includes species with high as well as low dispersal capacity. It has been shown that some Anisoptera (dragonflies) have the capacity to move long distances, even across oceans (Troast et al. 2016, Alvial et al. 2017), while other Anisoptera have difficulties to pass a narrow landscape barrier such as a motorway (Šigutová et al. 2017). The same applies for Zygoptera (damselflies): Many species are poor dispersers (Watts et al. 2007), while others are capable of making long-distance migration, but probably more aided by wind than species in the other suborder. Suhling et al. (2017) showed that in a desert environment, specimens of *Pseudagrion glaucescens* were found more than 270 km from the nearest suitable habitat. Although less than the distances found for anisopteran species, this indicates that also some Zygoptera have high dispersal possibilities. One example is *Ischnura hastata* on the Azores, 3300 km distant from the nearest Caribbean population (Lorenzo-Carballa et al. 2017). We used the body size (measured as the mean value of minimum and maximum hindwing length; Dijkstra and Lewington 2006) as a proxy for dispersal ability.

Statistical methods

We used 10% occupancy classes and number or percentage of odonate species in each class to represent the geographical variation in occupancy frequency distribution, as recommended by McGeoch and Gaston (2002). We used Pearson correlation to test the relationship between species richness and waterbody area. As our localities varied from small ponds to relatively large lakes, the waterbody area was $\log_{10}$-transformed before analyses. We used Spearman rank correlation to test the relationship between a species' geographical range and its wing length, and generalized linear models with type III errors (negative binomial distribution; log link) to test the relationship between a species' geographical range and the number of waterbodies occupied. We used the same method to test differences in occupancy frequency between the different breeding habitat types. In this model, the breeding habitat type was set as a factor, and the geographical range, as well as its wing length, was used as continuous covariates. We tested differences between breeding habitat types within a

Table 2. A list of species observed in 292 waterbodies in Finland and Sweden.

Species	Suborder	Habitat	Wing length	Range	SS (*n*)	CS (*n*)	SF (*n*)	CF (*n*)	Total (*n*)
Aeshna caerulea	Anisoptera	Specialist	80	508	. . .	1	. . .	. . .	1
Aeshna crenata	Anisoptera	Specialist	106	63	. . .	. . .	21	1	22
Aeshna cyanea	Anisoptera	Generalist	100	363	17	19		2	38
Aeshna grandis	Anisoptera	Generalist	102	700	59	58	51	39	207
Aeshna juncea	Anisoptera	Specialist	95	770	18	73	39	42	172
Aeshna mixta	Anisoptera	Specialist	85	205	6	5	. . .	. . .	11
Aeshna serrata	Anisoptera	Specialist	99	115	. . .	3	. . .	. . .	3
Aeshna subarctica	Anisoptera	Specialist	90	355	10	27	30	28	95
Aeshna viridis	Anisoptera	Specialist	87	88	1	2	5	. . .	8
Brachytron pratense	Anisoptera	Generalist	72	210	14	5	2	1	22
Calopteryx splendens	Zygoptera	Tourist	61	315	1	. . .	4	. . .	5
Calopteryx virgo	Zygoptera	Tourist	58	640	4	. . .	6	. . .	10
Coenagrion armatum	Zygoptera	Specialist	39	315	1	5	11	7	24
Coenagrion hastulatum	Zygoptera	Generalist	40	663	42	75	26	49	192
Coenagrion johanssoni	Zygoptera	Specialist	36	370	. . .	20	23	36	79
Coenagrion lunulatum	Zygoptera	Specialist	40	248	5	1	. . .	. . .	6
Coenagrion puella/pulchellum	Zygoptera	Generalist	41	405	46	45	19	11	121
Cordulia aenea	Anisoptera	Generalist	68	615	45	55	33	44	177
Enallagma cyathigerum	Zygoptera	Specialist	38	618	26	15	10	17	68
Epitheca bimaculata	Anisoptera	Specialist	85	150	2	. . .	4	1	7
Erythromma najas	Zygoptera	Generalist	43	495	46	28	23	28	125
Gomphus vulgatissimus	Anisoptera	Tourist	64	225	3	. . .	0	. . .	3
Ischnura elegans	Zygoptera	Specialist	35	333	44	. . .	1	. . .	45
Lestes dryas	Zygoptera	Specialist	45	270	. . .	1	. . .	1	2
Lestes sponsa	Zygoptera	Specialist	42	600	41	37	36	32	146
Lestes virens	Zygoptera	Specialist	39	78	1	. . .	. . .	. . .	1
Leucorrhinia albifrons	Anisoptera	Specialist	60	323	9	13	17	14	53
Leucorrhinia caudalis	Anisoptera	Specialist	64	238	2	4	10	22	38
Leucorrhinia dubia	Anisoptera	Specialist	53	610	7	47	35	35	124
Leucorrhinia pectoralis	Anisoptera	Specialist	66	263	4	13	2	0	19
Leucorrhinia rubicunda	Anisoptera	Specialist	66	645	3	40	3	30	76
Libellula depressa	Anisoptera	Specialist	76	323	. . .	2	. . .	. . .	2
Libellula qadrimaculata	Anisoptera	Generalist	75	630	54	69	33	38	194
Orthetrum cancellatum	Anisoptera	Specialist	77	305	9	1	. . .	. . .	10
Orthetrum coerulescens	Anisoptera	Generalist	60	165	3	2	1	. . .	6
Platycnemis pennipes	Zygoptera	Tourist	45	340	1	. . .	1	. . .	2
Pyrrhosoma nymphula	Zygoptera	Generalist	44	415	28	9	. . .	4	41
Somatochlora arctica	Anisoptera	Generalist	68	385	. . .	1	. . .	2	3
Somatochlora flavomaculata	Anisoptera	Specialist	76	290	6	12	4	9	31
Somatochlora metallica	Anisoptera	Generalist	78	743	27	17	11	27	82
Sympecma fusca	Anisoptera	Specialist	40	115	1	1	. . .	0	2
Sympetrum danae	Anisoptera	Generalist	46	603	14	36	34	21	105
Sympetrum flaveolum	Anisoptera	Specialist	55	405	3	1	10	13	27
Sympetrum sanguineum	Anisoptera	Generalist	55	245	24	12	. . .	. . .	36
Sympetrum striolatum	Anisoptera	Specialist	58	190	1	3	. . .	. . .	4
Sympetrum vulgatum	Anisoptera	Specialist	60	420	6	12	4	. . .	22

Notes: For each of the species, the following information is presented: suborder [Zygoptera (damselflies), Anisoptera (dragonflies)], breeding habitat (generalist is breeding in both standing and running water, specialist is breeding mainly in standing water, tourist is mainly breeding in running water but rarely also in standing water), mean hind wing length (mm; from Dijkstra and Lewington 2006), geographical range (1000 km^2, geographical range area in Finland and Sweden from Boudot and Kalkman 2015), and number of waterbodies (*n*) from which each species was collected in the four respective regions; southern Sweden (SS), central Sweden (CS), southern Finland (SF), central Finland (CF), and combined data (Total). Note that *Coenagrion puella* and *C. pulchellum* were pooled, since they are inseparable as larvae.

given geographical range with Kruskal–Wallis test, as data were not normally distributed.

We applied the multi-model inference approach to the regressions of empirically ranked species-occupancy curves (RSOCs; Jenkins 2011). For these analyses, each of the data sets (combined data and the four different areas; species listed in rows and waterbodies as columns), was processed separately (Jenkins 2011). All analyses described below are based on relative occupancy (presence/absence) data at individual waterbodies. First, we calculated the sum of areas of all waterbodies where a given species was observed. We then divided each occupancy area by the total area of all waterbodies, to get the relative proportion of the total waterbody area that each species occupied (Hanski 1999). Second, we sorted the species by their relative occupancy values in decreasing order, where R_i is the rank value for species i. We plotted the relative occupancy of the species (O_i) as a function of R_i, resulting in RSOC. Third, we compared which of the most common core–satellite species patterns (unimodal satellite dominant, bimodal symmetrical, or bimodal asymmetrical) gave the best fit for the assemblages (Jenkins 2011). We fitted each of the following three SOFD patterns:

1. Unimodal satellite mode (exponential concave): $O_i = y_0 + a \times \exp(-bR_i)$ where the initial parameters were $y_0 = 0.01$, $a = 1.0$, $b = 0.01$.
2. Bimodal symmetrical (sigmoidal symmetric): $O_i = a/(1 + \exp(-bR_i + c)$, where the initial parameters were $a = 1.0$, $b = -0.1$, $c = -1.0$.
3. Bimodal asymmetric (sigmoidal asymmetric): $O_i = a[1 - \exp(-bR_i^c)]$, where the initial parameters were $a = 1.0$, $b = -1.0$, $c = -1.0$,

where y_0, a, b, and c are estimated parameters.

The nonlinear regressions were used in the Levenberg–Marquardt algorithm (999 iterations) according to Jenkins (2011), and parameters were estimated by means of ordinary least squares (OLS) with IBM SPSS statistical package. We graphically evaluated the assumptions of the regressions for normality of residuals, homogeneity of variance, independent error terms, as well as the tails and shoulders of the data and models.

We used Akaike information criterion for small sample sizes (AIC_c) to compare the alternative models. The model with the smallest AICc is considered to be best with respect to expected Kullback–Leibler information (Burnham and Anderson 2000). The approach is powerful to detect differences between models if ΔAICc ($= AICc_i - AICc_{min}$) values are higher than 4 (Anderson et al. 2000, Jenkins 2011). All the data analyses were performed using the IBM SPSS statistical package, version 23.

Results

A total of 46 odonate species were recorded in the 292 waterbodies. On average, we found 8.4 [±3.6 standard deviation (SD)] species, ranging from 1 to 18 (Table 3). In the combined data, the number of species did not increase with ($\log_{10}$-transformed) area of the waterbody ($r = 0.06$, $n = 292$, $P = 0.292$). However, there were regional differences in the correlation between species number and waterbody area. In three out of the four regions, we found no such relationship (southern Finland, $r = 0.19$, $n = 58$, $P = 0.162$; southern Sweden, $r = -0.10$, $n = 94$, $P = 0.353$; and central Sweden, $r = 0.145$, $n = 91$, $P = 0.170$). Only in central Finland, there was a clear positive relationship between waterbody area and species number ($r = 0.45$, $n = 49$, $P = 0.001$).

Each species occurred in an average of 54 ± 62.4 (range: 1–209) waterbodies (Table 2). Overall, the species with a large geographical range occurred in a higher number of waterbodies (Fig. 2, Table 4). The model including breeding habitat and geographical range was considered the best of the tested models (Table 4). Generalists occurred in a larger number of waterbodies (mean: 96 ± 74 SD, $n = 14$) than specialists (39 ± 47, $n = 28$; generalized linear models, Wald = 4.64, df = 1, $P = 0.031$; Fig. 2). However, the geographical range did not differ between breeding habitat types (Kruskal–Wallis test, $H = 5.37$, df = 2, $P = 0.068$). Neither dispersal ability (measured by wing length) nor the geographical range of the species ($r_s = -0.08$, $n = 46$, $P = 0.593$) explained the species occupancy frequency in the waterbodies (Table 4).

In the combined data, the SOFD pattern of the odonate species followed a unimodal satellite pattern (Table 5, Fig. 3). All alternative models

Table 3. The number of species found and mean, standard deviation (SD), and maximum (max) number and percentage of waterbodies occupied by odonate species in Finland and Sweden.

Region	Species	Number of waterbodies			Percent of waterbodies		
		Mean	SD	Max	Mean	SD	Max
Southern Sweden	39	16.3	17.8	59	17.7	21.8	79.2
Central Sweden	38	20.3	22.5	75	21.1	23.5	73.1
Southern Finland	31	15.9	14.2	51	31.8	34.5	94.5
Central Finland	27	19.1	15.9	49	51.3	35.8	100.0
Combined	46	54.4	62.4	209	19.4	22.3	78.7

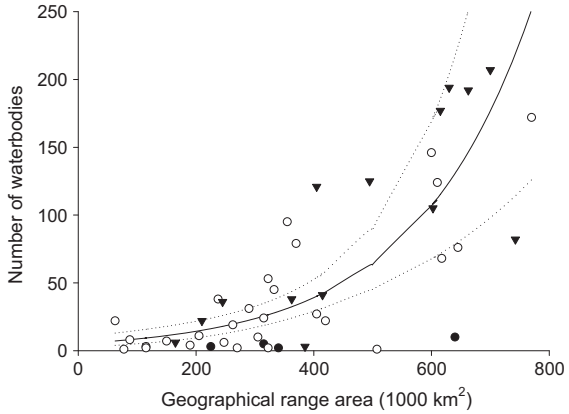

Fig. 2. Number of waterbodies occupied by each odonate species (n = 46) in relation to its geographical range in Finland and Sweden. Model prediction curve (continuous line) and 95% confidence intervals (dotted lines). The curve is based on the combined data set and calculated with generalized linear models. In the model, the number of lakes occupied by each odonate species was negatively binomial distributed with a logarithmic link function. The symbols denote the breeding habitat(s) of the species: Generalists (filled triangles) breed in both standing and running waters, specialists (open dots) breed in standing waters, and tourists (filled dots) breed mainly in running waters, but occasionally also in standing waters.

fitted less well with data (ΔAICc > 4; Table 5). There was a high number of satellite species, and half of the species (23 out of 46) occurred in <10% of the waterbodies. On the other hand, six species were found in at least half of the waterbodies (Fig. 3).

We found geographical variation in the SOFD patterns (Table 5, Fig. 4). The three northern regions (i.e., central Finland, southern Finland, and central Sweden; Fig. 4a, b, d) showed the best fit with the bimodal core–satellite pattern, whereas southern Sweden followed the unimodal satellite-dominant pattern (Table 5, Fig. 4c). All alternative models fitted less well with data (ΔAICc > 4; Table 5). More than half of the species occurred in <10% of the waterbodies in southern Sweden (Fig. 4c), but only about one-fourth in central Finland (Fig. 4b). Moreover, in Sweden, none of the species occurred in all waterbodies (Fig. 4c, d), whereas certain species, such as *Aeshna grandis*, *A. juncea,* and *Coenagrion hastulatum*, occurred in almost all of the studied Finnish lakes (Table 2, Fig. 4a, b).

Discussion

Species richness

We found a relatively high total number of odonate species in the studied waterbodies, about 77% (46 out of 60 species) of the total number occurring regularly in Sweden and Finland (Boudot and Kalkman 2015). We also found that species richness increased with waterbody area in central Finland, but not in southern Finland or in Sweden. The lack of a general relationship between waterbody area and species richness contrasts with the results of a previous study where larger ponds were shown to harbor a larger number of odonate species (Oertli et al. 2002). Larger lakes may have room for more niches, for example, different types/structures of aquatic plants, which increases odonate species richness (Oertli et al. 2002, Honkanen et al. 2011). However, the maximum waterbody size studied by Oertli et al. (2002) was 9.5 ha, whereas our waterbodies were much larger (up

Table 4. Generalized linear models for the occupancy frequency of 46 odonate species in 292 waterbodies in Finland and Sweden.

Model	Parameter estimates					Omnibus test			AICc values	
	I	Range	Generalist	Specialist	Wing	G^2	df	*P*	AICc	ΔAICc
Range + Habitat	**2.11**	**0.005**	**−2.37**	−0.34	—	48.39	3	<0.001	419.79	0.0
Range + Habitat + Wing	**2.07**	**0.005**	**−2.37**	−0.34	0.001	48.40	4	<0.001	422.31	2.52
Range	**1.66**	**0.005**	—	—	—	38.47	1	<0.001	425.02	5.23
Range + Wing	**1.57**	**0.005**	—	—	0.002	38.50	2	<0.001	427.28	7.49
Habitat	**4.57**	—	**−2.60**	**−0.90**	—	19.36	2	<0.001	446.42	26.63
Habitat + Wing	**4.57**	—	**−2.97**	**−0.90**	−0.006	19.51	3	<0.001	448.68	28.89
Wing	**4.09**	—	—	—	−0.004	0.06	1	0.815	463.43	43.64

Notes: Predictor variables were geographical range, breeding habitat (three categories: generalist, specialist, and tourist species as a reference category) and wing length of the species. Estimated parameters for the intercept (*I*) and predictor variables are shown in bold if they differed from zero ($P < 0.05$).The adequacy of each model was tested by the goodness-of-fit test (G^2), and Akaike information criterion for small sample sizes (AICc) and ΔAICc($= \text{AICc}_i - \text{AIC}_{c\min}$) values are presented. The model with the lowest AIC_c is considered as the best model of the tested. Em-dash indicates that the parameter(s) did not belong to the model.

Table 5. Results of odonate species occupancy frequency distributions (SOFD) in Finland and Sweden.

Region	Figure	Species	AICc	ΔAICc
Combined	3	46		
Unimodal satellite			−327.1	0.0
Bimodal symmetric			−322.8	4.3
Bimodal asymmetric			−204.7	122.4
Southern Sweden	4c	39		
Unimodal satellite			−315.4	0.0
Bimodal symmetric			−310.4	5.0
Bimodal asymmetric			−178.3	137.0
Central Sweden	4d	38		
Bimodal symmetric			−272.9	0.0
Unimodal satellite			−257.3	15.6
Bimodal asymmetric			−154.7	118.1
Southern Finland	4a	31		
Bimodal symmetric			−272.9	0.0
Unimodal satellite			−257.3	15.6
Bimodal asymmetric			−154.7	118.1
Central Finland	4b	27		
Bimodal symmetric			−149.0	0.0
Bimodal asymmetric			−130.5	18.6
Unimodal satellite			−126.0	23.0

Notes: The three most likely SOFD patterns (unimodal satellite dominant, bimodal symmetrical, and bimodal asymmetrical) were analyzed with combined data and separately for the four different locations (southern Sweden, central Sweden, southern Finland, and central Finland). Figure column joins statistical models with data figures. Species denote number of species in each study region. Akaike information criterion for small sample sizes (AICc) and ΔAICc ($= \text{AICc}_i - \text{AICc}_{\min}$) values are presented. The model with the lowest AIC_c is considered as the best of the tested models.

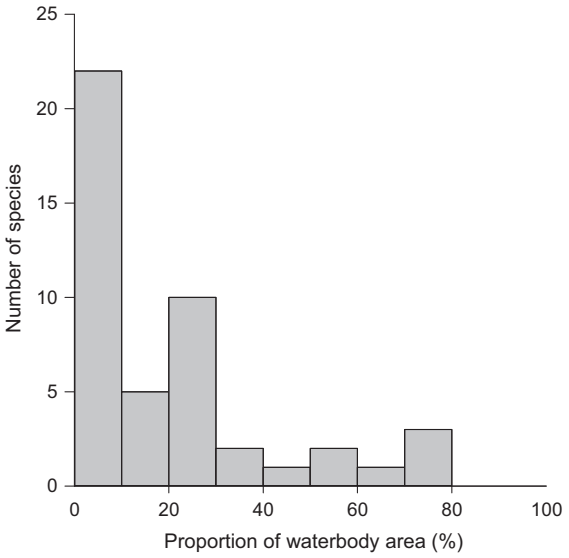

Fig. 3. Number of odonate species ($n = 46$) in relation to the proportion of the waterbody area occupied (%; $n = 292$ lakes) in Finland and Sweden.

to 247 ha). Moreover, diversity of many taxonomic groups are known to peak at high productivity (Dodson et al. 2000) rather than large area and previous studies have also noted that small lakes in forests often harbor a larger number of species than large ones (Flenner and Sahlén 2008, Koch et al. 2014).

The fact that such a high percentage of the total number of recorded odonate species was found in our relatively small subset of Swedish and Finnish waterbodies is interesting, as the lakes surveyed by us constitute much less than 0.1% of all lakes in the two countries (estimated at >151,000 lakes larger than 0.01 km^2; Henriksen et al. 1998). This may be because the number of species encountered at these northern latitudes

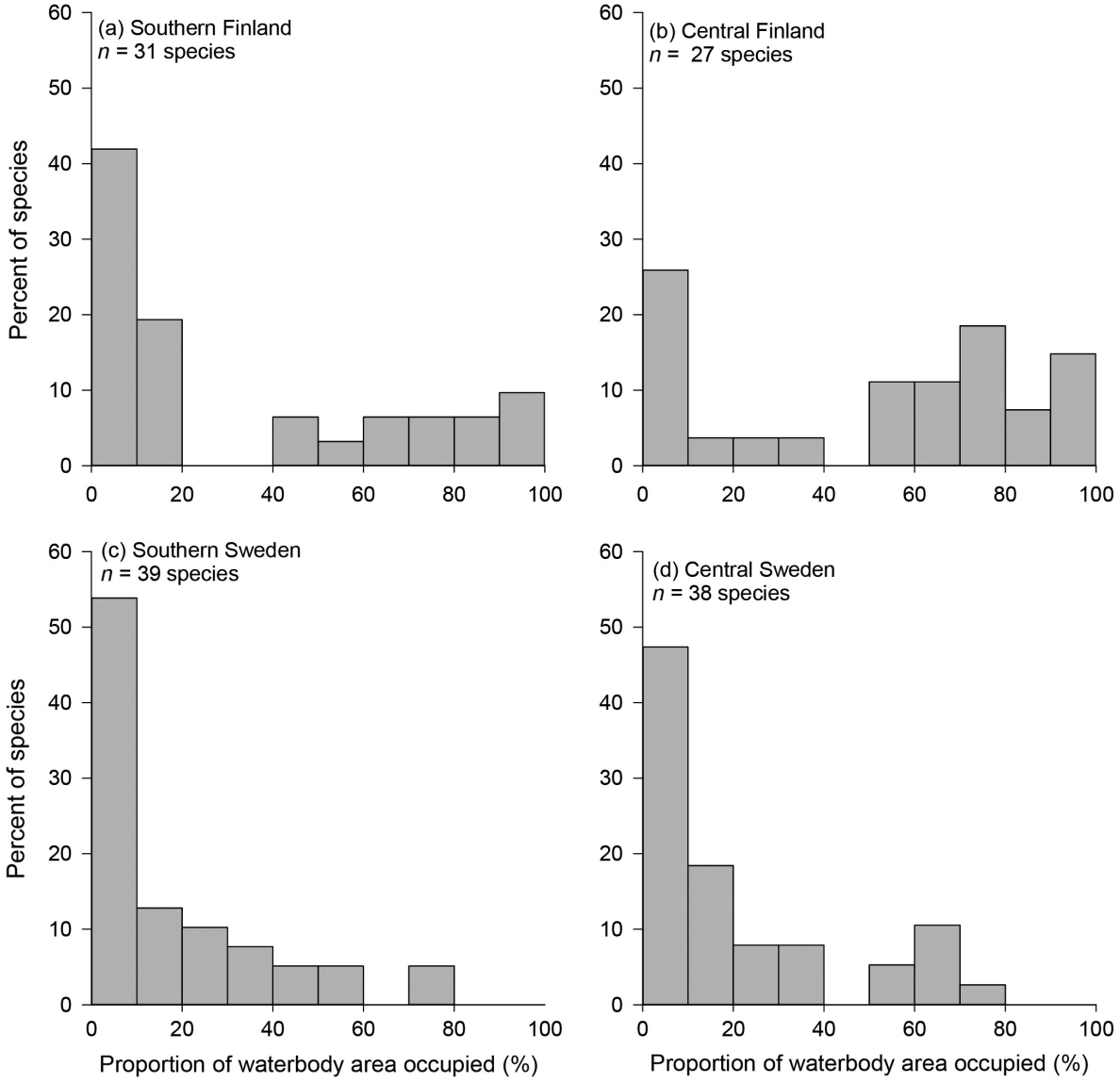

Fig. 4. Percentage of odonate species in relation to the proportion of waterbody area (%) occupied in Finland and Sweden. (a) Southern Finland, (b) central Finland, (c) southern Sweden, and (d) central Sweden.

is rather small (~60, Norling and Sahlén 1997), and the variation in community composition is thus limited. Moreover, we show that sampling only a small subset of the available habitats will give a fair picture of the number of species present in an area, providing our combined sampling methods are not biased. The species that occur there without being detected are probably rare in the area, or have a limited flight season/larval time—and it is well known that such species require specific or intense sampling efforts (Guisan et al. 2006).

Species occupancy frequency distribution in the waterbodies

Sampling artefacts.—Our results suggest that with increasing latitude, the SOFD pattern changes from unimodal satellite dominant to bimodal symmetric (Fig. 4). There are several

possible explanations to this variation in SOFD pattern between Fennoscandia waterbodies along latitudinal gradients (McGeoch and Gaston 2002, Jokimäki et al. 2016). The SOFD patterns may differ due to sampling methods, such as the number of samples and the extent of sampling (McGeoch and Gaston 2002, Heatherly et al. 2007). Data collected by different survey methods may produce different estimates of species richness and thus different SOFD patterns. We used different survey methods (collecting larvae, exuviae, and observed adults) in different studies and geographical regions (Table 1), but all methods we employed are known to detect the majority of species present at a waterbody, adult surveys detecting slightly more species than to larval surveys (Giugliano et al. 2011). Previous studies have shown that a single visit is not enough to capture species richness reliably (Bried et al. 2012*b*), and this is particularly true for adults and exuviae due to differences in species' emerging times. Reduced sampling is likely to result in situation where species are erroneously considered to be rarer than they actually are. As we used repeated sampling in most of our studies focusing on adults and exuviae and a large part of the larval studies, it is less likely that our results are biased. However, we cannot completely rule out the possibility that the regional differences found follow from the differences in sampling. Misidentification is unlikely, as we used only studies executed by researchers highly skilled in odonate species identification (cf., Foster and Soluk 2006, Bried et al. 2012*b*). Study plot size may also influence SOFD patterns (McGeoch and Gaston 2002). However, in our study, the sizes of the waterbodies only affected the species richness slightly in three of the four latitudinal regions—the northernmost one, central Finland, being the exception. Also, the sample size (number of waterbodies) was relatively large within each geographical region (at least 49 waterbodies). In general, samples from large areas are more heterogeneous than samples from smaller areas. They are therefore likely to contain many satellite (rare) species and exhibit unimodal species distributions (McGeoch and Gaston 2002). Our data partly support this hypothesis, as our combined data exhibit a unimodal satellite-dominated pattern, whereas bimodal SOFDs were often observed in subsamples of the data (Collins and Glenn 1997, Heatherly et al. 2007, Jokimäki et al. 2016).

Biological factors.—As predicted, we found that species which have a large geographical range occurred more often in the studied waterbodies (Fig. 3). It may be that locally common species become widely distributed because they have a low local extinction rate and a high colonization rate, as predicted by metapopulation theory (Hanski and Gyllenberg 1997, Hanski 1998). Several previous studies have shown that species with a narrow geographical range are susceptible to local extinctions (Hanski 1998, Korkeamäki and Suhonen 2002, Suhonen et al. 2014) and that the high risk of local extinctions may be due to smaller population size and higher environmental sensitivity compared to the widespread species (Suhonen et al. 2010, 2014, Korkeamäki 2013). Also, here we found that species with a small geographic range occupied a small number of waterbodies, although we did not specify the mechanistic basis underlying this pattern.

Odonate species occupancy frequencies may be affected by differences in dispersal ability and colonization rate between species (Collins and Glenn 1997). Naturally, the probability that all species would occur in all waterbodies decreases with increasing spatial scale. Dispersal capability is not fully understood in Odonata, although many large species have been shown or assumed to have a high dispersal ability (Andersen et al. 2016, Troast et al. 2016) and small ones are sometimes very poor dispersers (Rouquette and Thompson 2005). Moreover, one might assume that a species will have a high dispersal ability if the habitat it requires is scarce. This is, however, not the case in our study area, where lentic waterbodies are abundant (Henriksen et al. 1998). We found that body size, measured as hind wing length, did not affect species occupancy frequency in the waterbodies. This result is consistent with a previous study made in running waters (Heino 2015).

We found that generalist species occupied a larger number of waterbodies and had larger geographical ranges than specialist species or tourist species. The tourist species, such as *Gomphus vulgatissimus* and *Calopteryx* spp., are mainly breeding in running waters (Dijkstra and Lewington 2006). Hence, it is easy to understand why these species have very low occupancy

frequencies in our data (Table 2, Fig. 2). Generalist species frequently breed in both standing and running waters. For these species, the alternative habitat (see more details in Suhonen et al. 2010) might be a low-quality sink habitat (Pulliam 1988, Watkinson and Sutherland 1995), where the risk of local extinction probability is higher than in the main breeding habitat (Suhonen et al. 2010, 2014). Generalist species occurred in very high frequencies in standing waters (Fig. 2). This might be because these species are able to use low-quality habitat patches as stepping stones to colonize new high-quality patches. Moreover, it may be better to breed in low-quality habitat patches than not to breed at all, if high-quality habitats are not available. Generalist species with broad niches have a wide geographical distribution, whereas specialist species are limited by their narrower niches. Thus, this niche-based hypothesis mainly predicts a right-skewed unimodal SOFD pattern (Brown 1984) and our result is in concordance with this hypothesis at large spatial scale (Brown 1984, McGeoch and Gaston 2002, cf. Heino 2015).

We found that most of the species occurred in a small portion of the waterbodies, whereas only six species were found in at least half of the lakes. These results are best described by the unimodal satellite-dominant SOFD pattern (Fig. 3). The pattern that waterbodies have only a few common species and many rare ones follows the general theory of species community structure (Lennon et al. 2004). The theory suggests that habitat and climate heterogeneity increases with increasing distance between waterbodies at large spatial scale. This will increase the variation between waterbodies and reduce the likelihood that species inhabit numerous waterbodies. Our results were consistent with previous studies, where the percentage of species in the core group declined, and the percentage of species in the satellite group increased, as the spatial scale increased from regional (Fig. 4) to Fennoscandian (Fig. 3; Collins and Glenn 1997, Heatherly et al. 2007, Jokimäki et al. 2016).

We found that SOFD pattern varied between regions in Finland and Sweden. The symmetric core–satellite SOFD pattern gave the best fit with our data, except for southern Sweden, where the best-fitted SOFD pattern was unimodal satellite species dominant (Table 5, Fig. 4). Southern Sweden (Fig. 4c) had fewer core species and a larger number of satellite species than assemblages at higher latitudes (Fig. 4a, b, d). One important factor behind this was that the species pool was larger (54 species) in southern Sweden than in central Finland (44 species; Boudot and Kalkman 2015). The number of species encountered at northern latitudes is small, and the variation in community composition will thus be limited. Most of the species occur in most of the waterbodies, and there are relatively few specialist species. Thus species occupancy frequency fits well with the core–satellite SOFD pattern (McGeoch and Gaston 2002). On the other hand, in the regions further south, the species pool probably includes a larger number of specialist species which occupy only part of the potentially suitable habitats, and thus, the unimodal satellite species-dominant pattern fits well (McGeoch and Gaston 2002). Moreover, the species lists for the four regional data sets seem to be nested. Most of the species in Finland and central Sweden occur also in southern Sweden, where the species richness is higher (Boudot and Kalkman 2015).

Our results (Fig. 4) are in accordance with the SOFD theory (McGeoch and Gaston 2002): If the sampled sites are located in an area near the edge of the geographical range of many of the species present, the SOFD will be unimodal satellite dominant or bimodal satellite dominant. Our results also support the prediction that species at lower latitudes tend to have a smaller latitudinal range than high latitude species (Rapoport's latitude rule; Gaston et al. 1998). Southern Sweden is near the northern distribution limit of several (6 out of 54) odonate species (Boudot and Kalkman 2015), and we found that a unimodal satellite-dominant SOFD pattern fits the data best. As a consequence, small populations near the periphery of their range will be more susceptible to local extinction (Gaston 2003) and increase the proportion of satellite species in the assemblage. This is an important aspect to consider when setting up conservation measures for the rarer of the northern species.

Current global warming is shifting the range of southern odonate species toward the north (Hickling et al. 2005), particularly in southern Sweden (Parmesan et al. 2005, Flenner and Sahlén 2008) as the species pool is larger in central Europe than in the northern regions (Boudot

and Kalkman 2015). This geographical range shift increases both the species pool and the proportion of satellite species. In previous studies, it has been shown that the population density decreases from the distribution center of a species toward the periphery (Hengeveld and Haeck 1982, Brown 1984, Brussard 1984), and the proportion of occupied suitable patches also decreases (Svensson 1992). However, recent genetic studies have given only partial support to this center-periphery hypothesis. Johansson et al. (2013) suggested that the pattern is perhaps more complex. For example, if the geographical range of a satellite species shifts to the north, the species may also shift from satellite to core species and, consequently, the proportion of satellite species within a given region will remain unchanged. Therefore, further empirical and theoretical studies are needed to obtain more detailed information regarding how global warming influences the geographical SOFD variation.

We would also expect less change in species composition in the north as global warming, and other anthropogenic effects are likely to most probably affect the rare species. As the general pattern already today means few rare and more common species, these communities should be stable and less prone to change than those in the south where the species pool is dominated by specialists. On the other hand, the few rare northern species with narrow habitat requirements may become even rarer if the suitable habitats become too rare due to climate change or other anthropogenic disturbances.

To conclude, our results demonstrate that standing waterbodies conform to the prediction of variations in SOFD models at large geographical scale. In the southern regions, the SOFD pattern was satellite dominant, and in the northern ones, it was bimodal. Biological mechanisms such as geographical range and breeding habitat requirement (generalist or specialist species) explain the variation in species occupancy frequency. The different patterns observed by latitude are interesting when considering setting up conservation programs for rare or endangered species. In our northernmost area, species are in general common and occurring in a high number of waterbodies compared to the situation at lower latitudes (Fig. 4). Thus, protecting rare species in the north would require a higher effort to identify the scattered lakes occupied by a certain rare species. Our observations are consistent with previous studies over large spatial scales (Collins and Glenn 1991, 1997) and follow Brown's niche-based model (Brown 1984). Further empirical and theoretical studies are, however, needed to acquire more detailed information regarding geographical variation in SOFD for aquatic organisms and the ways in which range and size shifts of species affect species occupancy frequency.

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