COMMUNITY ECOLOGY - ORIGINAL PAPER

Deconstructing responses of dragonfly species richness to area, nutrients, water plant diversity and forestry

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Abstract Understanding large-scale variation in species richness in relation to area, energy, habitat heterogeneity and anthropogenic disturbance has been a major task in ecology. Ultimately, variation in species richness results from variation in individual species occupancies. We studied whether the individual species occupancy patterns are determined by the same candidate factors as total species richness. We sampled 26 boreal forest ponds for dragonflies (Odonata) and studied the effects of shoreline length, water vascular plant species density (WVPSD), availability of nutrients, intensity of forestry, amount of *Sphagnum* peat cover and pH on dragonfly species richness and individual dragonfly species. WVPSD and pH had a strong positive effect on species richness. Removal of six dragonfly species experiencing strongest responses to WVPSD cancelled the relationship between species richness and WVPSD. By contrast, removal of nine least observed species did not affect the relationship between WVPSD and species richness. Thus, our results showed that relatively common species responding strongly to WVPSD shaped the observed species richness pattern whereas the effect of least observed, often rare, species was negligible. Also, our results support the view that, despite of the great impact of energy on species richness at large spatial scales, habitat heterogeneity can still have an effect on species richness in smaller scales, even overriding the effects of area.

Keywords Extreme deconstruction · Disturbance · Habitat heterogeneity · Odonata · Species number

Communicated by Craig Osenberg.

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Introduction

Species richness is a fundamental character of biodiversity and extensive effort has been put to understand the large-scale variation in it. Traditionally, the changes in species richness at biogeographical scales have been explained by area and its counterpart, habitat heterogeneity. This view has been challenged by introducing a more general variable, energy (Wright 1983), which indeed seems to explain large-scale species richness patterns better than area or habitat heterogeneity (Field et al. 2009). However, ultimately, species richness and its variation are results of species-specific occupancies. This so-called deconstructive approach to species richness (Marquet et al. 2004) could yield deeper understanding of mechanisms driving species richness (Evans et al. 2006; Terribile et al. 2009).

Dragonfly (Odonata) species richness has been shown to react positively to area (Oertli et al. 2002; Ruggiero et al. 2008), different measures of energy (Samways and Steytler 1996; Heino 2002; Keil et al. 2008) and vascular plant species richness (Sahlén 1999; Heino 2002; Carchini et al. 2007; Keil et al. 2008), which could be seen as a measure of habitat heterogeneity. However, in some studies, clear relationships have not been found and thus the relative importance of the factors seems to vary (e.g., Johansson and Brodin 2003; Carchini et al. 2007; Ruggiero et al. 2008). Although the variability in the results may stem

from the interactions between the three variables, scale or location of the particular study, it may as well originate from species-specific occupancy responses. When species occurrences are not completely random, increase or decrease in species richness results from the presence or absence of some specific species, which are sensitive for certain environmental factors, such as area, energy or habitat availability.

In this study, we examined the relationship between dragonfly species richness and shoreline length, availability of nutrients, water vascular plant species density (WVPSD), amount of peat cover along the shoreline and pH. Instead of partitioning species richness into different species 'sets' based on some ecological characteristics (Marquet et al. 2004), we emphasized the fact that each species has a particular niche that determines its response to environmental factors (Terribile et al. 2009). We modeled the occupancy of each individual species in relation to the variables described above, resulting in extreme deconstruction of species richness (Terribile et al. 2009). Thus, we can discern whether or not the variation in species richness originates from a consistent response of individual species to environmental variation. There is also a growing body of literature that common species have a greater effect on species richness patterns than rare species (e.g., Jetz and Rahbek 2002; for a short review, see Gaston 2008) and one could predict that common species would be more closely related to environmental variables with which total species richness tends to covary (Gaston 2008). We also wanted to study what are the effects of common and rare species to species richness patterns.

Humans may clearly have an additional effect on species richness (see Pautasso 2007 and references therein). Forestry, one form of anthropogenic disturbance, has become the primary disturbance factor in boreal forests today (Niemelä 1999), and it has been found to affect dragonfly species richness negatively (Rith-Najarian 1998; Sahlén 1999). Thus, we additionally studied the effect of forestry on dragonfly species richness and individual species, and if this possibly results from changes in nutrients or WVPSD.

Materials and methods

Study site, sampling and study variables

We sampled 26 boreal forest ponds and small lakes (mean water area = 1.57 ha, min = 0.04 ha, max = 4.33 ha) situated in the boreal zone, Central Finland, representing geographical variation from c. 61N to c. 63N and c. 24W to c. 26W. Fourteen of the ponds were situated in protected areas (Isojärvi, Leivonmäki and Pyhä-Häkki National Parks) and 12 in the surrounding commercial forest

landscapes. All the areas were administered by the state forest enterprise Metsähallitus.

We measured area as shoreline length, which we assumed to reflect habitat area available for dragonfly larvae. The shoreline length was highly correlated with pond area (Spearman $r = 0.942$, $p < 0.001$). We sampled the ponds for dragonfly larvae twice, in June and July 2007, with a water-net (D-shape, mesh size 1 mm^2) and searched the shoreline for dragonfly exuviae. We standardized both of the sampling methods in order to keep equal sampling effort per unit area (shoreline length): the number of net sweeps for detecting larvae ranged from 15 to 90 (on average one net sweep 20 m^{-1} in June and 40 m^{-1} in July) and time for exuviae searching from 20 to 120 min (1 min 20 m^{-1} in both June and July). Since we used only larvae and exuviae, actual breeding of the species was confirmed and vagrants automatically excluded (Sahlén 1999). Larvae were fixed in 80% ethanol with an additive of 4% formaldehyde to preserve pigment patterns, and exuviae were sterilized in 95% alcohol and dried. Later, we determined them to species according to Norling and Sahlén (1997).

Although dragonflies as predatory insects on all life-stages do not directly feed on plants, they use vegetation for various actions in all life-stages (Buchwald 1992; Corbet 2004, p. 13). Thus, water plant species richness could represent habitat heterogeneity for dragonflies. We sampled water vascular plants during July, when vegetation cover was fully developed, by a 5-m-wide transect. Transects reached from the shoreline towards the center of the pond as far as there was vegetation. The number of transects were standardized according to shoreline length ranging from 2 to 12 (on average 1 transect 100 m^{-1}).

A wide variety of energy metrics can be divided into two main categories: solar and productive energy metrics (Evans et al. 2005). Solar energy metrics, such as temperature, measure the amount of solar energy available at a given location whereas productive energy metrics measure the amount of resources available for consumers. We used total phosphorus (TP) and total nitrogen (TN) as proxies for productive energy of ponds because these nutrients have been shown to be limiting factors in freshwater systems (Elser et al. 2007) and they have also been used in previous studies with ponds (e.g., Carchini et al. 2007). As TP and TN correlated strongly with each other ($r = 0.720$, $p < 0.001$) and provided congruent information of the nutrient availability in ponds, we ran a principal component analysis (PCA) in order to receive a single productive energy variable. PCA extracted one component which explained 71.19% of the total variation and was used in the further analyses.

Dragonfly communities react to forest harvesting in the surroundings of their aquatic habitat with a 5- to 15-year time lag (Sahlén 1999). Information on forestry measures

was derived from the Metsähallitus' SutiGis database, which covers only state-owned land and consequently information for private land was not available. For several ponds moving further away from the shoreline than 100 m resulted in inflated proportion of private land. Thus, we defined the intensity of the forestry as a percent of 5- to 15-old forest within 100 m from the shoreline. Some dragonfly species prefer ponds with *Sphagnum* peat cover along the shoreline (Dijkstra 2006). The longest distance between shoreline and forest edge was 17 m. Hence, we measured the amount of *Sphagnum* peat cover (hereafter peat) as a percent of the 17-m-wide zone (Topographic Database, National Land Survey of Finland, 2008). Additionally, we measured water pH since it has been shown an important variable for determining dragonfly community composition (Johansson and Brodin 2003).

Statistical analysis

For determining water vascular plant species density in a pond we used the equation

$$C = S \cdot A^{-z}$$

where S = number of species detected, A = number of transects and z = curvature of the power equation (Rosenzweig 2004). We first estimated the power function for the whole dataset producing average curvature, $z_a = 0.95$. We used this value to derive WVPSD for each pond as the number of species of aquatic vascular plants divided by the number of transects raised to 0.95. This procedure assumes that plant species richness in all ponds follows the same accumulation curve with increasing pond area. Because the number of transects was determined according to shoreline length, this results in sample-size-free estimate of the vascular plant species richness.

pH was transformed to hydrogen ion concentration to allow a linear relationship with species richness ($H^+ = 10^{-pH}$, H^+ was multiplied by 10^5). Thus, pH increases with decreasing H^+. We ran a set of 15 linear regression models with observed species richness as a dependent variable: six models with one explanatory variable (shoreline length, WVPSD, nutrients, intensity of forestry, peat, H^+) and nine models with two explanatory variables (peat or H^+ + shoreline length, WVPSD, nutrients, forestry) for controlling the possible effects of peat and H^+.

Species richness is likely to increase with increasing number of both individuals and samples (Gotelli and Colwell 2001). In order to control these effects, we further ran a set of models with a number of sampled individuals entered into every model. The same procedure was repeated for the number of samples. This resulted in three model sets representing observed species richness, species richness controlling for the sample size (number of individuals) and species richness controlling for the sampling effort. We used a second-order Akaike's information criterion (AIC_c) due to low amount of sites (26) to compare alternative models within a set (Burnham and Anderson 2002). The model with the smallest AIC_c value is estimated to be best in the sense of expected Kullback–Leibler information lost.

Naïve presence–absence data is liable to underestimate the true occupancy due to imperfect detection (MacKenzie et al. 2002). To account for this possible source of bias, we used single-season occupancy models which use repeated surveys of ponds to estimate species-specific occupancy (ψ) and detection (p) probabilities (MacKenzie et al. 2002). For each species, we fit the same 15 models as for species richness, plus an additional model with constant occupancy. All the model covariates were standardized to mean value 0 and standard deviation 1. Both the sampling methods (net sweeping, exuviae searching) and sampling times (June, July) were considered different sampling units resulting in four repeated surveys for each of the ponds. For all the models, detection probabilities were heterogeneous: it is likely that different sampling methods and times have different probabilities to detect the species. Thus, in every model, the detection probability (p) was dependent on the sampling mode (exuviae searching, net sweeping) and on time of visiting a pond (June, July) resulting in four survey-specific detection probabilities. For three species (*Lestes sponsa*, *Coenagrion johanssoni*, *Leucorrhinia rubicunda*), probability of observing exuviae was fixed to zero thus reducing the number of estimated parameters by one (Online Resource 1) because the probability of finding exuviae is essentially zero when species' (often weather-dependent) time of emergent has not yet begun or has been passed.

To assess model fit of our site-occupancy models, we used a method developed by MacKenzie and Bailey 2004. We calculated the Pearson chi-square and used parametric bootstrap procedure to determine whether the observed statistic distribution is unusually large. Model fit should be assessed for the most complicated model in the set (MacKenzie and Bailey 2004). As we had several models with the same number of parameters, we assessed model fit for all of these. The results were virtually identical, and after 5,000 bootstraps there was some evidence of poor fit for models of only one species (Online Resource 1). Consequently, $QAIC_c$ values following quasi-likelihood theory (Burnham and Anderson 2002) were used to compare these models, and a square-rooted over-dispersion factor, from the model with the poorest fit, was used to inflate standard errors for parameters of all the models.

We were able to perform the analysis for 12 individual species (Table 4; Online Resource 1). Nine species had too

few observations (occurred only in three or fewer ponds, or were observed less than 11 times from the total of 104 sampling units) and three species occupied almost all ponds (25 or 26) (Table 1). Due to over-parameterization, we were not able to perform the complete model set for four species (*L. sponsa*, *C. johanssoni*, *Leucorrhinia albifrons*, *L. rubicunda*) and thus only single explanatory variable models (7 models) were run for these species.

To assess whether species richness was determined by the same explanatory variables as individual species occupancies, we removed species strongly responding to the variable explaining species richness. Strength of response was considered to be the model-averaged estimate of parameter for the variable in question, that is, AIC$_c$ weights of the candidate models were used to obtain a weighted average of the individual parameter estimates (MacKenzie et al. 2006, p. 81). For a set of R models, the estimator is:

$$\hat{\theta}_A = \sum_{r=1}^{R} w_r \hat{\theta}_r$$

where w_r is the Akaike weight and θ_r the parameter in question of model r. Also, assessing model-averaged parameter estimates is a useful way to compare the effects of different variables when there seems to be no single best model. The estimators for peat and H$^+$ are not directly comparable to those of other variables, since for the eight species with the complete model set peat and H$^+$ occur in twice as many models as the other variables. Thus, their Akaike weights were divided by two when calculating the model-averaged parameter estimate.

We began to remove species from the data in order of their strength of response: first, we removed the species having the strongest response, then two species with the strongest responses, and so on. Each time, we ran a linear regression model for the new set of data and checked whether the relationship with the candidate variable and species richness remained. This was done by counting ΔAIC$_c$ between a model containing only number of individuals (or number of samples) and a model also containing the variable of interest. If ΔAIC$_c$ remained positive, the removal of the species did not change the relationship between species richness and variable of interest, i.e., the variable of interest still adds information to the model containing only number of individuals (or number of samples). When the value of ΔAIC$_c$ appeared to be negative, we stopped removing species and considered that the effect of variable of interest on species richness was cancelled. The same procedure was applied in detecting the effect of nine least observed species (to which we could not run species-specific occupancy models) on species richness patterns.

Because the mere removal of species from the analysis could have an effect on the relationship between species richness and the variable of interest, we re-ran the modeling procedures described above by randomly removing the corresponding number of species. We repeated this procedure 10,000 times and counted the mean and 95% confidence intervals for ΔAIC$_c$. If the removal of specific species deleted the relationship between species richness and variable of interest but random removal of the same number of species did not, it could be interpreted that the specific species produced the species richness pattern.

The fact that common species are likely to have a greater effect on species richness patterns may be due to pure statistical reasons (Šizling et al. 2009). Species for which the response strength could be calculated were all relatively common (occupancy from 7 to 23 of total sites). We wanted to ensure that mere removal of a certain number of common species, regardless of their response

Table 1 Species found from study ponds ($n = 26$), number of ponds they occupied and number of larvae and exuviae representing the species

Species	Ponds	Larvae	Exuviae
Lestes dryas (Kirby, 1890)	1	1	1
L. sponsa (Hansemann, 1823)	17	188	77
Coenagrion hastulatum (Charpentier, 1825)	26	1,882	37
C. johanssoni (Wallengren, 1894)	23	1,406	13
C. pulchellum (Vander Linden, 1825)	3	4	–
Erythromma najas (Hansemann, 1823)	13	94	25
Pyrrhosoma nymphula (Sulzer, 1776)	2	1	2
Enallagma cyathigerum (Charpentier, 1840)	7	30	333
Brachytron pratense (Müller, 1764)	1	1	1
Aeshna crenata (Hagen, 1856)	1	–	8
A. cyanea (Müller, 1764)	2	4	–
A. grandis (Linnaeus, 1758)	22	186	86
A. juncea (Linnaeus, 1758)	26	199	43
A. subarctica (Walker, 1908)	22	205	56
Cordulia aenea (Linnaeus, 1758)	23	101	913
Epitheca bimaculata (Charpentier, 1825)	1	–	1
Somatochlora metallica (Vander Linden, 1825)	14	25	89
Libellula quadrimaculata (Linnaeus, 1758)	16	87	136
Sympetrum danae (Sulzer, 1776)	7	26	1
S. flaveolum (Linnaeus, 1758)	1	–	1
Leucorrhinia albifrons (Burmeister, 1839)	7	13	51
L. caudalis (Charpentier, 1840)	9	107	66
L. dubia (Vander Linden, 1825)	25	1,657	327
L. rubicunda (Linnaeus, 1758)	9	53	9
Total	26	6,270	2,276

strength, does not cancel the relationship. Thus, we re-ran the previous analysis by removing a randomly specified number of those relatively common species. We also calculated whether the occupancy rate of species experiencing strong relationship with the variable of interest differs from those that do not.

The individual species analyses were conducted with PRESENCE 3.0 (beta) (MacKenzie et al. 2006), the procedure randomly removing species from data was done with MATLAB® (version R2008b), and other analyses were performed with SPSS 16.0 (SPSS, Chicago, IL, USA).

Results

We found a total of 24 dragonfly species (Table 1). The average observed number of dragonfly species per pond was 10.69 (SE ± 2.36) with a maximum of 15 and minimum of 7. WVPSD got strongest support explaining dragonfly species richness: it had a strong positive effect and appeared in the models ranked best (Fig. 1; Table 2a) even when controlling for the number of individuals and sampling effort (Table 2b, c). Thus, WVPSD increased both species richness and species density. By contrast, H^+ had a strong negative effect: ponds with low pH had lower species richness than ponds with relatively high pH (Fig. 2; Table 2a, b). In contrast, H^+ had relatively little effect on species density (Table 2c). Nutrient availability had a
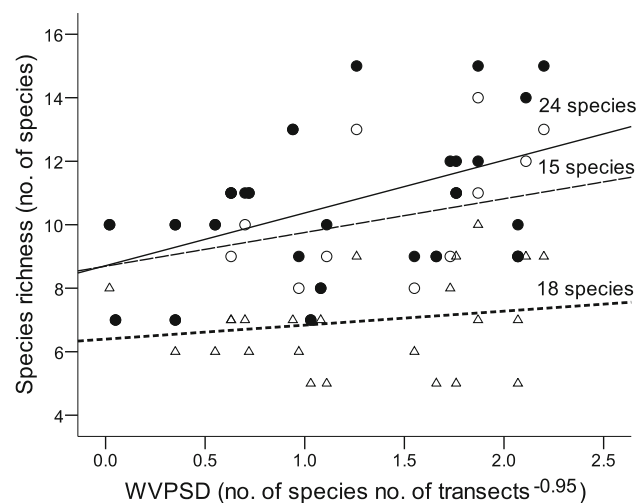
Fig. 1 Relationship between water vascular plant species density (*WVPSD*) and dragonfly species richness when total number of dragonfly species included is 24 (*filled circles, solid line*), 15 (9 rarest species removed; *open circles, dashed line*) and 18 (6 species with strongest relationship with WVPSD removed; *open triangles, dotted line*), n = 26. For 24 species: species richness = (1.66 × *WVPSD*) + 8.71; r^2 = 0.23; for 15 species: species richness = (0.44 × *WVPSD*) + 6.40; r^2 = 0.13; for 18 species: species richness = (1.66 × *WVPSD*) + 8.71; r^2 = 0.043

negative effect on species richness but not on species density whilst peat seemed to affect species density but not richness. However, the effects of nutrient availability and peat were relatively weak as shown by 95% confidence intervals of the parameters encompassing zero. Shoreline length and intensity of forestry got only weak support in explaining species richness or density (Table 2a–c) and intensity of forestry did not correlate with WVPSD or nutrients (Table 3). However, shoreline length, peat and H^+ were correlated: small ponds tended to have more peat cover on the shoreline and lower pH (Table 3).

For a number of species, there was not a single best site-occupancy model and all AIC_c (or $QAIC_c$) values lay within seven units indicating that these models had considerable less support than the top models but they could not be totally ruled out (Online Resource 1). For four species, the model likelihood for constant occupancy model was larger than 0.9, suggesting that these species did not respond to any of the explanatory variables (shoreline length, WVPSD, nutrients, forestry, peat, H^+) (Tables 4 and 5). Two species showed their strongest response (i.e. the largest value of model-averaged parameter estimates) to shoreline, WVPSD and H^+ whereas both peat and intensity of forestry affected strongest only one species each (Table 4). None of the species showed their strongest response to nutrients (Table 4).

After removing six species with the strongest response to WVPSD, the relationship between WVPSD and species richness disappeared ($\Delta AIC_c = -0.17$; Fig 1). In contrast, the relationship did not change after random removal of any six species (mean $\Delta AIC_c = 4.65$, 95% Confidence Intervals = 0.69, 10.13) or six relatively common species (random mean $\Delta AIC_c = 4.06$, 95% CI = 0.16, 9.14). Same applied for species density: removal of five species with the strongest response to WVPSD cancelled the relationship with WVPSD ($\Delta AIC_c = -0.99$) whereas random removal of any five species (random mean $\Delta AIC_c = 5.98$, 95% CI = 1.24, 12.15) or five relatively common species (random mean $\Delta AIC_c = 6.98$, 95% CI = 0.34, 15.36) did not. In addition, the relationship between H^+ and species richness disappeared after removal of six species with strongest relationship with H^+ ($\Delta AIC_c = -1.57$; Fig. 2). This value did not lie between 95% confidence intervals for removal of randomly selected six species (random mean $\Delta AIC_c = 3.17$, 95% CI = -1.17, 8.13) or randomly selected six relatively common species (random mean $\Delta AIC_c = 2.93$, 95% CI = -1.07, 8.21).

The mean number of occupied ponds for the six species with the strongest response to WVPSD was 16.3 (SD = 5.4) whereas for the six other relatively common species it was 14.0 (SD = 7.4). For the six species with the strongest response to H^+ occupancy rate was 15.2

Table 2 Linear regression models for 26 ponds with (a) observed species richness (b) species richness (number of sampled individuals included in all models) and (c) species density (number of samples included in all models)

Model	R^2	AIC_c	Δ_i	w_i	K	First parameter			Second parameter		
						β	95% CI		β	95% CI	
(a) Observed species richness											
WVPSD	0.225	41.59	0.00	0.23	2	1.661	0.426	2.896			
WVPSD + H$^+$	0.281	42.21	0.62	0.17	3	1.140	−0.293	2.573	−0.922	−2.272	0.428
H$^+$	0.205	42.25	0.66	0.16	2	−1.493	−2.669	−0.317			
Nutrients + H$^+$	0.251	43.27	1.68	0.10	3	−1.470	−3.896	0.956	−1.458	−2.626	−0.290
Shoreline + H$^+$	0.231	43.95	2.36	0.07	3	0.001	−0.003	0.005	−1.325	−2.636	−0.014
WVPSD + peat	0.225	44.16	2.57	0.06	3	1.662	0.400	2.924	−0.065	−3.023	2.893
Peat + H$^+$	0.209	44.68	3.09	0.05	3	0.533	−2.476	3.542	−1.518	−2.725	−0.311
Forestry + H$^+$	0.205	44.82	3.23	0.05	3	0.001	−0.034	0.036	−1.500	−2.731	−0.269
Shoreline	0.117	44.97	3.38	0.04	2	0.003	0.001	0.005			
Shoreline + peat	0.187	45.39	3.80	0.03	3	0.004	0.000	0.008	2.704	−1.061	6.469
Nutrients	0.056	46.71	5.12	0.02	2	−1.619	−4.283	1.045			
Forestry	0.008	48.00	6.41	0.01	2	−0.008	−0.045	0.029			
Peat	0.000	48.21	6.62	0.01	2	0.074	−3.213	3.361			
Nutrients + peat	0.056	49.28	7.69	0.00	3	−1.621	−4.341	1.099	0.110	−3.153	3.373
Forestry + peat	0.009	50.55	8.96	0.00	3	−0.009	−0.048	0.030	0.235	−3.181	3.651
(b) Species richness											
WVPSD	0.464	34.54	0.00	0.23	3	1.657	0.608	2.706			
WVPSD + H$^+$	0.506	35.27	0.73	0.16	4	1.209	−0.006	2.424	−0.794	−1.941	0.353
Nutrients + H$^+$	0.504	35.37	0.83	0.15	4	−2.005	−4.049	0.039	−1.344	−2.318	−0.370
H$^+$	0.420	36.60	2.06	0.08	3	−1.401	−2.430	−0.372			
WVPSD + peat	0.465	37.35	2.81	0.06	4	1.656	0.584	2.728	0.074	−2.441	2.589
Shoreline + H$^+$	0.430	38.97	4.43	0.02	4	0.001	−0.001	0.003	−1.245	−2.399	−0.091
Peat + H$^+$	0.426	39.14	4.60	0.02	4	0.638	−1.983	3.259	−1.431	−2.484	−0.378
Forestry + H$^+$	0.422	39.36	4.81	0.02	4	0.003	−0.028	0.034	−1.426	−2.502	−0.350
Nutrients	0.339	40.02	5.48	0.01	3	−2.171	−4.474	0.132			
Shoreline	0.314	40.96	6.42	0.01	3	0.002	0.000	0.004			
#	0.241	41.05	6.51	0.01	2						
Shoreline + peat	0.369	41.60	7.06	0.01	4	0.003	−0.001	0.007	2.402	−0.997	5.801
Nutrients + peat	0.340	42.79	8.25	0.00	4	−2.177	−4.531	0.177	0.274	−2.517	3.065
Forestry	0.244	43.51	8.97	0.00	3	−0.005	−0.038	0.028			
Peat	0.241	43.60	9.05	0.00	3	0.213	−2.713	3.139			
Forestry + peat	0.245	46.27	11.73	0.00	4	−0.006	−0.041	0.029	0.323	−2.725	3.371
(c) Species density											
WVPSD + peat	0.453	37.90	0.00	0.23	4	1.926	0.828	3.024	2.766	−0.370	5.898
WVPSD	0.379	38.41	0.51	0.18	3	1.866	0.725	3.007			
WVPSD + H$^+$	0.379	41.21	3.31	0.04	4	1.826	0.283	3.369	−0.060	−1.630	1.509
H$^+$	0.227	44.10	6.20	0.01	3	−1.277	−2.575	0.021			
Nutrients + H$^+$	0.283	44.93	7.03	0.01	4	−1.651	−4.105	0.803	1.187	−0.100	2.471
#	0.101	45.43	7.53	0.01	2						
Peat + H$^+$	0.261	45.71	7.81	0.00	4	1.914	−1.763	5.591	−1.171	−2.482	0.140
Nutrients	0.176	45.74	7.84	0.00	3	−1.889	−4.447	0.669			
Nutrients + peat	0.249	46.15	8.25	0.00	4	−2.083	−4.594	0.428	2.740	−0.943	6.423
Peat	0.159	46.29	8.39	0.00	3	2.423	−1.368	6.214			
Shoreline + H$^+$	0.243	46.34	8.44	0.00	4	0.009	−0.016	0.034	−1.130	−2.504	0.244
Shoreline	0.154	46.43	8.53	0.00	3	0.015	−0.010	0.040			

Table 2 continued

Model	R^2	AIC_c	Δ_i	w_i	K	First parameter			Second parameter		
						β	95% CI		β	95% CI	
Shoreline + peat	0.233	46.68	8.78	0.00	4	0.019	−0.006	0.044	2.890	−0.863	6.643
Forestry + H^+	0.227	46.90	9.00	0.00	4	0.002	−0.033	0.037	−1.289	−2.637	0.059
Forestry	0.103	47.94	10.04	0.00	3	−0.004	−0.041	0.033			
Forestry + peat	0.166	48.87	10.97	0.00	4	−0.008	−0.045	0.029	2.561	−1.347	6.469

For every model, explanatory variable(s) are included (# indicates that only the number of sampled individuals/samples is included), R^2 (percent of variance explained by the model), AIC_c values, Δ_i (deviation of AIC_c values between model i and the model with the smallest AIC_c), K (number of parameters), β and 95% confidence intervals for the variable(s) included are presented
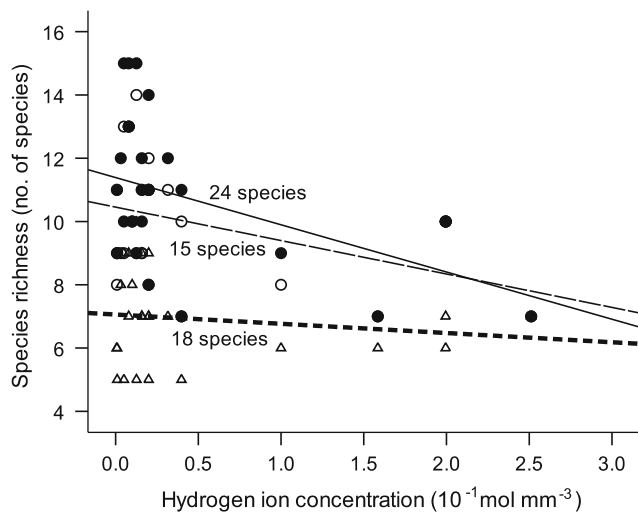
Fig. 2 Relationship between hydrogen ion concentration (H^+) and dragonfly species richness when total number of dragonfly species included is 24 (*filled circles, solid line*), 15 (9 rarest species removed; *open circles, dashed line*) and 18 (6 species with strongest relationship with H^+ removed; *open triangles, dotted line*), $n = 26$. For 24 species: species richness = $(−1.49 \times H^+) + 11.39$; $r^2 = 0.21$; for 15 species: species richness = $(−1.057 \times H^+) + 10.46$; $r^2 = 0.38$; for 18 species: species richness = $(−0.29 \times H^+) + 7.059$; $r^2 = 0.15$

Table 3 Spearman rank correlations between the explanatory variables used in the study ($n = 26$)

	Nutrients	WVPSD	Forestry	Peat	H^+
Shoreline	−0.071	−0.096	−0.036	−0.665***	−0.730***
Nutrients		−0.162	0.001	−0.030	0.220
WVPSD			0.059	−0.010	−0.318
Forestry				0.229	−0.078
Peat					0.502**

** Statistical significance at 0.01 level

*** Statistical significance at 0.001 level

(SD = 4.4) and for the six other relatively common species, the mean was also 15.2 (SD = 8.3).

Removal of nine rarest species did not change the relationship between WVPSD and species richness (Fig. 1; $\Delta AIC_c = 2.39$, random mean $\Delta AIC_c = 3.56$, 95% CI = −0.98, 9.86), between WVPSD and species density ($\Delta AIC_c = 2.96$, random mean $\Delta AIC_c = 5.01$, 95% CI = −0.84, 13.20) or between H^+ and species richness (Fig. 2; $\Delta AIC_c = 2.19$, random mean $\Delta AIC_c = 1.99$, 95% CI = −2.37, 5.06).

Discussion

Our results showed that WVPSD and pH where the main drivers of dragonfly species richness whilst shoreline length, nutrients, intensity of forestry or the amount of *Sphagnum* peat cover did not have a strong effect. This supports the view that, despite of the overall importance of energy availability (Keil et al. 2008; Field et al. 2009), habitat heterogeneity can still have an effect on species richness (Tews et al. 2004) and even override the effect of area, as also observed by Báldi 2008. Removal of the six relatively common species with strongest response to WVPSD removed the relationship between WVPSD and species richness and density. We could not entirely remove all statistical artifacts (Šizling et al. 2009) because the occupancy rate of relatively common species affecting species richness pattern differed a bit. However, not all relatively common species had a strong relationship with WVPSD and random removal of six of these species did not affect the relationship between species richness and WVPSD. Thus, it seems that species responding strongly to WVPSD and representing only one-quarter of the total species pool largely determined the whole observed species richness pattern. The removal of the nine rarest species did not change the relationship between the WVPSD (or pH) and species richness indicating that these rare species did not have a major contribution to overall species richness patterns in this study system.

Increasing dragonfly species richness with increasing WVPSD is not surprising: the positive relationship between plant and dragonfly species is also evident at the continental

Table 4 Model-averaged parameter estimates and model likelihood for the constant occupancy model $\psi(.)$ for 12 individual species

	Shoreline	WVPSD	Forestry	Nutrients	Peat	H⁺	$\psi(.)$
L. sponsa	0.06	0.04	−0.01	0.00	0.14	−0.23	**1.00**
C. johanssoni	−0.12	−0.01	0.01	0.24	0.06	**16.28**	0.08
E. najas[a]	0.14	0.06	−0.02	−0.01	0.00	−0.06	**1.00**
E. cyathigerum[a]	−0.04	−0.08	0.01	−0.24	0.00	0.21	**0.92**
A. grandis[a]	**1.90**	0.19	−0.01	−0.17	0.04	−0.25	0.09
A. subarctica[a]	0.18	−0.28	0.73	0.70	0.03	**9.25**	0.04
C. aenea[a]	0.00	**1.59**	−0.03	0.02	−0.01	−0.01	0.27
S. metallica[a]	**1.23**	0.05	0.02	−0.08	−0.34	−0.04	0.03
L. quadrimaculata[a]	0.09	0.04	**−0.39**	−0.01	0.00	−0.26	0.60
L. albifrons	−0.01	0.00	−0.03	0.00	**1.88**	0.00	0.13
L. caudalis[a]	0.01	**0.31**	−0.01	0.00	0.01	−0.24	0.78
L. rubicunda	0.06	0.02	0.06	0.03	−0.01	−0.02	**1.00**

For every species, the variable with the strongest effect is shown in bold, except for species with $\psi(.)$ having substantial support (model likelihood > 0.90)

[a] Akaike weights for H⁺ and peat were divided by two since these variables occur in twice as many models as the other variables

scale in Europe (Keil et al. 2008). Our results further support the view that many dragonfly species find their favored plant composition at least somewhere in a pond when vascular plant species richness is high (Sahlén 1999). More generally, vegetation offers various functions for dragonflies, including complex larval habitat (e.g., protection from predators) as well as important substrates for oviposition and basking for adult dragonflies (Buchwald 1992). Thus, the relationship likely stems from the several life stages of dragonflies benefiting from plant diversity.

Water acidity was also an important factor for dragonfly species richness: there was a lower number of species in ponds with low pH even after controlling for the number of individuals. By contrast, species density (species richness after controlling for sampling effort) was not affected by pH. Thus, the fact that species richness was affected but species density was not indicates that there was higher density of individuals of the same species at low pH. Water acidity has also been previously found to be an important variable explaining dragonfly community composition (Johansson and Brodin 2003), the suggested reason being an indirect effect mediated through fish predators (Eriksson et al. 1980; Bendell and McNicol 1987). Indeed, presence of fish strongly determines relative abundances of species in dragonfly communities (McPeek 1990; Johansson et al. 2006) and may have a positive, but relatively small, effect on dragonfly species richness (Johansson et al. 2006). During the net sweeping, we caught fish in half the ponds but we suspect that most, if not all, ponds fostered fish populations. Winter anoxia, pH, lake isolation and area were shown by Öhman et al. (2006) to be the main factors indicating fish presence, but we also found fish in relatively acidic, small ponds. Thus, we conclude that it is unlikely

that our main results concerning dragonfly species richness were biased due to unknown fish presence. The presence of fish in ponds may also be a mechanism for the positive association between WVPSD and species richness, as increased diversity of plants likely provides protection against larval predation by fish.

Despite the fact that two species had a strong positive response to shoreline length, this effect was not evident in species richness analyses. Also, neither species richness, species density nor any of the individual species reacted clearly to nutrient availability. Although it has been shown that TP and TN tend to be limiting factors in freshwater systems (Elser et al. 2007), it may be that they do not adequately reflect the amount of energy available for dragonflies in small boreal ponds. Similarly, Johansson and Brodin (2003) did not find any effect of TP on dragonfly community composition. Earlier studies have shown that solar energy-related factors such as temperature (Samways and Steytler 1996; Heino 2002) and actual evapotranspiration (Keil et al. 2008) are important for dragonfly species occurrence and species richness. These results highlight the fundamental role of solar energy in controlling all activities in poikilothermic organisms (Corbet 2004). We did not analyze solar energy-related variables because the limited geographic extent of our study effectively removes variation in solar energy.

Although intensity of forestry did not have an effect on dragonfly species richness or density, one species (*Libellula quadrimaculata*) negatively responded to it. In Sweden, the species has not been found suffering from forestry measures (Sahlén 1999). The difference in the results may arise from the fact that Sahlén (1999) did not study intensity of forestry but rather the time since forestry. Thus,

Table 5 Site-occupancy models for 12 individual species

Species	Model	AIC_c	Δ_i	w_i	K	$-2 \log(L)$	First parameter β	SE	Second parameter Beta	SE
L. sponsa[a]	$\psi(.)$	99.83	0.00	0.28	4	89.93				
	$\psi(H^+)$	100.11	0.28	0.25	5	87.11	−0.919	0.610		
	$\psi(peat)$	100.89	1.06	0.17	5	87.89	0.822	0.638		
C. johanssoni[b]	$\psi(H^+)$	66.03	0.00	0.69	5	53.03	23.594	12.111		
E. najas[c]	$\psi(.)$	56.68	0.00	0.34	5	90.85				
	$\psi(shoreline)$	58.57	1.89	0.13	6	87.66	0.781	0.678		
E. cyathigerum	$\psi(H^+)$	78.85	0.00	0.22	6	62.43	0.883	0.536		
	$\psi(.)$	79.02	0.17	0.20	5	66.02				
	$\psi(nutrients + H^+)$	80.49	1.64	0.10	7	60.27	−1.678	1.946	1.243	1.084
	$\psi(WVPSD)$	80.52	1.67	0.10	6	64.10	−0.663	0.500		
A. grandis	$\psi(shoreline)$	133.51	0.00	0.23	6	117.09	2.138	1.425		
	$\psi(H^+)$	135.01	1.50	0.11	6	118.59	−0.939	0.497		
	$\psi(nutrients + H^+)$	135.06	1.55	0.11	7	114.84	−1.078	0.580	−1.246	0.631
	$\psi(WVPSD)$	135.11	1.60	0.11	6	118.69	1.253	0.769		
	$\psi(.)$	135.33	1.82	0.09	5	122.33				
A. subartica	$\psi(forestry + H^+)$	136.83	0.00	0.24	7	116.61	3.018	1.680	30.014	16.343
	$\psi(H^+)$	137.44	0.61	0.18	6	121.02	13.285	7.969		
	$\psi(nutrients + H^+)$	137.86	1.03	0.14	7	117.64	3.734	2.730	19.327	12.673
	$\psi(WVPSD + H^+)$	138.04	1.21	0.13	7	117.82	−1.932	1.274	22.018	11.853
C. aenea	$\psi(WVPSD)$	120.76	0.00	0.50	6	104.34	2.323	1.422		
S. metallica	$\psi(shoreline)$	114.18	0.00	0.50	6	97.76	1.808	0.711		
L. quadrimaculata	$\psi(forestry + H^+)$	125.47	0.00	0.20	7	105.25	−1.135	0.646	−1.112	0.600
	$\psi(H^+)$	125.61	0.14	0.18	6	109.19	−0.961	0.540		
	$\psi(forestry)$	125.85	0.38	0.16	6	109.43	−0.930	0.521		
	$\psi(.)$	126.50	1.03	0.12	5	113.50				
L. albifrons	$\psi(peat)$	69.30	0.00	0.77	6	52.88	2.439	1.553		
L. caudalis	$\psi(WVPSD)$	88.65	0.00	0.24	6	72.23	0.919	0.505		
	$\psi(H^+)$	89.12	0.47	0.19	6	72.70	−1.297	1.070		
	$\psi(.)$	89.15	0.50	0.19	5	76.15				
L. rubicunda[b]	$\psi(.)$	72.27	0.00	0.38	4	62.37				

Only models with substantial support (i.e., $\Delta_i < 2$) are presented. For every model explanatory variable(s) included [$\psi(.)$ indicates a model with constant probability of occupancy], AIC_c values, Δ_i (deviation of AIC_c values between model i and the model with the smallest AIC_c), K (number of parameters), $-2 \log(L)$ (-2 log-likelihood), β and standard error for first and second variables included. For all of the models detection probabilities are survey-specific

[a] Probability of finding exuviae in June fixed to 0

[b] Probability of finding exuviae in July fixed to 0

[c] $QAIC_c$ values with an over-dispersion factor 2.08 used and standard errors inflated with $\sqrt{2.08}$

although *L. quadrimaculata* is considered a generalist, occupying both agricultural areas and forest ponds (Sahlén 2006), it can still respond negatively to intense forestry. Additionally, two rare species (*Aeshna crenata*, *Epitheca bimaculata*) were found exclusively in ponds surrounded by pristine forest. In summary, we conclude that, even though clear-cutting of forests surrounding the ponds may negatively affect some species, it is not a main driver of species richness in these boreal ponds.

In conclusion, our results supported the view that habitat heterogeneity can drive both species richness and species density on relatively small spatial scales. We also showed that species richness patterns can arise from responses of relatively small number of species responding to the same environmental variable. Although these species were relatively common, as predicted by Gaston (2008), it seems that mere commonness does not result in a species having a strong impact on species richness pattern; also, a strong

response to the environmental variable is needed. Hence, the fact that species richness of common species tends to be more strongly correlated with some environmental variables than that of rare species (Gaston 2008) could be due to a few common species closely related to these variables. By contrast, rare species did not seem to contribute much to variation in species richness patterns. Thus, from a conservation perspective, selecting sites for protection based on their species richness does not necessarily provide a network of sites that would effectively cover the rare species that are often the ones in need of special conservation attention.

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