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Aquatic plant biodiversity at high latitudes: patterns of richness and rarity in Finnish freshwater macrophytes

Jani Heino1) and Heikki Toivonen2)

1) *Finnish Environment Institute, Research Programme for Biodiversity, P.O. Box 413, FI-90014 University of Oulu, Finland (e-mail: jani.heino@ymparisto.fi)*
2) *Finnish Environment Institute, Research Programme for Biodiversity, P.O. Box 140, FI-00251 Helsinki, Finland (e-mail: heikki.toivonen@ymparisto.fi)*

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We examined patterns, causes, and implications of freshwater macrophyte richness and rarity in Finland. The provincial richness of all macrophyte species and that of rare species showed strong declines with latitude, and this pattern did not vary between helophytes, hydrophytes, and shore plants. Aquatic mosses deviated from the patterns found for the other groups. Nationally rare species showed strong preferences for mesotrophic and eutrophic conditions, while nationally common species occurred more evenly across the whole gradient of trophic conditions. Although some species classified as rare in Finland were also rare in other regions in Europe, the majority of nationally rare species appeared to be inclined to eutrophic conditions and do well in the more southerly regions. By contrast, many species that are still common in Finland tended to be either endangered in or absent from regions further south in Europe. Such contrasting patterns of species' rarity among regions call for international evaluation in the conservation efforts for freshwater macrophyte biodiversity.

Introduction

The main goal of conservation is to preserve as much of the Earth's biodiversity as possible, with emphasis on those elements that are most critically threatened by anthropogenic activities (Angermeier and Schlosser 1995). This goal is not easy to achieve, because the definitions of what constitute the most valuable biotic elements and their degree of vulnerability may differ from one region to another. Furthermore, the lack of rigorous information on the distributions of species and consequent evaluation of conservation priorities makes it difficult to implement successful conservation programs in many regions. This is especially true for freshwater biodiversity, which is poorly understood in comparison to terrestrial biodiversity and at the same time severely threatened by invasive species, climatic change, land-use alterations, and degradation of ecosystem conditions (Sala *et al.* 2000). Thus, Abell (2002) presented pleas for the increase of conservation-oriented freshwater studies and for integrating conservation programs across terrestrial and freshwater realms. The present situation for freshwater biotas clearly calls for (i) the identification of general biodiversity patterns, (ii) assessment of the most critically threatened components, and (iii) comparison of these assessments between different regions and countries.

Macrophytes constitute a major component of freshwater biodiversity in terms of biomass, ecosystem functioning, and species richness (Hutchinson 1975, Wetzel 2001). This valuable component of biodiversity is severely endangered in many countries, for example, due to land-use changes and consequent increases in nutrient levels in freshwater ecosystems (Sand-Jensen *et al*. 2000 and references therein). These changes in local-scale biodiversity may have feedback effects on regional scale, and several species of macrophytes have indeed been classified as endangered or threatened in many countries (Ingelög *et al*. 1993, Korneck *et al*. 1996). However, changes due to anthropogenic activities may differ among countries (cf. Rintanen 1996 and Sand-Jensen *et al*. 2000), and increases in nutrient levels, for example, may have contrasting effects on macrophyte diversity in regions that differ naturally in the representation of different types (oligotrophic *vs*. eutrophic) of freshwater ecosystems. Therefore, macrophyte species that are rare in one region may be common in others, and vice versa, often due to the contrasting natural and altered states of freshwater ecosystems. Such differences between regions and countries in macrophyte rarity should be taken into consideration in international conservation planning, and a good example of this is the emerging concept of national responsibility species. In short, responsibility species are those that are common in a given country but generally rare or absent elsewhere. This is the reasoning that underpins the responsibility species concept that was used in the third Finnish Red List on plants and animals (Rassi *et al*. 2001). However, direct assessments of the regional distribution and overlap in the rarity and commonness of such responsibility species, as well as other macrophyte species, are not yet well developed.

In this study, we assessed general patterns, causes, and implications of freshwater macrophyte diversity and rarity in Finland. Firstly, we examined the species richness of all groups of macrophytes, as well as the species richness of hydrophytes, helophytes, shore plants, and aquatic mosses (definitions of these groups followed Hutchinson 1975), in relation to regional-scale ecological variables. Secondly, we were interested in determining the relationships between species rarity and trophic preference, and the implications of such associations for freshwater conservation at the national and international levels. Thirdly, we compared the degree of rarity and trophic preference of Finnish hydrophyte species with their status in a number of other regions in Europe. This comparison was conducted to assess the importance of the primarily oligotrophic freshwater ecosystems of Finland for the conservation of freshwater biodiversity in Europe, and to forecast possible changes in Finnish macrophyte biodiversity due to anticipated environmental changes related to land use changes and consequent eutrophication.

Material and methods

Study area, regional characteristics and macrophyte data

Finland is located from 20°E to 32°E and 60°N to 70°N, representing a major latitudinal gradient from hemiboreal ecoregion in the south to subarctic-alpine ecoregion in the north (*see* Heino *et al*. 2002). The region is characterised by the legacy of the last ice age and its post-glacial history in the past ca. 10 000 years. As a result of this legacy, various types of waterbodies are common in most parts of the country, especially in the large lake district in southeastern Finland. The inland waters of Finland have generally low calcium levels, are poor in nutrients, and vary widely in their humic content. Relatively few inland waters are naturally nutrient-rich, but many waterbodies have become eutrophic due to anthropogenic influences, especially in the agricultural regions of southern Finland (Hallanaro and Pylvänäinen 2002). Vegetation in Finnish freshwater bodies can be characterised by the following: (i) extensive beds of either isoetids and aquatic bryophytes that are inclined to oligotrophic conditions; (ii) *Phragmites australis*, *Equisetum fluviatile and Nuphar lutea* that are indifferent to trophic conditions; and (iii) *Typha latifolia* that prefers mesotrophic to eutrophic conditions (mainly in southern Finland).

Regional distribution patterns of Finnish hydrophyte and helophyte species were first summarised in the 1930s (Linkola 1933), with little summarising work done thereafter. We updated this older information, incorporating also shore plants and aquatic lake mosses in the analysis. Regional differences in the richness and rarity of the four life form groups (i.e. hydrophytes, helophytes, shore plants, aquatic mosses) were examined based on their distribution in the 20 biogeographical provinces of Finland. These provinces have been used as the basis of floristic and faunistic work in Finland for a very long time (Lahti *et al.* 1988, Hämet-Ahti *et al.* 1998). Although such atlas material is admittedly very coarse with respect to both spatial resolution (large-sized provinces covering the whole country) and species commonness–rarity classification (absent, rare, common) we considered the data to be robust enough for our present purposes to reveal general regional patterns.

The species included in this study were either aquatic vascular plants or aquatic mosses occurring in inland lakes, ponds, marshes, and major rivers. The macrophyte flora of Finland is rather diverse, with 72 hydrophyte species, 29 helophyte species, and 25 lake moss species that were defined as obligatory aquatic in this study. Furthermore, we included 54 species of shore plants that often occur in shallow water (HT, expert judgement). The occurrence data (i.e. absent, rare, common) and origin (i.e. indigenous, archaeophytes, neophytes) of vascular plants in each province were compiled from Hämet-Ahti *et al.* (1998) for vascular plants and Koponen *et al.* (1995) for aquatic mosses. However, because archaeophytes and neophytes are not well-represented in the Finnish macrophyte flora, and because they show as strong latitudinal diversity gradient as indigenous species, we only present the results for all species and separately for rare species in each macrophyte group. The species were considered either rare or common in Finland based on the categorisation given in Hämet-Ahti *et al.* (1998). Although a species could be regarded as rare, it does not necessarily have to be threatened or near-threatened in Finland. The characterisation of the trophic preferences of vascular plants mainly followed Toivonen and Huttunen (1995), with supplementary information taken from Ellenberg *et al.* (1991) and Hill *et al.* (1999). The trophic characterisation of species was as follows: o = oligotrophic, o-m = oligo-mesotrophic, m = mesotrophic, i = indifferent, m-e = meso-eutrophic, e = eutrophic.

We used mean provincial latitude and longitude, as well as the area extent of main land use and land cover types (i.e. province land area, surface water area, forests, fields, open land, built up areas, roads; derived via GIS) as explanatory variables for variation in the number of macrophyte species in the Finnish provinces. The land use and land cover data were derived from the land use and land cover classification of the National Land Survey of Finland. Two variables reflecting the intensity of anthropogenic influence were constructed from the original variables: Humarea (intensively human influenced area) is the sum of fields, built-up areas, and road areas (km^2), whereas the Humindex is the percentage proportion of the Humarea from the total area of a province. These latter variables, as well as the area extent of fields, were considered as proxy variables for the degree of anthropogenic eutrophication in the provinces. These measures are also largely proxies for favourable soils in Finland (Atlas of Finland 1990).

Finally, we compiled additional information on the Red List status of common and rare hydrophyte species in Finland, as well as in the more southerly regions of Europe. Hydrophytes were chosen as the exemplary group for this comparison, because (i) they show a wide range of trophic preferences and (ii) they are typically sensitive to anthropogenic changes (e.g. Sand-Jensen *et al.* 2000). The status of Finnish hydrophyte species in other northern and central European regions was derived from the Red Data Book of the Baltic Region (Ingelög *et al.* 1993) for Finland (1990), Sweden (1990), St. Petersburg district in Russia, Estonia, Latvia, Lithuania, and Poland, whereas Korneck *et al.* (1996) was consulted for the information for the regions in Germany, and http://www.sns.dk/netpub/rodliste/73.htm was used for Denmark. For Finland and Sweden, species status was also derived from recent Red Data Books that use the new IUCN categories (Rassi *et al.* 2001, Gärdenfors 2000). To our knowledge, such comprehensive categorisations are not available for the other regions surrounding the Baltic Sea. The Finnish responsibility species were based on the categorisation in Rassi *et al.* (2001).

Data analysis

We used regression analysis to examine the relationships between provincial species richness and mean provincial latitude and longitude, as well as the four regional-scale variables that describe surface water area, field area, and human land-use in each province. In addition, partial regression analyses were conducted to examine the relationships between provincial species richness and the four regional variables when latitude and longitude were controlled for. Regression and partial regression analyses were conducted separately for all macrophyte species together and rare species only. Similar analyses were conducted for the different life form groups of macrophytes (i.e. hydrophytes, helophytes, shore plants, aquatic mosses). No correction for province area was done, because preliminary analyses indicated that it was not significantly (and often negatively) correlated to all measures of species richness (Pearson correlation analyses: $P > 0.15$). Qualitatively similar results to the regression analyses of species richness were obtained by using ordination analyses on species composition data, with a very strong latitudinal gradient existing for both measures of provincial macrophyte assemblages. Chi-square test was used to examine the associations between commonness–rarity and trophic preference of species. Similar tests were also used to examine the relations between commonness–rarity and trophic preference within each life form group, as well as between commonness–rarity and life form groups. All analyses were conducted using SPSS ver. 11.5 (SPSS Inc. 2002).

Results

Species richness patterns were generally similar among all macrophyte groups, with the exception of aquatic mosses. In general, species richness declined strongly with latitude and increased with the indices of human land use (i.e. Fields, Humarea, Humindex) (Table 1 and Fig. 1). There were no significant relationships between species richness and surface water area or longitude. When geographical location (i.e. latitude, longitude) was controlled for in partial regression analyses, the correlation between species richness and human land-use decreased, suggesting that species richness was primarily determined by biogeographical factors rather than by the covarying patterns of land use. Significant relationships were only found between helophytes and Fields, as well as between helophytes and Humarea (Table 1). Mosses deviated from the patterns found for the other life form groups in that no variable was significantly related to their species richness, except Humarea in partial analysis.

Species richness patterns of rare macrophytes did not differ appreciably from those for all species. Species richness in all life form groups, with the exception of aquatic mosses, was strongly related to latitude, with a decrease of diversity with increasing latitude. Species richness was also positively related to human land-use (Table 2). In partial regression analyses, these latter variables were no longer significant. Mosses differed again from the other macrophyte groups in that their species richness was not significantly related to any of the measured variables. Partial regression analyses indicated, however, that the species richness of rare mosses was positively related to Humarea.

For the Finnish freshwater macrophyte flora, rarity and trophic preference were strongly related (Table 3). This relationship applied to all macrophytes, including the species in each of the three life forms of vascular macrophytes (Chi-square tests: all $P < 0.01$). As a general tendency, nationally rare species were strongly inclined towards meso-eutrophic and eutrophic conditions, whereas common species showed more even distribution among the trophic classes (Table 3). There were no differences in the degree of commonness and rarity between the three vascular plant groups (Chi-square test: $P = 0.357$).

A comparison of Red List status between the hydrophyte floras of Finland, Sweden and those of more southerly regions showed interesting patterns. Some species classified as rare or threatened in Finland tended to be either extinct, endangered, or vulnerable in other European regions (Table 4). Amongst the most threatened ones were *Najas tenuissima*, *N. flexilis* and *Crassula aquatica*, the first two of which

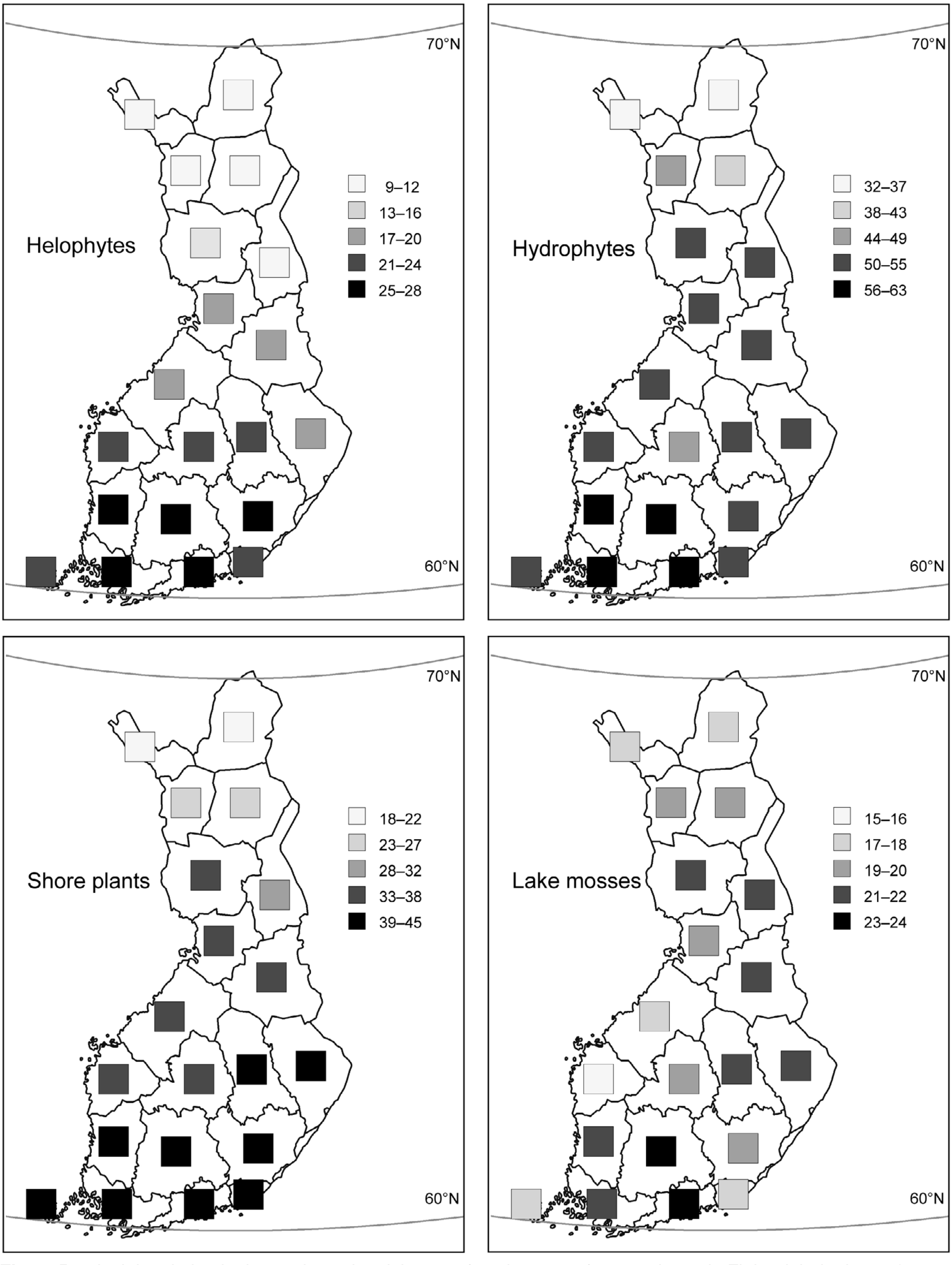

Fig. 1. Provincial variation in the total species richness of each group of macrophytes in Finland: helophytes (*n* = 29 species in Finland), hydrophytes (*n* = 72), shore plants (*n* = 54), and lake mosses (*n* = 25). For macrophyte names and species lists of the provinces of Finland, *see* Hämet-Ahti *et al*. (1998) and Koponen *et al*. (1995).

are severely endangered in Finland. They are also included in the Annex II of the EU Habitats directive. Furthermore, several rare species, though not threatened in Finland (e.g. *Nymphaea tetragona*, *Myriophyllum sibiricum*, *Ranunculus confervoides*, *Utricularia stygia*, *U. ochroleuca*), are either absent from or severely threatened in the regions further south, implying that these species belong to the most valuable part of the Finnish hydrophyte flora from the European perspective. These rare species showed preferences towards oligotrophic to mesotrophic conditions, and they represent the northern floral element in Europe. Furthermore, some widely-distributed species considered rare everywhere across their ranges (e.g. *Pilularia globulifera*, *Potamogeton polygonifolius, P. rutilus*) are also valuable from the viewpoint of conservation. The remaining two thirds of rare hydrophyte species represent mostly the southern floral element in Finland, and these species generally do well in eutrophic waters in more southerly regions (Table 4).

Perhaps more importantly, many hydrophyte species that are common in Finland tended to be included in the Red Lists of other European regions (Table 5). These species included the northern *Elatine orthosperma* and *Sparganium hyperboreum* that are absent from the regions further south from Finland and Sweden (the former species extinct in the St. Petersburg region). The group of common hydrophytes in Finland also included several Finnish responsibility species

Table 1. Results of regression analyses and partial regression analyses (latitude and longitude controlled for) for the relationships between total macrophyte species richness and provincial-scale variables. Significant relationships are set in boldface.

Variable		Normal			Partial		
Dependent	Independent	r	R^2	P	r	R^2	P
All species	Latitude	**–0.897**	**0.804**	< **0.001**			
	Longitude	–0.127	0.016	0.593			
	Water	0.173	0.030	0.466	–0.051	0.002	0.840
	Fields	**0.673**	**0.452**	**0.001**	0.353	0.124	0.151
	Humarea	**0.698**	**0.487**	**0.001**	0.380	0.144	0.119
	Humindex	**0.763**	**0.582**	< **0.001**	0.138	0.019	0.586
Helophytes	Latitude	**–0.933**	**0.870**	< **0.001**			
	Longitude	–0.285	0.081	0.224			
	Water	0.155	0.024	0.514	0.178	0.031	0.480
	Fields	**0.735**	**0.540**	< **0.001**	**0.530**	**0.281**	**0.024**
	Humarea	**0.758**	**0.575**	< **0.001**	**0.665**	**0.442**	**0.003**
	Humindex	**0.842**	**0.701**	< **0.001**	0.219	0.047	0.383
Hydrophytes	Latitude	**–0.792**	**0.627**	< **0.001**			
	Longitude	–0.112	0.013	0.639			
	Water	0.091	0.008	0.702	–0.161	0.098	0.523
	Fields	**0.659**	**0.434**	**0.001**	0.358	0.128	0.145
	Humarea	**0.676**	**0.457**	**0.001**	0.367	0.135	0.135
	Humindex	**0.697**	**0.486**	< **0.001**	0.173	0.030	0.492
Shore plants	Latitude	**–0.927**	**0.859**	< **0.001**			
	Longitude	–0.076	0.006	0.751			
	Water	0.165	0.027	0.487	–0.261	0.068	0.295
	Fields	**0.582**	**0.338**	**0.007**	0.029	0.001	0.909
	Humarea	**0.604**	**0.365**	**0.005**	0.042	0.001	0.868
	Humindex	**0.750**	**0.563**	< **0.001**	0.016	0.000	0.950
Aquatic mosses	Latitude	–0.307	0.094	0.188			
	Longitude	0.174	0.030	0.462			
	Water	0.386	0.149	0.092	0.257	0.066	0.303
	Fields	0.280	0.078	0.232	0.137	0.019	0.587
	Humarea	0.321	0.105	0.167	**0.549**	**0.301**	**0.018**
	Humindex	0.177	0.031	0.455	–0.043	0.002	0.865

Table 2. Results of regression analyses and partial regression analyses (latitude and longitude controlled for) for the relationships between rare macrophyte species richness and the provincial-scale variables. Significant relationships are set in boldface.

Variable		Normal			Partial		
Dependent	Independent	*r*	R^2	*P*	*r*	R^2	*P*
All rare species	Latitude	–**0.830**	**0.689**	< **0.001**			
	Longitude	–0.285	0.081	0.223			
	Water	0.035	0.001	0.884	–0.086	0.007	0.736
	Fields	**0.574**	**0.329**	**0.008**	0.119	0.014	0.639
	Humarea	**0.607**	**0.368**	**0.005**	0.158	0.025	0.530
	Humindex	**0.799**	**0.638**	< **0.001**	0.291	0.085	0.241
Helophytes	Latitude	–**0.818**	**0.669**	< **0.001**			
	Longitude	–0.398	0.158	0.082			
	Water	0.099	0.010	0.677	0.227	0.052	0.366
	Fields	**0.625**	**0.391**	**0.003**	0.247	0.061	0.324
	Humarea	**0.655**	**0.429**	**0.002**	0.285	0.081	0.252
	Humindex	**0.813**	**0.661**	< **0.001**	0.270	0.073	0.279
Hydrophytes	Latitude	–**0.722**	**0.521**	< **0.001**			
	Longitude	–0.334	0.112	0.150			
	Water	–0.092	0.008	0.700	–0.189	0.036	0.452
	Fields	**0.528**	**0.279**	**0.017**	0.131	0.017	0.604
	Humarea	**0.549**	**0.301**	**0.012**	0.148	0.022	0.559
	Humindex	**0.721**	**0.520**	< **0.001**	0.219	0.048	0.382
Shore plants	Latitude	–**0.876**	**0.767**	< **0.001**			
	Longitude	–0.165	0.027	0.487			
	Water	0.024	0.001	0.919	–0.361	0.130	0.141
	Fields	0.424	0.180	0.062	–0.332	0.110	0.178
	Humarea	**0.458**	**0.266**	**0.042**	–0.296	0.088	0.233
	Humindex	**0.803**	**0.645**	< **0.001**	0.346	0.120	0.159
Aquatic mosses	Latitude	–0.428	0.205	0.060			
	Longitude	0.130	0.017	0.585			
	Water	0.348	0.121	0.133	0.202	0.041	0.420
	Fields	0.345	0.119	0.137	0.128	0.016	0.612
	Humarea	0.386	0.149	0.093	**0.539**	**0.291**	**0.021**
	Humindex	0.305	0.093	0.191	0.011	0.000	0.965

Table 3. Preferences for different trophic states by common (C) and rare (R) vascular macrophyte species. The three life form groups (i.e. helophytes, hydrophytes, and shore plants) are also shown separately. There were significant relationships between rare and common species and their preferences for trophic states in all life form groups (Chi-square tests: $P < 0.01$). C = common, R = rare.

	Helophytes		Hydrophytes		Shore plants		All vasculars	
Trophic state	C	R	C	R	C	R	C	R
Oligotrophic	0	0	6	1	0	0	6	1
Oligo-mesotrophic	1	0	8	6	4	1	13	7
Mesotrophic	1	0	8	2	13	3	22	5
Indifferent	8	0	7	1	4	0	19	1
Meso-eutrophic	6	1	5	6	8	5	19	12
Eutrophic	2	10	3	19	4	12	9	41
Total	18	11	37	35	33	21	88	67

Table 4. Rare hydrophyte species in Finland, and their Red List status in other regions in northern and central Europe. Finnish responsibility species are in bold, and species included in the Annex II of the EU Habitats Directive are indicated with asterisks (*). Abbreviations: FIN20 = Finnish red data list 2000; FIN90 = Finnish red data list 1990; SWE20 = Swedish red data list 2000; SWE90 = Swedish red data list 1990; LEN = St. Petersburg district in Russia; EST = Estonia; LAT = Latvia; LIT = Lithuania; POL = Poland; DEN = Denmark; GER = whole Germany; GMEC = Mecklenburg-Vorpommern in Germany; GSCH = Schleswig-Holstein in Germany; GBAY = Bayern in Germany. Threat categories for FIN20 and SWE20: CR = critically endangered; EN = endangered; VU = vulnerable; NT = near-threatened; LC = of least concern or not threatened. Status categories for FIN90, SWE90 and other regions: 0 = extinct, 1 = endangered; 2 = vulnerable; 3 = care demanding; LC = not threatened, ? = indeterminate. Trophic codes are given in Material and methods. Nomenclature follows Hämet-Ahti *et al.* (1998).

Species	Trophic	FIN20	FIN90	SWE20	SWE90	LEN	EST	LAT	LIT	POL	DEN	GER	GMEC	GSCH	GBAY
Crassula aquatica	**m**	**NT**	**LC**	**NT**	**LC**	**2**	**0**	**0**		**0**	**1**	**0**		**0**	
Najas tenuissima*	**m-e**	**EN**	**2**			**1**									
*Najas felixilis**	m-e	EN	1	CR	1	1	1	1		2	1	1			
Nymphaea tetragona	o-m	LC	LC			2									
Myriophyllum sibiricum	e	LC	LC	LC	LC										
Pilularia globulifera	o-m	VU	3	VU	3					1	2	3	0	1	1
Utricularia stygia	o-m	LC	LC	LC	LC			LC			0	2			2
Utricularia ochroleuca	o-m	LC	LC	LC	LC			1		2	2	2			2
Ranunculus confervoides	m-e	LC	LC	LC	LC	3	?	?	-	-	-	3	-	-	3
Potamogeton polygonifolius	o	NT	3	LC	LC					2	LC	3	1	2	1
Littorella uniflora	o-m	LC	LC	LC	LC	1	1	2		3	LC	2	1	2	1
Ranunculus peltatus subsp. *baudotii*	e	LC	LC	LC	LC	3	LC	2	-	?	LC	LC	LC	3	-
Najas marina	e	LC	LC	LC	LC	2	3	2	2	LC	1	2 or 3	2	1	2
Potamogeton rutilus	e	NT	3	EN	3	LC	LC	3	LC	LC	1	1	0	1	1
Potamogeton friesii	e	NT	3	VU	LC	LC	LC	LC	LC	LC	LC	2	2	2	3
Callitriche hamulata	o-m	LC	LC	LC	LC					LC	LC	LC	1	3	LC
Utricularia australis	i	LC	LC	LC	LC			LC		LC	LC	3	1	2	3
Ceratophyllum submersum	e			NT	3		LC	2	3	LC	LC	LC	LC	LC	LC
Callitriche hermaphroditica	e	LC	LC	LC	LC	LC	LC	2	LC	LC	LC	G	1	2	0
Ranunculus aquatilis var. *aquatilis*	e	?	1	LC	LC	3	LC	LC	LC	LC	LC	LC	2	LC	3
Zannichellia palustris	e	LC	LC	LC	LC	3	LC	3		LC	LC	LC	LC	LC	LC
Limosella aquatica	m-e	LC	LC	LC	LC	LC	LC	LC	LC	LC	2	LC	3	2	3
Potamogeton compressus	e	LC	LC	VU	LC	LC	LC	LC	LC	LC	LC	2	2	2	3
Potamogeton filiformis	e	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC	2	1	1	2
Potamogeton praelongus	m-e	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC	2	1	2	2
Potamogeton pusillus	e	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC	3	3	3
Stratiotes aloides	e	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC	3	2	3	2
Ranunculus aquatilis var. *diffusus*	m-e	LC	2	LC	LC	LC	LC	LC	LC	LC	LC	LC	2	LC	LC
Elodea canadense	m-e	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC
Lemna gibba	e	LC	LC	LC	LC	3	LC	LC	LC	LC	LC	LC	LC	LC	LC
Lemna trisulca	e	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC
Potamogeton crispus	e	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC
Potamogeton lucens	e	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC	3	LC
Potamogeton pectinatus	e	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC
Ranunculus circinatus	e	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC
Spirodela polyrrhiza	e	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC

that are in severe decline in other European regions, with Sweden being an exception (Table 5, species in bold). Finland and Sweden are thus important havens for these nationally common, yet internationally rare and threatened species that show clear affinities to low-nutrient conditions typical of boreal freshwater ecosystems. Good examples are isoetid species (e.g. *Lobelia dortmanna*, *Isoëtes echinospora*, *I. lacustris* and *Subularia aquatica*). These species comprise a characteristic component of the natural habitats types 3110 and 3160 of the EU Habitats Directive (Council Directive 92/43/EEC).

Discussion

The species richness of both all macrophytes and that of rare species was strongly related to latitude and the three variables describing land-use in the biogeographical provinces of Finland. In partial regression analyses where geographical location was controlled for, the influence of these land-use variables declined, and significant relationships were found only between helophyte and moss richness and the extent of human land-use. Species' degree of rarity showed strong associations with their trophic preference, with nationally rare species being inclined towards eutrophic conditions, whereas common species occurred more evenly across the whole range of trophic conditions. These patterns remained generally the same irrespective of a life form group. In the following, we will discuss these findings in relation to biogeographic constraints, local limiting factors, and anthropogenic influences.

The relatively high numbers of aquatic macrophytes in temperate regions has long been recognised (Hutchinson 1975), and it has been suggested that the diversity of freshwater macrophytes deviates from the general pattern of decreasing diversity towards poles (Crow 1993, *see* also Willig *et al*. 2003). Such patterns may well occur in studies where geographic extent ranges from the tropics to the poles, but different patterns are likely to be found when studies are conducted within the boreal region only. In all regression analyses, latitude was the most consistent and strongest correlate of macrophyte species richness, mirroring the marked decrease of species richness with increasing latitude. In this context, latitude was likely a proxy for climatic and historical factors that are known to be strongly related to the regional diversity patterns of freshwater organisms (Heino 2001, 2002) and other biota across the study area (Lahti *et al*. 1988, Pedersen 1990, Väisänen and Heliövaara 1994).

However, the relative importance of these factors is difficult to judge. If one assumes that the dispersal of macrophytes after the last ice age has been rapid and that most species have attained their distributional limits to correspond to present-day conditions, then diversity patterns would be primarily under environmental control. This reasoning is supported by the findings that latitudinal patterns in diversity are often related to parallel variation in regional environmental productivity and climatic severity (Currie 1991, Wright *et al*. 1993). Undoubtedly, both are important in determining the distribution patterns of freshwater macrophytes, as was already suggested by Linkola (1933). Furthermore, although not directly separated from environmental productivity, the length of growing season and the duration of ice cover may severely limit the distribution of macrophytes in boreal regions. Circumstantial evidence for this was seen in the rapid decline of species richness in the four northernmost provinces in the study area, where harsh winter conditions are likely to severely limit macrophyte growth and distributions, despite the fact that the aquatic medium may to some extent balance the effects of harsh climate. Helophytes that occur in the littoral zones of lakes are especially sensitive to the effects of harsh winter conditions, during which factors such as ice erosion and freezing of benthic sediments in the littoral zone may destroy whole macrophyte beds (e.g. Hellsten 2001). Large-sized isoetids may also be sensitive to ice erosion (e.g. Rørslett 1984), and such sensitivity in one important group may also be reflected in overall latitudinal gradients of macrophyte diversity. However, we stress that the strength of the latitudinal diversity gradients may be affected to some degree by grain size, i.e., depending upon whether the species richness values are based on data for single lakes across which local abiotic factors can vary widely (e.g. Rørslett 1991) or on

Table 5. Common hydrophyte species in Finland, and their Red List status in other regions in northern and central Europe. Finnish responsibility species are in bold. Abbreviations: FIN20 = Finnish red data list 2000; FIN90 = Finnish red data list 1990; SWE20 = Swedish red data list 2000; SWE90 = Swedish red data list 1990; LEN = St. Petersburg district in Russia; EST = Estonia; LAT = Latvia; LIT = Lithuania; POL = Poland; DEN = Denmark; GER = whole Germany; GMEC = Mecklenburg-Vorpommern in Germany; GSCH = Schleswig-Holstein in Germany; GBAY = Bayern in Germany. Threat categories for FIN20 and SWE20: CR = critically endangered; EN = endangered; VU = vulnerable; NT = near threatened; LC = of least concern or not threatened. Status categories for FIN90, SWE90 and other regions: 0 = extinct, 1 = endangered; 2 = vulnerable; 3 = rare and care demanding; LC = not threatened, ? = indeterminate. Trophic codes are given in Material and Methods. Nomenclature follows Hämet-Ahti *et al.* (1998).

Species	Trophic	FIN20	FIN90	SWE20	SWE90	LEN	EST	LAT	LIT	POL	DEN	GER	GMEC	GSCH	GBAY
Sparganium hyperboreum	**o**	**LC**	**LC**	**LC**	**LC**										
Sagittaria natans	**m-e**	**LC**	**LC**	**LC**	**LC**	**3**									
Elatine triandra	**m**	**LC**	**LC**	**LC**	**LC**	**3**				**1**		**3**			**2**
Isoëtes echinospora	**o**	**LC**	**LC**	**LC**	**LC**	**3**	**1**	**1**		**1**	**2**	**2**		**0**	
Subularia aquatica	**o**	**LC**	**LC**	**LC**	**LC**	**3**	**1**	**2**			**1**	**0**		**0**	**0**
Isoëtes lacustris	**o**	**LC**	**LC**	**LC**	**LC**	**3**	**2**	**2**	**1**	**2**	**2**	**2**	**0**	**1**	**0**
Lobelia dortmanna	**o**	**LC**	**LC**	**LC**	**LC**	**3**	**2**	**2**	**1**	**2**	**LC**	**1**	**0**	**1**	
Sparganium gramineum	m	LC	LC	LC	LC	LC	LC	2							
Elatine orthosperma	m	LC	LC	VU	3	0									
Nymphaea alba subsp. *candida*	i	LC	LC	LC	LC	LC	LC	3	LC	LC		2			1
Nuphar pumila	o-m	LC	LC	LC	LC	LC	2	3	2	LC	3	1	1		1
Elatine hydropiper	m	LC	LC	LC	LC	LC	3	1	3	LC	2	3	1	2	2
Sparganium angustifolium	o	LC	LC	LC	LC	LC	LC	2	LC	2	LC	2		1	1
Myriophyllum alterniflorum	o-m	LC	LC	LC	LC	3	1	2	1	LC	LC	2	2	1	1
Juncus supinus	o-m	LC	LC	LC	LC	3	3	LC	LC	LC	LC	LC	2	LC	LC
Potamogeton gramineus	m	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC	2	2	1	2
Ranunculus peltatus subsp. *peltatus*	m	LC	LC	LC	LC	LC	3	2		LC	LC	LC	3	LC	LC
Utricularia minor	o-m	LC	LC	LC	LC	3	LC	LC	LC	LC	LC	2	2	2	3
Ranunculus reptans	o-m	LC	LC	LC	LC	LC	LC	LC	LC	2	2	1	1	1	1
Eleocharis acicularis	o-m	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC	3	2	3	LC
Hydrocharis morsus-ranae	e	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC	3	3	LC	2
Myriophyllum verticillatum	e	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC	2	3	LC
Sparganium natans	o-m	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC	2	2	2	3
Utricularia intermedia	o-m	LC	LC	LC	LC	3	LC	LC	LC	LC	LC	2	2	0	3
Utricularia vulgaris	i	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC	3	3	3	LC
Potamogeton alpinus	i	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC	3	2	2	3
Potamogeton obtusifolius	m-e	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC	3	2	2	3
Potamogeton berchtoldii	m-e	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC	3	3	3
Nymphaea alba subsp. *alba*	i	LC	LC	LC	LC	3	LC	3	2	LC	LC	LC	LC	LC	3
Callitriche cophocarpa	m	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC
Callitriche palustris	m	LC	LC	LC	LC	LC	LC	LC	LC	LC	1	LC	LC	3	LC
Ceratophyllum demersum	e	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC
Lemna minor	m-e	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC
Potamogeton perfoliatus	m	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC	3
Nuphar lutea	i	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC
Persicaria amphibia	m-e	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC
Potamogeton natans	i	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC

regional counts of species (e.g. Heino 2002).

A pattern deviating from the clear decline of species richness with latitude was shown by aquatic lake mosses. In contrast to other macrophytes, many species of mosses may not prefer such meso-eutorphic and eutrophic conditions as are required by the majority of helophytes, hydrophytes, and shore plants. Rather, many aquatic mosses may be inclined towards oligotrophic and often humic conditions (e.g. Rintanen 1996), which is also suggested by the moderate diversity of mosses in primarily oligotrophic waters of headwater streams in boreal regions (e.g. Heino *et al*. 2005). Although not much is known about the ecological requirements of aquatic bryophytes, it is also possible that phytoplankton and common hydrophytes, for example, are superior competitors to mosses in more eutrophic conditions (Hutchinson 1975, Syrjänen and Toivonen 2000), thereby limiting their occurrence in some southern eutrophic freshwater ecosystems in the study area. Although this reasoning remains speculative, it may provide a reasonable working hypothesis for assessing the effects of anthropogenic eutrophication on freshwater bryophyte versus hydrophyte diversity at the local ecosystem level. Findings from within-region analyses of multiple lakes indeed suggest that most moss species along with several species of isoetids and characeans may be vulnerable to the direct and indirect effects of eutrophication (Blindow 1992, Karttunen and Toivonen 1995, Syrjänen and Toivonen 2000, Sand-Jensen *et al*. 2000).

Provincial surface-water area was not significantly related to macrophyte species richness. This result may seem counterintuitive, as species richness should increase with habitat area (e.g. Rosenzweig 1995). However, it is likely that factors other than area *per se* are important in determining macrophyte diversity at the regional scale. Firstly, total surface water area may not be the primary factor determining macrophyte species richness, but the amount of available littoral habitat may be more important. Thus, a set of small, shallow lakes is likely to be more important for macrophytes than a single large and deep lake. Secondly, most of the lakes in Finland are oligotrophic, whereas more nutrient-rich lakes that generally harbour a high local diversity of macrophytes are more scattered in their occurrence. Thus, it appears that regions containing a large number of mesotrophic and eutrophic lakes, and perhaps also a high variability of lake types that vary in nutrient levels and other factors (e.g. Heegard 2004), are likely to have the greatest species diversity at the regional level. However, it has to be stressed that this reasoning applies only to regions located at approximately similar latitude, as biogeographical constraints clearly set the strongest filter for species distributions and regional species pools (Tonn 1990, Heino 2001). Nevertheless, there is a strong potential for feedback effects of local species richness and species turnover on regional diversity, which may also be related to anthropogenic land use patterns.

Land use in terms of agricultural areas and human disturbance was strongly related to the species richness of macrophytes. Although one could easily envisage that such relationships are negative, with increasing anthropogenic stress leading to a loss of biodiversity, we found positive relationships between macrophyte diversity and anthropogenic disturbance. This finding is by no means unexpected, because rich macrophyte floras typically occur and actually did occur prior to human interference in those areas that are also the most suitable, both climatically and edaphically, for human settlements and agriculture (*see* also Araujo 2003). Although the relationship between anthropogenic influences and macrophyte diversity was mainly driven by the strong latitudinal gradient, as well as the tendency of anthropogenic influences to be more extensive in southern Finland, this finding may also have important implications for our understanding of the regional dynamics of macrophyte diversity in boreal regions. Firstly, given that many nationally rare species show a clear affinity to eutrophic conditions typical of intensively altered landscapes, some degree of eutrophication of naturally oligotrophic freshwater ecosystems may actually be beneficial for macrophyte diversity in boreal regions (Rintanen 1996, Toivonen and Huttunen 1995). As macrophyte species richness at the local scale of lakes generally increases from oligotrophic to slightly eutrophic conditions (Rørslett 1991, Toivonen and Huttunen 1995), such effects are also likely to have feedback effects on regional diversity.

However, more importantly, as some species are clearly inclined to oligotrophic conditions, lakes located along a widely varying gradient of nutrient levels are likely to yield most species regionally.

Although slight eutrophication is likely to increase diversity at both local and regional scales, as well as increase the availability of suitable habitats for some species classified as rare in Finland (Toivonen 1985), we by no means advocate the increasing trend of freshwater eutrophication. Rather, we advocate the contrary on two grounds. Firstly, although eutrophication is likely to lead to increased diversity in the beginning of the process, hypereutrophic conditions are known for decreased macrophyte diversity. This is a situation common for lakes in more southerly regions of Europe (Arts *et al.* 1990, Klein 1993, Sand-Jensen *et al.* 2000). Secondly, oligotrophic freshwater ecosystems common in Finland are less numerous in more southerly regions, as evidenced by a considerable number of species that are rare or threatened in these regions, but still common in Finland. Thus, from the international point of view, many species showing preference for eutrophic conditions are, although rare in Finland, internationally under no threat. By contrast, many Finnish responsibility species and other species showing preference for oligotrophic conditions clearly qualify as the most important component of the Finnish macrophyte flora in terms of the conservation of biodiversity in Europe.

Changes in freshwater macrophyte diversity at local scales may not only feed back to regional diversity, but may also have effects on other organisms associated with suitable macrophyte beds or even single macrophyte species. Macrophytes are important for other organisms, for example, by providing habitat for invertebrates and fish (e.g. Eadie and Keast 1984), and therefore they could be termed as keystone structures in freshwater ecosystems (cf. Tews *et al.* 2004). Local-scale changes in such keystone structures will inevitably lead to dramatic changes in wholesale biodiversity, although not much is known about their actual importance in freshwater ecosystems. A safe policy is to guarantee that minimally affected local communities and ecosystems typical to each region are preserved, along with their most important structural components, such as macrophytes in the oligotrophic freshwater ecosystems of Finland. This endeavour may not be an easy one to accomplish, however, and it entails considering processes at several scales. Although the effects of climate change on biodiversity are difficult to prevent, more localised effects of land use and subsequent impacts on local freshwater ecosystems are more easily counteracted by appropriate management and conservation planning at the landscape and regional scales. A balanced approach to conservation planning must consider interactions between processes important for population and community persistence at various scales (Opdam and Wascher 2004), but such understanding is not thus far well-developed for freshwater macrophyte diversity.

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