Sun J, Hunter P, Tyler A & Willby N (2018) The influence of hydrological and land use indicators on macrophyte richness in lakes – A comparison of catchment and landscape buffers across multiple scales, *Ecological Indicators*, 89, pp. 227-239.

DOI: 10.1016/j.ecolind.2018.02.016

The influence of hydrological and land use indicators on macrophyte richness in lakes – a comparison of *catchment and landscape buffers* across multiple scales

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Abstract

In biogeography it is well established that environmental variables often have scale-dependent effects on abundance and distribution of organisms. Here we present results from a study on scale-dependency of macrophyte (aquatic plant) richness to hydrology and land use indicators. Hydrological connectivity and land use within the landscape surrounding 90 UK lakes, at nine buffer sizes varying from 0.25 km to 10 km from the shoreline, with (*catchment buffer*) and without (*landscape buffer*) adherence to the catchment boundary, were constructed using GIS. These variables were used to explain variation in macrophyte richness derived from field surveys. The results revealed strong scale-dependency. The effects of land use were most apparent at small buffer sizes and grossly outweighed the importance of hydrology at all spatial scales. The total richness of macrophytes was most strongly determined by land use and hydrology within 1 km of the lake for *landscape buffers* and 500 m for *catchment buffers*. The nature of the scale-dependent effect also varied with macrophyte growth habit. In terms of growth form composition, the effects of hydrological connectivity were stronger than those of land use, being greatest at an intermediate distance (~ 5 km) from the lake. Our results indicate the value of maintaining some lake catchments with less intensive land use, at least within 1 km of the lake shore, while also minimising alterations to catchment hydrology (e.g. through drainage or impoundment) over distances extending at least 5 km from the lake shore.

Key words

Catchment, buffer analyses, lake macrophyte, landscape pattern, species richness

1. Introduction

Freshwater macrophytes are a fundamental component of aquatic food webs and their species richness is implicitly linked to ecosystem structure and function (Bouchard et al., 2007; Engelhardt and Ritchie, 2001). The degradation of aquatic vegetation is often associated with the loss of native species and invasion by non-native species (Di Nino et al., 2005; Hussner and Lösch, 2005; Willby, 2007). The impact of eutrophication can also lead to a shift from small submerged aquatic plants towards predominantly floating and emergent species (Egertson et al., 2004), followed by entire collapse in the aquatic vegetation (Madgwick et al., 2011). Studies characterising the anthropogenic controls on lake water quality and macrophyte abundance have typically been undertaken from two different perspectives: the landscape (Pedersen et al., 2006) and the stricter topographic catchment.

Lake riparian buffer zones or lake marginal zones are a common target area for tools designed to reduce impacts of anthropogenic activity on lake water quality and aquatic vegetation in the landscape surrounding a lake (Lee et al., 2004). The effects of land cover on macrophyte species richness, and the extent to which this relationship is scale-dependent, have been explored in a number of previous studies. Pedersen et al. (2006), for example, used buffers of different size (i.e. varying distances from the lake shore) to examine the effect of land cover on macrophyte species in Danish lakes. The results showed that land use within the < 3 km buffer zone exerted a stronger effect on the occurrence of *Littorella uniflora* than that observed with coarser scale buffers. Others have also shown that landscape diversity and the proportion of managed land within the immediate vicinity of a lake has a significantly greater influence on macrophyte richness than the effect measured over larger units, e.g. wider landscape or entire catchment (Steffan-Dewenter et al., 2002). There is also evidence that the scale-dependent effect of land cover on macrophyte richness varies depending on macrophyte growth form (Akasaka et al., 2010) and that the size of the effect is proportional to the area of the lake (Alahuhta et al., 2012). Hydrological pathways are considered to determine the effectiveness of buffer strips and, thus, a catchment-wide perspective on lake riparian management was advocated by Wissmar and Beschta (1998).

The topographic catchment of a lake is defined as the basin of land that drains surface and sub-surface water with sediments and other materials into the receiving water body. The topography within a catchment is a major determinant of surface hydrological processes and conditions (Hwang et al., 2012) including the extent of connectivity between discrete habitats. Water flow via the river network is the major pathway via which materials including nutrients, and stressors such as heavy metals are distributed between lakes, and simultaneously provides the network via which many aquatic organisms disperse (Bornette et al., 1998; Bracken and Croke, 2007; Jencso et al., 2009). Thus, when connectivity is disrupted by, for example, dam construction, the dispersal of macrophytes is impacted (Oťaheľova et al., 2007). The landscape connectivity between limnological networks is considered to be a key variable in shaping the macrophyte communities of lowland rivers (Demars and Harper, 2005). Flooding, water velocity and the resulting impacts on lake water level regime have also been shown to be closely correlated with macrophyte species distribution and abundance (Baart et al., 2010; Baattrup-Pedersen et al., 2008; Barendregt and Bio, 2003; Steffen et al., 2014; Thomaz et al., 2007).

Different land use types and patterns within the catchment also influence nutrient availability and thus can impact on downstream lake water quality and primary production through overland flow and runoff (Gorman et al., 2014; Lee et al., 2009). Downstream water quality and macrophyte abundance are linked with (i) the proportion of urban or industrial land within the upstream catchment (Sass et al., 2010; Tong and Chen, 2002; White and Greer, 2006); (ii) the proportion of agricultural land, which influences nutrient loading and thus primary production (Gorman et al., 2014; Knoll et al., 2003); and (iii) the type of agricultural land, for example, arable crops have a higher N:P stoichiometry compared with pasture (Arbuckle and Downing, 2001). Whilst it is generally understood that nutrient loading from land has an important impact on the trophic status of lakes and the abundance and structure of phytoplankton (Downing and McCauley, 1992; Smith and Bennet, 1999), areas of localised nutrient enrichment can also directly affect macrophyte growth (Lacoul and Freedman, 2006).

Despite the apparent importance of the runoff regime in regulating macrophyte communities in lakes, the nature of this process is not well documented. With the exception of Ecke (2009) who examined the relationship between the density of drainage ditching within a Swedish catchment and lake macrophyte composition, few studies have addressed the effect of stream density and lake spatial structure on macrophyte richness and composition. This is probably because of the difficulty in measuring some hydrological attributes at relevant scales. For the present work, stream density and lake density in different buffer types and sizes were derived to explore the relationship between hydrological attributes and macrophyte species richness. In particular, the landscape pattern method (O'Neill et al., 1988) was incorporated into our analyses to assess the influence of lake physical structure and spatial connectivity on macrophyte species richness in lakes over multiple scales rather than at a single scale.

This work firstly proposes the concept of the *catchment buffer* to allow the scale-dependent influence of hydrology and land use on the lake macrophyte richness to be contrasted with the *landscape buffer* (i.e. the area encircling a lake up to a given distance (buffer size) from its shore without adherence to the catchment boundary). Previous studies have concluded that land cover within *landscape buffers* has a more important impact on macrophyte communities than land cover in the topographic catchment (Pedersen et al., 2006; Sass et al., 2010). We then compare the effects of land use and hydrological connectivity on macrophyte species richness and ask to what extent these effects depend on buffer size within the contrasting topographic *catchment and the landscape buffer* types. Two hypotheses are explored:

(i) Lake macrophyte richness is less affected by hydrology and land use within the topographic catchment than the landscape over comparable distances;

(ii) Hydrological connectivity and land use in the immediate vicinity of a lake exert a stronger influence on macrophyte species richness than at larger distances, but the strength of this effect also varies with macrophyte growth form.

Our approach is designed to shed new light on connectivity and macrophyte dispersal and to identify the optimal spatial scale of the buffer zone for conserving macrophyte biodiversity in lakes.

2. Methods

2.1. Study sites

This study focused on 90 lakes within mainland Britain, selected from a larger database of physicochemical and macrophyte data for 2584 lakes surveyed between 1985 and 2000 under the auspices of the Joint Nature Conservation Committee (JNCC) and the UK environmental agencies. The lakes selected for this study met two requirements: (i) the shoreline was at least 10 km from the sea such that the *landscape buffers* were entirely terrestrial in nature; (ii) the minimum distance from the lake shoreline to the catchment boundary was at least 10 km to enable a complete set of *catchment buffers* to be constructed (Fig. 1). Previous studies of the impact of anthropogenic disturbance on lake macrophytes were mostly conducted on a small scale (< 3 km) using *landscape buffers* (Akasaka et al., 2010; Alahuhta et al., 2012; Pedersen et al., 2006). Our study used incremental buffer sizes up to a maximum of 10 km as the buffer spatial scale because many of the study lakes had large catchments. This allows for the overall trend in the impact of hydrology and land use in *landscape buffers* and *catchment buffers* on lake macrophyte richness to be compared across a wide range of spatial scales.

Fig. 2 shows the latitudinal gradient of the study lakes, ranging from northern Scotland to the midlands of England and Wales. The distribution of the study sites reflects the fact that the majority of lakes in Great Britain are located in the north west. The population of study lakes varied considerably in terms of their morphology, chemistry and landscape location. The characteristics of these lakes are summarised in Appendix A.

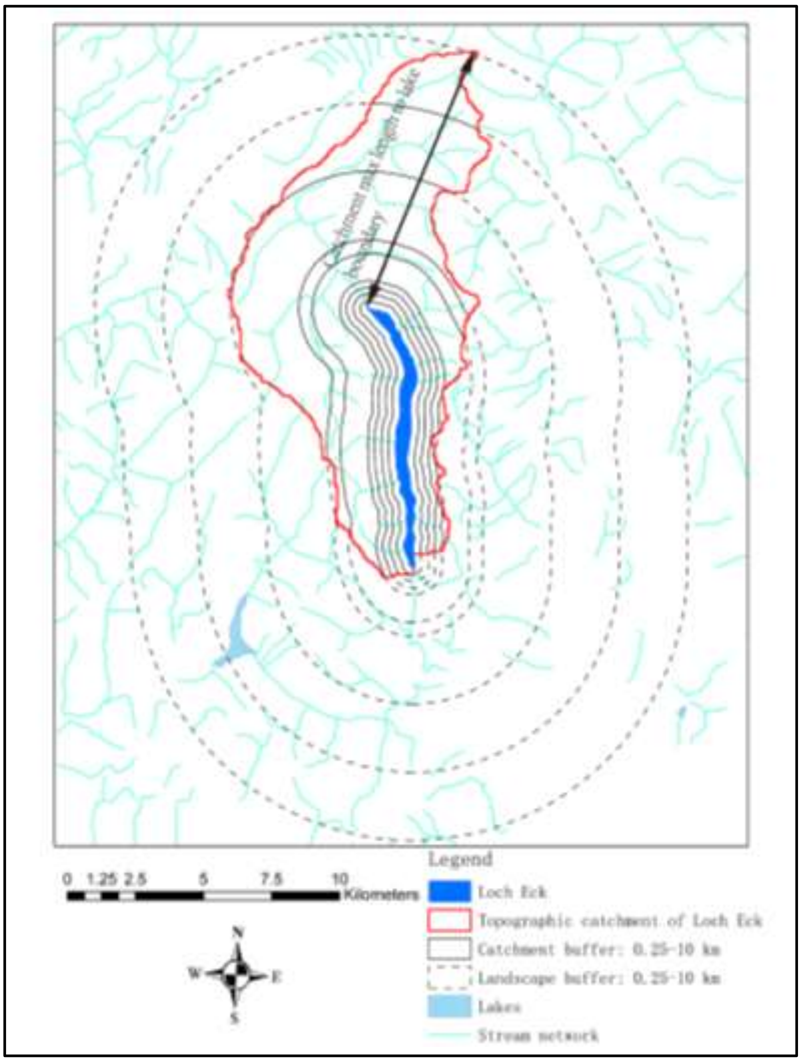

Fig. 1 Explanation of *catchment and landscape buffer* types. Example shown is for Loch Eck (WBID24996, Catchment area: 103.24 km^2).

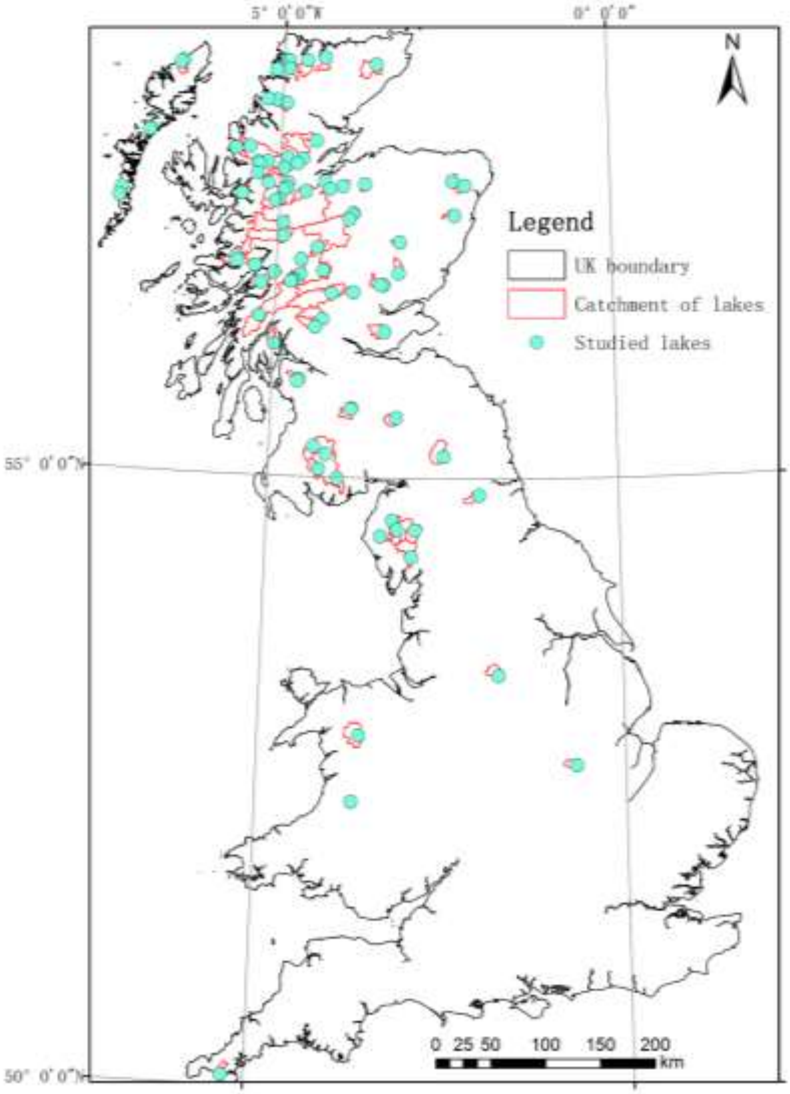

Fig. 2 Geographical positions of the study lakes and their catchments

2.2. Lake and macrophyte sampling

Macrophytes were surveyed by traversing each water body in a boat along multiple transects and by wading within the shallower parts of the littoral zone (Gunn et al., 2010). A rake was usually used to collect samples but in shallow water a bathyscope was also used to locate plants. Surveys were conducted between July and September. The recorded species were assigned to different exclusive growth form categories: emergent, free-floating, floating-leaved and submersed. The emergent category included only those emergent plants growing in standing water and does not reflect the full complement of emergent and marginal plants in a lake. Total macrophyte richness was calculated as the sum of the species in different growth form categories.

For each lake, water samples were taken near the outflow in summer and winter. Variables such as conductivity and alkalinity showed little change on a decadal level (Willby et al., 2012), whilst total phosphorus, total nitrogen and pH, where measured, sometimes exhibited marked variation. Alkalinity was considered the key variable to represent water chemistry (Vestergaard and Sand-Jensen, 2000a) and has been widely found to be a major driver of macrophyte composition in lakes (Vestergaard and Sand-Jensen, 2000b), probably due to its influence on inorganic carbon supply and co-variation with major nutrient concentrations (Kolada et al., 2014). A significant positive relationship ($R^2 = 0.531$; $p < 0.001$) between total phosphorus and alkalinity for lakes within the database (349 of the 2584 lakes had both TP and alkalinity data) supported this assumption. Lake area, a major determinant of macrophyte richness (Rorslett, 1991), was determined subsequently using GIS.

2.3. GIS analysis

2.3.1. Catchment definition

The topographic catchments of the 90 study lakes were generated using Arc Hydro Tools in ArcGIS (v 10.2; ESRI, U.S.A) with application of the vectorised lake boundaries and Digital terrain model (DTM) at a 50 m grid resolution using data from the UK Ordnance Survey (MERIDIAN^{TM} 2 and OS Terrain 50). Concentric buffers at spatial distances of 0.25, 0.5, 0.75, 1, 2, 2.5, 5, 7.5 and 10 km from the lake shoreline were subsequently calculated using Buffer Tool in ArcGIS. These are hereafter termed *landscape buffers* since they take no account of the boundary of the topographic catchment. The *landscape buffers* were subsequently intersected with the polygon layer representing the topographic catchment for each lake to derive the *catchment buffers* (Fig. 1) at each aforementioned buffer distance.

2.3.2. Hydrological and land use indicators

Hydrological indices were generated from two-dimensional vector maps of the lakes and rivers network of the UK supplied by the Ordnance Survey (MERIDIAN^{TM} 2) in order to construct the framework for estimating the effect of lake hydrological connectivity on macrophyte richness. From this, stream density, lake density and lake coverage were calculated in each of the incremental spatial scales for the two buffer types.

A 1:25000 UK land cover map (LCM2007: http://www.ceh.ac.uk/services/land-cover-map-2007) was used to estimate the influence of anthropogenic disturbance on lake macrophyte richness. The percentage cover of the most impacted land use types was quantified within each size of *landscape buffer* and *catchment buffer* for each lake. Two broad categories of land use were considered as indicators of land use intensity: (i) agriculture, consisting of improved grassland, arable cereals, arable horticulture and arable non-rotational; and (ii) urban, defined by suburban/rural developed land in addition to designated urban areas.

Indices of landscape pattern were calculated using land cover map (LCM2007) in Fragstat 4.1 to characterise the physical structure and arrangement of water and land cover patches within the different sizes and types of buffer for each lake. The effect on biota of either the structure of the habitats surrounding lakes, or the landscape diversity, will vary with the scale of *landscape* and *catchment buffers* (Steffan-Dewenter et al., 2002). Since different landscape diversity indices are inter-correlated only those variables listed in Appendix B were used. Table 1 shows the mean and range of the hydrological and land use indicators in the *landscape buffers* and *catchment buffers*. With the exception of the variables Euclidean nearest-neighbour distance (ENN, as defined in Appendix B), Landscape division index and Agriculture coverage, all mean values decrease with increasing buffer size as a result of simple scale effects.

Table 1

Mean value of hydrological and land use indicators of the study lakes within *landscape buffers* and *catchment buffers* across continuous buffer distances from 0.25 km to 10 km (The table summarises the minimum and maximum value of the selected variables across two buffer types and the buffer sizes in which these values were encountered)

Explanatory variables		***Landscape buffers***		***Catchment buffers***	
	Unit	Minimum value (Buffer size / km)	Maximum value (Buffer size / km)	Minimum value (Buffer size / km)	Maximum value (Buffer size / km)
Hydrological attributes					
Stream density	km/km^2	0.69 (B10)	1.46 (B0.25)	0.77(B10)	1.48(B0.25)
Water body coverage	%	2.78(B10)	33.7(B0.25)	4.93(B10)	34.0(B0.25)
Lake density	$1/km^2$	0.15(B10)	1.15(B0.25)	0.21(B10)	1.27(B0.25)
Lake fractal index	-	1.07(B10)	1.09(B0.25)	1.08(B10)	1.09(B0.25)
Core area percentage of landscape	%	1.34(B10)	17.2(B0.25)	2.51(B10)	17.3(B0.25)
Disjunct core area density	$1/km^2$	0.044(B10)	0.50(B0.25)	0.08(B10)	2.08(B0.5)
Euclidean nearest-neighbour distance	m	85.4(B0.25)	845.9(B10)	78.6(B0.25)	895.2(B7.5)
Proximity index	%	17.3(B10)	22.2(B1)	15.9(B10)	21.1(B1)
Interspersion juxtaposition index	%	64.1(B7.5)	68.4(B0.25)	62.7(B2)	68.3(B0.25)
Cohesion index	%	96.1(B10)	96.3(B0.25)	94.9(B0.5)	95.9(B0.25)
Landscape division index	%	0.86(B0.25)	1.0(B10)	0.86(B0.25)	0.99(B10)
Land use indicators					
Urban coverage	%	0.72(B5)	0.98(B0.25)	0.47(B10)	1.03(B0.25)
Agriculture coverage	%	8.22(B0.25)	12.7(B2.5)	8.09(B0.25)	12.28(B1)
Urban patch density	$1/km^2$	0.23(B10)	1.10(B0.25)	0.28(B10)	1.09(B0.25)
Agriculture patch density	$1/km^2$	0.96(B10)	3.80(B0.25)	1.16(B10)	3.94(B0.25)

2.4. Statistical analyses

The distribution of all hydrological and land use indicators (Table 1) was normalised by $\log_{10}$ transformation and values were then standardised to zero mean and unit standard deviation. Principal components analysis (PCA) was performed to prioritise the non-correlated variables from the sets of hydrological and land use indicators for each buffer type (catchment and landscape) and for each buffer size (from 0.25 km to 10 km). Three components, “PCA1- lake spatial dispersal”, “PCA2-land use” and “PCA3-lake shape and connectivity”, were extracted and explained over 70% of the total variation for each buffer spatial scale (Table 4). The bivariate correlations between the derived PCA components were calculated for each buffer size. If the value of the correlation coefficient r was greater than 0.6, we filtered the most highly correlated variables, such as alkalinity, conductivity and pH, then repeated the initial PCA analyses before the non-correlated PCA components were extracted.

Univariate regression was used to identify the key hydrological and land use predictors of lake macrophyte richness for each growth form. Due to low group membership of two growth forms, free-floating and floating-leaved were aggregated into a single group for the analysis. To identify the local environmental factors (Appendix A) best explaining the richness of each growth form, generalized linear models with a Poisson log link function (GLLM) were initially used since the response variable was count data. However, to reduce over-dispersion in some cases a negative binomial generalized linear model (GLM-NB) was used in preference.

Based on the optimal model for each growth form, separate models were fitted along with each hydrological / land use predictor and PCA gradients for each buffer type (catchment and landscape) and for each buffer size (from 0.25 km to 10 km). The Akaike Information Criterion (AIC) was used to compare the goodness of fit for each model. Finally, ΔAIC of each GLLM model was calculated to identify the optimal buffer size for explaining macrophyte richness for each macrophyte growth form by each hydrological / land use indicator and PCA gradients separately.

Partial Redundancy Analysis (Partial RDA) was used to identify the size of *catchment* and *landscape buffer* that best explained growth form composition, as defined by the relative number of species in the major growth forms. First, using the 'corvif' function from the 'aed' package in R (Zuur et al., 2009), the variance inflation factor (threshold of 3) of all variables was determined within the separate environmental (Appendix A), hydrological and land use variable data sets (Table 1) to reduce collinearity among model predictors. Thus, the variables stream density, lake proximity index, water body coverage, lake density, Euclidean nearest-neighbour distance and lake fractal index were retained within the hydrological dataset. Similarly, agricultural coverage, urban coverage and agricultural patch density were retained within the land use dataset. An automated, forward stepwise selection of variables within the Partial RDA was then used to identify the environmental variables that best explained macrophyte growth form composition. The adjusted R^2 of the Partial RDA models based on the selected hydrological and land use indicators were then compared between *catchment buffers* and *landscape buffers* respectively. We evaluated the uncertainty of the explanatory power of the Partial RDA model using bootstrapping. This was performed by random resampling (using a loop created in R programming to generate 89 random lake observations) with replacement from the original sample (n=90) (Quinn and Keough, 2004). The bootstrapping procedure allows the Partial RDA model to be repeated using the randomly resampled lake observations. The coefficient of determination (i.e. Adjusted-R^2) from the bootstrapped models was calculated from the standardized error to test the uncertainty of the Partial RDA model.

All of the statistical analyses were conducted in R (v3.1.3, R Core Team 2015). Estimates of coefficients for the GLM models in Fig. 3 and measures of their confidence (2.5%-97.5%) are provided in Supporting information (Appendix C). The GLM-NB model was fitted using the “mass” package (Venables and Ripley, 2002). PCA analysis was conducted in “ade4” package (Dray and Dufour, 2007) and Partial RDA was performed in the “vegan” package (Oksanen et al., 2007).

3. Results

3.1. Response of macrophyte richness to hydrological and land use indicators

All of the environmental variables defined for the 90 study lakes in Appendix A were considered as candidate explanatory variables to predict macrophyte species richness. The results for the GLM-NB models showed that the drivers of macrophyte richness differed with macrophyte growth form (Table 2). In particular, the key factors explaining emergent macrophyte richness were lake area and alkalinity, while the richness of floating macrophytes was best explained by lake conductivity alone. Overall, lake area, conductivity and pH were the most significant variables explaining total macrophyte richness within the 90 study lakes.

Table 2

The best performing GLM-NB models using environment variables to predict the richness for each macrophyte growth form, based on AIC. The significance of each predictor in GLLM models was tested through the analysis of variance (ANOVA) Chi-square test (*p<0.1; **p<0.01)

Predictor	Model selected	Step forward results for GLLM model	Residual deviation on d.f.	AIC
Total plant richness	GLM-NB	Lake Area* + lake Conductivity + lake pH	95.63, 88	579.63
Submersed plants	GLM-NB	Lake Area** + lake Alkalinity* + lake Conductivity*	97.85, 88	501.56

Emergent plants	GLLM with Poisson	Lake Area + lake Alkalinity*	77, 90	327.51
Floating plants	GLLM with Poisson	Lake Conductivity	91.55, 90	325.34

Table 3

The ΔAIC value of GLLM models for explaining macrophyte richness by key hydrological and land use predictors based on the most significant environmental factors for each growth form. The (+ or -) indicates the positive or negative coefficient for the factor. AIC values that indicate an improvement from the basic environmental model (Table 2) are shown in italics.

Predictor		Total richness		Submersed richness		Emergent richness		Floating richness	
Buffer type		Landscape	Catchment	Landscape	Catchment	Landscape	Catchment	Landscape	Catchment
Original AIC		579.63		501.56		327.51		325.34	
Stream density	B0.25	1.75	2	1.72	1.99	1.78	1.76	*-0.27(+)*	1.28
	B0.5	0.13	1.84	0.4	1.86	1.78	1.98	*-2.31(+)*	0.79
	B0.75	*-0.68(+)*	1.85	*-0.48(+)*	1.83	1.46	1.95	*-3.33(+)*	0.77
	B1	*-1.96(+)*	1.59	*-1.18(+)*	1.7	1.22	1.93	*-5.80(+)*	**-0.3**
	B2	1.17	1.93	1.91	1.62	1.48	1.92	*-3.55(+)*	0.1
	B2.5	1.1	1.94	1.62	1.73	1.56	1.95	*-1.36(+)*	0.43
	B5	0.21	2	0.48	1.99	1.12	1.99	*-0.12(+)*	1.14
	B7.5	*-0.40(+)*	1.92	*-0.18(+)*	1.79	1.13	1.96	0.01	1.64
	B10	*-1.17(+)*	1.97	*-0.88(+)*	1.99	0.88	1.92	*-0.18(+)*	1.05
Lake density	B0.25	2	1.51	1.99	1.7	1.68	1.48	1.05	1.99
	B0.5	1.9	1.78	1.99	1.76	1.99	1.87	0.48	1.91
	B0.75	1.99	1.9	1.93	1.75	1.71	1.96	1.7	1.93
	B1	1.98	1.99	1.98	1.96	1.6	1.92	1.57	1.83
	B2	1.88	1.99	1.99	1.89	0.55	1.31	0.85	1.36
	B2.5	1.89	2	1.99	1.71	*-0.10(+)*	0.88	0.67	1.15
	B5	1.98	1.99	1.8	1.56	0.44	1.03	0.88	1.25
	B7.5	1.96	2	1.93	1.78	0.05	0.92	1.25	1.17
	B10	1.92	2	1.99	1.63	0.04	0.89	1.3	1.19
Lake coverage	B0.25	1.45	1.44	*-0.39(-)*	*-0.27(-)*	1.08	1.04	1.09	1.25
	B0.5	1.75	1.83	0.7	0.93	1.09	1.03	0.99	0.84
	B0.75	1.94	1.98	1.53	1.62	0.97	0.83	0.85	0.56
	B1	2	1.99	1.92	1.96	0.76	0.5	0.54	0.11
	B2	1.25	1.39	1.39	1	0.64	*-0.32(+)*	*-0.46(+)*	*-0.57(+)*
	B2.5	1.38	1.31	1.14	*-0.19(-)*	0.02	*-1.50(+)*	0.49	0.1
	B5	1.82	0.66	1.62	*-2.83(-)*	*-0.02(+)*	*-1.03(+)*	1.74	0.92
	B7.5	2	1.25	1.99	*-1.22(-)*	*-0.33(+)*	*-1(+)*	2	1.68
	B10	0.56	1.53	0.22	*-0.60(-)*	*-1.80(+)*	*-1.32(+)*	1.18	1.91
Lake fractal index	B0.25	1.42	1.62	1.41	1.38	1.31	1.78	1.39	1.67
	B0.5	1.01	1.49	1.61	1.45	1.72	2	1.07	1.44
	B0.75	1.65	1.44	1.69	1.33	1.94	1.88	1.92	1.75
	B1	1.72	1.44	1.65	1.16	1.95	1.85	1.93	1.77
	B2	2	0.55	1.98	*-0.20(-)*	1.95	1.6	1.54	1.75
	B2.5	0.71	*-2.88(-)*	1.57	*-2.88(-)*	*-0.76(-)*	*-0.20(-)*	2	0.31
	B5	1.7	*-2.75(-)*	1.69	*-5.35(-)*	1.83	1.5	1.08	1.35
	B7.5	1.07	0.38	0.98	*-0.66(-)*	1.99	1.8	0.57	1.86
	B10	0.37	0.11	*-0.05(-)*	*-1.03(-)*	1.99	1.34	*-2.05(+)*	1.95
Land use/ Agriculture	B0.25	*-200(+)*	*-200(+)*	*-173(+)*	*-173(+)*	*-109(-)*	*-109(-)*	*-111(+)*	*-111(+)*
	B0.5	*-189(+)*	*-194(+)*	*-165(+)*	*-169(+)*	*-103(-)*	*-106(-)*	*-102(+)*	*-107(+)*
	B0.75	*-160(+)*	*-188(+)*	*-140(+)*	*-164(+)*	*-86(-)*	*-103(-)*	*-86(+)*	*-104(+)*
	B1	*-160(+)*	*-176(+)*	*-140(+)*	*-154(+)*	*-86(-)*	*-95(-)*	*-85(+)*	*-96(+)*
	B2	*-114(+)*	*-160(+)*	*-99(+)*	*-140(+)*	*-59(-)*	*-86(-)*	*-60(+)*	*-88(+)*
	B2.5	*-92(+)*	*-148(+)*	*-81(+)*	*-131(+)*	*-47(-)*	*-80(-)*	*-46(+)*	*-81(+)*
	B5	*-36(+)*	*-133(+)*	*-32(+)*	*-116(+)*	*-16(-)*	*-72(-)*	*-17(+)*	*-74(+)*
	B7.5	*-15(+)*	*-133(+)*	*-13(+)*	*-115(+)*	*-7(-)*	*-72(-)*	*-7(+)*	*-74(+)*
	B10	*-3.4(+)*	*-132(+)*	*-2.5(+)*	*-115(+)*	*-1(-)*	*-72(-)*	*-1(+)*	*-74(+)*

Land use/ Urban	B0.25	*-382(+)*	*-382(+)*	*-327(+)*	*-327(+)*	*-217(-)*	*-217(-)*	*-214(+)*	*-214(+)*
	B0.5	*-358(+)*	*-363(+)*	*-307(+)*	*-311(+)*	*-205(-)*	*-207(-)*	*-200(+)*	*-204(+)*
	B0.75	*-352(+)*	*-352(+)*	*-302(+)*	*-302(+)*	*-201(-)*	*-201(-)*	*-196(+)*	*-196(+)*
	B1	*-329(+)*	*-335(+)*	*-283(+)*	*-288(+)*	*-187(-)*	*-191(-)*	*-185(+)*	*-188(+)*
	B2	*-297(+)*	*-329(+)*	*-256(+)*	*-282(+)*	*-168(-)*	*-188(-)*	*-167(+)*	*-183(+)*
	B2.5	*-254(+)*	*-316(+)*	*-217(+)*	*-271(+)*	*-140(-)*	*-180(-)*	*-143(+)*	*-177(+)*
	B5	*-174(+)*	*-302(+)*	*-148(+)*	*-261(+)*	*-97(-)*	*-171(-)*	*-94(+)*	*-167(+)*
	B7.5	*-133(+)*	*-290(+)*	*-114(+)*	*-251(+)*	*-69(-)*	*-164(-)*	*-71(+)*	*-161(+)*
	B10	*-92(+)*	*-290(+)*	*-77(+)*	*-251(+)*	*-48(-)*	*-164(-)*	*-49(+)*	*-161(+)*

The ΔAIC value of the GLLM model (Table 3) for *landscape buffers* and *catchment buffers* indicated that the majority of the different hydrological and land use indicators could be used to individually explain macrophyte richness separately when the different growth forms were considered. Land use explained far greater variation in macrophyte richness than hydrological attributes. Urban land cover explained a greater proportion of macrophyte species richness than did agriculture, regardless of buffer type or size. For hydrological attributes, the best three variables for predicting macrophyte species richness were stream density, lake coverage and lake fractal index. In addition, the most important hydrological attribute(s) differed between macrophyte growth forms. For example, stream density (*landscape buffer*) was related more closely with floating plant richness, whilst the lake fractal index (*catchment buffer*) had a closer relationship with submersed plant richness. For each variable, the coefficient of determination changed with increasing buffer size, demonstrating a scale dependency in the model predictions. The estimation of all coefficients including their confidence intervals are provided in the supplementary information.

Furthermore, the comparison of buffer types demonstrated that for land use indicators and some hydrological variables (i.e. lake coverage and lake fractal index), the *catchment buffers* explained more of the variation in lake macrophyte richness (lower ΔAIC value) than *landscape buffers*. By contrast, for other hydrological attributes (e.g. stream density) *landscape buffers* were generally better predictors of macrophyte richness than *catchment buffers*.

3.2. Optimal spatial distances for explaining total species richness

The first three PCA axes explained over 70% of the variation in all selected variables for *landscape buffers* and *catchment buffers*, with almost equal amounts being explained by PC axes 1 and 2. Variables in each PC axis were very similar for *landscape* and *catchment buffers* (Table 4). Specifically, PC axis 1 was positively associated with variables related to lake area (e.g. water body coverage, largest lake index and lake cohesion index) and negatively correlated with lake structural variables (e.g. lake density, stream density and lake division index). The second axis was positively associated with land use characteristics such as extent of agriculture. PC axis 3, explained 9.5% to 11.6% of the variation and, was positively related to lake shape index and lake proximity index.

Table 4

Summary of correlation coefficients for three PC axes based on the hydrological and land use indicators. Ranges show the differences in a buffer type across buffer sizes from 0.25 to 10 km.

Landscape Buffer			
PCA components	PC axis1 Lake spatial dispersal	PC axis2 Land use	PC axis3 Lake shape and connectivity
Explained range (lowest to highest / Buffer distance (km))	23.9%(B5) to 31.3%(B0.25)	24.9%(B5) to 30.9%(B1)	9.5%(B10) to 11.6(B5)
Variables (correlation coefficients with PC axis)	Stream density (-0.593 to -0.397)	Agriculture coverage (0.747 to 0.938)	Proximity index (0.493 to 0.782)
	Water body coverage (0.834 to 0.978)	Agriculture patch density (0.779 to 0.926)	Lake fractal index (0.518 to 0.826)
	Lake density (- 0.815 to -0.560)	Urban coverage (0.382 to 0.846)	
	Largest patch index (0.953 to 0.985)	Urban patch density (0.674 to 0.921)	
	Cohesion (0.637 to 0.762)		
	Division (- 0.951 to -0.893)		
Catchment Buffer			
PCA component	PC axis1 Lake spatial dispersal	PC axis2 Land use	PC axis3 Lake shape and connectivity
Explained range (lowest to highest / Buffer distance (km))	24.6%(B2.5) to 31.04%(B0.25)	24.5%(B2) to 27.5%(B7.5)	9.01%(B10) to 11.4(B0.75)
Variables (correlation coefficients with PC axis)	Stream density (-0.593 to -0.329)	Agriculture coverage (0.838 to 0.955)	Proximity index (0.437 to 0.782)
	Water body coverage (0.924 to 0.980)	Agriculture patch density (0.871 to 0.935)	Lake fractal index (0.542 to 0.806)
	Lake density (- 0.846 to -0.532)	Urban coverage (0.646 to 0.880)	
	Largest patch index (0.945 to 0.984)	Urban patch density (0.652 to 0.938)	
	Cohesion (0.551 to 0.744)		
	Division (- 0.952 to -0.921)		

The GLM-NB model of total macrophyte richness, after taking account of lake area, conductivity and pH (Table 2), included at least one significant PCA component in each size of buffer, indicating that richness of macrophytes was explained partially by the hydrological and land use indicators (Fig. 3). The total richness of macrophyte species was best explained by PCA components at the finer buffer scales - specifically at the **1 km** scale for the *landscape buffers* and the **0.5 km** scale for the *catchment buffers*.

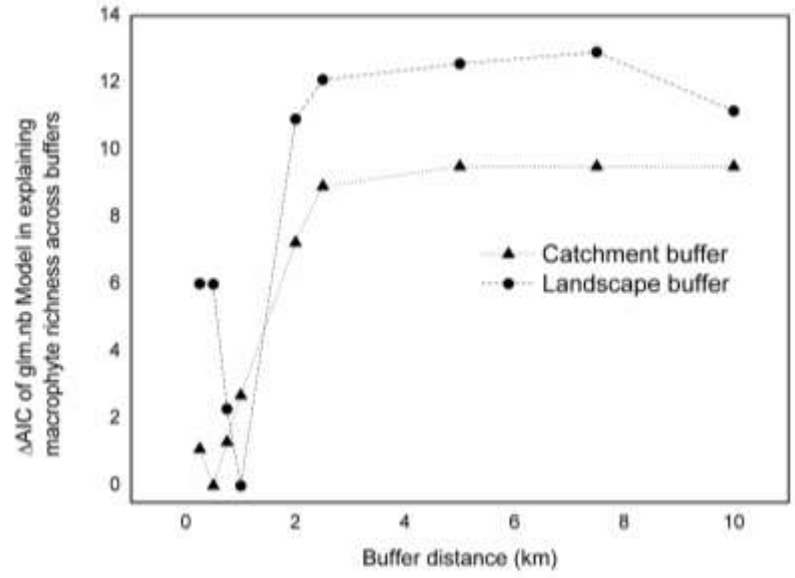

Fig. 3 Comparison of the fitted GLM-NB models applying hydrology and land use in different buffer types and sizes to explain lake macrophyte species richness

The independent variable is the residual from the model based on lake area and chemistry, and explanatory variables are PCA components (three PCA axes described in Table 4) according to *landscape buffers* and *catchment buffers*. ΔAIC shows the variation among AIC values of the model at each buffer size (from 0.25 to 10 km), the best model being indicated by the lowest ΔAIC.

3.3. Effect of hydrological and land use indicators on macrophyte growth form composition at the optimal buffer size

Adjusted R^2 values from the Partial RDA models for the multiple spatial scales (Fig. 4) showed different trends in terms of explaining macrophyte growth form composition using hydrological and land use datasets separately. For land use indicators (Fig. 4A), the total variance explained for both *landscape buffers* and *catchment buffers* increased before peaking at around **1** km, followed by a drop with increasing buffer distance. For the hydrological dataset (Fig. 4B), a similar trend is shown for the *landscape buffer*, with a buffer size of **1** - **2** km being the most important in terms of explaining growth form composition. However, using *catchment buffers* variation in growth form composition was best explained by a buffer size of **5** km (13%), with models using hydrological predictors in *catchment buffers* proving non-significant at the finest buffer sizes (<1km). Moreover, there was a turning point at about **1.5** km marking a shift in importance from *landscape buffer* to *catchment buffer* in explaining macrophyte growth form composition across coarser buffer sizes.

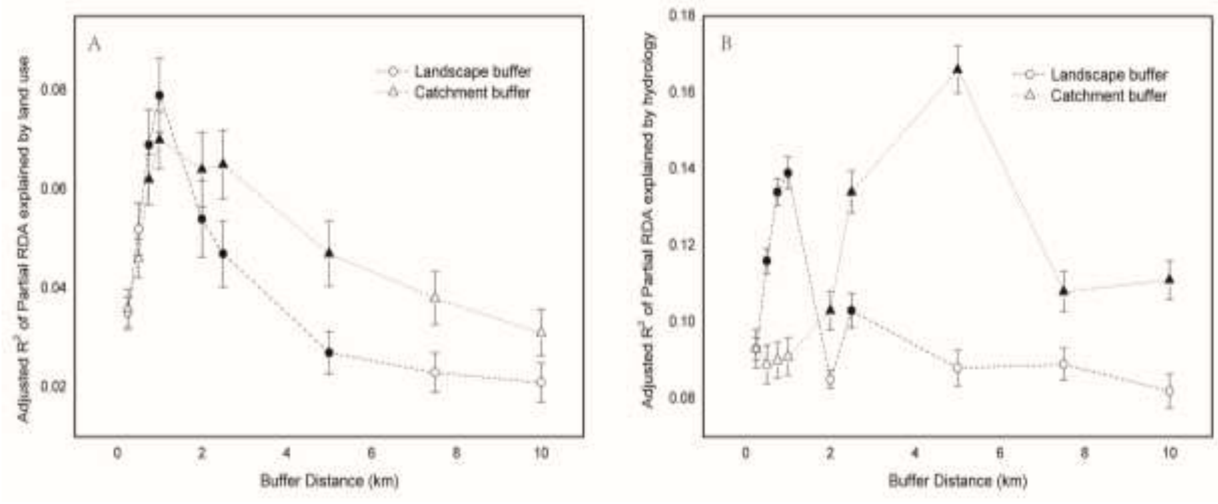

Fig. 4 Spatial dependency of Partial Redundancy models in explaining macrophyte growth form composition using land use (Fig. 4A) and hydrological (Fig. 4B) indicators within a *landscape buffer* or *catchment buffer*. The solid points represent significant ($P < 0.05$) Partial RDA models, whilst the hollow points represent non-significant models.

Fig.5 illustrates how the Partial RDA of macrophyte richness in different growth forms corresponded to the key hydrological and land use indicators at the buffer size where the relationship between the explanatory variables and composition was strongest in *landscape buffers* or *catchment buffers*. For hydrological attributes (see Fig. 5B, Fig. 5D), lake fractal index was a key variable, as defined by a forward selection model, to explain richness for all growth forms. It was negatively correlated to relative richness of submersed and free-floating macrophytes. Lake proximity index was positively correlated with the relative richness of emergent macrophytes and floating-leaved macrophytes at the optimal size of *landscape buffer* or *catchment buffer*. For land use indicators (see Fig. 5A, Fig. 5C), urban coverage was closely correlated with the relative richness of free-floating and submersed macrophytes, whilst agricultural extent was strongly negatively related to the relative richness of floating-leaved and emergent macrophytes at a size of 1 km in the *landscape buffer*.

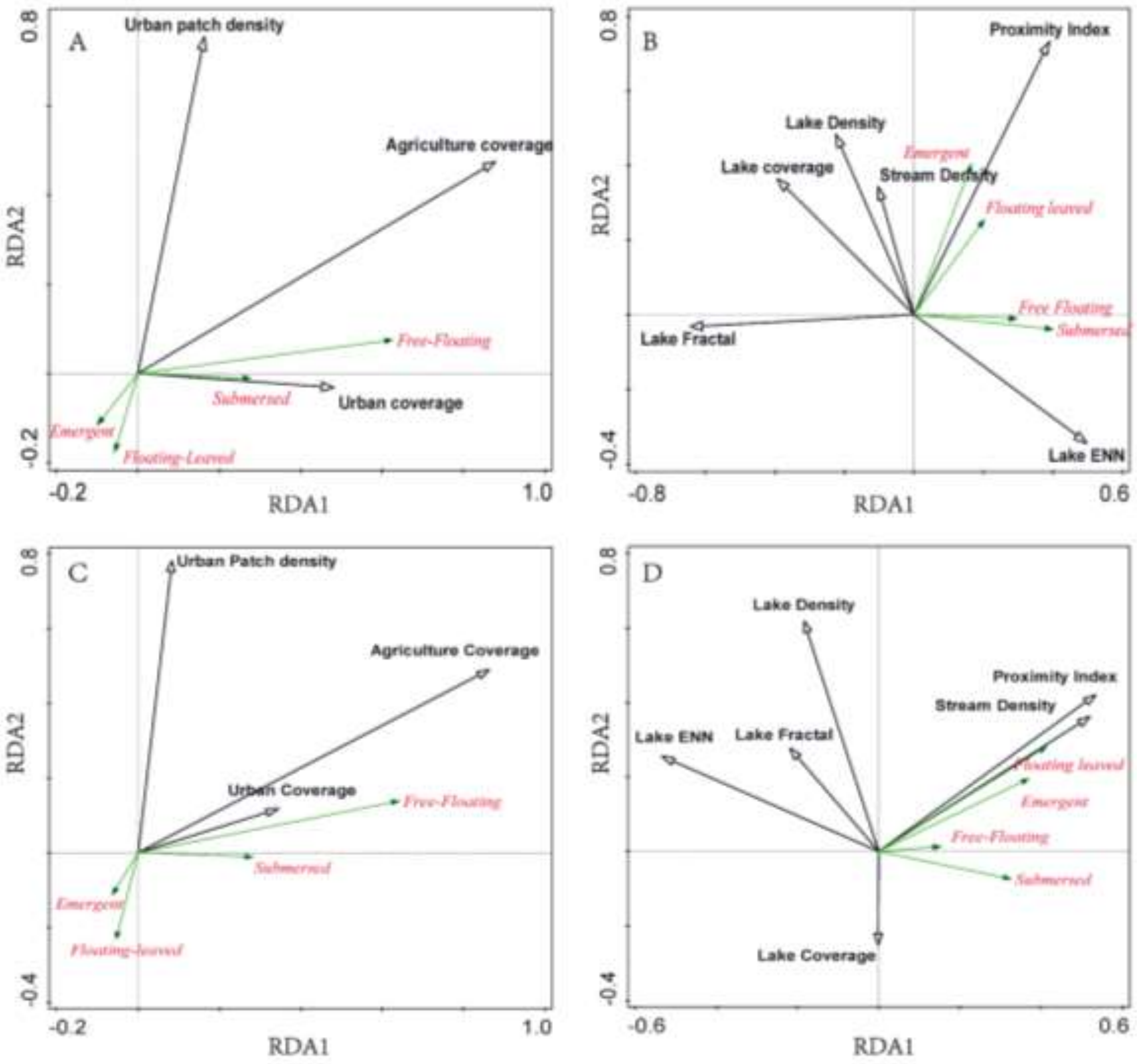

Fig. 5 Partial Redundancy Analyses of macrophyte growth form composition related to the key hydrological and land use indicators at the optimal size of *landscape buffer* or *catchment buffer*. Fig.

5A - Scale of 1 km in *catchment buffer* explained by land use; Fig. 5B - Scale of 5 km in *catchment buffer* explained by hydrological attributes; Fig. 5C - Scale of 1 km in *landscape buffer* explained by land use; Fig. 5D - Scale of 1 km in *landscape buffer* explained by hydrological attributes.

4. Discussion

4.1. Effect of buffer-scale drivers on macrophyte richness

The landscape perspective was more important in determining the biogeographical distribution of aquatic plants that disperse mainly through biological vectors (e.g. birds or mammals) or wind-assistance, while the catchment perspective was more closely related to the distribution of macrophyte species that are dependent on hydrochory.

The impact of hydrological and land use indicators on macrophyte richness differed depending on plant growth form (Table 3). The richness of floating plants was more strongly associated with stream density within *landscape buffers* (Table 3). This might be explained by floating macrophytes being more reliant on the hydrological network, and flood events in particular, for dispersing between water bodies (Thomaz et al., 2007). Interestingly, however, the relationship between stream density and floating plant richness was significant from the landscape rather than catchment perspective, especially at smaller buffer sizes, suggesting that, despite their buoyancy, floating plants and their seeds can disperse by means other than direct hydrochory. Floating plants probably transfer readily to other lakes at a small spatial scale (probably < 1 km) via a variety of mechanisms, while physical attributes of their seeds facilitate transfer to upstream or nearby lakes by wind, and over larger buffer sizes by birds (Santamaria, 2002).

Numerous studies have shown that lake chemistry is strongly impacted by inputs and processing from the stream network and surrounding environment (Lottig et al., 2011), whereas the density of the drainage network increases the contribution of processing in determining lake water quality (Nilsson and Håkanson, 1992). Systems with a dense drainage network are expected to exhibit greater similarities in water chemistry between lakes and streams. Thus one might expect agricultural inputs to lakes will be accelerated in catchments with a higher density stream network leading to greater fertility of lake water (Downing et al., 2008). Such conditions generally favour free-floating macrophytes over other growth forms (Heegaard et al., 2001; Meerhoff et al., 2003; Vestergaard and Sand-Jensen, 2000b).

The richness of emergent macrophytes was generally related to the extent of standing water in both *landscape buffers* and *catchment buffers*. Our result support previous observations of a positive relationship between lake-surface area and richness of emergent plants in ponds (Alahuhta et al., 2011; Møller et al., 1985). PCA revealed that lake coverage was negatively correlated with lake density in the two buffer types (Table 4); lake buffer zones with high lake coverage and low lake density are characterised by a few large surface-area lakes. Regions with a high extent of shallow open water are likely to be beneficial to emergent macrophyte species simply through the increased provision of habitat (Friday, 1987; Rorslett, 1991) but will also be attractive to avian dispersal vectors.

The positive relationship between land use intensity and macrophyte species richness found in this study is unsurprising since the majority of lakes in the north of Britain are naturally nutrient poor and thus moderate nutrient subsidies from low intensity agriculture are likely to stimulate macrophyte diversity (Heino and Toivonen, 2008). The emergent growth form was the only one where richness was negatively influenced by managed land coverage. This may reflect increased dominance by typical competitive emergent species (e.g. *Typha latifolia* or *Phragmites australis*) that benefit from eutrophication (Maemets and Freiberg, 2004; Partanen et al., 2009). Alternative causes may include loss of shallow water habitat associated with physical impacts of land use, or deterioration of habitat quality, e.g. through increased fine sediment inputs (Jones et al., 2012).

4.2. Effect of buffer-level drivers on macrophyte growth form composition

The main determinants of macrophyte species richness in previous studies include geographical distribution (e.g. latitude), lake water quality (e.g. alkalinity and major nutrient concentrations), climate (e.g. mean annual temperature) and land use (e.g. human disturbance) (Alahuhta, 2015; Alahuhta et al., 2012; Chappuis et al., 2012). More recently, factors such as habitat heterogeneity have also been related to macrophyte species richness and composition (Kreft and Jetz, 2007; Rolon et al., 2008; Shi et al., 2010). Our results indicate that both hydrological and land use indicators influenced macrophyte species richness at *catchment and/or landscape buffer* scale once the effects of the local environment were excluded.

The Partial RDA showed that the impact of hydrological variables (adjusted R^2 varying from 0.08 to 0.17, Fig. 4A) on macrophyte growth form composition was stronger than that of land use (adjusted R^2 varying from 0.02 to 0.09, Fig. 4B). This implies that hydrological indicators, whether in *catchment or landscape buffers* are the principle additional drivers of aquatic vegetation structure in the study catchments. The study areas have a highly-developed river channel network (Scotland alone has over 6000 rivers with a total length more than 100000 km (Gilvear et al., 2002) plus a high density of lakes (>21000 water bodies >0.25 ha in area)). These hydrological attributes (e.g. stream density, lake density) evidently influence the distribution of different macrophyte growth forms between lakes via the stream network. Physical connectivity of rivers, and practices such as flow regulation, water diversion or abstraction, impoundment or channel engineering, are therefore likely to affect plant dispersal, with consequences for the distribution of some species (Johansson et al., 1996).

Our findings differ from previous studies indicating that aquatic plants of inland lakes are distributed mainly according to a gradient of land use intensity within the catchment (Lougheed et al., 2001), although our results confirm that this is indeed a major determinant of the richness of the overall flora and individual growth forms. Most catchments considered in our study have good water quality or, where historical impacts have occurred, water quality has been restored through management actions (Marsden and Mackay, 2001). A predominance of low intensity land use combined with regulatory control over anthropogenic disturbance, especially diffuse pollution, therefore means that runoff from agriculture plays a lesser role in determining macrophyte species richness in lakes in northern Britain.

4.3. Importance of catchment versus landscape

The most appropriate spatial extent over which to target nutrient reduction as part of lake restoration strategies has been found to vary, probably reflecting differences in climate, lake size, connectivity, water depth and macrophyte composition. Previous studies have reported the strongest effects on macrophyte richness at spatial extents ranging from 3000 m (Pedersen et al., 2006) to 1000 m (Akasaka et al., 2010) and 500 m (Alahuhta et al., 2012). However, these studies only considered relationships within *landscape buffers*. In our study, 1 km was regarded as the most relevant *landscape buffer* for determining effect of land use on lake macrophyte richness in different growth forms, while a 5-km *catchment buffer* showed the strongest relationship between macrophyte growth form composition and hydrological attributes.

Riparian buffer zones are widely implemented to improve water quality by reducing nutrient inputs and soil erosion (Buckley et al., 2012; Correll, 2005) and their use to protect aquatic vegetation is well supported (Akasaka et al., 2010; Alahuhta et al., 2012). Guidelines for lake protection often advise controlling land use in close proximity to the shore because the terrain adjacent to a lake’s shoreline has more direct contact with the lake, and thus greater ability to influence the status of macrophytes, compared with the whole topographic catchment (Akasaka et al., 2010; Pedersen et al., 2006; Sass et al., 2010). Our results are consistent with previous findings that the strongest relationships with land-use and hydrological variables occur when considered from a *landscape buffer* perspective rather than the more restricted catchment buffer perspective, with the strength of the effect being broadly inversely proportional to the distance from the lake. However, we suggest that guidelines for lake protection would be more effective if they transcend catchment boundaries due specifically to the higher significance of the *landscape buffer* in explaining species richness (Fig. 4). Moreover, we observed the impact of drivers in *catchment buffers* was stronger than those for *landscape buffers* when the buffer distance was greater than 1.5 km. This is possibly because land use can only affect lake condition at coarser scales (e.g. > 1.5 km in this study) if there is adequate connectivity through the hydrological network (i.e. in *catchment buffers*), while at short distance (e.g. < 1.5 km in this study), this effect can occur independently of hydrological connectivity (i.e. in *landscape buffers*). The results further suggest that the scale-dependency of land use effects may be associated with direct anthropogenic effects from the riparian zone and indirect hydrological connectivity impacts originating in headwater streams and lakes (Alahuhta et al., 2012).

Our results highlight the importance of buffer strips from both catchment (through runoff processes) and landscape perspectives (through indirect influences, such as groundwater exchange beyond the topographic catchment, or availability of dispersal vectors) in conserving freshwater biodiversity. We recommend, wherever possible, limiting management activity and modification of the drainage network in close proximity (~1 km) of a lake's shoreline. This approach will be most effective if not just restricted to the catchment boundary (i.e. a *landscape buffer* is utilised). However, at larger buffer sizes, catchment plays the dominant role in governing lake macrophyte diversity, probably through the impact of runoff-related processes. Alleviating artificial barriers to connectivity between freshwater within *catchment buffers* may serve to naturalise plant growth form composition. However, such actions may also serve to disperse invasive species or redistribute stressors linked to artificial land use which, as our analyses show, is a primary determinant of plant species richness in lakes.

5. Conclusions

Our study aimed to compare the impact of hydrological attributes (lake spatial pattern and lake connectivity) and land use on lake macrophyte richness in *landscape buffers* and *catchment buffers* and to determine if these relationships are scale sensitive. A larger spatial extent (5 km) of *catchment buffers* dominated by hydrological attributes had the greatest overall influence on lake macrophyte growth form composition. This research sheds new light on the links between limnology and macrophyte dispersal and identifies the scales over which human disturbance exerts most influence on the vegetation of lakes. The study demonstrates that characteristics of *landscape buffers* within

1.5 km drive growth form composition of lake macrophytes, while the impact of *catchment buffers* was strongest at coarser scales. Moreover, the most significant hydrological and land use indicators to explain macrophyte richness differed between growth forms. Thus, floating macrophytes were most affected by stream density within *landscape buffers*, suggesting proportionally more reliance on biological vectors or wind-aided transport at small spatial scale and more dependence on water-borne dispersal (hydrochory) at larger buffer sizes. Conversely, emergent macrophytes were more closely related to lake coverage in *catchment buffers*, potentially because their seeds disperse more easily via wind or biological vectors and benefit from the increased edge habitat associated with water body extent.

Our study also highlights the key spatial extent of *landscape* or *catchment buffers* for restricting adverse effects of human activities, such as drainage, stream engineering and farming, on lake ecosystems, especially those with protected status. 1 km of *landscape buffer* from the lake shoreline is regarded as the most relevant area influenced by agriculture and urbanization, while alterations to the drainage network (e.g. ditching, impoundment, abstraction) within 5 km of the lake upper area (within *catchment buffer*) should be minimised to reduce impacts on macrophyte species richness.

Acknowledgements

We are grateful to JNCC for making available the lake macrophyte survey data used in this study. We also thank Laurence Carvalho (Centre for Ecology & Hydrology), and Alan Law and Luc Bussiere (University of Stirling) for their advice on statistical analyses and comments on a draft manuscript. Partial funding support for this work was provided by University of Stirling.

Appendices A-C. Supplementary data

Supplementary data associated with this article can be found in the end of the manuscript.

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