Interaction between patch area and shape: lakes with different formation processes have contrasting area and shape effects on macrophyte diversity

Concise title: Interaction between lake area and shape

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Abstract

Although both patch area and shape are key factors driving biodiversity in fragmented terrestrial landscapes, researchers have had limited and mixed success in documenting the effects of these two factors on aquatic ecosystems. Here we examined the effects of lake area and shape on macrophyte species richness in a lowland floodplain by considering the differences in lake types, i.e. marsh, oxbow and man-made lakes. We surveyed species richness of native macrophytes in 35 lakes including 11 marshes, 11 oxbow and 13 man-made lakes with various complex shapes ranging covering from 0.25 to 46.3 ha. Model selection clearly supported the existence of interaction between area and shape effects: large-circular and small-complex lakes supported higher macrophyte species richness while it was lower in large-complex and small-circular lakes. Among the three lake types, marsh lakes were more circular and man-made lakes had more complex shapes, while oxbow lakes were intermediate between these two. Also, marsh lakes had positive species-area relationships while man-made lakes had negative relationships. Our results suggest the opposing shape complexity and species-area relationships of these two contrasting lake types are the result of the interactions between lake area and shape. These results indicate that different lake types result in variations in their conservation value for preserving macrophyte diversity. We suggest that small complex-shaped patches (especially oxbow lakes), which are often given the lowest conservation priority in terrestrial ecosystems, cannot be disregarded when conserving macrophyte biodiversity in aquatic ecosystems.

Keywords: area-shape interaction, edge effect, floodplain lake, macrophyte assemblages, management, oxbow lake

Introduction

Loss and fragmentation of natural habitats form the primary threat to biodiversity at local, regional and global scales (Fahrig 2003; Foley et al. 2005). Since the positive relationship between patch area and species richness (i.e. species-area relationship) is called one of the '*general laws in ecology*' (e.g. Lawton 1999), patch area is the most important driver of species richness in fragmented landscapes because large patches have high colonization rates (Lomolino 1990) and low extinction rates (Hanski 1999; MacArthur and Wilson 1967) compared with small ones. Moreover, large patches may be more heterogeneous and provide more complex habitats, enabling them to support a higher number of species (e.g. Connor and McCoy 1979; Russell et al. 2006). For these reasons, a need exists to focus on patch-interior species, because large patches are believed to have higher conservation values (see also Diamond 1975).

The edge effects of both patch area and shape complexity have large effects on local species diversity and population size in fragmented habitats (Laurance and Yensen, 1991; Ewers et al. 2007; Ewers and Didham 2007; Yamaura et al. 2008). Ewers et al. (2007) and Ewers and Didham (2007) suggested that small patches and those with complex shapes have much stronger edge effects because of a strong synergistic interaction between area and edge effects. In such patches, interior species are likely to be detrimentally affected by a loss of area and shape complexity (Yamaura et al. 2008), because the ratio of edge habitat increases in small patches and in those with complex shapes (Laurace and Yensen 1991; Ewers and Didham 2007). However, studies testing the interaction between area and shape effects are scarce and limited in terrestrial ecosystems (e.g. Ewers et al. 2007). Testing such interaction is important because if shape complexity affects species-area relationships, conservation plans and actions designed to mitigate area loss that do not consider shape complexity would be ineffective: i.e. species conservation is not always accomplished by simply increasing patch size.

In aquatic ecosystems, lakes support higher species diversity and more unique species of macroinvertebrates and macrophytes than other lotic habitats (e.g. rivers, streams and ditches), and have been called hotspots that could greatly contribute to the regional diversity (Williams et al. 2004; Biggs et al. 2005). Moreover, because lentic habitats are easily distinguished from other landscape elements such as ‘aquatic islands’ (De Meester et al. 2005), we can easily use lentic habitats to examine the relative importance of patch area and shape on biodiversity. In aquatic ecosystems, the biogeographical principle that a larger area supports more species has been tested many times (Moller and Rordam 1985; Gee et al. 1997; Jeffries 1998; Biggs et al. 2005). Although the relationships between patch shape and species diversity in terrestrial ecosystems are receiving increasing attention (e.g. Laurance and Yensen 1991), those of aquatic ecosystems are mostly unknown. Because patch area and shape could easily be measured and these factors have strong effects on species diversity, they were considered to be one of the most fundamental factors needing consideration when one is planning the preservation and restoration of nature reserves (e.g. Yamaura et al. 2008). Therefore, to prevent future species loss caused by landscape change and to conserve and manage these species, we need to understand how lake area and shape affect species diversity.

In the last few decades, biodiversity of aquatic habitats has declined drastically (Jenkins 2003). In particular, human activities have caused a widespread loss and degradation of floodplains, making biodiversity conservation and management of floodplain lakes one of the most important tasks for land managers in recent years (Sparks 1995; Tockner and Stanford 2002). Here, we examined the effects of lake area, shape and their interaction on macrophyte species richness in floodplain lakes that are considered appropriate model systems for testing those effects because many lakes take on various shapes and sizes. Generally, preserving foundation species must be incorporated into conservation strategies because they make habitat conditions more favorable for other species (Crain and Bertness 2006; Halpern et al. 2007). Macrophytes serve this function in aquatic ecosystems. For example, the physical structure of wetland macrophytes and their ability to help maintain water quality leads to lakes providing habitat and refugia to other aquatic organisms (Hatzenbeler et al. 2000; Miranda et al. 2000; Burks et al. 2001). Therefore, understanding how lake area and shape affect wetland macrophyte species richness is crucial during the management and conservation of floodplain biodiversity. In floodplain ecosystems, habitat edge can be clearly defined as “shoreline area”. For wetland macrophyte species, unlike many terrestrial organisms, “habitat edge” (i.e. shoreline area) offers a stable habitat for macrophytes, rather than unstable habitats (Jeppesen et al. 1990). Therefore, when the interactive effect of lake area and shape is evident, such an interaction pattern may be different from those reported in terrestrial ecosystems (e.g. Ewers et al. 2007).

Methods

Study area

Our study lakes are located in the downstream part of the floodplain of the Ishikari River (Fig. 1), which originates in the Taisetsu mountain system and flows into the Japan Sea. The 268 km long Ishikari River has the second largest watershed in Japan (14,330 km^2). The Ishikari was previously a typical meandering river and was drastically straightened during the 1900s. Starting in 1918, channel modification for flood control and agricultural land reclamation straightened the meandering river, and levee construction isolated many lakes and wetlands from the main channel. By the late 1970s, most lakes and wetlands occurred within agricultural and residential areas. Three types of lakes occur in the study area: i.e. back-water marsh lakes (marsh lakes hereafter), oxbow lakes, and short-cut lakes (man-made lakes) (Hayashida et al. 2010). Marsh lakes tend to occur in relatively downstream areas while oxbow lakes tend to be in upstream areas. Over the last century, man-made lakes have been increasingly created by channel modifications (i.e. “man-made” oxbow lakes).

Study lakes and vegetation survey

A total of 35 lakes ranging from 0.25 to 46.3 ha were selected (Fig. 1), including 11 marsh, 11 oxbow, and 13 man-made lakes (Appendix A). Lake types were classified as reported in Hayashida et al. (2010). No relationship exists between the rank order of lakes from upstream to downstream and macrophyte species richness (Spearman’s rank correlation, r =–0.15, p =0.21), indicating no cline of macrophyte species richness from upstream to downstream in our study area.

Individual surveys were conducted at each lake site during a single visit during August in either 2003, 2004, 2005, or 2006. We used an inflatable boat to observe and record all macrophyte species present on the sampling routes. Two people spent 5 hours surveying each lake or a total of 10 man-hours. Identifications of macrophyte species were based on observation of a part of the mature plant body (i.e. flowers, seeds and turions). We photographed macrophyte species and created specimens of species, which could be identified in the field. Finally, we counted the number of plant species present after identifying the macrophyte species following the taxonomy of Kadono (1994). In this study, we recorded submerged, floating-leaved, and emergent plant species.

A geographic information system (ArcView ver. 3.2, ESRI, CA) and large-scale aerial photographs (1:2,500 scale) were used to quantitatively assess the lake area and shape complexity. To describe the shape of each lake, we calculated a shape index (SI) proposed by Laurance and Yansen (1991) as follows: $SI = P/200[(\pi TA)^{0.5}]$, where P is the perimeter length of the lake (m) and TA is the total area of the lake (ha). The SI describes the deviation of each patch from simplicity (≥ 1), which means that as the value of SI increases, the lake shape becomes more complex (see also Appendix B). Although water depth and slope are important factors determining the distribution of aquatic macrophytes (Duarte and Kalff 1986; Van Geest et al. 2003), we did not measure these parameters because of the difficulty in characterizing these parameters. Water depths and slopes are highly variable within lakes. Therefore, we would have needed to develop a detailed bathymetric map showing lake-bottom topography in each lake to assess the depth and slope effects (Remillard and Welch 1993), which is beyond the scope of the present study. Rather, we were interested in how accurately macrophyte diversity can be predicted using only lake area and shape without measures requiring additional labor and expense.

Statistical analysis

To examine the relative importance of lake area, shape and the interaction between lake area and shape on macrophyte species richness, we used generalized linear models (GLMs) with a Poisson distribution and a log link function. The number of macrophyte species in each lake was used as a response variable, and lake area, shape index in each lake and their interaction term (area × shape) were used as explanatory variables. Lake area (ha) was log-transformed. To select the best models among all five possible combination models, we used *Akaike's Information Criterion* (*AIC*, Burnham and Anderson 2002). The *AIC* for each model quantifies its parsimony (based on the trade-off between the model fit and the number of parameters included) relative to other models considered. All of the models were ranked by ΔAIC ($\Delta AIC_i = AIC_i - AIC_{\min}$; where AIC_i and $AIC_{\min}$ represents the i^{th} model and the best model in the model subsets, respectively) such that the model with the minimum *AIC* had a value of 0. Models for which $\Delta AIC \leq 2$ were considered to have substantial support (Burnham & Anderson 2002). The plausibility of each model is quantified by its relative likelihood, which is proportional to the exponent of $-0.5 \times \Delta AIC$ given our data. For each candidate model, we divided this likelihood by the sum of the all models and compiled the *Akaike weights* (w_i). We conducted these analyses using the "dredge" function from the "MuMIn" package (ver. 1.0.0) (Barton 2009). The explanatory power of each model was tested by the percentage of deviance explained by each model to a null model (i.e., a model not containing any explanatory variables). We calculated this value as follows: % deviance explained = (1 – residual deviance/null deviance) × 100. GLMs were structured for all types of lakes combined (i.e. total lakes or all lakes irrespective of lake types) and separately for each of the three different types of lakes as three separate groups.

Differences of lake area, shape complexity and species richness among three lake types were tested by general linear hypotheses, using the "glht" function from the "multcomp" package (ver. 1.2.12; Hothorn et al. 2012). In this analysis, we used Poisson and Gaussian (normal) distribution for macrophyte species richness, and for lake area and shape, respectively. All of the analyses were conducted using the R software package (ver. 2.12.0, R Development Core Team).

Results

In total, we found 52 macrophyte species in 35 lakes (Table 1). Although two exotic species (*Nelumbo nucifera*, *Iris pseudacorus*) were found, they were excluded from the analyses. Among 50 native macrophytes, three species (*Monochoria korsakowii*, *Sparganium erectum*, and *Utricularia australis*) and two species (*Sparganium simplex* and *Typha angustifolia*) were classified as Near Threatened species (NT species hereafter) by the Red Data Book (Ministry of the Environment (Japan) 2000) and Rare species (R species hereafter) by the Red Data Book in Hokkaido (Hokkaido government 2001), respectively.

Biotic and abiotic features of three lake types

Macrophyte species richness was significantly lower in the man-made lakes than in the marsh and oxbow lakes (Fig. 2a). Among the three lake types, lake areas were not significantly different (Fig. 2b). However, marsh lakes had significantly lower SIs (i.e. simple shape) and man-made lakes tended to have high SIs (i.e. complex shape) (Fig. 2c). Additionally, man-made lakes tend to show a positive correlation between lake area and shape complexity ($r = 0.54$, $p = 0.09$). Also, marsh and oxbow lakes had negative correlations between lake area and shape complexity (marsh: $r = –0.52$, $p = 0.07$; oxbow lake: $r = –0.71$, $p < 0.05$).

Interactions between area and shape effects

For total lakes (including all three lake types), model selection based on *AIC* showed that the full model (containing all three explanatory variables) was best supported (Table 2), suggesting an interactive effect exists between lake area and shape complexity on macrophyte species richness. Scatter plots (Fig. 3a) and prediction of the full model (Fig. 3b) showed that large-simple lakes and small-complex lakes had higher species richness than those with other combinations of area and shape complexity. In contrast, macrophyte species richness was low in large-complex lakes and small-simple lakes. In particular, differences of species richness between large-complex and large-simple lakes were clearest (Fig. 3a). Scatter plots of the different lake types (Fig. 3b) showed that these two contrasting lake types (i.e. large-complex and large-simple lakes) were composed of mainly man-made and marsh lakes, respectively (Fig. 3b).

For marsh and man-made lakes, the ΔAIC values for the top two models were > 2.0 (Table 2), indicating that Model 1 had the strongest support (Burnham and Anderson, 2002). Therefore, positive and negative correlations between macrophyte species richness and lake area were strongly supported for marsh and man-made lakes, respectively. For oxbow lakes, the null model was best supported (Table 2), suggesting that macrophyte species richness in oxbow lakes could not be well explained by lake area and shape.

Discussion

Interactions between lake area and shape

In this study, we found a significant interaction between lake area and shape effects on macrophyte species richness. However, mechanisms underlying such interaction in our study are considered to be different from those assumed in terrestrial ecosystems for the following two main reasons. First, the interaction pattern in our study is different from previous findings in fragmented forest areas. Generally, species richness is lowest in small-complex areas and highest in large-circular patches (Ewers et al. 2007). However, in our study, high species richness was found not only in large-simple lakes but even in small-complex lakes. Second, interaction between lake area and shape was only evident in analysis using all three lake types as a single unit for analysis, but we could not observe such interaction when analyzing different types of lakes separately. Overall, interaction between lake area and shape in this study may not be the result of direct effects of area loss and increasing edge area as reported in terrestrial ecosystems (Ewers et al. 2007).

It was initially puzzling that such a clear interaction between area and shape effects was observed in our study. Close examinations of species-area relationships specific to each of the different types of lakes provided insights into the process behind such an interaction. In this study, positive species-area relationships were found in simple-shaped lakes and negative relationships were found in complex-shaped lakes. As previously mentioned, marsh lakes had the simplest shape (Fig. 2c) and a positive relationship between species richness and lake area. In contrast, man-made lakes tended to have complex shapes and a negative relationship between species richness and lake area. Thus, these two lake types, marsh and man-made lakes that have contrasting shape complexity and species-area relationships, would result in these types of interactions.

A driver of variable area-species richness relationships

A positive relationship between lake area and macrophyte species richness was observed only in marsh lakes. In this region, marsh lakes tend to occur along the downstream segments where main channels are constrained by relatively stable natural levees. Overbank deposition of transported sediment that gradually buries scroll-bar topography results in flat and shallow lakes (Mertes et al. 1996). Such a shallow area was the preferred habitat for macrophytes because low water depth decreases wind-stress (Hudon et al. 2000) and increases light availability (Middelboe and Markager 1997). Therefore, in marsh lakes, increasing lake area may directly increase the extent of stable habitat available for macrophytes.

Oxbow lakes exhibited no clear relationship between lake area and macrophyte species richness. The most important difference in species occurrence patterns between marsh and oxbow lakes is that, for oxbow lakes, even small lakes had relatively high species richness compared with that of large lakes. Several mechanisms can be suggested to explain the advantage small lakes have in relation to species diversity. First, fish abundance may be low in small lakes because of the high risk of oxygen depletion (Jeppesen et al. 1990); an abundance of fish can negatively affect macrophyte diversity through predation (Scheffer et al. 2006) and bioturbation (Matsuzaki et al. 2007). Second, macrophyte growth in small lakes may be less hampered by wind-stress (Hudon et al. 2000). In our study, small oxbow lakes (i.e., Lake #1, 2) had relatively high shape complexity (Appendix A), indicating such small lakes have a higher ratio of shoreline to surface area (panel (b) in Appendix B). Because shoreline acts as a refuge for herbivorous zooplankton (Burks et al. 2001), which could lead to a reduction in phytoplankton populations, complex shorelines could allow sunlight to penetrate into the water and so promote the growth of submerged macrophytes (Jaspen et al. 1990). Overall, in oxbow lakes, such an advantage of small lakes may obscure significant positive species-area relationships.

Man-made lakes had the lowest macrophyte species richness of the three lake types (Fig. 2) and they also have a negative species-area relationship. Artificially disconnected floodplain lakes tend to have different bottom morphometry compared with those formed naturally. For example, they could be relatively deep for a given surface area (Miranda 2005); this is possibly a result of their short history of receiving deposition of sediment and organic matter from floods. As a result, wave stress on macrophytes, which is a function of depth and surface area to some extent, may be stronger in man-made lakes, especially in large man-made lakes. Therefore, in man-made lakes, we found a negative species-area relationship exists that is in contrast to island biogeographic theory (MacArthur and Wilson, 1967). These results suggest that species-area relationships would be different among the three lake types, which have different formation processes and geomorphic characteristics. However, in this study, we only used lake area and shape as habitat parameters and did not measure bottom morphometric characteristics (e.g., water depth). Therefore, in future studies, combining both two- and three-dimensional lake morphometry may allow us to predict and understand macrophyte community and population dynamics comprehensively (Van Geest et al., 2003).

The role of small lakes with complex shapes in floodplain conservation

Marsh had a positive species-area relationship, suggesting that larger marsh lakes have high conservation value for macrophytes. In contrast, for oxbow and man-made lakes, small lakes had higher species richness when compared with large lakes, suggesting that small lakes are as important as large lakes in terms of species richness. Based on these results, in the upstream regions where mostly man-made and oxbow lakes are found mixed along the floodplains, given that the surface areas are equivalent, conserving small oxbow lakes may be important for macrophyte diversity conservation. In this study, NT and R species were frequently observed in oxbow and marsh lakes (Appendix A); therefore conserving small oxbow lakes rather than small man-made lakes would be desirable. Even small lakes, such as small oxbow lakes, would serve an important role for maintaining local biodiversity in floodplain ecosystems. Because maintaining small lakes is relatively easy, such lakes cannot be disregarded in conservation planning and land management.

On the other hand, in the downstream region where marsh and man-made lakes are found together more frequently, large marsh lakes would have the highest conservation priority. Without considering lake formation processes or types, we may misunderstand the value of small lakes with complex shape. In this study, we focused only on macrophyte species, but other taxa that have a commensal relationship with macrophytes may show similar responses to lake area and shape (e.g., aquatic insects, Randall et al. 1996 and Hatzebeler et al. 2000; plankton, Burks et al. 2001; birds, Ruggles 1994 and Taut et al. 2004). Examining the responses of multiple taxa to lake morphometry (inclusive of bed topography) with the consideration of not only local but also regional species richness will help facilitate regional planning for better management of biodiversity.

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Figure legends

Fig. 1

Location of the study region in Hokkaido, Japan (inset) and 35 study lakes along the Ishikari River.

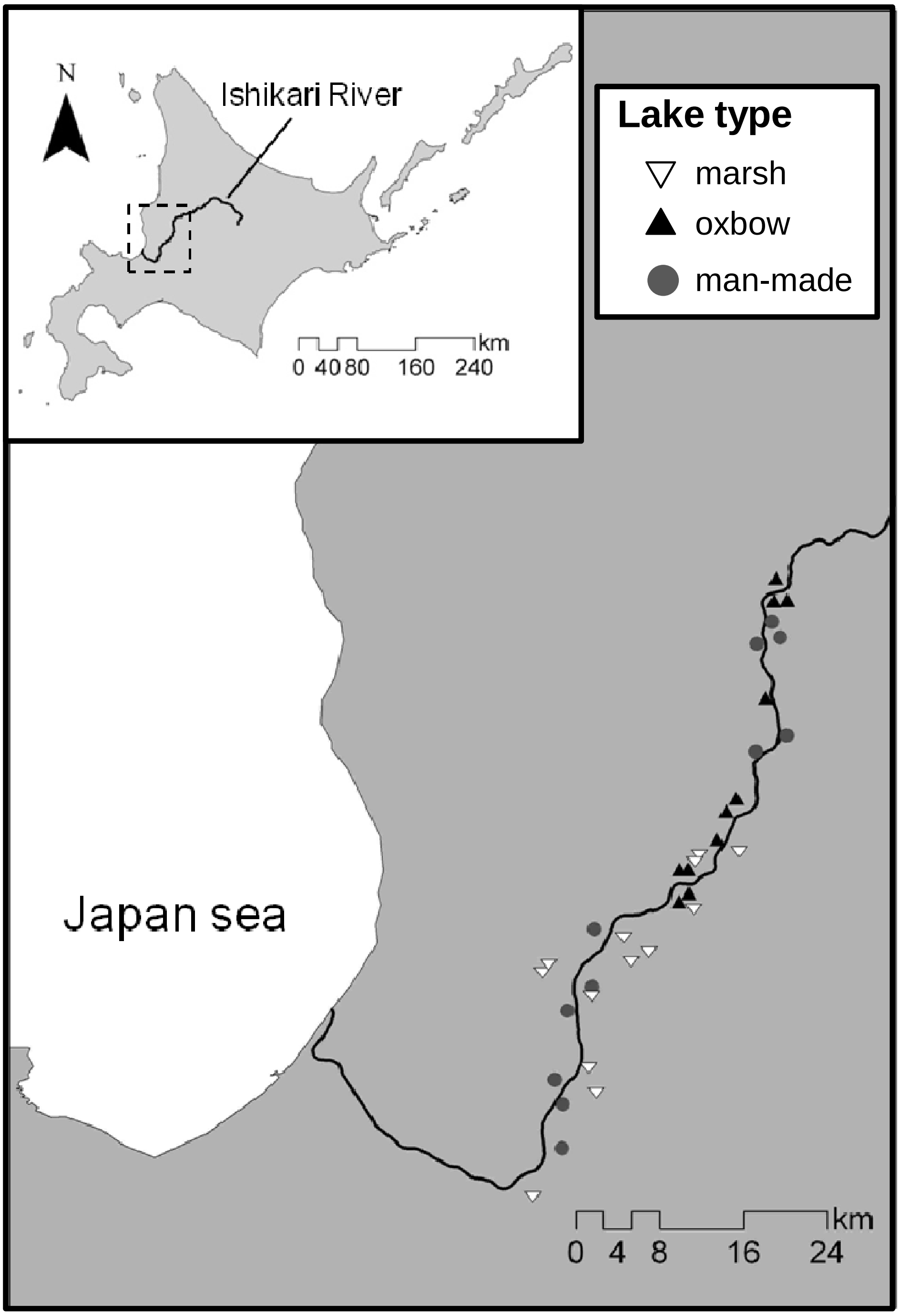
Fig. 2

Macrophyte species richness (a), lake area (b), and lake shape complexity (c) for the three lake types. The central bar in the boxplot indicates the median, the ends of the boxes indicate the interquartile range, and the whiskers indicate the 10^{th} and 90^{th} quantiles. These differences were tested by general linear hypotheses (* $p < 0.05$, ** $p < 0.01$).

Fig. 3

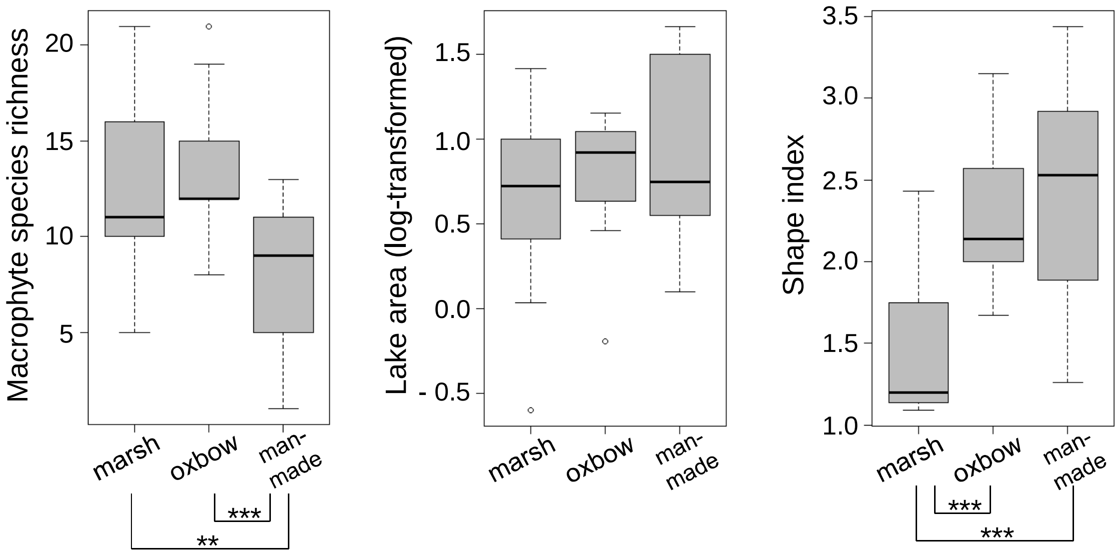
Relationships between lake area, lake shape, and macrophyte species richness. In panel (a), the size of bubble shows observed macrophyte species richness. In panel (b), white triangles, black triangles, and white circles indicate marsh, oxbow and man-made lakes, respectively. Contour lines show macrophyte species richness predicted in the best model (full model) in total lakes in Table 2: macrophyte species richness = exp $(1.06 \times A + 0.17 \times SI - 0.46 \times A \times SI + 2.13)$.

476 **Fig. 1**


N
Ishikari River
0 40 80 160 240 km
Lake type
marsh
oxbow
man-made
Japan sea
0 4 8 16 24 km

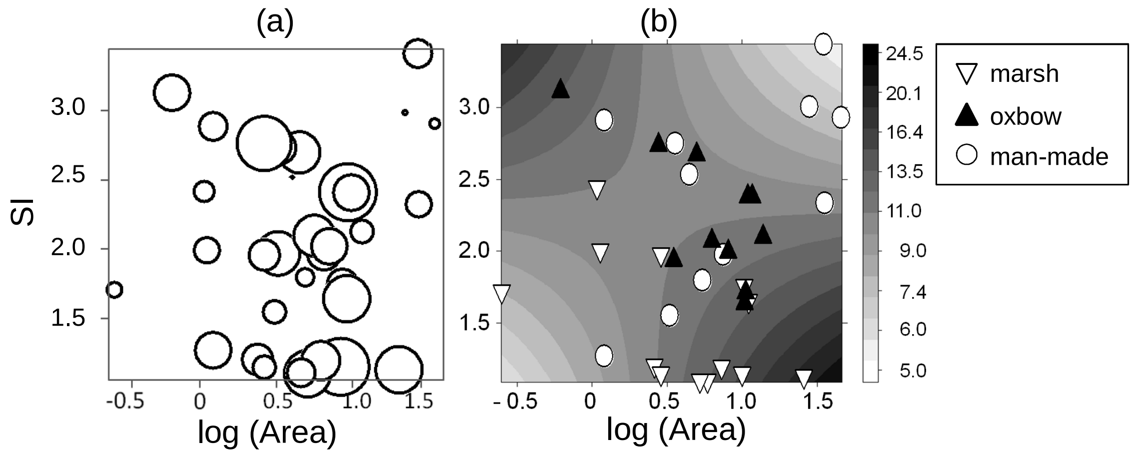
477

Fig. 2



Macrophyte species richness
20
15
10
5
marsh
oxbow
man-made
***
**
Lake area (log-transformed)
1.5
1.0
0.5
0.0
- 0.5
marsh
oxbow
man-made
Shape index
3.5
3.0
2.5
2.0
1.5
1.0
marsh
oxbow
man-made
***
***

Fig. 3



(a)
(b)
SI
3.0
2.5
2.0
1.5
-0.5
0
0.5
1.0
1.5
log (Area)
24.5
20.1
16.4
13.5
11.0
9.0
7.4
6.0
5.0
marsh
oxbow
man-made

Table 1

List of 52 macrophyte species observed in our study area. Lake ID corresponds to Appendix A.

Species	Lake ID																																			Life-form	Rank**
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35		
Equisetum fluviatile	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●			●	●			●							●	●	●		E	-
Equisetum palustre	●												●			●	●																			E	-
Persicaria amphibia		●	●		●																						●							●		E	-
Nulumbo nucifera			●																																	E	E
Nuphar japonicum	●	●	●	●		●				●	●	●	●	●	●			●		●				●	●	●		●		●				●	●	E	-
Nymphaea hybrida			●															●							●			●							●	E	-
Nymphaea tetragona		●								●			●											●	●	●										F	-
Ceratophyllum demersum	●	●	●				●			●		●						●							●	●		●		●					●	F	-
Elatine triandra													●					●																		S	-
Trapa japonica	●	●	●		●	●	●		●	●	●	●	●		●	●	●	●	●		●	●	●	●	●	●		●		●		●			●	F	-
Myriophyllum spicatum																														●					●	S	-
Myriophyllum verticillatum		●		●	●		●			●		●					●																		●	S	-
Menyanthes trifoliata																												●							●	E	-
Callitriche verna						●																														S	-
Utricularia australis							●					●								●	●			●						●						F	NT
Utricularia tenuicaulis																																			●	F	-
Alisma canaliculatum													●								●					●										S	-
Alisma plantago-aquatica												●						●				●											●			E	-
Sagittaria aginashi																																				E	-
Sagittaria trifolia						●	●				●										●												●			E	-
Hydrilla verticillata																									●	●		●								S	-
Potamogeton compressus		●	●							●								●																		S	-
Potamogeton crispus																	●																			S	-
Potamogeton distinctus	●			●																																F	-
Potamogeton fryeri																																			●	F	-
Potamogeton maackianus			●							●								●										●							●	S	-
Potamogeton natans		●																																		F	-
Potamogeton octandrus	●	●	●	●			●										●	●	●		●		●			●				●		●			●	F	-
Potamogeton oxyphyllus																														●					●	S	-
Potamogeton perfoliatus																																			●	S	-
Potamogeton pusilla							●					●						●												●						S	-
Monochoria korsakowii									●				●																							E	NT
Iris pseudacorus	●	●		●	●	●	●			●	●					●	●		●								●				●			●		E	E
Murdannia keisak																					●	●														E	-
Phragmites australis	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	E	-
Zizania latifolia		●		●	●				●	●	●	●	●		●	●		●		●	●	●	●	●	●	●		●		●		●	●	●	●	E	-
Acorus calamus	●		●					●	●	●					●			●	●		●	●					●								●	E	-
Lemna aoukikusa													●		●					●			●	●				●		●		●				F	-
Lemna minor		●		●	●			●	●	●		●				●	●	●				●				●							●	●		F	-
Spirodela polyrhiza		●		●	●		●			●		●	●	●		●	●	●	●	●	●	●	●	●	●	●				●		●			●	F	-
Sparganium erectum		●				●	●	●				●										●								●		●				E	NT
Sparganium simplex	●	●		●																																E, F,	R
Typha angustifolia																					●					●				●						E	R
Typha latifolia	●	●		●		●	●	●		●	●	●			●	●	●	●	●	●	●	●	●	●	●	●		●		●		●			●	E	-
Eleocharis acicularis						●			●		●		●					●														●	●			E	-
Eleocharis intersita																																				E	-
Eleocharis mamillata																			●							●										E	-
Scirpus hotarui											●		●					●			●												●			E	-
Scirpus juncoides						●																														E	-
Scirpus tabernaemontani	●	●	●		●	●	●				●	●	●	●	●	●	●	●	●		●	●	●	●		●				●		●	●	●	●	E	-
Scirpus triangulatus											●											●											●		●	E	-
Scirpus triqueter		●			●	●					●																						●			E	-
Scirpus yagara													●				●	●			●									●					●	E	-
Total species richness	13	20	13	12	11	13	14	6	8	15	13	15	16	5	9	10	13	21	9	7	16	13	8	10	11	15	4	11	1	17	2	11	11	8	21		

* E: emergent plants, F: floating plants, S: submerged plants.

** NT: near threatened species, R: rare species, E: exotic species. NT and R species were defined by Red Data Book in Japan (Ministry of the Environment (Japan) 2000) and Hokkaido (Hokkaido 2001), respectively.

Table 2

Results of model selection base on AIC.

Rank	*Variables* (intercept)	A	SI	A × SI	*K* *	*Deviation*	*AIC*	⊿*AIC**	w_i *	*% deviance explained*
Total lakes (*N* = 35)										
Model 1	1.92	1.15	0.19	-0.50	4	-103.58	216.5	0.00	0.95	22.35
Model 2	2.80		-0.19		2	-109.50	223.4	6.88	0.03	0.08
Model 3	2.78	0.04	-0.20		3	-109.41	225.6	9.10	0.01	0.08
Model 4	2.42				1	-112.59	227.3	10.80	0.00	0.00
Model 5	2.41	0.02			2	-112.57	229.5	13.02	0.00	0.00
Marsh lakes (*N* = 13)										
Model 1	2.10	0.61			2	-31.01	67.2	0.00	0.76	68.61
Model 2	2.44	0.53	-0.20		3	-30.66	70.0	2.77	0.19	72.12
Model 3	3.25		-0.52		2	-34.42	74.0	6.81	0.03	34.35
Model 4	2.41	0.58	-0.18	-0.03	4	-30.66	74.3	7.10	0.02	72.14
Model 5	2.50				1	-37.83	78.0	10.80	0.00	0.00
Oxbow lakes (*N* = 11)										
Model 1	2.61				1	-29.83	62.1	0.00	0.56	0.00
Model 2	2.12		0.21		2	-29.19	63.9	1.77	0.23	11.62
Model 3	2.71	-0.14			2	-29.61	64.7	2.62	0.15	3.95
Model 4	1.97	0.07	0.25		3	-29.16	67.8	5.65	0.03	12.05
Model 5	4.39	-2.97	-0.57	1.09	4	-27.19	69.1	6.95	0.17	47.76
Artificial lakes (*N* = 11)										
Model 1	2.43	-0.41			2	-32.89	71.3	0.00	0.56	17.06
Model 2	2.06				1	-35.18	73.5	2.20	0.19	0.00
Model 3	2.69		-0.27		2	-34.14	73.8	2.51	0.16	8.91
Model 4	2.62	-0.39	-0.10		3	-32.74	74.9	3.63	0.09	18.02
Model 5	2.63	-0.42	-0.11	0.01	4	-32.74	80.1	8.87	0.01	18.02

* *K* : Number of model parameters, ⊿*AIC* : *AIC* differences, w_i : Akaike weights.

Appendix A

Characteristics of 35 sample lakes, listed in the order of longitudinal positions from upstream to downstream along the Ishikari River.

Lake ID	Macrophyte species richness	Lake area (ha)	Shape index	Lake type*	Number of NT and R species**	Year of contruction
1 Tanba-no-numa	13	0.64	3.15	O	1	
2 Uryu-numa	20	2.87	2.78	O	2	
3 Ebeotsu-kyutyome	13	8.32	2.03	O	-	
4 Tako-no-kubi	12	3.68	2.75	MM	1	1938-1939
5 Ike-no-mae	11	35.20	3.44	MM	-	1939-1941
6 Shisun-numa	13	1.25	1.26	MM	1	1939-1941
7 Naka-toppu	14	5.10	2.72	O	3	
8 Hokko-numa	6	5.60	1.80	MM	1	1941-1951
9 Shimo-toppu	8	3.40	1.55	MM	-	1964-1969
10 Pira-numa	15	6.50	2.10	O	-	
11 Toi-numa	13	11.89	2.42	O	-	
12 Urausu-numa	15	3.60	1.97	O	3	
13 Tyashinai-numa	16	11.04	1.64	M	-	
14 Utsugi-numa	5	0.25	1.71	M	-	
15 Tsuki-numa	9	1.13	2.00	M	-	
16 Higashi-numa	10	10.77	1.75	O	-	
17 Nishi-numa	13	10.65	1.67	O	-	
18 Hishi-numa	21	11.23	2.42	O	1	
19 Ito-numa	9	14.18	2.14	O	-	
20 Sakura-numa	7	1.08	2.43	M	1	
21 Miyajima-numa	16	25.87	1.12	M	2	
22 Omagari-ugan	13	7.62	1.97	MM	1	1941-1955
23 Tegata-numa	8	2.88	1.14	M	-	
24 Sankaku-numa	10	5.24	1.10	M	-	
25 O-numa(Tsukiga-ko	11	10.30	1.75	M	-	
26 Ko-numa(Tsukiga-k	15	7.22	1.19	M	1	
27 Karisato-numa	4	46.26	2.93	MM	-	1939-1940
28 Kagami-numa	11	2.58	1.20	M	-	
29 Kawakami-numa	1	4.55	2.53	MM	-	1940-1949
30 O-numa	17	5.84	1.09	M	4	
31 Hukuro-tappu	2	28.52	3.01	MM	-	1934-1939
32 Naga-numa	11	2.88	1.96	M	1	
33 Horo-tappu	11	1.25	2.91	MM	-	1934-1939
34 Tomoe-nojyo	8	35.69	2.33	MM	-	1935-1938
35 Echigo-numa	21	9.99	1.14	M	-	

* M: marsh, MM: man-made, and O: oxbow lakes
** NT and R species were defined by Red Data Book in Japan (Environment Agency of Japan 2000) and Hokkaido (Hokkaido 2001), respectively.

Appendix B

Examples of lakes with lowest (a) and highest (b) SI. Both broken lines and arrows indicate the surface of lakes.