



Title	Interaction between patch area and shape: lakes with different formation processes have contrasting area and shape effects on macrophyte diversity
Author(s)	Soga, Masashi; Ishiyama, Nobuo; Sueyoshi, Masanao; Yamaura, Yuichi; Hayashida, Kazufumi; Koizumi, Itsuro; Negishi, Junjiro N.
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1 **Interaction between patch area and shape: lakes with**
2 **different formation processes have contrasting area and shape**
3 **effects on macrophyte diversity**

4 **Concise title:** Interaction between lake area and shape

5 Masashi Soga^a, Nobuo Ishiyama^a, Masanao Sueyoshi^a, Yuichi Yamaura^a, Kazufumi
6 Hayashida^{b,c}, Itsuro Koizumi^d, Junjiro N. Negishi^e

7 ^a*Division of Environmental Resources, Graduate School of Agriculture, Hokkaido University, Nishi
8 9, Kita 9, Kita-ku, Sapporo 080-8589, Japan*

9 ^b*Watershed Environmental Engineering Research Team, Civil Engineering Research Institute for
10 Cold Region, Hiragishi 1–3, Toyohira-ku, Sapporo 062-8602, Japan*

11 ^c*Division of Biosphere Science, Graduate School of Environmental Science, Hokkaido University,
12 Nishi 9, Kita 9, Kita-ku, Sapporo 060-0809, Japan*

13 ^d*Creative Research Institution, Hokkaido University, Kita 21, Nishi 10, Kita-ku, Sapporo 001-0021,
14 Japan*

15 ^e*Faculty of Environmental Earth Science, Hokkaido University, Kita 10, Nishi 5, Kita-ku, Sapporo
16 060-0810, Japan*

17 **Corresponding author:** Masashi Soga

18 Division of Environmental Resources, Graduate School of Agriculture, Hokkaido University, Nishi 9,
19 Kita 9, Kita-ku, Sapporo 080-8589, Japan

20 E-mail address: soga06154053@yahoo.co.jp

21

22 **Abstract**

23 Although both patch area and shape are key factors driving biodiversity in fragmented
24 terrestrial landscapes, researchers have had limited and mixed success in documenting
25 the effects of these two factors on aquatic ecosystems. Here we examined the effects of
26 lake area and shape on macrophyte species richness in a lowland floodplain by
27 considering the differences in lake types, i.e. marsh, oxbow and man-made lakes. We
28 surveyed species richness of native macrophytes in 35 lakes including 11 marshes, 11
29 oxbow and 13 man-made lakes with various complex shapes ranging covering from
30 0.25 to 46.3 ha. Model selection clearly supported the existence of interaction between
31 area and shape effects: large-circular and small-complex lakes supported higher
32 macrophyte species richness while it was lower in large-complex and small-circular
33 lakes. Among the three lake types, marsh lakes were more circular and man-made lakes
34 had more complex shapes, while oxbow lakes were intermediate between these two.
35 Also, marsh lakes had positive species-area relationships while man-made lakes had
36 negative relationships. Our results suggest the opposing shape complexity and
37 species-area relationships of these two contrasting lake types are the result of the
38 interactions between lake area and shape. These results indicate that different lake types
39 result in variations in their conservation value for preserving macrophyte diversity. We
40 suggest that small complex-shaped patches (especially oxbow lakes), which are often
41 given the lowest conservation priority in terrestrial ecosystems, cannot be disregarded
42 when conserving macrophyte biodiversity in aquatic ecosystems.

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

46 **Introduction**

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

58 The edge effects of both patch area and shape complexity have large effects on
59 local species diversity and population size in fragmented habitats (Laurance and Yensen,
60 1991; Ewers et al. 2007; Ewers and Didham 2007; Yamaura et al. 2008). Ewers et al.
61 (2007) and Ewers and Didham (2007) suggested that small patches and those with
62 complex shapes have much stronger edge effects because of a strong synergistic
63 interaction between area and edge effects. In such patches, interior species are likely to
64 be detrimentally affected by a loss of area and shape complexity (Yamaura et al. 2008),
65 because the ratio of edge habitat increases in small patches and in those with complex
66 shapes (Laurace and Yensen 1991; Ewers and Didham 2007). However, studies testing
67 the interaction between area and shape effects are scarce and limited in terrestrial
68 ecosystems (e.g. Ewers et al. 2007). Testing such interaction is important because if
69 shape complexity affects species-area relationships, conservation plans and actions

70 designed to mitigate area loss that do not consider shape complexity would be
71 ineffective: i.e. species conservation is not always accomplished by simply increasing
72 patch size.

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

91 In the last few decades, biodiversity of aquatic habitats has declined drastically
92 (Jenkins 2003). In particular, human activities have caused a widespread loss and
93 degradation of floodplains, making biodiversity conservation and management of

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

112

113 **Methods**

114 **Study area**

115 Our study lakes are located in the downstream part of the floodplain of the Ishikari
116 River (Fig. 1), which originates in the Taisetsu mountain system and flows into the
117 Japan Sea. The 268 km long Ishikari River has the second largest watershed in Japan
118 (14,330 km²). The Ishikari was previously a typical meandering river and was
119 drastically straightened during the 1900s. Starting in 1918, channel modification for
120 flood control and agricultural land reclamation straightened the meandering river, and
121 levee construction isolated many lakes and wetlands from the main channel. By the late
122 1970s, most lakes and wetlands occurred within agricultural and residential areas. Three
123 types of lakes occur in the study area: i.e. back-water marsh lakes (marsh lakes
124 hereafter), oxbow lakes, and short-cut lakes (man-made lakes) (Hayashida et al. 2010).
125 Marsh lakes tend to occur in relatively downstream areas while oxbow lakes tend to be
126 in upstream areas. Over the last century, man-made lakes have been increasingly created
127 by channel modifications (i.e. “man-made” oxbow lakes).

128

129 **Study lakes and vegetation survey**

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

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

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

160 additional labor and expense.

161

162 **Statistical analysis**

163 To examine the relative importance of lake area, shape and the interaction between lake
164 area and shape on macrophyte species richness, we used generalized linear models
165 (GLMs) with a Poisson distribution and a log link function. The number of macrophyte
166 species in each lake was used as a response variable, and lake area, shape index in each
167 lake and their interaction term (area \times shape) were used as explanatory variables. Lake
168 area (ha) was log-transformed. To select the best models among all five possible
169 combination models, we used *Akaike's Information Criterion* (*AIC*, Burnham and
170 Anderson 2002). The *AIC* for each model quantifies its parsimony (based on the
171 trade-off between the model fit and the number of parameters included) relative to other
172 models considered. All of the models were ranked by ΔAIC ($\Delta AIC_i = AIC_i - AIC_{\min}$;
173 where AIC_i and AIC_{\min} represents the i^{th} model and the best model in the model subsets,
174 respectively) such that the model with the minimum *AIC* had a value of 0. Models for
175 which $\Delta AIC \leq 2$ were considered to have substantial support (Burnham & Anderson
176 2002). The plausibility of each model is quantified by its relative likelihood, which is
177 proportional to the exponent of $-0.5 \times \Delta AIC$ given our data. For each candidate model,
178 we divided this likelihood by the sum of the all models and compiled the *Akaike weights*
179 (w_i). We conducted these analyses using the "dredge" function from the "MuMIn"
180 package (ver. 1.0.0) (Barton 2009). The explanatory power of each model was tested by
181 the percentage of deviance explained by each model to a null model (i.e., a model not
182 containing any explanatory variables). We calculated this value as follows: % deviance
183 explained = (1 – residual deviance/null deviance) \times 100. GLMs were structured for all

184 types of lakes combined (i.e. total lakes or all lakes irrespective of lake types) and
185 separately for each of the three different types of lakes as three separate groups.

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

192

193 **Results**

194 In total, we found 52 macrophyte species in 35 lakes (Table 1). Although two exotic
195 species (*Nelumbo nucifera*, *Iris pseudacorus*) were found, they were excluded from the
196 analyses. Among 50 native macrophytes, three species (*Monochoria korsakowii*,
197 *Sparganium erectum*, and *Utricularia australis*) and two species (*Sparganium simplex*
198 and *Typha angustifolia*) were classified as Near Threatened species (NT species
199 hereafter) by the Red Data Book (Ministry of the Environment (Japan) 2000) and Rare
200 species (R species hereafter) by the Red Data Book in Hokkaido (Hokkaido government
201 2001), respectively.

202

203 **Biotic and abiotic features of three lake types**

204 Macrophyte species richness was significantly lower in the man-made lakes than in the
205 marsh and oxbow lakes (Fig. 2a). Among the three lake types, lake areas were not
206 significantly different (Fig. 2b). However, marsh lakes had significantly lower SIs (i.e.
207 simple shape) and man-made lakes tended to have high SIs (i.e. complex shape) (Fig.
208 2c). Additionally, man-made lakes tend to show a positive correlation between lake area
209 and shape complexity ($r = 0.54, p = 0.09$). Also, marsh and oxbow lakes had negative
210 correlations between lake area and shape complexity (marsh: $r = -0.52, p = 0.07$; oxbow
211 lake: $r = -0.71, p < 0.05$).

212

213 **Interactions between area and shape effects**

214 For total lakes (including all three lake types), model selection based on *AIC* showed

215 that the full model (containing all three explanatory variables) was best supported
216 (Table 2), suggesting an interactive effect exists between lake area and shape
217 complexity on macrophyte species richness. Scatter plots (Fig. 3a) and prediction of the
218 full model (Fig. 3b) showed that large-simple lakes and small-complex lakes had higher
219 species richness than those with other combinations of area and shape complexity. In
220 contrast, macrophyte species richness was low in large-complex lakes and small-simple
221 lakes. In particular, differences of species richness between large-complex and
222 large-simple lakes were clearest (Fig. 3a). Scatter plots of the different lake types (Fig.
223 3b) showed that these two contrasting lake types (i.e. large-complex and large-simple
224 lakes) were composed of mainly man-made and marsh lakes, respectively (Fig. 3b).

225 For marsh and man-made lakes, the ΔAIC values for the top two models were >
226 2.0 (Table 2), indicating that Model 1 had the strongest support (Burnham and Anderson,
227 2002). Therefore, positive and negative correlations between macrophyte species
228 richness and lake area were strongly supported for marsh and man-made lakes,
229 respectively. For oxbow lakes, the null model was best supported (Table 2), suggesting
230 that macrophyte species richness in oxbow lakes could not be well explained by lake
231 area and shape.

232

233 **Discussion**

234 **Interactions between lake area and shape**

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

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

257 complexity and species-area relationships, would result in these types of interactions.

258

259 **A driver of variable area-species richness relationships**

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

269 Oxbow lakes exhibited no clear relationship between lake area and macrophyte
270 species richness. The most important difference in species occurrence patterns between
271 marsh and oxbow lakes is that, for oxbow lakes, even small lakes had relatively high
272 species richness compared with that of large lakes. Several mechanisms can be
273 suggested to explain the advantage small lakes have in relation to species diversity. First,
274 fish abundance may be low in small lakes because of the high risk of oxygen depletion
275 (Jeppesen et al. 1990); an abundance of fish can negatively affect macrophyte diversity
276 through predation (Scheffer et al. 2006) and bioturbation (Matsuzaki et al. 2007).
277 Second, macrophyte growth in small lakes may be less hampered by wind-stress
278 (Hudon et al. 2000). In our study, small oxbow lakes (i.e., Lake #1, 2) had relatively
279 high shape complexity (Appendix A), indicating such small lakes have a higher ratio of

280 shoreline to surface area (panel (b) in Appendix B). Because shoreline acts as a refuge
281 for herbivorous zooplankton (Burks et al. 2001), which could lead to a reduction in
282 phytoplankton populations, complex shorelines could allow sunlight to penetrate into
283 the water and so promote the growth of submerged macrophytes (Jaspen et al. 1990).
284 Overall, in oxbow lakes, such an advantage of small lakes may obscure significant
285 positive species-area relationships.

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

303

304 **The role of small lakes with complex shapes in floodplain conservation**

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

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

328 management of biodiversity.

329

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335

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455 **Figure legends**

456

457 **Fig. 1**

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

459 Ishikari River.

460

461 **Fig. 2**

462 Macrophyte species richness (a), lake area (b), and lake shape complexity (c) for the
463 three lake types. The central bar in the boxplot indicates the median, the ends of the
464 boxes indicate the interquartile range, and the whiskers indicate the 10th and 90th
465 quantiles. These differences were tested by general linear hypotheses (* $p < 0.05$, ** $p <$
466 0.01).

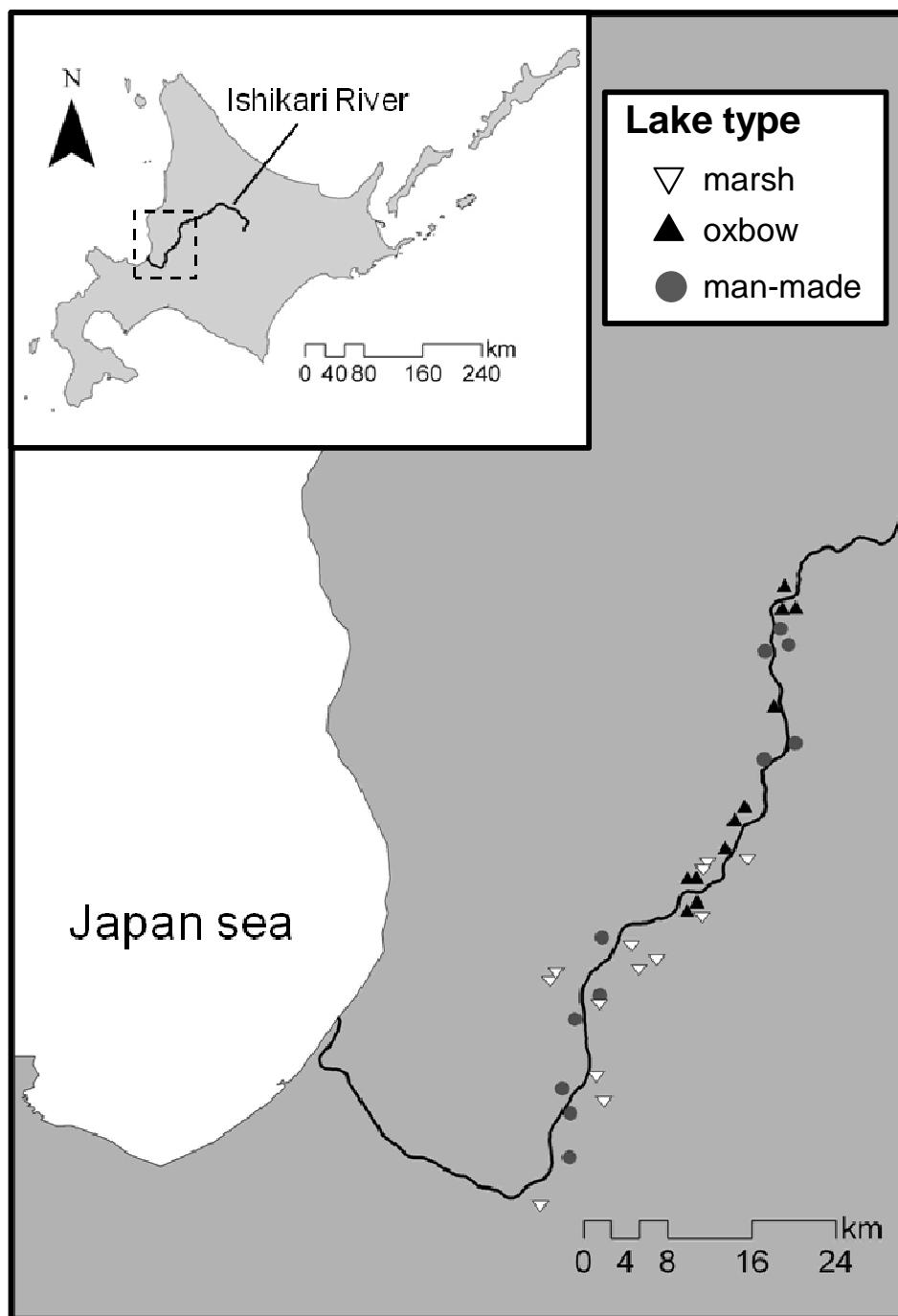
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468 **Fig. 3**

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

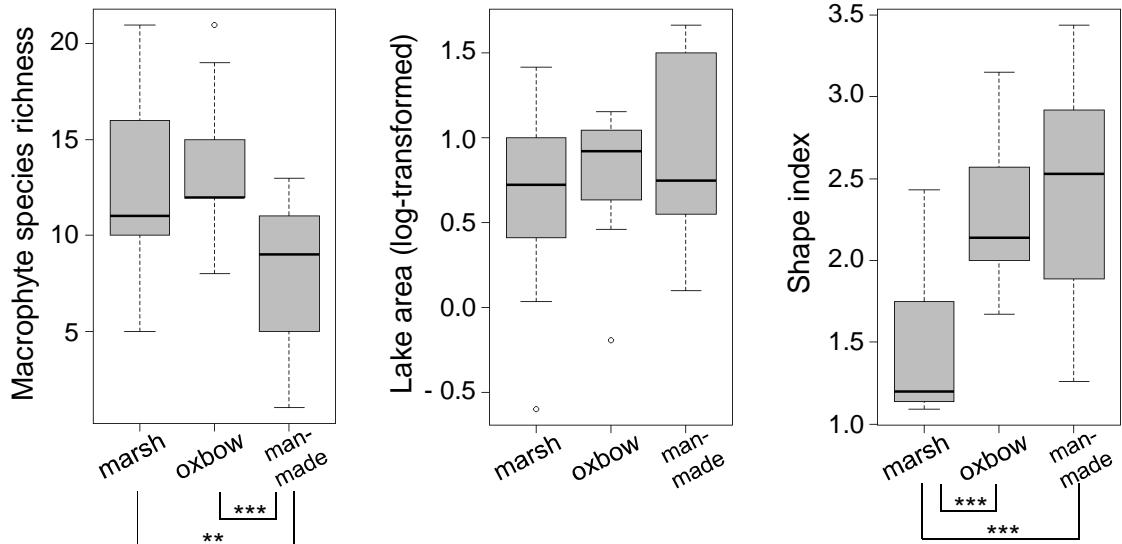
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476 **Fig. 1**

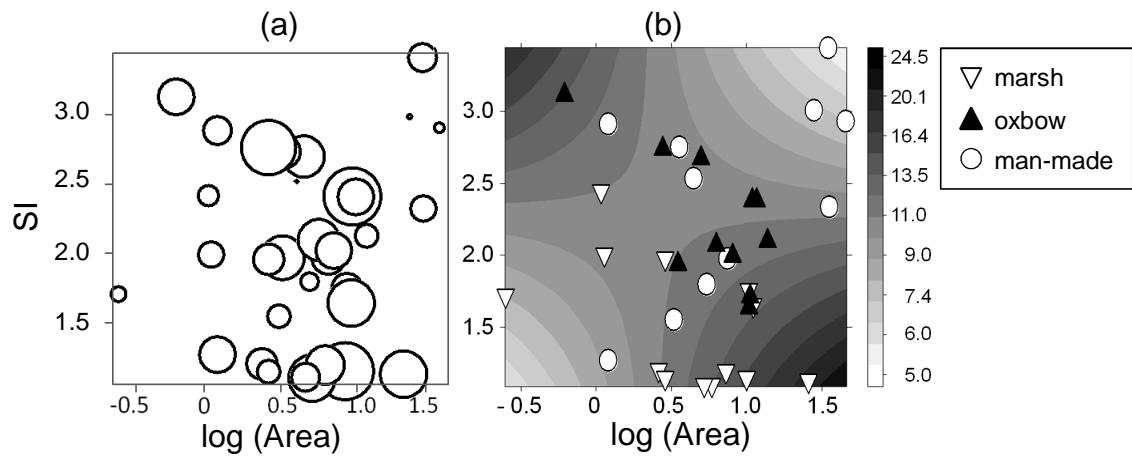


478 **Fig. 2**

479



480 **Fig. 3**



481

Table 1

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

* 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.

485 **Table 2**

486 Results of model selection base on AIC.

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

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

488

489 **Appendix A**490 Characteristics of 35 sample lakes, listed in the order of longitudinal positions from
491 upstream to downstream along the Ishikari River.

492

Lake ID	Macrophyte species richness	Lake area (ha)	Shape index	Lake type*	Number of NT and R species**	Year of construction
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-ko	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.

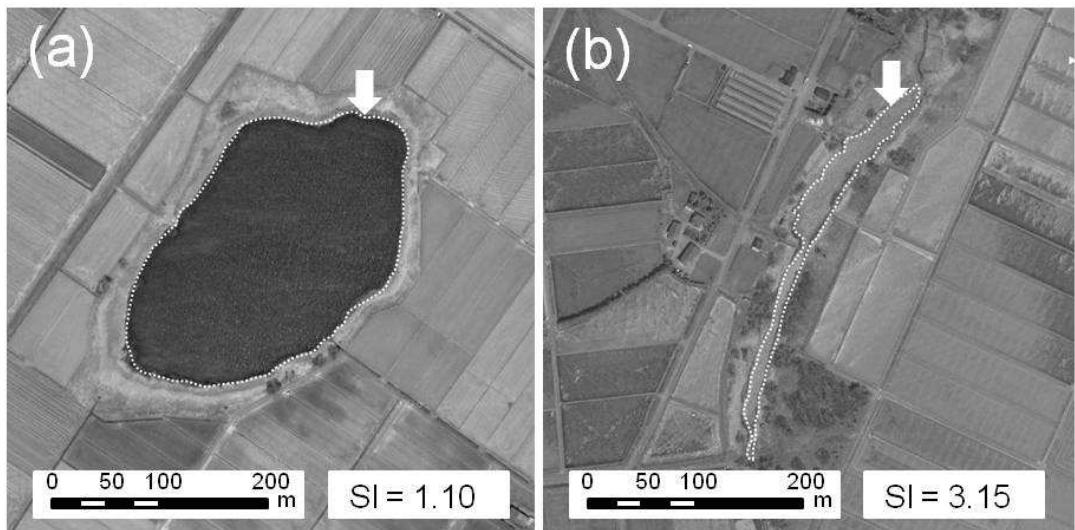
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496 **Appendix B**

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



499

500