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3 Imperiled freshwater mussels in drainage channels associated with rare agricultural 4 landscape and diverse fish communities

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Abstract

Identification of landscape structures that predict the distribution of aquatic organisms has the potential to provide a practical management tool for species conservation in agricultural drainage channels. We tested the hypothesis that sites with imperiled freshwater mussels have distinct rural landscape structures, and are characterized by the presence of diverse fish communities. In central Japan, the proportion of developed land-use in surrounding areas was compared among sites with mussel populations (mussel sites) and randomly chosen sites (random sites) across multiple spatial scales (with a radius ranging from 100 to 3000 m). Mussel sites were characterized by a much lower proportion of developed land (means = 5-18%) compared with random sites (means = 32-35%) at a scale of ≤ 300 m. The areas that met the landscape criteria for mussel sites across multiple scales constituted only 0.23% of the area that presumed to have suitable slope and elevation as mussel habitat. Landscape metrics derived from mussel sites to locate unknown populations had a low predictability (16.7%). Sites with mussels were located close to each other and had fish communities with higher taxonomic diversity than in sites without mussels. In addition, mussel taxonomic richness was a good predictor of fish community diversity. The quantitative measures of landscape structure may serve as a useful tool when prioritizing or identifying areas for

conservation of mussels and fish if spatially auto-correlated distribution of habitat and other critical environmental factors such as habitat connectivity are also considered.

Keywords: development, indicator, paddy fields, Unionoida, urbanization

Introduction

In Japan, rice paddy fields, which constitute approximately 7% of national land as the most widespread cropland type (>50%; Sato 2001), have been a part of landscapes for centuries, providing habitats for unique sets of species (Natuhara 2012). Of particular importance are the environmental characteristics similar to those of natural floodplains (Elphick 2000) and the presence of a mosaic of different landscape components (i.e., paddy-fields, forests, ponds, and networks of small creeks and ditches) that are closely coupled through food webs (Katoh et al. 2009). Modernization of landscape elements (i.e., land consolidation that converts small land parcels into larger ones with the installation of pipeline systems for irrigation water management) and the urbanization of fields (i.e., land use conversion) are both pressing causes of reduced species diversity in rice-paddy landscapes (Takahashi 1994; Natuhara 2012).

There is a growing body of literature on the ecological roles of drainage channel networks in agricultural landscapes (Herzon and Helenius 2008). The relative importance of ditch communities to regional species diversity has been relatively well studied, with unique species being often identified (Armitage et al. 2003; Williams 2004). Degradation of ditch habitat quality has been related to runoff from agricultural crop fields with high levels of agro-chemicals (pesticides and fertilizers) (Janse et al.

61 1998; Biggs et al. 2007). Physical modifications of channel structures including
62 concrete lining and the placement of migration barriers, such as vertical drops, have
63 been also related to decreased species diversity in drainage channel systems (Katano et
64 al. 2003; Nagayama et al. 2012; Natuhara 2012). Recent ecological studies with the aim
65 of developing species conservation strategies have emphasized the importance of
66 landscape structure in accounting for species distribution across multiple spatial scales
67 (Gergel 2002; Marchand 2004). Such attempts have been made for organisms in riverine
68 channels (e.g., Wang et al. 2001; Cao et al. 2013) but not in drainage channel networks.
69 The latter tends to be smaller in size, located in more upstream areas, and regulated
70 more strongly (i.e., flow rate) (e.g., Negishi and Kayaba 2009), and thus better
71 understanding of ecosystem processes characteristic of drainage channels is needed.
72 Identification of areas that harbor high species richness at the local scale and/or
73 make high contributions to species diversity at the regional scale would greatly facilitate
74 prioritization of sites for conservation (Moilanen and Wilson 2009). Such a
75 prioritization approach is critically important in paddy-dominated landscapes because
76 drainage channel management for species conservation inevitably assumes secondary
77 importance to that of increased agricultural production (Herzon and Helenius 2008).
78 Among aquatic organisms, freshwater mussels (Order: Unionoida) can be used as an

79 indicator for biodiversity in low-land aquatic ecosystems, especially other
80 macroinvertebrates and fish (Aldridge et al. 2007; Negishi et al. 2013). Besides,
81 freshwater mussels are one of the most imperiled groups of organisms (Lydeard et al.
82 2004; Negishi et al. 2008). Several empirical relationships between the community
83 structure and distribution of freshwater mussels and landscape metrics, such as
84 catchment geology, have been reported (Arbuckle and Downing 2002; Daniel and
85 Brown 2013).
86 Landscape structure in the surrounding areas may affect mussel distribution in
87 agricultural drainage channel. First, urbanization could affect mussel habitat quality
88 because effluents from industrial and household sources impair water quality (Onikura
89 et al. 2006). Local hydraulic conditions, which are a strong factor determining mussel
90 distribution (Morales et al. 2006; Allen and Vaughn 2010), may be altered as a result of
91 flashier runoff hydrograph from impervious urban surfaces (Xu and Wu 2006). Second,
92 the encroachment of non-agricultural human land-uses in surrounding areas often
93 coincide with improvements in agricultural infrastructure in the area, such as the
94 modernization of ditch structures and irrigation systems (J.N. Negishi, personal
95 observation). We hypothesized that sites with remaining populations of freshwater
96 mussels have distinct rural landscape structures. This study aimed to develop a practical

97 scheme for the identification of locations of mussel habitat, where diverse fish
98 communities also occur based on landscape metrics over a large area (> 10,000 km^2).
99 Specific objectives were to: 1) identify the landscape structures (i.e., the areal
100 proportion of non-agricultural areas in surrounding areas) characteristic of mussel
101 habitats at various spatial scales; 2) to test the efficacy of the identified landscape
102 structures in predicting potential mussel habitats; and 3) to test the use of mussel
103 community structure as an indicator of fish community structure. We predicted that
104 mussel habitats in drainage channels are associated with rural landscapes having low
105 levels of non-agricultural human land-uses, and are characterized by the presence of fish
106 communities with relatively high species richness.
107
108 **Methods**
109 Study site
110 The study was conducted in the period between April and August, 2011, in the lowlands
111 of Tokai region, including Aichi, Gifu, and Mie prefectures (Fig. 1). We collected as
112 much information about the locations of existing unionoid mussel populations in
113 agricultural channel networks *a priori* as we could find in the published literature,
114 unpublished records, and knowledge from local people and researchers (see

115 Acknowledgements). Between 23rd and 26th April, each location was visited to confirm
116 the presence of mussels. Our criteria for study site selection were: 1) sites were located
117 in agricultural channels for single (drainage) or dual (irrigation and drainage)
118 purpose(s); 2) sites had > 10 individual live mussels with an approximately 2 person
119 hours search; 3) sites were located a minimum of 800-m channel length from each
120 other; and 4) sites were not connected to each other within the same drainage channel
121 networks before connecting to main river channels in downstream areas. The sites
122 located immediately downstream of agricultural ponds (reservoirs for irrigation water
123 supply) were excluded because there was the possibility that local populations were
124 largely maintained by emigrants from the source populations within the ponds.
125 Consequently, we identified 26 sites (hereafter mussel sites; Fig. 1 and 2). These sites
126 had one of the following unionoid taxa: *Anodonta* spp., *Unio douglasiae nipponensis*
127 Martens, *Inversidens brandti* Kobelt, *Obovalis omiensis* Heimburg, *Pronodularia*
128 *japanensis* Lea, or *Lanceolaria grayana* Lea. It was later found that one of the mussel
129 sites located downstream of the other in the same drainage channel, and excluded when
130 conducting fish and mussel surveys. Landscape analyses were redone by excluding this
131 site, but it did not change the interpretation of statistical results and negligibly affected
132 the criteria used to quantify landscape structures.

133

134 Delineation of habitable area

135 We conducted our study in three regions that contained mussel sites, each of which
136 comprised several neighboring watersheds (Fig. 1). This approach was employed to
137 reduce the possibility that our analyses contained the area in which distribution of
138 mussels is biogeographically limited by the legacy of marine transgressions. The entire
139 area of the three regions is hereafter referred to as the total area (Fig. 2). We recorded
140 the geographical locations of the mussel sites using GPS (CS60, Garmin Co., USA) and
141 registered on GIS (Arcmap, ver. 9.3, ESRI Co., USA). Using the surface elevation
142 distribution (50-m resolution, Geospatial Information Authority of Japan), a digital
143 elevation model (DEM) was generated. A ground surface slope distribution model
144 (50-m resolution; DSM) was also created based on DEM. We calculated the average
145 elevation and slope of each site by calculating average DEM and DSM values within
146 the 100-m radius buffer polygon surrounding each site. We carefully examined the data
147 and excluded the slope values where the 100-m buffer polygon enclosed unusual
148 topographic variations such as adjacent hill slopes because the DSM was particularly
149 sensitive to such errors (this occurred at five sites). Channel slope can limit mussel
150 distribution by potentially mediating hydraulic forces on the benthic habitat conditions

151 (Arbuckle and Downing 2002). Temperature can also limit mussel distribution because
152 of the physiological thermal tolerance of mussels and/or that of their host fish species
153 whose distribution can determine the distribution of mussels (Galbraith et al. 2010;
154 Schwalb et al. 2011; Negishi et al. 2013; Schwalb et al. 2013). Thus, we have delineated
155 the area that fell within the range of slopes (0.001–3.45%) and elevations (13.0–86.71
156 m) as a proxy of temperature variation of the mussel sites as potentially habitable for
157 mussels (hereafter habitable area) within the total area (Fig.1 and 2).
158
159 Landscape structures of mussel sites
160 To examine how rare the landscape structures of the mussel sites were in the study area,
161 we randomly chose sites (random sites) within the habitable area (total of 26 sites) (Fig.
162 2). Random sites were used to represent the average landscape structure present within
163 the habitable area and we did not confirm the occurrence of mussels in random sites.
164 First, continuous square grid cells of 500 × 500 m were generated to cover the habitable
165 area so that all cells were completely contained within (grid cells). A total of 26 grid
166 cells (random cells) was selected so that the number of selections in each region equaled
167 the numbers of mussel sites within each region. Central points of each random cell were
168 considered as random sites (Fig.1). The use of 500 × 500 m grid cells was to assure that

169 randomly selected sites were apart from each other and from mussel sites at least by
170 800-m channel length (i.e., minimum distances among mussel sites).
171 We defined the developed areas whose surface was covered by landscape
172 components that are not agricultural fields or natural features such as forests and water
173 bodies (i.e., rivers and lakes). We used nation-wide land use census data (land use
174 database in 1997, Ministry of Land, Infrastructure, Transport and Tourism, 50-m grid
175 resolution), and assigned golf courses, residential areas, transportation fields (e.g., roads
176 and airports), barren land, and commercial districts as the developed landscape
177 components. We created 50-m raster data, with each grid cell being assigned 1
178 (developed) or 0 (other land-uses). We calculated the proportion of developed areas for
179 mussels as well as random sites at multiple spatial scales (circles with a buffer radius of
180 100, 200, 300, 500, 1,000, or 3,000 m) using the GIS buffering and zonal and focal
181 statistics functions (Fig. 1).
182
183 Locating potential sites containing unknown mussel populations
184 Based on the landscape structures of known mussel sites defined by land-use patterns at
185 multiple spatial scales, we attempted to identify the locations of unknown sites with
186 mussel populations (i.e., potential sites). We delineated and calculated the area that met

187 the landscape structure criteria for the mussel sites at respective spatial scales; the
188 criteria were set at 95% confidence intervals of the means of the proportion of the
189 developed area for mussel sites. We determined the area that met the criteria of each
190 spatial scale, as well as all spatial scales (i.e., potential areas) from the habitable area
191 using the GIS focal statistics function. For example, the potential area constrained by
192 criteria at all spatial scales refer to the area, any given locations within which had the
193 proportion of developed land in surrounding areas within the criteria for mussel sites at
194 all spatial scales examined (Fig. 2).

195 We excluded habitable areas in Mie prefecture (see Fig. 1) from the further
196 analyses because distant locations rendered frequent visiting for observations and
197 sampling impractical. We initially attempted to randomly choose candidates for
198 potential sites within the potential area as was done for the selection of random sites
199 using the 500 m grid cells; the selected cells were referred to as candidate cells. We
200 chose 18 candidate cells, the number same as that of initially designated mussel sites.
201 However, preliminary analyses revealed that the number of cells meeting such criteria
202 was too small (< 10 cells) to conduct a random selection (see results for more detail). As
203 an alternative, we selected cells based on the criteria set based on the maximum value of
204 the proportion of developed area at a spatial scale of 500 m (53.8%), which provided >

100 cells. When randomly chosen 18 candidate cells were placed on areas dominated by large rivers (> 90%), or the areas without noticeable agricultural drainage channel networks, candidate cells were re-chosen by a random selection procedure (this occurred once).

Mussel and fish surveys

Fish and mussel communities were surveyed in the summer period between 8th and 13th August when flow is stable and no noticeable precipitation was recorded in the preceding 2 weeks. In the water management cycles for rice cultivation in the area, this period typically provides the largest amount of water within the channel (Negishi et al. 2013). The exact locations of the potential sites within candidate cells were determined as follows: The geographical coordinates for the central points of chosen grid cells were determined by GIS and located in the field by GPS. The sampling sites were chosen by the following criteria: Upon arrival at the location, the closest drainage channel was located. The site suitability was confirmed when it was for drainage or irrigation/drainage purpose(s), had decent water quality and perennial flow, and was of a comparable size to that of the mussel sites. The presence of perennial flow with decent water quality was confirmed by the occurrence of freshwater Mollusca such as

223 *Pleuroceridae* sp. and *Viviparidae* sp. Only those whose wetted channel width was
224 within the range of that in the mussel sites were selected. When the closest one did not
225 meet these criteria, the next closest ones were progressively examined until the criteria
226 were met.
227 At each study site, two sections having a longitudinal length 10 times the
228 average wetted surface width (range = 45–320 cm) were set for mussel surveys with a
229 distance of 20 times the width between each section. In each section, electrical
230 conductivity (EC), pH, and water temperature (°C) were recorded using a
231 multi-parameter water quality probe (WM-22EP; DKK-TOA Co., Japan). Mussels were
232 quantified by collecting all mussels within the belt transects (a dimension of 25 × the
233 wetted channel width) equally spaced along a longitudinal profile. The total number of
234 transects was proportional to the section length (n = 4–32) and total areas searched
235 ranged from 0.9 to 36.8 m^2. Mussels were collected by thoroughly sieving the sediment
236 using baskets (1-cm mesh), identified, enumerated, and measured along their longest
237 shell axes. Fish communities were surveyed by enclosing a section (20 times the length
238 of the wetted width) in the area upstream of the mussel survey sections. To avoid
239 disturbing the fish communities, the survey was conducted prior to the mussel survey.
240 Fish were caught by conducting two passes of catches using triangular scoop nets

241 (34-cm wide and 33-cm high mouth opening; 44-cm long; 2-mm mesh) aligned
242 perpendicularly to the channel. Furthermore, specific areas such as those with a fast
243 current and along the channel edge were thoroughly searched for fishes using scoop nets
244 (up to 5 min by two or three personnel depending on the channel size). Fish were
245 identified, enumerated, and photographed to digitally estimate their body sizes.
246 Collected organisms were released back to the capture area immediately after the
247 measurements had been taken.
248
249 Statistical analyses
250 Repeated measures two-way analysis of variance (ANOVA) was conducted to examine
251 the effects of spatial scale and site characteristics (mussel sites vs. random sites, or
252 mussel sites vs. potential sites), and their interactions on the proportion of developed
253 areas in surrounding areas. Site identity was included as a repeated measures factor.
254 When significant interaction terms were detected, the proportion of developed lands was
255 compared between site types at each scale using Student's t-tests. A correlogram of
256 Moran’s *I* was constructed to assess the degree of spatial autocorrelation in the
257 presence/absence data obtained from field surveys on mussels; presence data from
258 present sites (initially designated mussel sites in addition to some potential sites with

mussel populations) whereas absence data from absent sites (remaining potential sites without mussels). Environmental variables (GIS-calculated elevation and slope, water temperature, pH, EC, and flow rate) were compared between present and absent sites using Welch's t-tests. Fish community metrics were calculated as abundance, taxonomic richness, and Shannon-Wiener index. These fish metrics, calculated for both communities, included all taxa and those excluding bitterlings; bitterlings require live mussels for spawning (Negishi et al. 2013). Mussel community metrics were calculated with the pooled data from two sections in terms of abundance and mussel taxonomic richness. Fish and mussel abundance were expressed as density (the number of individuals either per 1 m^2 or 100 m^2). Mussel indicator roles were examined in two ways. First, fish community metrics were compared between present and absent sites using Welch's t-tests. Second, relationships between mussel and fish community metrics were examined by regression analysis (12 cases in total) with the former as independent and the latter as dependent variables. All statistical analyses were conducted in R 2.10.1 (R Development Core Team, 2008) with a significance level of 0.05. The Bonferroni correction was applied to the statistical significance level when appropriate.

Results

277 The change pattern of the proportions of developed lands in the surrounding areas in
278 response to variable spatial scales differed between the sites with known mussel
279 populations and those of randomly chosen sites (interaction effect: $F_{5, 245}$= 6.8, p <
280 0.001). The differences in landscape structures between two types of sites were
281 particularly high at relatively small spatial scales (Fig. 3A). The proportions of
282 developed lands were significantly lower for the sites with known mussel populations
283 compared with those of randomly chosen sites (site effect: $F_{1, 49}$ = 12.22, p < 0.001; Fig.
284 3A). The proportions of developed lands were significantly lower at sites with mussels
285 at the spatial scales of 100, 200, and 300 m when compared at respective spatial scales
286 (Fig. 3A).
287 The areal extent of lands (potential areas) that fell within the landscape
288 conditions of mussel sites at different spatial scales became disproportionately less with
289 decreasing spatial scale (Table 1). Approximately 7% of the total area was selected as
290 within the slope and elevation range of sites with existing mussel populations (habitable
291 area). The areal extent of the potential area that met the landscape-level criteria of
292 mussel sites across all spatial scales only constituted 0.23% of the habitable area. The
293 potential sites, which were selected based on the criteria of maximal areal proportion of
294 developed land at a scale of 500 m (53.8%), had landscape structures similar to those of

295 mussel sites (Fig. 3B). The change pattern of the proportions of developed lands in the
296 surrounding areas in response to variable spatial scales did not differ between two types
297 of sites (interaction effect: $F_{5, 165} = 0.17$, $p = 0.97$). The potential sites had a proportion
298 of developed lands similar to that of mussel sites in surrounding area (site effect: $F_{1, 33} =$
299 1.16, $p = 0.29$; Fig. 3B) with a significant effect of spatial scale ($F_{5, 165} = 18.84$, $p <$
300 0.001).

301 In total, 2, 128 individuals were found: 1, 764 *P. japanensis*, 118 *L. grayana*,
302 56 *O. omiensis*, 78 *Inversidens brandti*, 107 *Anodonta* spp., and 5 *U. douglasiae*
303 *nipponensis*. We found mussels in three out of 18 potential sites (at least one live
304 individual in the quadrat survey) (Fig. 4A). A clear spatial structure was revealed in the
305 distribution of present and absent sites with Moran's correlogram indicating statistically
306 significant positive autocorrelation for small-distance categories (Fig. 4B). It is
307 important to note that three potential sites with mussels were close to each other or close
308 to the sites with known mussel populations, augmenting the patchy distribution. Sites
309 with mussels (including the three potential sites with mussels) and those without
310 mussels were similar to each other in the measured environmental variables (Table 2).
311 Mean (±SD) mussel density (individuals/m^2), irrespective of taxon, at sites with mussel
312 populations was 29.6 (±57.3) individuals/m^2. In total, 2,390 fish, consisting of 24 taxa,

were collected (Appendix); their body length was <15 cm. When compared between sites with and without mussels, fish species richness with all taxa included and taxa excluding bitterling species were both higher at the sites with mussels compared with those without (Fig. 5; $p < 0.001$). The Shannon-Wiener index did not differ among site type ($p > 0.20$). Mussel taxonomic richness was positively associated with fish species richness (both with and without bitterlings) and the Shannon-Wiener index calculated from all taxa included (Fig. 6). Mussel abundance did not have any predictive effect on fish community metrics ($p > 0.12$).

Discussion

We demonstrated that the landscape structure surrounding agricultural drainage channels with imperiled unionoid mussels was characterized by rural landscapes having a significantly lower level of land development compared with common landscapes in the area with similar elevation and slope ranges. This difference was more pronounced when landscape structure was examined at relatively small spatial scales. These results agree with our prediction that mussel habitats possess relatively rare rural landscape features in the region. The interpretation of our findings requires caution because we did not compare landscape structures between the sites with and without mussels. Also, we

331 did not constrain our analyses to the areas where only the landscape structures varied,
332 with other important factors (see the next paragraph) being more or less controlled when
333 selecting random sites.

334 The absence of GIS-ready digital data resources of drainage channel networks
335 across a large area prevented us from taking into the account spatial attributes of
336 drainage channel networks when delineating areas potentially suitable as mussel habitat.
337 For example, drainage density (i.e., total length of channels in a given unit area; see
338 Benda et al. 2004), which is analogous to habitat availability, could have been
339 particularly meaningful. Thus, it is possible that some of the random sites were selected
340 from areas where highly urban landscapes dominated and as a result few drainage
341 channels existed (relatively low habitat availability). Consequently, the differences in
342 landscape structure between the mussel and random sites can be partly a reflection of
343 the differences in land-use patterns (rural vs. urban) and not necessarily those around
344 drainage channels. Despite such limitations, the results implied that a quantitative
345 measure of rare landscape structure is useful when narrowing down the areas where
346 mussel habitat likely to occur.

347 We showed that areas with landscape structures characteristic of mussel sites
348 across multiple spatial scales constituted only a fraction of habitable area in the region

349 (0.23%) and was much less when compared with the areas estimated at respective
350 spatial scales (Table 2). This suggests that mussel sites can be more accurately defined
351 by considering landscape metrics quantified at multiple spatial scales. Our findings
352 underscore the importance of considering landscape structures at multiple spatial scales
353 when explaining organism distribution patterns (also see Marchand 2004; Stephens et al.
354 2004). Furthermore, landscape structure characteristic of mussel sites were more
355 pronounced and became rarer at relatively small spatial scales. Cao et al. (2013)
356 examined the relationships between landscape metrics and riverine mussel habitat
357 conditions and also reported the disproportionately strong influences of landscape
358 conditions in a close proximity (i.e., riparian zone). In the study region, the increase of
359 developed land surface within the area in a relatively short distance from mussel sites
360 likely causes a disproportionately large drop in potential habitat availability and may
361 degrade mussel habitat quality more severely.
362 Unknown mussel populations were found at only a few potential sites (16.7%),
363 indicating limited usefulness of landscape structure as a single predictor of mussel
364 habitat distribution. A patchy distribution of sites with mussels was apparent, and an
365 understanding and incorporation of its cause can improve the predictive model of
366 mussel distribution. Patchy distribution of mussels (mussel beds) is relatively well

367 reported at within-channel scales as well as at broader regional to continental scales
368 (Vaughn and Taylor, 2000; Strayer 2008). At larger scales, in particular, host fish species
369 distribution may be the one of the most important factors (Vaughn and Taylor 2000;
370 Schwalb et al. 2011). A patchy distribution can be caused by natural barriers (e.g.,
371 drainage divide) for the dispersal of mussels (or host fish species), or as a result of
372 human-induced fragmentation and shrinkages of formerly broad distribution range
373 (Strayer 2008). Fish migrate up from rivers to drainage channels or rice paddies via
374 drainage channels seasonally (e.g., Katano et al. 2003). The placements of vertical drops
375 impassable for fish is common in modernized drainage channel networks (Miyamoto
376 2007). In agricultural channels, therefore, the reduction or loss of connectivity among
377 channels and/or between channels and downstream rivers might have fragmented
378 mussel habitat by limiting movement of host fish with attached glochidia. Other
379 potentially important factors on a local scale, such as flow velocity, hydraulic forces,
380 and physical channel structures, may also play a role in controlling the distribution of
381 mussels (Allen and Vaughn 2010; Matsuzaki et al. 2011; Nagayama et al. 2012; Negishi
382 et al. 2013). These factors independently or in a combination with other factors can
383 affect habitat conditions of mussels directly or indirectly by limiting distribution of host
384 fish species. Future studies should examine the relative importance of multiple factors

385 such as habitat fragmentation and local habitat conditions in relation to natural dispersal
386 ranges of host fish species (Schwalb et al. 2011; Cao et al. 2013; Schwalb et al. 2013).
387 Fish species richness was higher at sites with mussels compared to sites
388 without mussels despite of similar physico-chemical habitat conditions. This is
389 consistent with the findings that the occurrence of mussels is associated with the
390 presence of relatively species-rich fish communities (e.g., Vaughn and Taylor, 2000;
391 Negishi et al. 2013). Mussel species such as *I. brandti*, *O. omiensis*, and *P. japanensis*
392 co-occur with bitterlings through host-parasite relationships (Kitamura 2007; Terui et al.
393 2011). Importantly, when the bitterlings were removed, significant differences in fish
394 community species richness remained. This implies that the greater fish species richness
395 observed in the mussel sites was not the sole consequence of the addition of species
396 having a commensal relationship with mussels, but also several other ecological
397 processes (Negishi et al. 2013). Furthermore, the mussel taxonomic diversity gradient
398 predicted fish community taxonomic richness with mussels and the Shannon-Wiener
399 index relatively well. We previously tested fish and mussel communities in a <100 m^2
400 area including some of the mussel sites used in the present study and reported the
401 relationships between fish and mussel community structure in different seasons (Negishi
402 et al. 2013). A discrepancy with the present study is that Negishi et al. (2013) reported

403 less explanatory power of mussels for fish community structure in the summer period. A
404 cause of such a discrepancy may be scale-dependent relationships between community
405 structure of fish and mussels (e.g., Schwalb et al. 2013). The mechanisms between
406 species richness and fish community structure also merit future research. We argue that
407 unionid mussel can be used as an indicator of fish habitat quality over a large scale (>
408 10,000 km^2) at least within the area having elevation and slope ranges of mussel sites.
409 Our overall findings suggest that the quantitative measures of landscape
410 structure may serve as a useful tool when prioritizing or identifying areas for
411 conservation of mussels and fish if spatially auto-correlated distribution of habitat and
412 other critical environmental factors such as local habitat quality and habitat connectivity
413 are also considered. It is important to recognize the landscape structure in rural
414 landscape has changed in recent decades largely because of abandonment of agricultural
415 lands and land development associated with urbanizations (Nakamura and Short 2001;
416 Fujihara et al. 2005). Therefore, the landscape criteria quantified in the present study
417 should not be taken as an ideal habitat condition for mussels. Information on historical
418 distribution of mussels and land-use changes across a large area would provide crucial
419 insights into optimal habitat condition for mussels.
420

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Table 1: Areal extent of the potential area that met the criteria of mussel site landscape structures at different spatial scales and their relative availability (%) relative to total and habitable areas. For example, 7.41% of total area is considered suitable for mussel habitat based on the range of elevation and slope of sites with mussels; 9.64% of the habitable area was considered suitable for mussel habitat when considering landscape structure obtained for the surrounding area of mussel sites at the scale of 100 m (the area within a circular buffer having a radius of 100 m).

	Area (km^2)	Availability (%)
Total area	6,399.32	
Habitable area	473.89	7.41
3000-m buffer criteria	131.26	27.70*
1000-m buffer criteria	113.55	23.96*
500-m buffer criteria	97.68	20.61*
300-m buffer criteria	64.63	13.64*
200-m buffer criteria	58.24	12.29*
100-m buffer criteria	45.68	9.64*
Multiple-scale criteria	1.07	0.23*

* These values were calculated as a proportion relative to the habitable area

Table 2 General characteristics of study reaches with (present) and without (absent) freshwater mussels. Means ± SD are shown. Statistical significance as the result of Weltch's t-tests are also shown; significance level is Bonferroni-corrected (p = 0.05/6).

	Present (n=20†)	Absent (n=15)	Statistical significance
Elevation (m)	43.61±18.16	32.88±16.72	p = 0.08
Slope (%)	0.69±0.57	0.57±0.43	p = 0.67
Temp. (˚C)	27.45±2.10	26.42±1.35	p = 0.08
pH	7.12±0.69	7.80±0.62	p = 0.01
EC (μS/cm)	9.81±7.15	9.41±3.52	p = 0.83
Flow rate (m^3)	0.19±0.31	0.15±0.11	p = 0.63

† Sample size was 15 for slope as the 5 sites were excluded because of unusual land surface slope was estimated due to the presence of steep hillslope near the channel.

Appendix: Taxon list and general characteristics of fish communities in the study reaches. Abundances for the sites with and without mussels are shown; mean ± SD (maximum values; minimum values were all zero).

Family	Species name	Present (n = 20)	Absent (n = 15)
Cyprinidae			
	Rhodeus ocellatus ocellatus	17.12±45.86 (194.44)	0
	Tanakia lanceolata	35.81±94.88 (395.83)	0
	Tanakia limbata	190.86±404.25 (1693.12)	0
	Carassius sp.	6.43±18.00 (74.07)	2.22±8.31 (33.33)
	Nipponocypris sieboldii	85.78±173.04 (732.64)	40.30±150.77 (604.44)
	Nipponocypris temminckii	46.37±101.26 (324.79)	2.47±9.24 (37.04)
	Zacco platypus	6.82±23.67 (105.82)	10.15±21.54 (71.11)
	Abbottina rivularis	9.29±39.31 (180.56)	0
	Gnathopogon elongatus	65.12±208.52 (958.33)	3.54±9.16 (30.86)
	Hemibarbus barbus	0	1.19±4.43 (17.78)
	Pseudogobio esocinus	4.83±11.91 (48.61)	0
	Sarcocheilichthys variegatus variegatus	0.17±0.76 (3.47)	0
	Rhynchocypris logowskii steindachneri	1.10±4.07 (18.52)	7.11±21.78 (86.42)
	Rhynchocypris oxycephalus jouyi	0.17±0.76 (3.47)	0
	Pseudorasbora parva	4.08±16.63 (76.39)	0
Adrianichthyidae			
	Oryzias latipes	59.48±183.58 (833.33)	225.91±613.96 (2455.56)
Cobitidae			
	Cobitis biwae	1.66±4.48 (15.87)	29.71±107.92 (433.33)
	Cobitis sp.	1.19±5.19 (23.81)	0
	Misgurnus anguillicaudatus	63.48±103.56 (370.37)	109.06±199.33 (740.74)
	Paramisgurnus dabryanus	0	3.29±12.32 (49.38)
Gobiidae			
	Rhinogobius sp.	42.67±36.65 (128.47)	75.64±134.90 (444.44)
Odontobutidae			
	Odontobutis obscura	0.69±3.03 (13.89)	0
Petromyzontidae			

	Lethenteron reissneri	0	0.82±3.08 (12.35)
Siluridae			
	Silurus asotus	0	0.46±1.73 (6.94)

Figure captions

Figure 1: Location of the study area (A), study sites where unionoid mussel populations were present (mussel sites; n = 26) (B), an example of measurements of landscape structure in relation to multiple buffers surrounding the study sites (C), an example of the area potentially suitable as mussel habitat (habitable area; see the text for details) shown in white within region A (D), and an example of sites with mussels (mussel sites; filled circles) and sites randomly selected (random sites; open circles) (E). The regions A, B, and C in (B) denote watersheds within which random site selections were conducted. The sites enclosed with a broken line (n = 18) in (B) were used when testing mussel/fish relationships. The gray areas in (C) and scratched area in (E) denote the land use categorized as non-agricultural developed use such as urban areas.

Figure 2: A diagram depicting the procedure of delineating total area, habitable area, and potential area in association with sites with mussels (mussel sites), random sites, and potential sites.

Figure 3: Means ± SE of proportion of developed non-agricultural areas surrounding the study sites with mussels (mussel sites; filled circles) and randomly chosen sites (random sites; open triangles) at different spatial scales of buffer radii used to calculate landscape metrics. In (A), random sites (n = 26) were selected within the boundary of several watersheds and the range of elevation and ground surface slopes for the mussel sites (Fig. 1). In (B), the selection of potential sites (n = 18) was further constrained by the range of landscape characteristics at the spatial scale of 500 m. Asterisks indicate statistically significant pair-wise differences at respective spatial scales using Student's t-tests with Bonferroni corrections (p = 0.05/6; p = 0.005).

Figure 4: Spatial distribution of sites with mussels (filled circles) and without mussels (open circles) (A) and spatial correlogram of the occurrence (presence or absence) of mussels, where the abscissa is distance classes and the ordinate Moran's *I* coefficient (B). In (A), three sites accompanied by arrow denote sites that were initially chosen as potential sites and had mussel populations whereas the gray areas denote the habitable area. **Significant with Bonferroni-corrected probability (p = 0.05/10; p = 0.005). *Significant at the probability level p = 0.05 (i.e., before applying the Bonferroni correction).

Figure 5: Box plots showing median (central thick lines), 25%, and 75% quartile ranges around the median (box width) of taxonomic richness of fish community of all data (A) and data excluding bitterling species (B) for sites with (present) and without (absent) mussels. The sample size for each group was 21 and 15 for present and absent sites, respectively. Only those with statistically significant differences are shown; the statistical significance of Welch's t-test was corrected with Bonferroni corrections ($p = 0.05/6$; $p = 0.008$).

Figure 6: Relationships between mussel taxonomic richness and fish community metrics; Shannon-Wiener index of fish community (A), taxonomic richness of fish community (B), and taxonomic richness of fish community of data excluding bitterling species (C). Statistically significant regressions are shown as solid lines with coefficients of determination (R^2). Only those with statistically significant differences regressions are shown; statistical significance levels were corrected with Bonferroni corrections ($p = 0.05/6$; $p = 0.008$).

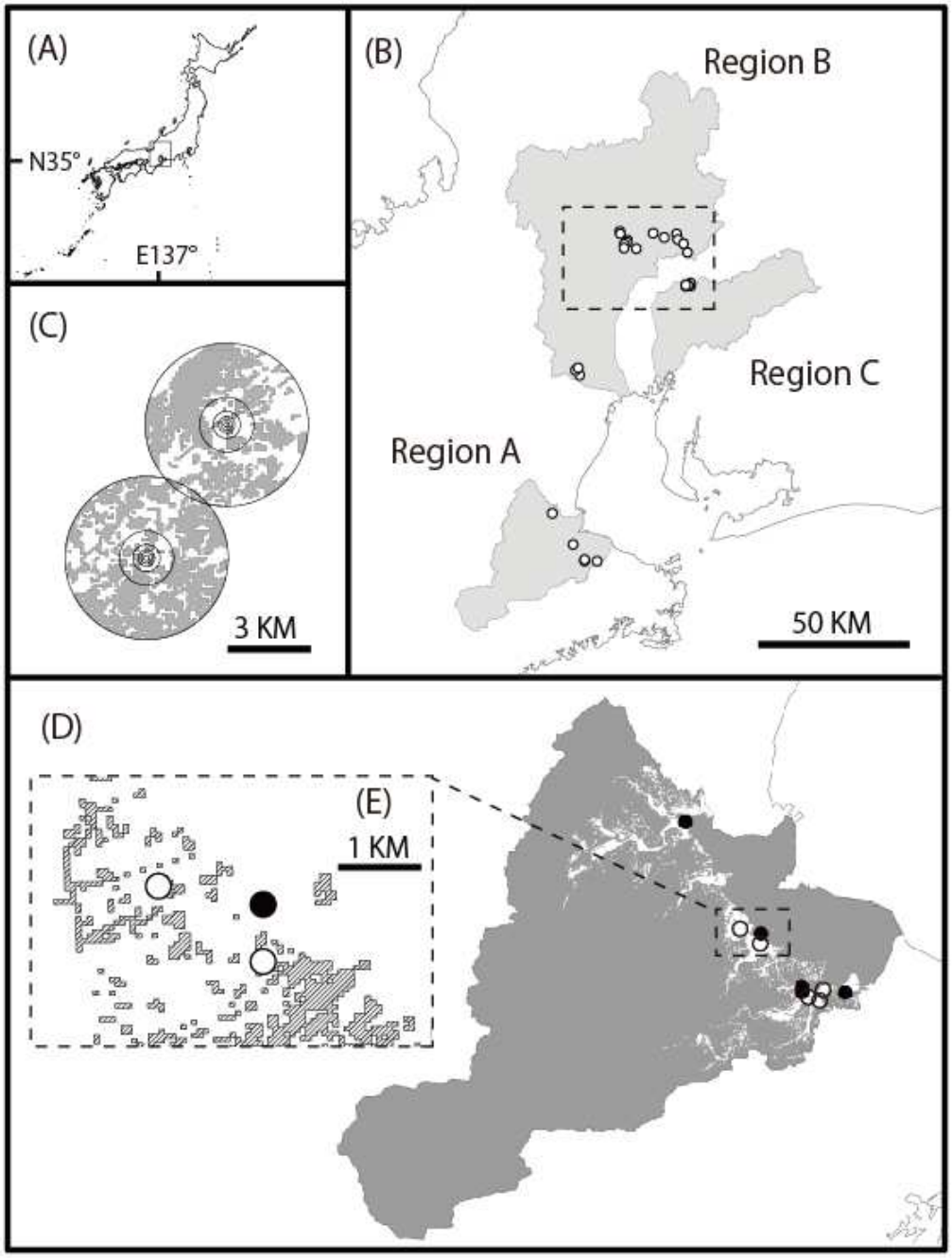


Fig. 1 Negishi et al.

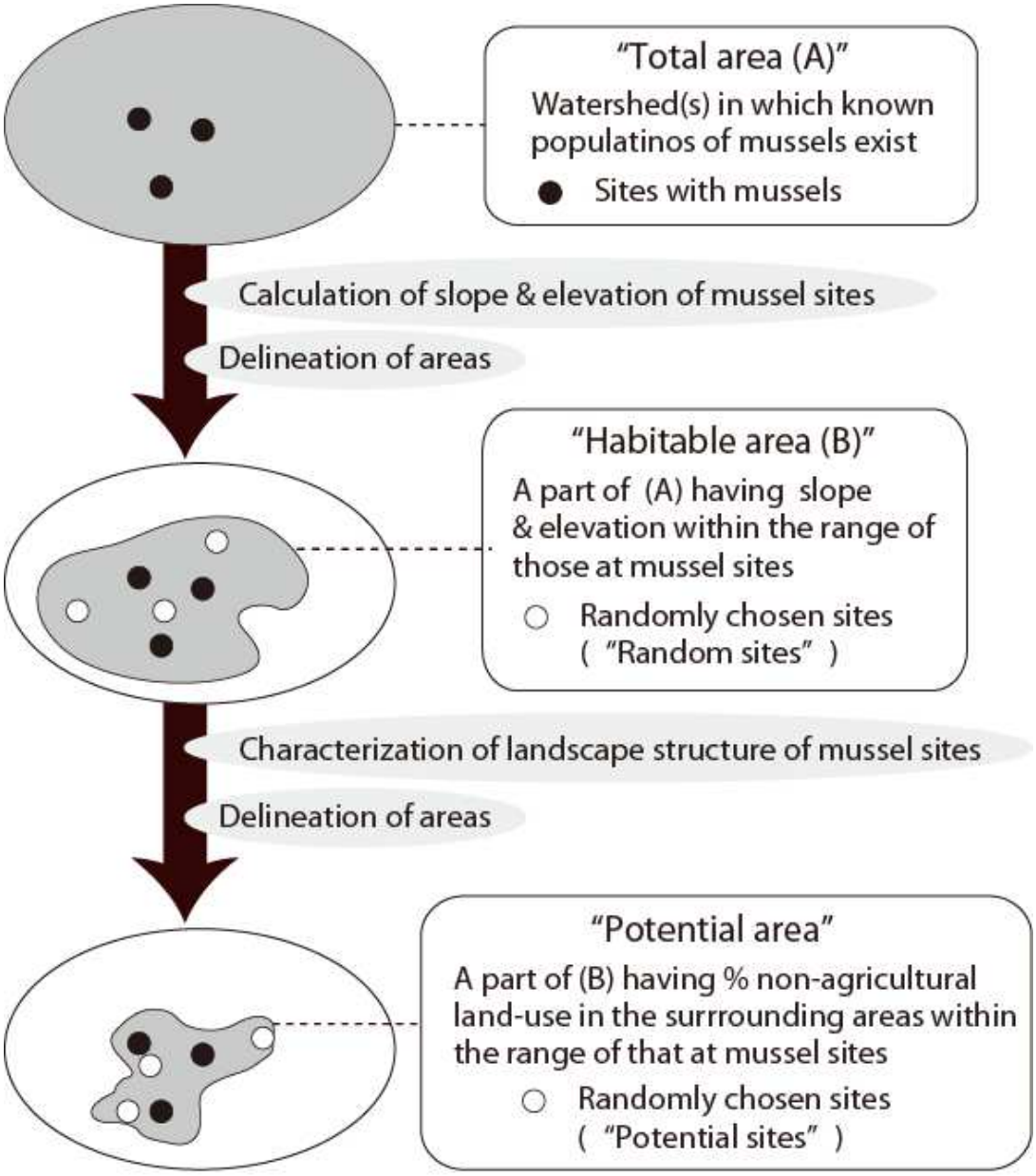


Fig. 2 Negishi et al.

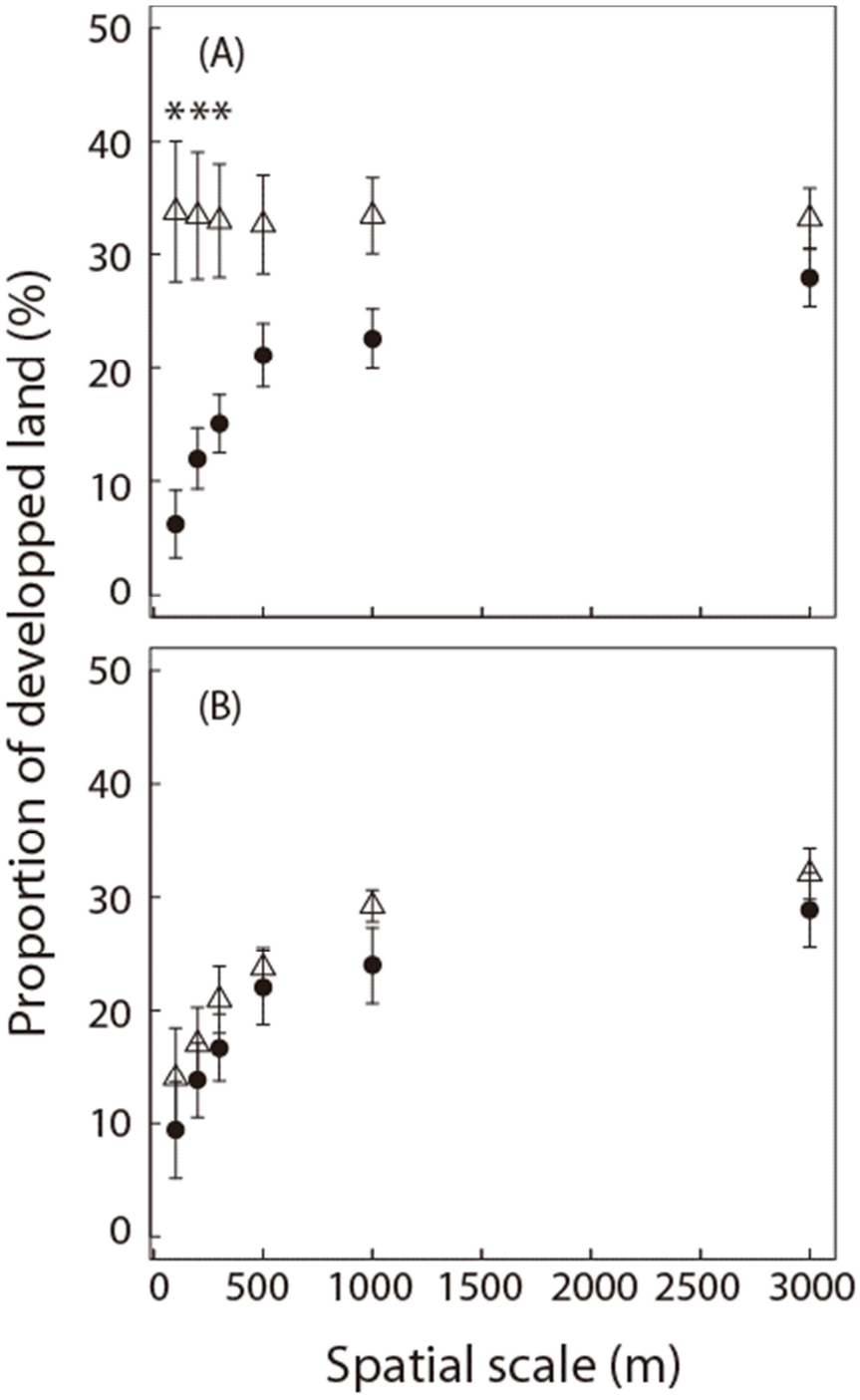


Fig. 3 Negishi et al.

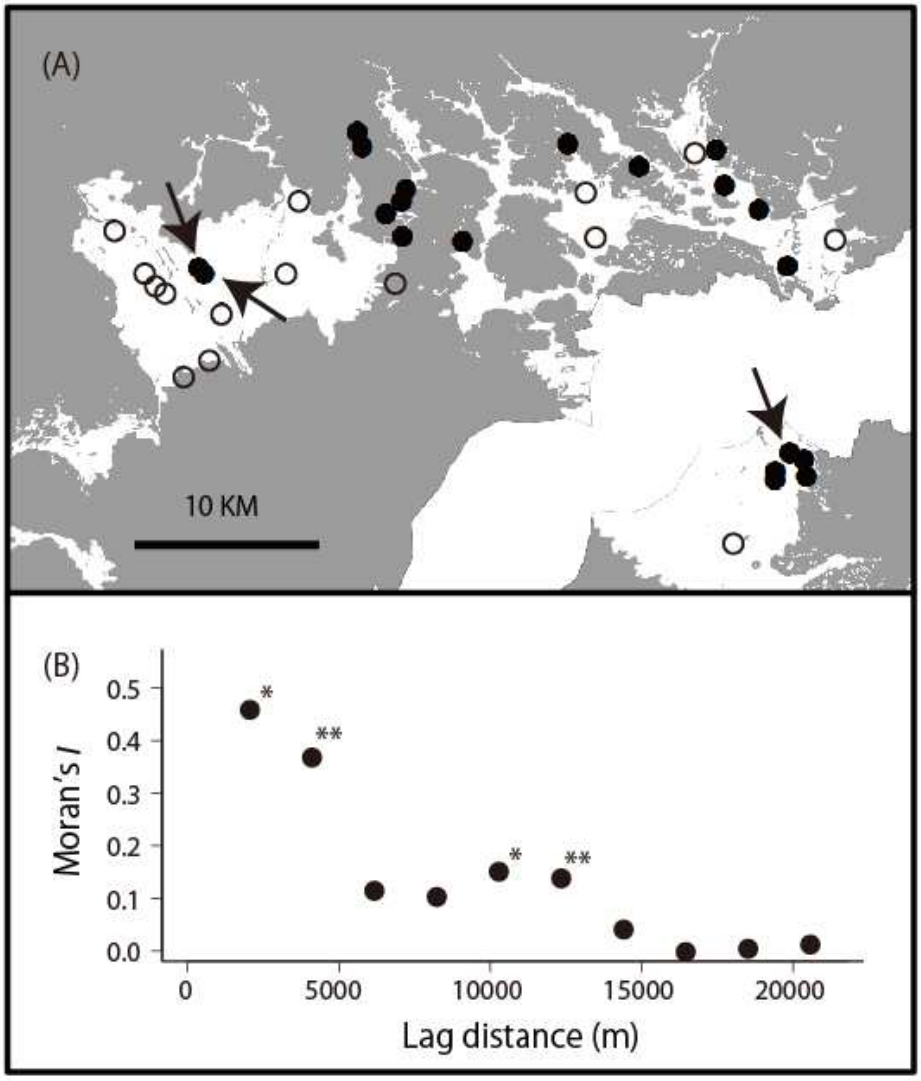


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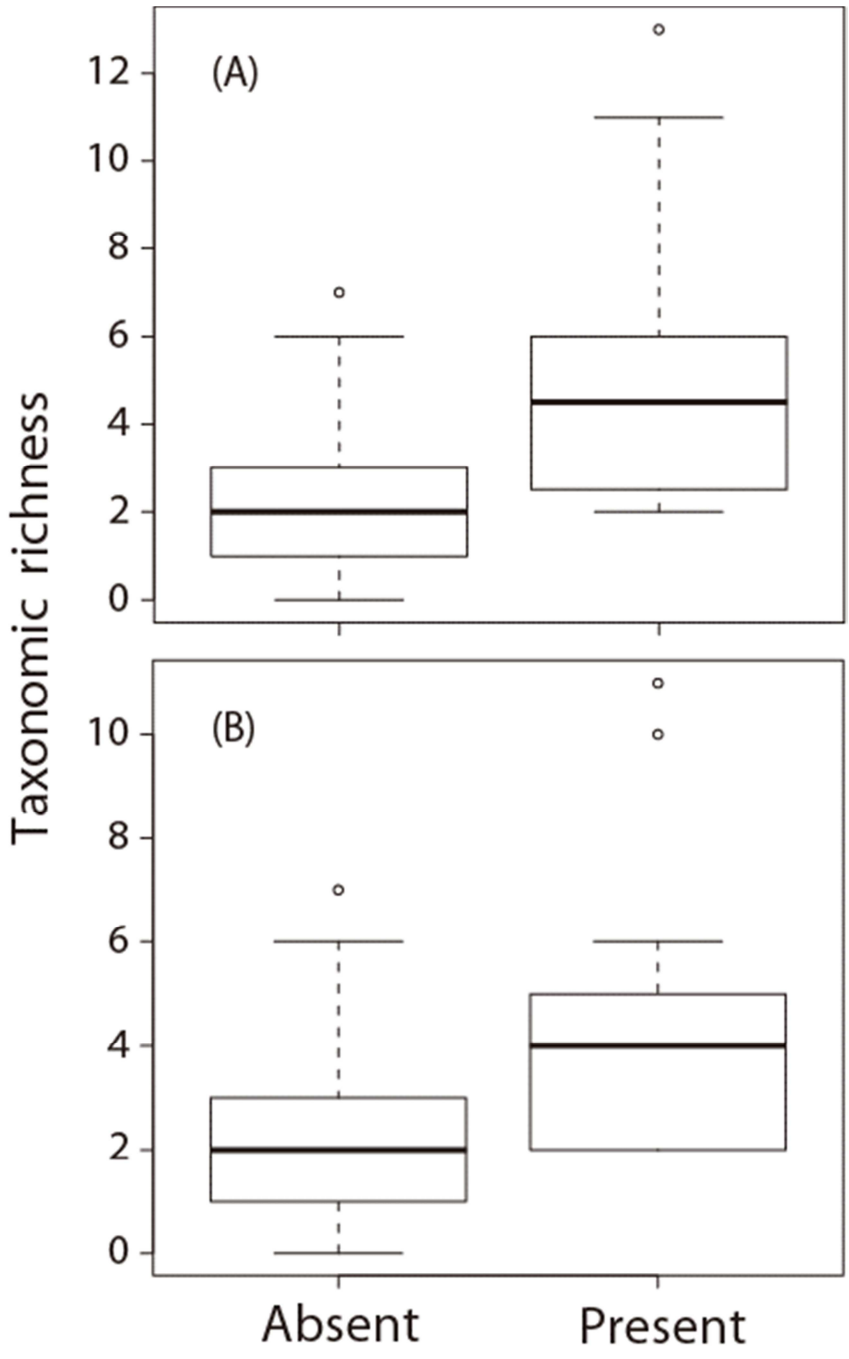


Fig. 5 Negishi et al.

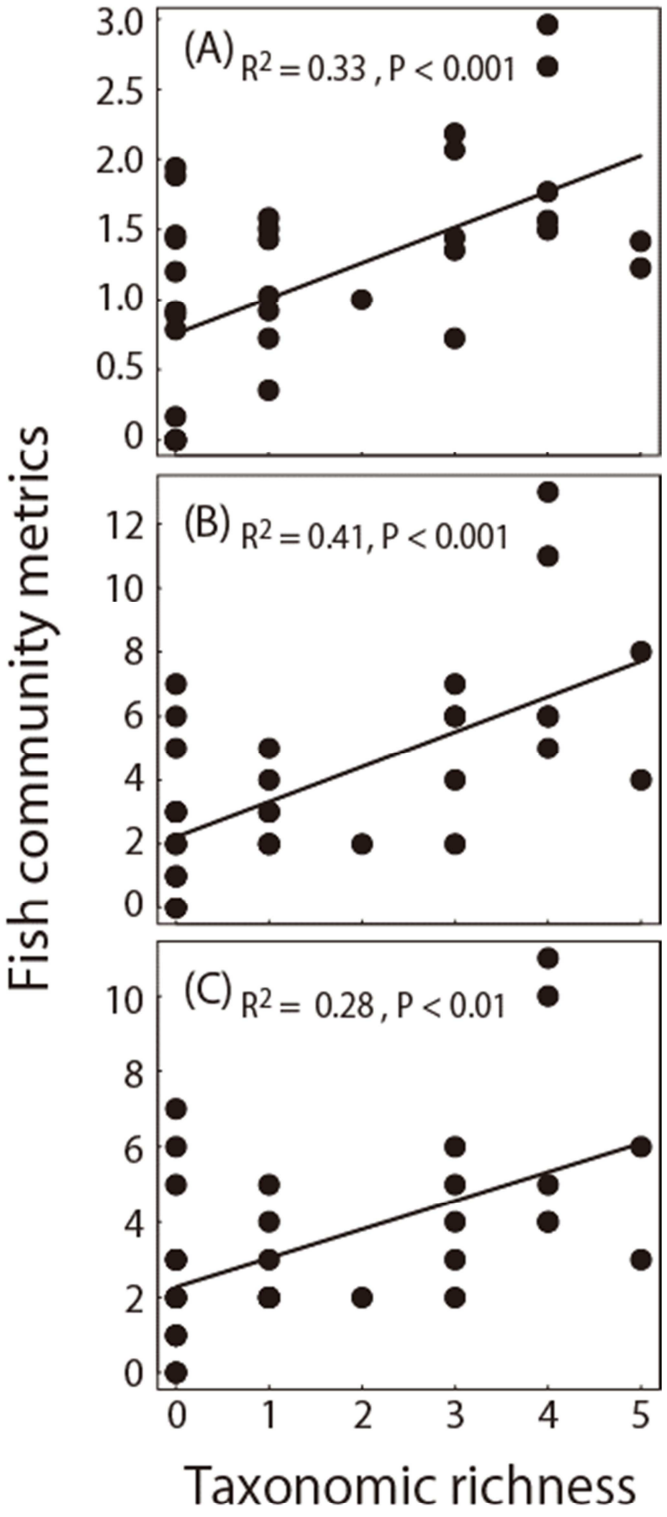


Fig. 6 Negishi et al.