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1 **Geology-dependent impacts of forest conversion on stream fish diversity**

2 **Ishiyama N, Miura K, Inoue T, Sueyoshi M & Nakamura F**

3
4 **Abstract**

5 Forest conversion is one of the greatest global threats to biodiversity, and land-use change and
6 subsequent biodiversity declines sometimes occur over a variety of underlying geologies.
7 However, how forest conversion and underlying geology interact to alter biodiversity is
8 underappreciated, although spatial variability in geology is considered an integral part of
9 sustaining ecosystems. We aimed to examine the effects of forest conversion to farmland,
10 underlying geology and their interaction on the diversity as well as species richness, evenness and
11 abundance of stream fishes in northeastern Japan. We disentangled complex pathways between
12 abiotic and biotic factors with structural equation modellings and found that the species diversity
13 of stream fishes was indirectly shaped by the interplay of land use and underlying geology.
14 Specifically, species diversity declined due to nutrient enrichment associated with farmlands,
15 which was mainly caused by changes in evenness rather than by changes in species richness. In
16 addition, this impact was stronger in streams with volcanic geology containing large substrates.
17 The interplay may result from the differential responses of abundant stream fishes to nutrient
18 enrichment (i.e., dominance) and the high dependency of these fishes on large streambed

19 materials during their life cycles. Our findings provide key insights into future land-use
20 management. First, the present study suggests that remediation of deforested or degraded forest
21 landscapes would be more efficiently conducted by considering the interaction between land use
22 and underlying geology. For example, the negative impacts of farmland on evenness were stronger
23 in streams with volcanic geology in the present study, suggesting that riparian forest restoration
24 along such streams would efficiently provide restoration benefits to stream fishes. Our findings
25 also have a wider application to future land-use development: land clearing around such streams
26 should be avoided to conserve the species evenness of stream fishes.

27

28 **Introduction**

29 Forest conversion is one of the greatest global threats to biodiversity (Brook et al.2003;
30 Gibson et al.2011), and agricultural development is among its largest direct causes. Hosonuma et
31 al. (2012) reported that commercial agriculture causes approximately 80 % of deforestation in
32 developing countries, and Curtis et al. (2018) attributed global forest loss from 2001 to 2015 to
33 shifting agriculture (24 %). The loss of forest cover directly eliminates habitat or corridors for
34 forest-dwelling species (Maretensen et al. 2008). In addition, forest conversion to farmland alters
35 the microclimatic and physicochemical characteristics of the surrounding habitat (Williams-
36 Linera et al., 1998; Schmidt et al. 2017), which in turn affects community structure and

37 biodiversity. Due to a wide range of negative impacts of forest conversion, the restoration of
38 previously forested land has evolved into a global initiative known as the ‘Bonn Challenge’; this
39 global effort aims to restore 150 million hectares of deforested and degraded forest landscapes by
40 2020 and 350 million hectares by 2030 to achieve the goals of restoring biodiversity and
41 mitigating climate change (Verdone & Seidl 2017). Given the serious anthropogenic impacts of
42 forest conversion, understanding the interactive effects of stressors on biodiversity is necessary
43 to manage habitats appropriately as well as to reliably project biodiversity change.

44 Ecological impacts of anthropogenic activities can vary along natural environmental
45 gradients (Peters et al.2019). Underlying geology (i.e., Earth’s subsurface rock lithology) controls
46 many environmental characteristics, such as soil properties and hydrology, which determine
47 habitat quality for plants and animals (Poff et al. 1997; Hjort et al. 2015). Indeed, understanding
48 the relationship between biodiversity and spatial variation in geological features is emerging as a
49 key issue (Schrodt et al.2019; Alahuhta et al.2020), and a few studies have shown that geological
50 variation affects the species richness of freshwater organisms (Toivanen et al. 2019; Kärnä et al.
51 2019). Forest conversion and subsequent biodiversity declines sometimes occur over a variety of
52 underlying geologies. However, how forest conversion and underlying geology interact to change
53 biodiversity is underappreciated, although interactions between variations in forest cover and
54 other major natural environmental factors, such as climate and geomorphology, have been

55 demonstrated (e.g., Ryo et al. 2018; Peters et al. 2019).

56 Running waters are among the most threatened ecosystems (Vörösmarty et al. 2010). The
57 conversion of forest to farmland in catchments has substantially altered the physicochemical
58 conditions of stream ecosystems, such as streambed materials and water quality, resulting in the
59 loss of biodiversity (Harding et al. 1998; Sueyoshi et al. 2017). Underlying geology, as well as
60 anthropogenic land use, intrinsically controls aquatic habitat conditions, such as substrate
61 composition and water chemistry (Carrie et al. 2015; Tashiro & Tsujimoto 2015). Given the
62 important independent effects of deforestation and underlying geology in running waters, testing
63 their combined effects is a necessary next step in strategic planning for the restoration of
64 catchment forests.

65 Here, we examine the effects of forest conversion, underlying geology and their interactions
66 on stream fish diversity on eastern Hokkaido Island, northern Japan. The underlying geology in
67 the region exhibits spatial variation, and natural forests have been widely converted to farmland
68 (Fig. 1). We hypothesize that 1) fish diversity will decrease with the loss of catchment forests
69 (e.g., increases in the amount of current farmland) due to alterations of instream environments
70 and 2) the impact will change along the gradient of underlying geology that governs physical
71 habitat quality. We disentangle the complex pathways from anthropogenic and natural factors to
72 stream fish diversity by using structural equation modeling (SEM).

73

74 **Methods**

75 - **Study Sites**

76 To clarify the pathways by which underlying geology and forest conversion to farmland
77 interact to change biodiversity, a field study was conducted on eastern Hokkaido Island (Fig. 1a).
78 We selected our study sites within the same climatic region and eco-region (Watanabe 2012; Inoue
79 et al. 2017) to eliminate confounding factors such as climatic and faunal gradients. Since the early
80 1900s, forest cover in the region has been rapidly converted to farmland such as pasture and crop
81 fields (Fig. 1b). The geology in the study area is largely characterized by Quaternary volcanic or
82 sedimentary materials (Geological Survey of Japan, National Institute of Advanced Industrial
83 Science and Technology). Volcanic rock is primarily composed of pyroclastic flow volcanic rocks
84 and volcanic ash originating from the Akan and Mashyu volcanoes. Sedimentary rocks originate
85 from marine and nonmarine sediments or swamp deposits. In the study region, we set 42 study
86 reaches with wetted widths of 4.9 ± 2.0 m (mean \pm sd). Biodiversity and its relationships with
87 abiotic factors can change along elevational gradients. We therefore restricted the study reaches
88 to the same low-elevational area, where the mean elevation was 26 ± 17 m (mean \pm sd).

89

90 - **Fish Sampling and Biotic Variables**

91 We collected fish in each study reach from August to September 2017 and 2018. In each
92 reach, we carried out two-pass electrofishing with a backpack electrofisher (Smith-Root; Model
93 LR-20B; Smith-Root Inc., Vancouver, Washington, USA) and counted the total number of
94 individuals for each species. An individual reach was approximately 10 times the length of the
95 wetted width (55 ± 21 m: mean \pm sd). Species diversity was calculated using Shannon and
96 Simpson indices. Both indices combine the number of taxa and their evenness across sites, but
97 the former is more sensitive than the latter to the responses of species with low abundances
98 (Magurran 2004). In addition, species richness, Pielou's evenness and the abundance of each
99 species were quantified to examine the processes creating patterns in fish diversity. We quantified
100 the abundance of each species according to individual density (inds./100 m²). We focused only
101 on native species and excluded the rainbow trout *Oncorhynchus mykiss* (Table 1; abundance: 2 %,
102 prevalence: 19 %) from calculations of the following diversity indices because the present study
103 aimed to conserve indigenous fish communities. We compared observed species richness with
104 estimated species richness using rarefaction-extrapolation analysis (Hsieh et al. 2016) to verify
105 the adequacy of our sampling efforts. Fish sampling was undertaken with permission from the
106 Fisheries Adjustment Rules of Hokkaido Prefecture.

107

108 - **Local-Scale Abiotic Variables**

109 In each study reach, we measured electrical conductivity (EC: ms/m), substrate coarseness,
110 water depth (cm), and current velocity (cm/s) during the fishing survey. We used EC as a water
111 quality index of nutrient enrichment because EC was positively correlated with total nitrogen
112 (TN: mg/L) and total phosphorus (TP: mg/L) in the study region (Fig. S1). We measured EC in
113 the uppermost section of each study site (WM-32EP, TOA DKK Co., Japan). For other
114 measurements, we established ten equally spaced transects with three measurement points in each
115 study reach. Water depth and current velocity were determined at each measurement point, and
116 the means of these variables in each reach were used for analysis. Current velocity was measured
117 at a 60 % depth from the water surface using a propeller-based flow meter (model CR-11; Cosmo-
118 riken Inc., Tokyo, Japan). At each measurement point, substrates were identified by visual
119 observation and classified as one of the following types: bedrock, silt (<0.063 mm), sand (0.063–
120 2 mm), gravel (2–32 mm), pebble (32–64 mm), cobble (64–128 mm) or boulder (>128 mm).
121 These categories were then coded as follows: bedrock = 0, silt = 1, sand = 2, gravel = 3, pebble =
122 4, cobble = 5 and boulder = 6. The recorded values were averaged to represent reach-scale
123 substrate coarseness. To assess habitat complexity in each reach, the coefficients of variation
124 (CVs) of water depth, current velocity and substrate coarseness were calculated by using the
125 values at 30 measurement points. We integrated the three CVs into one habitat complexity index
126 with principal component analysis and used the index for the following analyses. All of the CVs

127 were positively correlated with the habitat complexity index; that is, a high value indicated high
128 physical complexity (Fig. S2).

129

130 - **Landscape-Scale Abiotic Variables**

131 We applied catchment size, stream slope, catchment land use and underlying geology to
132 represent the landscape-scale abiotic variables that can influence local-scale abiotic and biotic
133 conditions. Catchment size (km²) and stream slope were obtained from a 10-m digital elevation
134 model (DEM) published by the Geospatial Information Authority of Japan. For the calculation of
135 stream slope, we clipped river lines around study sites using a 1-km-diameter buffer and divided
136 the length of the clipped river lines by the change in elevation. Land-use calculations were
137 conducted based on high-resolution land-use and land cover maps around 2010 with 11 thematic
138 classes (version 16.09, Jaxa 2016). We used the proportion of farmland in the catchments as an
139 index of forest conversion; proportions of farmland and forest were highly and negatively
140 correlated in the current landscape ($r = -0.99$). We defined ‘crops’ and ‘grassland’ as farmland and
141 calculated the proportion of farmland in the catchments (%). We calculated the proportion of
142 volcanic rocks within a 1-km-diameter buffer around each study site as an index of underlying
143 geology. The procedures used to select spatial scales for the calculation of land use and underlying
144 geology are shown in Table S1. Geological calculation was based on the 1:200,000 Seamless

145 Digital Geological Map of Japan (Geological Survey of Japan, National Institute of Advanced
146 Industrial Science and Technology). All geospatial analyses were performed in ArcMap (Esri,
147 version 10.6.1).

148

149 - **Statistical Analyses**

150 We applied structural equation models (SEM) to clarify the pathways by which underlying
151 geology and forest conversion interact to change biodiversity. SEM is a powerful technique for
152 evaluating multivariate causal relationships, including direct and indirect effects of the variables
153 (Fan et al. 2016); however, the results depend on sample size, similar to other statistical
154 approaches. The risk of Type I or II errors can increase when the sample size is too small or too
155 large (Wolf et al. 2013), and models with small sample sizes sometimes fail to converge (Rosseel
156 2020). We constructed multiple structural equation models, which included the Shannon index,
157 the Simpson index, species richness, evenness and the abundance of each species as biotic
158 response variables. In each model, we included four landscape-scale (catchment size, slope, land
159 use and geology) and three reach-scale abiotic variables (water quality index, substrate coarseness
160 and habitat complexity index) (Fig. 2). Lithological differences and the resultant effects on
161 bedrock resistance and particle size are likely to control sediment supply (Thompson et al. 2006),
162 and strong effects of underlying geology on substrate composition have been demonstrated in

163 Japanese streams (Tashiro & Tsujimoto 2015). We therefore applied a direct path from underlying
164 geology to substrate coarseness. Furthermore, geomorphic factors such as streambed slope and
165 catchment size were set as landscape-scale variables that control physical habitat conditions. We
166 applied a path from land use in the catchment to nutrient enrichment (i.e., EC), assuming an
167 influence of farmland on water quality. Elevated fine sediment is another possible impact of
168 human land use on aquatic biota (Kemp et al. 2011). However, we found no relationship between
169 fine sediment deposition and fish diversity in the study region (Fig. S3). Therefore, to simplify
170 model structure, we did not include the amount of fine sediment in the models. For the same
171 reason, we did not use the amount of woody cover or summer water temperature as an abiotic
172 variable (Fig. S3). In addition, we expected that the negative impact of land use (i.e., water
173 quality) on fish diversity would vary with underlying geology (i.e., substrate characteristics) and
174 thus included interactive terms between water quality and substrate coarseness to test for a
175 geology-land use interaction (Fig. 2). The proportion of volcanic materials and abundance of each
176 species were log-transformed to ensure multivariate normality, and we applied SEM using the
177 estimation method based on maximum likelihood. To avoid overfitting, any path with a small
178 coefficient (< 0.15) was removed from the model when it was not significant (Fujii et al. 2017;
179 Ishiyama et al. 2020). We repeatedly adjusted the models to find an adequate model with
180 standardized root mean square residual (SRMR) values, with values < 0.09 suggesting an

181 adequate fit. The fit of the model was also checked with a χ^2 test associated with a p value >
182 0.05 and the comparative fit index (CFI > 0.95). We used the ‘lavaan’ and ‘semTools’ libraries in
183 R software 3.3.2.

184

185 **Results**

186 In the study region, twelve native fish species were found, and the species richness measured
187 by fish sampling reflected 93 % of the estimated species richness on average (Table S2). The three
188 most abundant species were the stone loach *Barbatula barbatula* (841 inds., 29.4 %), white-
189 spotted char *Salvelinus leucomaenis* (684 inds., 23.9 %) and masu salmon *Oncorhynchus masou*
190 (631 inds., 22.1 %) (Table 1). Both the Shannon and Simpson diversity indices were more strongly
191 correlated with evenness than with species richness (Fig. 3). To model the abundance of each
192 species, we excluded species with a low prevalence rate (<25 %) from the SEM analyses and
193 targeted seven species because species with such a low prevalence may occur more randomly in
194 samples and not be well represented by distribution modeling (Table 1).

195 The final models for species diversity showed adequate model fits (Table 2) and explained
196 15 % of the total variance in the Shannon index and 17 % of that in the Simpson index (as R^2). In
197 the final models, the proportion of farmland in catchments had a direct positive effect on EC
198 (nutrient enrichment) (Fig. 4). Underlying geology (proportion of volcanic rocks) and stream

199 geomorphology (stream slope) calculated with a 1-km-diameter buffer positively affected
200 substrate coarseness (Fig. S4). Stream slope also positively affected stream habitat complexity. In
201 addition, significant interactive effects of EC and substrate coarseness on both the Shannon and
202 Simpson indices were found (Fig. 4a, b); species diversity declines due to increased nutrients
203 were more evident in streams with larger substrate materials (Fig. 5a, b). These results indicate
204 that anthropogenic land use indirectly and interactively shapes stream fish diversity with
205 underlying geology and stream geomorphology through the control of local habitat conditions.

206 The final models for species richness and evenness also showed adequate model fits (Table
207 2), explaining 30 % and 26 % of the total variance, respectively. Evenness showed similar
208 significant pathways with species diversity indices in the final models (Fig. 4d). On the other
209 hand, species richness was influenced only by catchment size; larger streams supported higher
210 species richness than did smaller streams (Fig. 4c).

211 We succeeded in modeling the abundance of six of the seven modeled species, namely, *S.*
212 *leucomaeniss*, *O. masou*, *B. barbatula*, *L. reissneri*, *Gymnogobius* sp. and *Pungitius* sp., with an
213 average of 29 % of the total variance explained (Table 2). For *O. masou*, *B. barbatula* and
214 *Gymnogobius* sp., we found a significant interactive effect of land use and geology on the
215 diversity indices and evenness (Fig. 6b, c, e). However, the three species showed different
216 responses to water quality degradation. The abundances of *O. masou* and *Gymnogobius* sp.

217 decreased with increasing EC, and the relationship was most evident in streams with larger
218 streambed materials (Fig. 5d, f). On the other hand, the abundance of *B. barbatula* positively
219 responded to increasing EC, with the clearest response observed for larger streambed materials
220 (Fig. 5e). The abundances of the other three species were influenced by catchment size. *S.*
221 *leucomaenis* abundance was negatively related to catchment size, whereas *L. reissneri* and
222 *Pungitius* sp. abundances responded positively to catchment size (Fig. 6a, d, f).

223

224 **Discussion**

225 In recent years, forest cover has been converted to farmland throughout the world, which has
226 deteriorated biodiversity. We disentangled the complex pathways among abiotic and biotic factors
227 by using SEM and found that the species diversity of stream fishes was indirectly shaped by the
228 interplay of land-use change and underlying geology, as expected (Fig. 4). Specifically, species
229 diversity declined due to forest conversion (i.e., nutrient enrichment), which was most evident in
230 streams with volcanic geology occupied by large streambed materials. Due to a wide range of
231 threats from forest loss and anthropogenic land use, the restoration of previously forested land
232 has led to the establishment of global targets such as the ‘Bonn Challenge’ (Verdone & Seidl
233 2017). The key findings of this study suggest that the effects of forest restoration on biodiversity
234 can vary with underlying geology. Of course, further studies are needed to deeply understand the

235 interplay of land-use change and underlying geology, but the present study suggests that
236 management of deforested or degraded forest landscapes would be more efficiently conducted by
237 considering the interaction.

238 Given limited conservation resources, landscape managers need to set priorities for habitat
239 restoration based on an understanding of the process by which human impacts affect
240 biodiversity. In the present study, we used the Shannon and Simpson diversity indices, which
241 are composed of two main elements: richness, which represents the number of species, and
242 evenness, which represents the variability in species abundance (Magurran 2004). Sites with
243 low species diversity tend to be given high restoration priority. However, species richness and
244 evenness can respond differently to the environment (e.g., Reitalu et al. 2009; Corcos et al.,
245 2018). We therefore have to thoroughly understand the processes by which environmental
246 stressors can alter these two components of species diversity. In the study region, the diversity
247 indices were more positively correlated with evenness than with species richness (Fig. 3), and
248 we detected a significant interactive effect of land use and underlying geology only on evenness
249 (Fig. 4c, d). For species richness, we detected a significant effect of catchment size but a
250 nonsignificant effect of anthropogenic land use. These findings suggested that land use and
251 underlying geology interactively affect species diversity mainly through changes in the

252 abundance of each species (i.e., evenness) and management efforts should be preferentially
253 focused on restoring evenness rather than species richness in the study region.

254 Even under high human impacts, presence/absence cannot change when at least one
255 individual is present. Therefore, evenness often responds more quickly than species richness to
256 anthropogenic disturbances (Chapin et al. 2000), which is also supported by our results.
257 Increasing evenness theoretically reduces invasibility because more local niches can be filled by
258 natives in even communities than in communities dominated by few species (see review by
259 Hillebrand et al. 2008). In addition, some empirical studies have shown that vigorous ecosystem
260 function is sustained by high evenness. For example, Crowder et al. (2010) showed that organic
261 farming practices promoted the evenness of natural enemy communities, which triggered a
262 powerful trophic cascade beneficial to plants and harmful to herbivores (i.e., natural pest
263 control). Given the various benefits of greater evenness, conserving and promoting evenness
264 would mitigate the negative impacts of anthropogenic land use on community resistance and
265 ecosystem functions.

266 Three of the seven modeled species, *O. masou*, *B. barbatula* and *Gymnogobius* sp., were
267 also affected by the interplay of land use and geology (Fig. 5), with the first two among the
268 three most abundant species in the study region (Table 1). However, the impacts of forest
269 conversion to farmland (i.e., nutrient enrichment) differed between the two species: the

270 abundance of *O. masou* responded negatively and indirectly to the proportion of farmland in
271 catchments, while that of *B. barbatula* showed a positive response. Nutrient enrichment caused
272 by agricultural development and its ecological impacts in running waters have already been
273 widely reported (e.g., Yuan 2010). The direct and indirect effects of elevated nutrient levels are
274 probable causes of ecological changes. In European running waters, 1 mg/L NH₄ has been used
275 as a threshold for ensuring trout survival (EIFAC 2013), which is well above our observed
276 range of ammonium concentrations, which was 0.029 to 0.123 mg/L (Table S3). This difference
277 suggests that direct toxic effects on *O. masou*, which exhibited decreased abundance in this
278 study, are unlikely. Another possible cause is an indirect effect through food-web modification.
279 For example, nutrient enrichment may shift benthic invertebrates from EPT taxa that are
280 sensitive to eutrophication-related water quality to non-EPT taxa such as small chironomids
281 (Harding et al. 1999; Quinn & Hickey 1990), which is consistent with a trend observed in other
282 streams on Hokkaido Island (Fig. S5). Quinn & Hickey (1990) also suggested that the loss of
283 large drifting macroinvertebrates and their replacement by small chironomids and mollusks
284 reduces the feeding efficiency of drift-feeding fishes. *O. masou* is a drift-feeding trout, and
285 ephemeropteran and trichopteran species are major aquatic food resources of this species
286 (Hashimoto & Ishida 1977; Nagasaka 1997). Therefore, such changes in the prey community
287 may be unsuitable, causing the abundance of *O. masou* to negatively respond to the proportion

288 of farmland in catchments. On the other hand, *B. barbatula* is a benthivorous fish that prefers
289 small and consistently abundant prey, such as chironomids (Worischka et al. 2015), suggesting
290 that the above changes in the prey community can have positive impacts on benthic fish. These
291 indirect effects of forest conversion on stream fishes may be reflected in community
292 composition (i.e., evenness), manifesting as a decrease in fish species diversity.

293 Why did the negative impact of anthropogenic land use on fish species diversity change
294 with spatial variability in underlying geology? As expected, the size of the substrate in the
295 studied streams was significantly affected by underlying geology, consistent with results in
296 previous studies (Thompson et al. 2006; Tashiro & Tsujimoto 2015). Lithological differences
297 and the resultant effects on bedrock resistance and particle size are likely to control the sediment
298 supply and resulting reach-scale streambed conditions, as suggested by Thompson et al. (2006).
299 Streambed conditions were more influenced by reach-scale geology than by catchment-scale
300 geology (Table S1). We selected study sites in low-elevation areas, a setting that may explain
301 the results. Lowland streams with gentle stream slopes tend to have low stream power and
302 would be more sensitive than other streams to sediment supply controlled by local geology.
303 Substrate coarseness plays a key role in the life histories of some stream fish and other aquatic
304 organisms. For the two most abundant species, namely, *O. masou* and *B. barbatula*, abundance
305 was affected by the interplay of land use and geology, similar to evenness. *O. masou* uses

306 middle- to large-sized substrates as spawning (Urabe et al. 2004) and overwintering (Nagayama
307 & Nakamura 2007) habitats. As the name suggests, the stone loach *B. barbatula* prefers gravel
308 streambeds that provide abundant interstitial shelter (Vlach et al. 2005). Therefore, the
309 influences of forest conversion on these species would become apparent in streams with high
310 substrate coarseness (Fig. 5) because the abundances of these species in small-particle streams
311 are inherently limited, regardless of the negative impact of anthropogenic land use. The
312 sensitivity of stream fishes to catchment land use in large-particle-sized streams (i.e., a large
313 proportion of volcanic geology) may be reflected in spatial trends of evenness, which will
314 change species diversity.

315 In the present study, we also detected interactive effects on species diversity between land
316 use and stream slope as well as underlying geology; declines in species diversity associated with
317 forest conversion were most evident in steep streams containing large streambed materials. It is
318 generally known that spatial variability in geomorphology governs habitat structure in running
319 waters. Stream slope, one of the key components of stream geomorphology, is directly related to
320 sediment transport capacity, and many studies (including the present study) have shown that
321 stream slope controls streambed composition (e.g., Coulombe-Pontbriand & Lapointe 2004). In
322 general, a steep slope consists of coarse bed materials. Thus, species diversity changes along
323 stream slopes and forest cover gradients can be regulated by the same mechanisms as species

324 diversity changes along underlying geology gradients (i.e., the dominant fish species in the
325 investigated streams prefer coarse substrates for their aquatic food resources and habitat, but the
326 response to nutrient enrichment differed among the species). The importance of the interaction
327 between forest land cover and geomorphology for stream biodiversity was also supported by
328 previous studies (e.g., Ryo et al. 2018). The findings of our study re-emphasize that the
329 interplay of geomorphology and land use should be considered in the management of deforested
330 landscapes.

331 The importance of the interactions between multiple stressors in ecosystem management
332 has been widely recognized, and interactions between natural and chemical (anthropogenic)
333 stressors, as revealed by our findings, are also well documented (see review by Holmstrup et al.
334 2010). However, to the best of our knowledge, few studies have clearly demonstrated that such
335 interplays result from the combined effects of land use and underlying geology. Our findings
336 emphasize that considering the interplay of geology and land use could significantly contribute
337 to future forest restoration projects. Restoration of whole-catchment land use is an ideal practice
338 but is nearly impossible due to substantial social impacts. Previous studies have shown that
339 riparian forests filter nutrients supplied from catchments (e.g., Vought et al. 1994; Nakamura &
340 Yamada 2005). Thus, reconvertng farmland along streams to forest will provide double the
341 ecological benefits (i.e., reduce nutrient sources and enhance filtering effects) while minimizing

342 social impacts. In addition, Nagasaka & Nakamura (1999) showed that the amount and volume
343 of large wood should substantially decrease with agricultural development, such as riparian
344 forest cutting. Cover provided by large woody debris can enhance the abundance of stream
345 fishes (e.g., Inoue & Nakano 2001), although we did not find a significant relationship between
346 the cover ratio and fish diversity. In the study region, the impacts of farmland on evenness are
347 higher in streams with larger substrates, suggesting that riparian forest restoration along such
348 streams with volcanic backgrounds or steep slopes would efficiently provide restoration benefits
349 to stream fishes. Farmland has been abandoned during the period of economic growth after the
350 1950s in developed countries, including Japan (e.g., Kobayashi et al. in press); utilization of
351 such degraded lands with depopulation is increasingly recognized as a tool for biodiversity
352 conservation (e.g., Nakamura et al. 2020). These previous studies and our findings strengthen
353 the argument that forest restoration using abandoned farmlands along streams with a volcanic
354 underlying geology is one of the best solutions for meeting ecological and social requirements.
355 Our findings have a wider application to future land-use development: land clearing around
356 such streams should be avoided in order to conserve species evenness. As we discussed,
357 degradation of upstream forest changes downstream environmental factors such as water quality
358 and the amount of organic matter. Therefore, our findings will also help conserve the health of
359 downstream ecosystems.

360 In our models, the pathways in models were simplified to test our hypothesis with limited
361 samples; however, the model identifies potential relationships between landscape geology,
362 channel substrates, land use, and fish species diversity. Underlying geology can cause spatial
363 variability in many instream environments as well as substrate composition. Large wood,
364 sediment and flow are the three key components of dynamic river ecosystems (Nakamura et al.
365 2017). In the present study, we considered large wood and sediment as candidate explanatory
366 variables, but flow regime was not measured, although the impacts of flow disturbance on
367 freshwater biodiversity can change with agricultural development (e.g., Sueyoshi et al. 2017). In
368 addition, not only local habitat quality but also the spatial configuration of habitat in
369 watercourse networks affects species diversity and abundance (e.g., Ishiyama et al. 2014, 2015).
370 The unexplained variance in our models may be related to these factors. Further studies which
371 test these unexplored factors are needed to improve our understanding of the interplay between
372 land use and underlying geology, and our findings can be further confirmed by future related
373 studies targeting various biotas and regions.

374

375 **Supporting Information**

376 Relationship of electrical conductivity with total nitrogen and total phosphorus (Fig. S1);
377 relationship of the habitat complexity index with the CVs of water depth, current velocity and

378 substrate coarseness (Fig. S2); relationships of fish diversity with the percentage of fine
379 sediment, percentage of woody cover and summer mean water temperature (Fig. S3);
380 relationships among the underlying geology, stream slope and substrate coarseness (Fig. S4);
381 and relationships of benthic macroinvertebrate abundance with nutrient enrichment in streams
382 of northern Hokkaido (Fig. S5) are available online. The procedures used to select the spatial
383 scales for land use and geology (Table S1), the observed and estimated species richnesses in
384 each study site (Table S2), the water chemical variables of the study reaches (Table S3) and
385 abiotic and biotic data for the statistical analyses (Table S4) are also available online. The
386 authors are solely responsible for the content and functionality of these materials. Queries (other
387 than those regarding absence of the material) should be directed to the corresponding author.
388

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540 **Table 1** List of captured fish species and information on their abundance and presence/absence.

541 The seven species used for abundance modeling are shown in bold.

Species	Total catch ^a	Abundance % ^b	Prevalence % ^c
Native			
<i>Salvelinus leucomaenis</i>	684	23.9	90.7
<i>Salvelinus malma</i>	1	0.0	2.3
<i>Oncorhynchus masou</i>	631	22.1	72.1
<i>Hucho perryi</i>	5	0.2	7.0
<i>Barbatula barbatula</i>	841	29.4	79.1
<i>Lethenteron reissneri</i>	244	8.5	74.4
<i>Cottus nozawae</i>	12	0.4	14.0
<i>Rhinogobius</i> sp.	48	1.7	4.7
<i>Gymnogobius</i> sp.	122	4.3	25.6
<i>Pungitius tymensis</i>	145	5.1	62.8
<i>Pungitius</i> sp.	35	1.2	25.6
<i>Trinbolodon</i> sp.	27	0.9	14.0
Non-native			
<i>Oncorhynchus mykiss</i>	63	2.2	19.0

543 ^a Total catch is the total number of fish caught in the 42 study reaches.

544 ^b Abundance % shows the number of each species relative to the total number of fish caught.

545 ^c Prevalence % shows the reaches with target species relative to the total number (42) of

546 reaches.

547 **Table 2** Structural equation modeling (SEM) fit statistics.

Biotic response variable	Chi p value ^a	CFI ^b	SRMR ^c	R ² ^d
Shannon index	0.937	1.000	0.064	0.15
Simpson index	0.865	1.000	0.068	0.17
Species richness	0.771	1.000	0.045	0.30
Evenness	0.825	1.000	0.065	0.26
Abundance				
<i>Salvelinus leucomaenis</i>	0.238	0.959	0.064	0.38
<i>Oncorhynchus masou</i>	0.970	1.000	0.055	0.30
<i>Barbatula barbatula</i>	0.901	1.000	0.056	0.36
<i>Lethenteron reissneri</i>	0.862	1.000	0.047	0.11
<i>Gymnogobius</i> sp.	0.87	1.000	0.060	0.19
<i>Pungitius tymensis</i>	—	—	—	—
<i>Pungitius</i> sp.	0.465	0.996	0.056	0.39

548 ^a Chi p value is the p value for chi-squared tests.

549 ^b The comparative fit index (CFI) represents the amount of variance accounted for in the
550 covariance matrix and is less affected by sample size than chi-squared tests. The CFI values range
551 from 0.0 to 1.0. A higher CFI value indicates a better model fit, which should be close to or higher
552 than 0.95 (Fan et al. 2016).

553 ^c Standardized root mean square residual (SRMR) is defined as the standardized difference
554 between the observed and predicted correlations.

555 ^d The R² statistics indicate the overall fit of the model to the biotic response variables.

556

557 **Figure Captions**

558 **Fig. 1** Characteristics of the study region. (a) Study sites and spatial configuration of the
559 geology and land use in the study region. (b) Land-use transitions around the study region; the
560 study region is divided with a 2 km × 2 km square grid, and the dominant land-use type in each
561 grid is shown on the map. We obtained data from LUIS Web
562 (<http://db.cger.nies.go.jp/dataset/luis/ja/index.html>) in the Global Environmental Database,
563 Center for Global Environmental Research, National Institute for Environmental Studies, Japan,
564 and modified maps of land-use changes in Hokkaido. The historical land-use data used in this
565 study were generated by Yukio Himiyama, Hokkaido University of Education, and Shouichirou
566 Arizono, Aichi University (Himiyama 1995; Arizono 1995).

567

568 **Fig. 2** Hypothetical model used to represent the direct and indirect pathways from abiotic
569 factors to biotic responses. We hypothesized that forest conversion indirectly and negatively
570 affects the species diversity of stream fishes through nutrient enrichment, and this effect of land-
571 use change depends on underlying geology, which forms a physical habitat template for stream
572 fishes. WQ×Sub is the term for the interaction between water quality and substrate coarseness.

573 **Fig. 3** Relationships of species richness and evenness with species diversity indices.

574

575 **Fig. 4** Path diagram based on a parsimonious model obtained with structural equation modeling
576 (SEM) for species diversity, species richness and evenness. WQ×Sub is the term for the
577 interaction between water quality and substrate coarseness. The standardized path coefficients
578 and R² values are shown; path thickness is proportional to the size of the standardized
579 coefficient. Asterisks indicate the statistical significance of each path: *P < 0.1, **P < 0.05, and
580 ***P < 0.01. Black and gray paths indicate positive and negative effects, respectively.

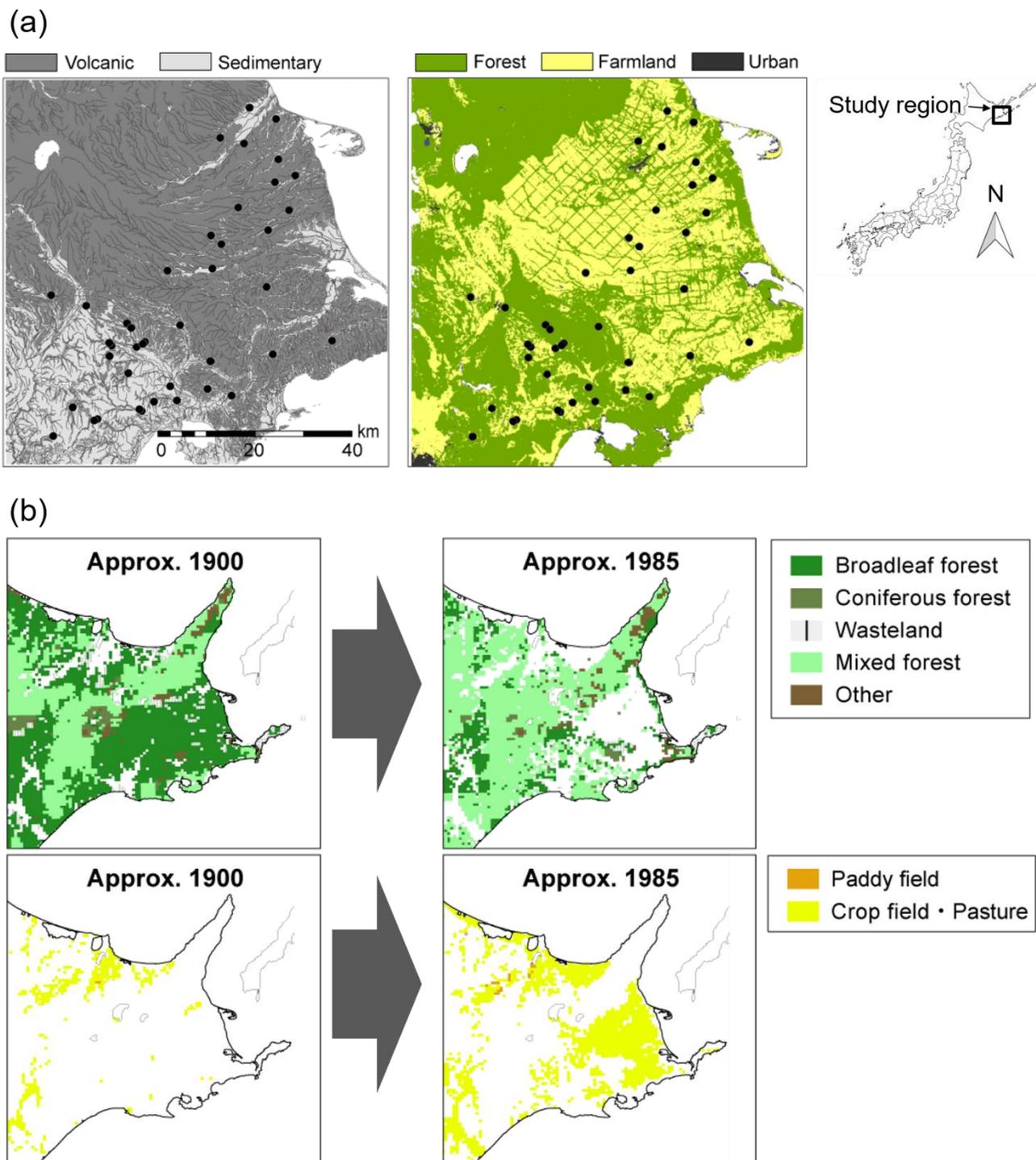
581

582 **Fig. 5** Interactive effects of water quality (i.e., land-use gradient) and substrate coarseness (i.e.,
583 geological gradient) on biotic variables. The abundance of each species was log-transformed.
584 Estimates were calculated by using generalized linear models (GLMs) with a Gaussian error
585 distribution and identity link function. EC, substrate coarseness and their interaction term were
586 used as explanatory variables.

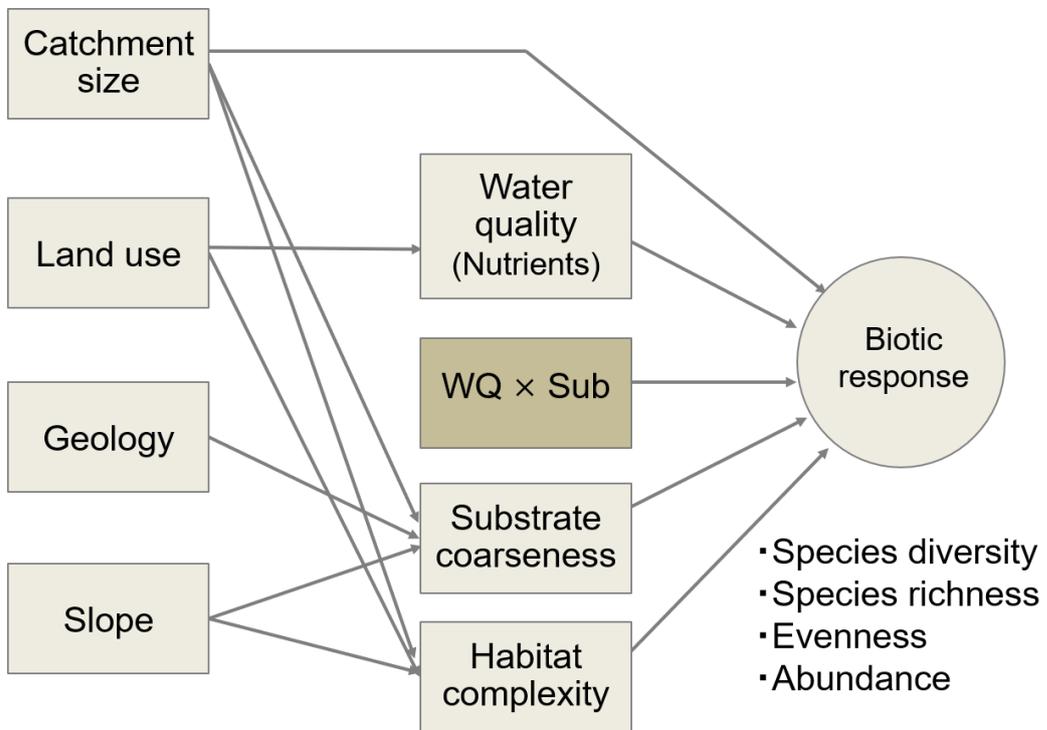
587

588 **Fig. 6** Path diagram based on a parsimonious model obtained with structural equation modeling
589 (SEM) for fish abundance. WQ×Sub is the term for the interaction between water quality and
590 substrate coarseness. The standardized path coefficients and R² values are shown; path thickness
591 is proportional to the size of the standardized coefficient. Asterisks indicate the statistical

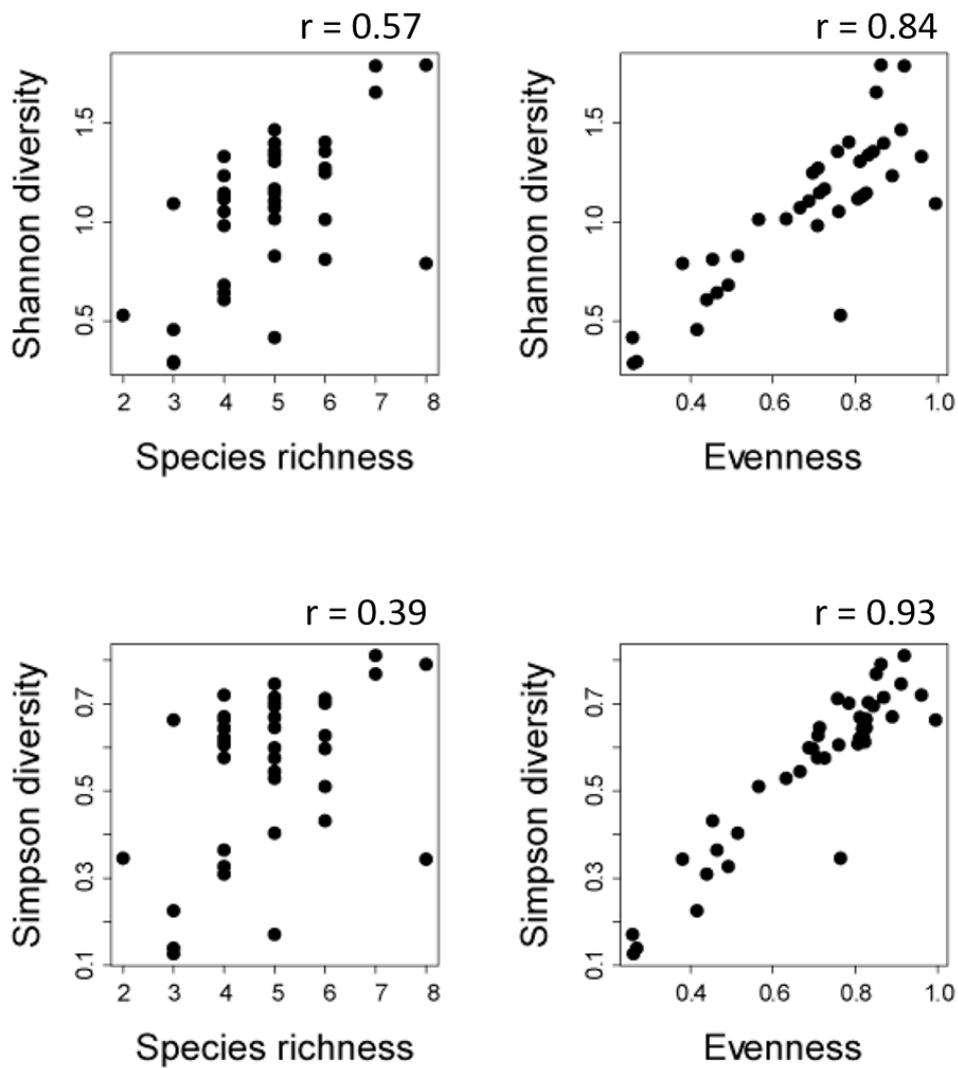
592 significance of each path: *P < 0.1, **P < 0.05, and ***P < 0.01. Black and gray paths indicate
593 positive and negative effects, respectively.



597 **Figure 2**

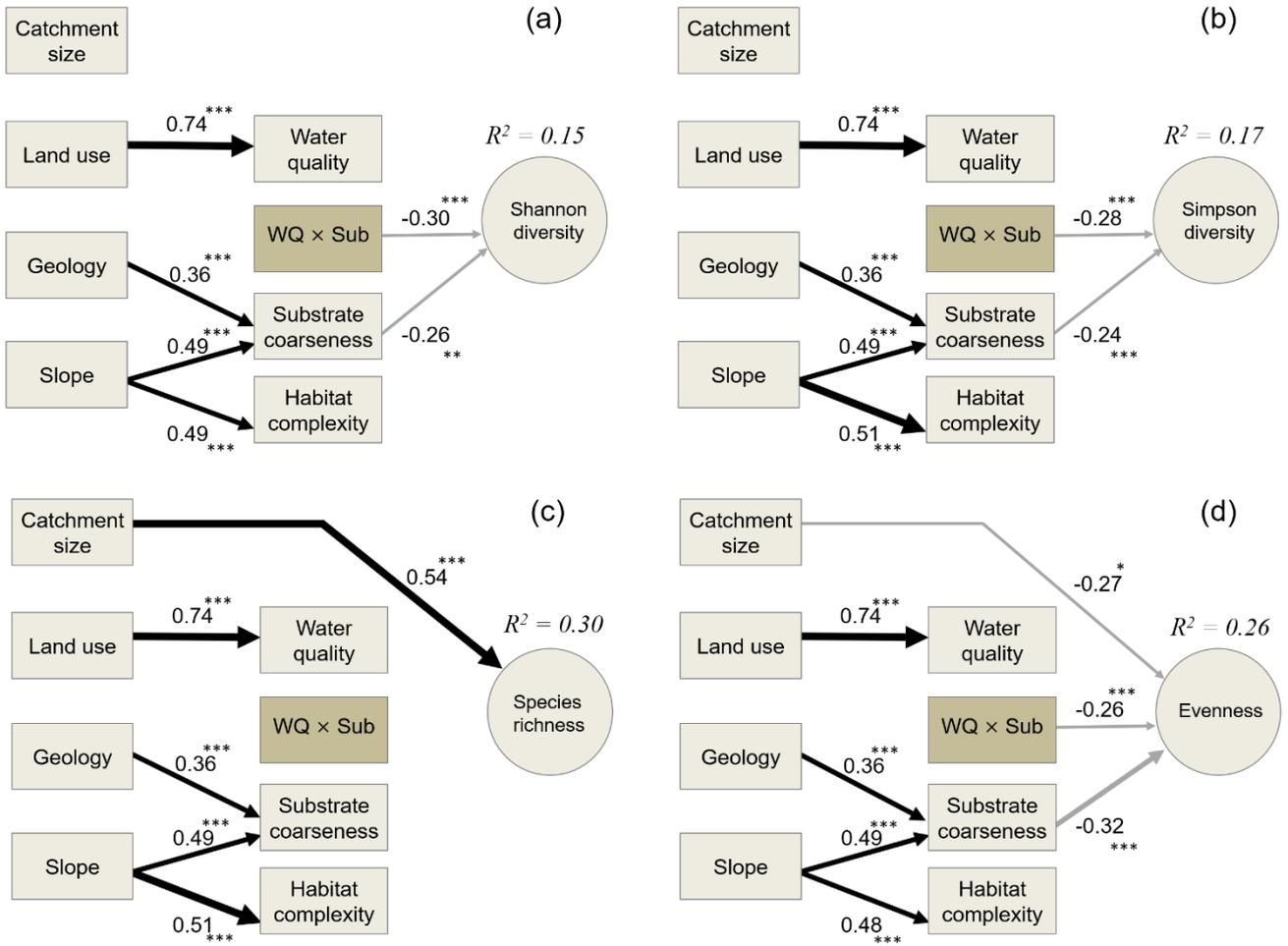


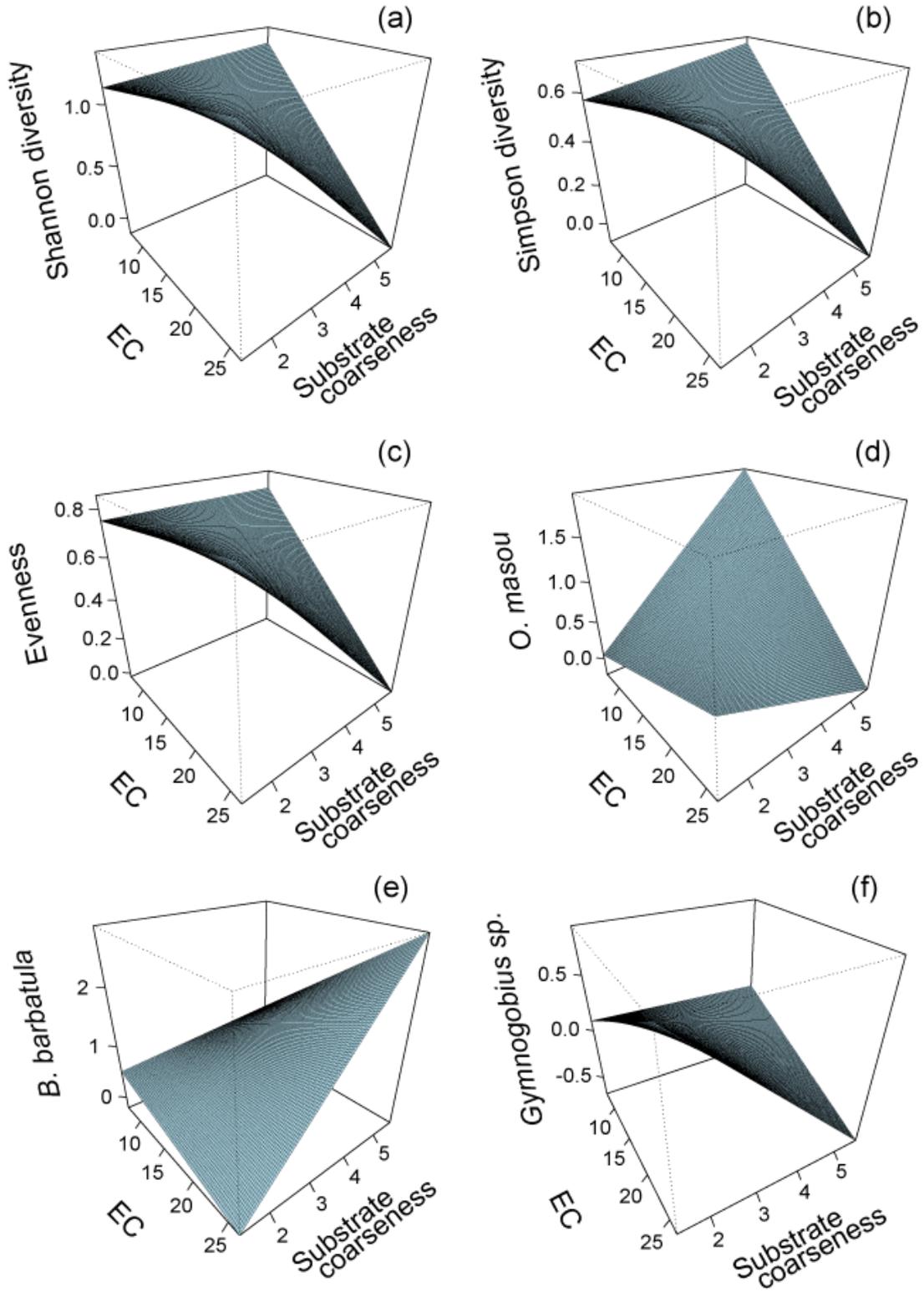
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601 **Figure 4**

602





604 **Figure 6**
605

