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Geology-dependent impacts of forest conversion on stream fish diversity

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Abstract

Forest conversion is one of the greatest global threats to biodiversity, and land-use change and subsequent biodiversity declines sometimes occur over a variety of underlying geologies. However, how forest conversion and underlying geology interact to alter biodiversity is underappreciated, although spatial variability in geology is considered an integral part of sustaining ecosystems. We aimed to examine the effects of forest conversion to farmland, underlying geology and their interaction on the diversity as well as species richness, evenness and abundance of stream fishes in northeastern Japan. We disentangled complex pathways between abiotic and biotic factors with structural equation modellings and found that the species diversity of stream fishes was indirectly shaped by the interplay of land use and underlying geology. Specifically, species diversity declined due to nutrient enrichment associated with farmlands, which was mainly caused by changes in evenness rather than by changes in species richness. In addition, this impact was stronger in streams with volcanic geology containing large substrates. The interplay may result from the differential responses of abundant stream fishes to nutrient enrichment (i.e., dominance) and the high dependency of these fishes on large streambed materials during their life cycles. Our findings provide key insights into future land-use management. First, the present study suggests that remediation of deforested or degraded forest landscapes would be more efficiently conducted by considering the interaction between land use and underlying geology. For example, the negative impacts of farmland on evenness were stronger in streams with volcanic geology in the present study, suggesting that riparian forest restoration along such streams would efficiently provide restoration benefits to stream fishes. Our findings also have a wider application to future land-use development: land clearing around such streams should be avoided to conserve the species evenness of stream fishes.

Introduction

Forest conversion is one of the greatest global threats to biodiversity (Brook et al.2003; Gibson et al.2011), and agricultural development is among its largest direct causes. Hosonuma et al. (2012) reported that commercial agriculture causes approximately 80 % of deforestation in developing countries, and Curtis et al. (2018) attributed global forest loss from 2001 to 2015 to shifting agriculture (24 %). The loss of forest cover directly eliminates habitat or corridors for forest-dwelling species (Maretensen et al. 2008). In addition, forest conversion to farmland alters the microclimatic and physicochemical characteristics of the surrounding habitat (Williams-Linera et al., 1998; Schmidt et al. 2017), which in turn affects community structure and biodiversity. Due to a wide range of negative impacts of forest conversion, the restoration of previously forested land has evolved into a global initiative known as the ‘Bonn Challenge’; this global effort aims to restore 150 million hectares of deforested and degraded forest landscapes by 2020 and 350 million hectares by 2030 to achieve the goals of restoring biodiversity and mitigating climate change (Verdone & Seidl 2017). Given the serious anthropogenic impacts of forest conversion, understanding the interactive effects of stressors on biodiversity is necessary to manage habitats appropriately as well as to reliably project biodiversity change.

Ecological impacts of anthropogenic activities can vary along natural environmental gradients (Peters et al.2019). Underlying geology (i.e., Earth’s subsurface rock lithology) controls many environmental characteristics, such as soil properties and hydrology, which determine habitat quality for plants and animals (Poff et al. 1997; Hjort et al. 2015). Indeed, understanding the relationship between biodiversity and spatial variation in geological features is emerging as a key issue (Schrodt et al.2019; Alahuhta et al.2020), and a few studies have shown that geological variation affects the species richness of freshwater organisms (Toivanen et al. 2019; Kärnä et al. 2019). Forest conversion and subsequent biodiversity declines sometimes occur over a variety of underlying geologies. However, how forest conversion and underlying geology interact to change biodiversity is underappreciated, although interactions between variations in forest cover and other major natural environmental factors, such as climate and geomorphology, have been demonstrated (e.g., Ryo et al. 2018; Peters et al. 2019).

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

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

Methods

- Study Sites

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

- Fish Sampling and Biotic Variables

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

- **Local-Scale Abiotic Variables**

In each study reach, we measured electrical conductivity (EC: ms/m), substrate coarseness, water depth (cm), and current velocity (cm/s) during the fishing survey. We used EC as a water quality index of nutrient enrichment because EC was positively correlated with total nitrogen (TN: mg/L) and total phosphorus (TP: mg/L) in the study region (Fig. S1). We measured EC in the uppermost section of each study site (WM-32EP, TOA DKK Co., Japan). For other measurements, we established ten equally spaced transects with three measurement points in each study reach. Water depth and current velocity were determined at each measurement point, and the means of these variables in each reach were used for analysis. Current velocity was measured at a 60 % depth from the water surface using a propeller-based flow meter (model CR-11; Cosmo-riken Inc., Tokyo, Japan). At each measurement point, substrates were identified by visual observation and classified as one of the following types: bedrock, silt (<0.063 mm), sand (0.063–2 mm), gravel (2–32 mm), pebble (32–64 mm), cobble (64–128 mm) or boulder (>128 mm). These categories were then coded as follows: bedrock = 0, silt = 1, sand = 2, gravel = 3, pebble = 4, cobble = 5 and boulder = 6. The recorded values were averaged to represent reach-scale substrate coarseness. To assess habitat complexity in each reach, the coefficients of variation (CVs) of water depth, current velocity and substrate coarseness were calculated by using the values at 30 measurement points. We integrated the three CVs into one habitat complexity index with principal component analysis and used the index for the following analyses. All of the CVs were positively correlated with the habitat complexity index; that is, a high value indicated high physical complexity (Fig. S2).

- Landscape-Scale Abiotic Variables

We applied catchment size, stream slope, catchment land use and underlying geology to represent the landscape-scale abiotic variables that can influence local-scale abiotic and biotic conditions. Catchment size (km^2) and stream slope were obtained from a 10-m digital elevation model (DEM) published by the Geospatial Information Authority of Japan. For the calculation of stream slope, we clipped river lines around study sites using a 1-km-diameter buffer and divided the length of the clipped river lines by the change in elevation. Land-use calculations were conducted based on high-resolution land-use and land cover maps around 2010 with 11 thematic classes (version 16.09, Jaxa 2016). We used the proportion of farmland in the catchments as an index of forest conversion; proportions of farmland and forest were highly and negatively correlated in the current landscape (r = -0.99). We defined ‘crops’ and ‘grassland’ as farmland and calculated the proportion of farmland in the catchments (%). We calculated the proportion of volcanic rocks within a 1-km-diameter buffer around each study site as an index of underlying geology. The procedures used to select spatial scales for the calculation of land use and underlying geology are shown in Table S1. Geological calculation was based on the 1:200,000 Seamless

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

- Statistical Analyses

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

Japanese streams (Tashiro & Tsujimoto 2015). We therefore applied a direct path from underlying geology to substrate coarseness. Furthermore, geomorphic factors such as streambed slope and catchment size were set as landscape-scale variables that control physical habitat conditions. We applied a path from land use in the catchment to nutrient enrichment (i.e., EC), assuming an influence of farmland on water quality. Elevated fine sediment is another possible impact of human land use on aquatic biota (Kemp et al. 2011). However, we found no relationship between fine sediment deposition and fish diversity in the study region (Fig. S3). Therefore, to simplify model structure, we did not include the amount of fine sediment in the models. For the same reason, we did not use the amount of woody cover or summer water temperature as an abiotic variable (Fig. S3). In addition, we expected that the negative impact of land use (i.e., water quality) on fish diversity would vary with underlying geology (i.e., substrate characteristics) and thus included interactive terms between water quality and substrate coarseness to test for a geology-land use interaction (Fig. 2). The proportion of volcanic materials and abundance of each species were log-transformed to ensure multivariate normality, and we applied SEM using the estimation method based on maximum likelihood. To avoid overfitting, any path with a small coefficient (< 0.15) was removed from the model when it was not significant (Fujii et al. 2017; Ishiyama et al. 2020). We repeatedly adjusted the models to find an adequate model with standardized root mean square residual (SRMR) values, with values < 0.09 suggesting an adequate fit. The fit of the model was also checked with a x^2 test associated with a p value > 0.05 and the comparative fit index (CFI > 0.95). We used the ‘lavaan’ and ‘semTools’ libraries in R software 3.3.2.

Results

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

The final models for species diversity showed adequate model fits (Table 2) and explained 15 % of the total variance in the Shannon index and 17 % of that in the Simpson index (as R^2). In the final models, the proportion of farmland in catchments had a direct positive effect on EC (nutrient enrichment) (Fig. 4). Underlying geology (proportion of volcanic rocks) and stream geomorphology (stream slope) calculated with a 1-km-diameter buffer positively affected substrate coarseness (Fig. S4). Stream slope also positively affected stream habitat complexity. In addition, significant interactive effects of EC and substrate coarseness on both the Shannon and Simpson indices were found (Fig. 4a, b); species diversity declines due to increased nutrients were more evident in streams with larger substrate materials (Fig. 5a, b). These results indicate that anthropogenic land use indirectly and interactively shapes stream fish diversity with underlying geology and stream geomorphology through the control of local habitat conditions.

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

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

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

Discussion

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

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

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

Three of the seven modeled species, *O. masou*, *B. barbatula* and *Gymnogobius* sp., were also affected by the interplay of land use and geology (Fig. 5), with the first two among the three most abundant species in the study region (Table 1). However, the impacts of forest conversion to farmland (i.e., nutrient enrichment) differed between the two species: the abundance of *O. masou* responded negatively and indirectly to the proportion of farmland in catchments, while that of *B. barbatula* showed a positive response. Nutrient enrichment caused by agricultural development and its ecological impacts in running waters have already been widely reported (e.g., Yuan 2010). The direct and indirect effects of elevated nutrient levels are probable causes of ecological changes. In European running waters, 1 mg/L NH_4 has been used as a threshold for ensuring trout survival (EIFAC 2013), which is well above our observed range of ammonium concentrations, which was 0.029 to 0.123 mg/L (Table S3). This difference suggests that direct toxic effects on *O. masou*, which exhibited decreased abundance in this study, are unlikely. Another possible cause is an indirect effect through food-web modification. For example, nutrient enrichment may shift benthic invertebrates from EPT taxa that are sensitive to eutrophication-related water quality to non-EPT taxa such as small chironomids (Harding et al. 1999; Quinn & Hickey 1990), which is consistent with a trend observed in other streams on Hokkaido Island (Fig. S5). Quinn & Hickey (1990) also suggested that the loss of large drifting macroinvertebrates and their replacement by small chironomids and mollusks reduces the feeding efficiency of drift-feeding fishes. *O. masou* is a drift-feeding trout, and ephemeropteran and trichopteran species are major aquatic food resources of this species (Hashimoto & Ishida 1977; Nagasaka 1997). Therefore, such changes in the prey community may be unsuitable, causing the abundance of *O. masou* to negatively respond to the proportion of farmland in catchments. On the other hand, *B. barbatula* is a benthivorous fish that prefers small and consistently abundant prey, such as chironomids (Worischka et al. 2015), suggesting that the above changes in the prey community can have positive impacts on benthic fish. These indirect effects of forest conversion on stream fishes may be reflected in community composition (i.e., evenness), manifesting as a decrease in fish species diversity.

Why did the negative impact of anthropogenic land use on fish species diversity change with spatial variability in underlying geology? As expected, the size of the substrate in the studied streams was significantly affected by underlying geology, consistent with results in previous studies (Thompson et al. 2006; Tashiro & Tsujimoto 2015). Lithological differences and the resultant effects on bedrock resistance and particle size are likely to control the sediment supply and resulting reach-scale streambed conditions, as suggested by Thompson et al. (2006). Streambed conditions were more influenced by reach-scale geology than by catchment-scale geology (Table S1). We selected study sites in low-elevation areas, a setting that may explain the results. Lowland streams with gentle stream slopes tend to have low stream power and would be more sensitive than other streams to sediment supply controlled by local geology. Substrate coarseness plays a key role in the life histories of some stream fish and other aquatic organisms. For the two most abundant species, namely, *O. masou* and *B. barbatula,* abundance was affected by the interplay of land use and geology, similar to evenness. *O. masou* uses middle- to large-sized substrates as spawning (Urabe et al. 2004) and overwintering (Nagayama & Nakamura 2007) habitats. As the name suggests, the stone loach *B. barbatula* prefers gravel streambeds that provide abundant interstitial shelter (Vlach et al. 2005). Therefore, the influences of forest conversion on these species would become apparent in streams with high substrate coarseness (Fig. 5) because the abundances of these species in small-particle streams are inherently limited, regardless of the negative impact of anthropogenic land use. The sensitivity of stream fishes to catchment land use in large-particle-sized streams (i.e., a large proportion of volcanic geology) may be reflected in spatial trends of evenness, which will change species diversity.

In the present study, we also detected interactive effects on species diversity between land use and stream slope as well as underlying geology; declines in species diversity associated with forest conversion were most evident in steep streams containing large streambed materials. It is generally known that spatial variability in geomorphology governs habitat structure in running waters. Stream slope, one of the key components of stream geomorphology, is directly related to sediment transport capacity, and many studies (including the present study) have shown that stream slope controls streambed composition (e.g., Coulombe-Pontbriand & Lapointe 2004). In general, a steep slope consists of coarse bed materials. Thus, species diversity changes along stream slopes and forest cover gradients can be regulated by the same mechanisms as species diversity changes along underlying geology gradients (i.e., the dominant fish species in the investigated streams prefer coarse substrates for their aquatic food resources and habitat, but the response to nutrient enrichment differed among the species). The importance of the interaction between forest land cover and geomorphology for stream biodiversity was also supported by previous studies (e.g., Ryo et al. 2018). The findings of our study re-emphasize that the interplay of geomorphology and land use should be considered in the management of deforested landscapes.

The importance of the interactions between multiple stressors in ecosystem management has been widely recognized, and interactions between natural and chemical (anthropogenic) stressors, as revealed by our findings, are also well documented (see review by Holmstrup et al. 2010). However, to the best of our knowledge, few studies have clearly demonstrated that such interplays result from the combined effects of land use and underlying geology. Our findings emphasize that considering the interplay of geology and land use could significantly contribute to future forest restoration projects. Restoration of whole-catchment land use is an ideal practice but is nearly impossible due to substantial social impacts. Previous studies have shown that riparian forests filter nutrients supplied from catchments (e.g., Vought et al. 1994; Nakamura & Yamada 2005). Thus, reconverting farmland along streams to forest will provide double the ecological benefits (i.e., reduce nutrient sources and enhance filtering effects) while minimizing social impacts. In addition, Nagasaka & Nakamura (1999) showed that the amount and volume of large wood should substantially decrease with agricultural development, such as riparian forest cutting. Cover provided by large woody debris can enhance the abundance of stream fishes (e.g., Inoue & Nakano 2001), although we did not find a significant relationship between the cover ratio and fish diversity. In the study region, the impacts of farmland on evenness are higher in streams with larger substrates, suggesting that riparian forest restoration along such streams with volcanic backgrounds or steep slopes would efficiently provide restoration benefits to stream fishes. Farmland has been abandoned during the period of economic growth after the 1950s in developed countries, including Japan (e.g., Kobayashi et al. in press); utilization of such degraded lands with depopulation is increasingly recognized as a tool for biodiversity conservation (e.g., Nakamura et al. 2020). These previous studies and our findings strengthen the argument that forest restoration using abandoned farmlands along streams with a volcanic underlying geology is one of the best solutions for meeting ecological and social requirements. Our findings have a wider application to future land-use development: land clearing around such streams should be avoided in order to conserve species evenness. As we discussed, degradation of upstream forest changes downstream environmental factors such as water quality and the amount of organic matter. Therefore, our findings will also help conserve the health of downstream ecosystems.

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

Supporting Information

Relationship of electrical conductivity with total nitrogen and total phosphorus (Fig. S1); relationship of the habitat complexity index with the CVs of water depth, current velocity and substrate coarseness (Fig. S2); relationships of fish diversity with the percentage of fine sediment, percentage of woody cover and summer mean water temperature (Fig. S3); relationships among the underlying geology, stream slope and substrate coarseness (Fig. S4); and relationships of benthic macroinvertebrate abundance with nutrient enrichment in streams of northern Hokkaido (Fig. S5) are available online. The procedures used to select the spatial scales for land use and geology (Table S1), the observed and estimated species richnesses in each study site (Table S2), the water chemical variables of the study reaches (Table S3) and abiotic and biotic data for the statistical analyses (Table S4) are also available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than those regarding absence of the material) should be directed to the corresponding author.

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Table 1 List of captured fish species and information on their abundance and presence/absence. The seven species used for abundance modeling are shown in bold.

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

[a] Total catch is the total number of fish caught in the 42 study reaches.

[b] Abundance % shows the number of each species relative to the total number of fish caught.

[c] Prevalence % shows the reaches with target species relative to the total number (42) of reaches.

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				
Salvelinus leucomaenis	0.238	0.959	0.064	0.38
Oncorhynchus masou	0.970	1.000	0.055	0.30
Barbatula barbatula	0.901	1.000	0.056	0.36
Lethenteron reissneri	0.862	1.000	0.047	0.11
Gymnogobius sp.	0.87	1.000	0.060	0.19
Pungitius tymensis	—	—	—	—
Pungitius sp.	0.465	0.996	0.056	0.39

[a] Chi p value is the p value for chi-squared tests.

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

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

[d] The R^2 statistics indicate the overall fit of the model to the biotic response variables.

Figure Captions

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

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

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

Fig. 4 Path diagram based on a parsimonious model obtained with structural equation modeling (SEM) for species diversity, species richness and evenness. WQ×Sub is the term for the interaction between water quality and substrate coarseness. The standardized path coefficients and R^2 values are shown; path thickness is proportional to the size of the standardized coefficient. Asterisks indicate the statistical significance of each path: $*P < 0.1$, $**P < 0.05$, and $***P < 0.01$. Black and gray paths indicate positive and negative effects, respectively.

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

Fig. 6 Path diagram based on a parsimonious model obtained with structural equation modeling (SEM) for fish abundance. WQ×Sub is the term for the interaction between water quality and substrate coarseness. The standardized path coefficients and R^2 values are shown; path thickness is proportional to the size of the standardized coefficient. Asterisks indicate the statistical significance of each path: *$P < 0.1$, **$P < 0.05$, and ***$P < 0.01$. Black and gray paths indicate positive and negative effects, respectively.

Figure 1

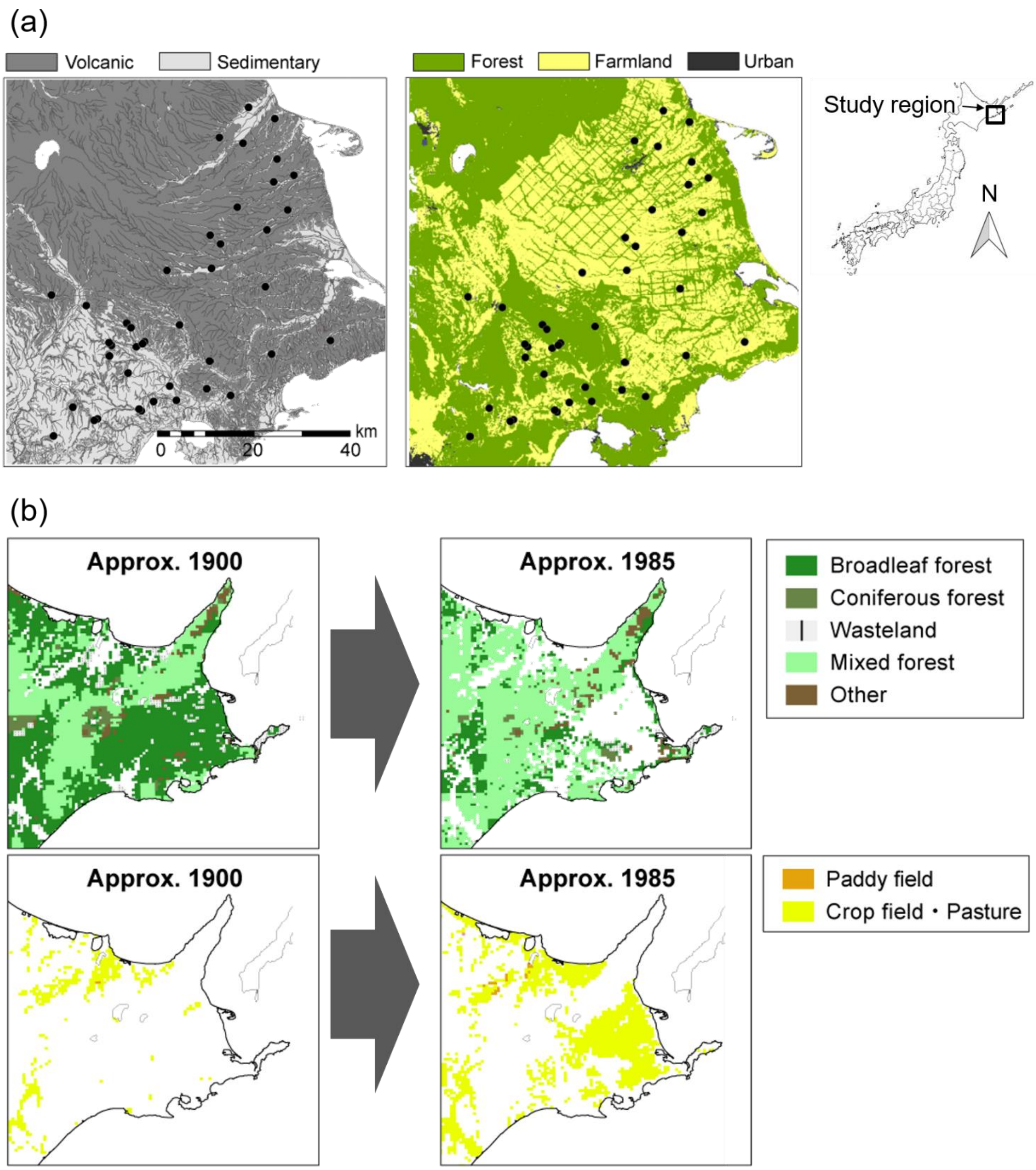

(a)
Volcanic
Sedimentary
Forest
Farmland
Urban
km
0
20
40
Study region
N
(b)
Approx. 1900
Approx. 1985
Broadleaf forest
Coniferous forest
Wasteland
Mixed forest
Other
Approx. 1900
Approx. 1985
Paddy field
Crop field・Pasture

Figure 2

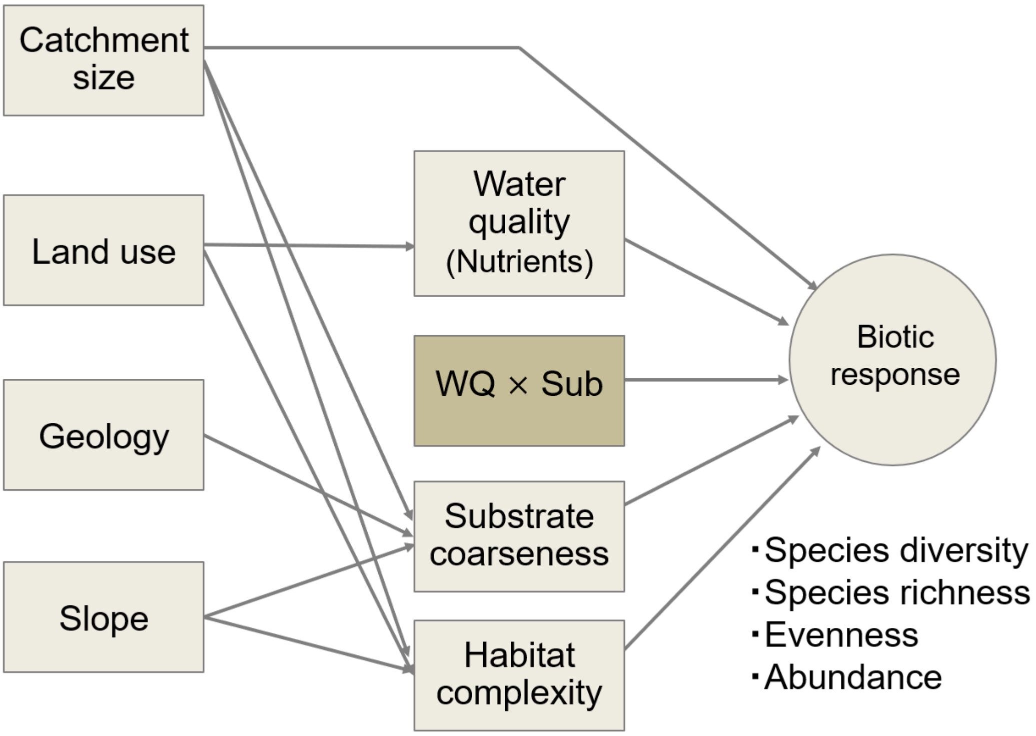

Catchment size
Land use
Geology
Slope
Water quality (Nutrients)
WQ × Sub
Substrate coarseness
Habitat complexity
Biotic response
▪Species diversity
▪Species richness
▪Evenness
▪Abundance

Figure 3

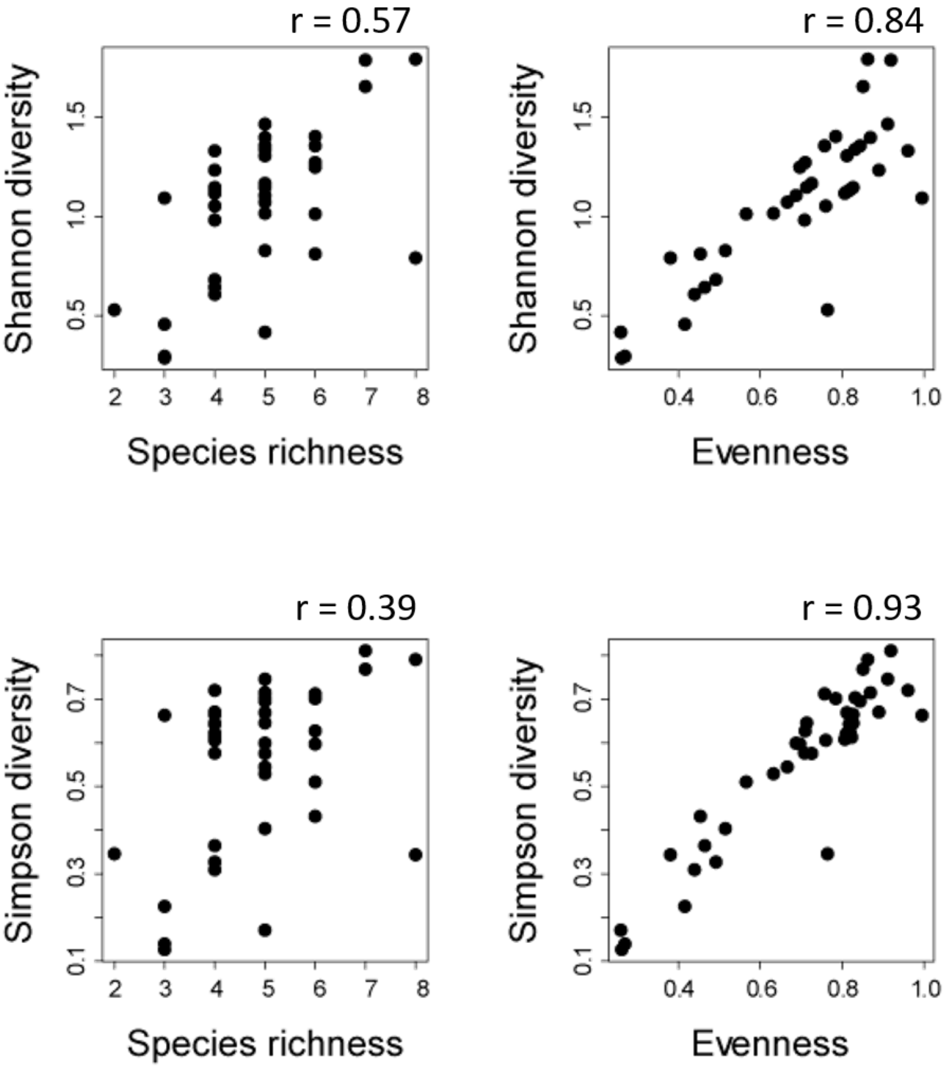

r = 0.57
Shannon diversity
0.5
1.0
1.5
2
3
4
5
6
7
8
Species richness
r = 0.84
Shannon diversity
0.5
1.0
1.5
0.4
0.6
0.8
1.0
Evenness
r = 0.39
Simpson diversity
0.1
0.3
0.5
0.7
2
3
4
5
6
7
8
Species richness
r = 0.93
Simpson diversity
0.1
0.3
0.5
0.7
0.4
0.6
0.8
1.0
Evenness

Figure 4

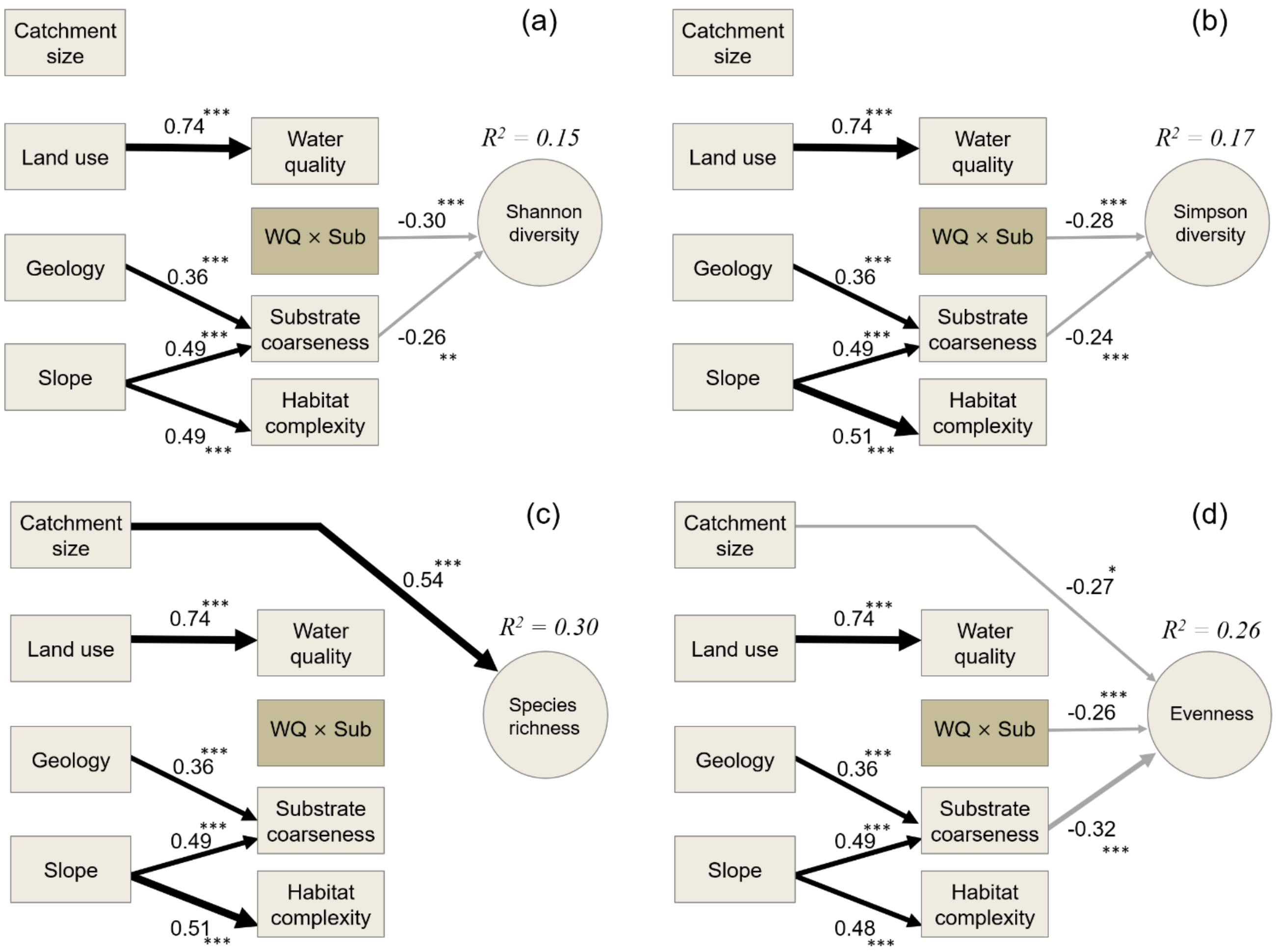

(a)
Catchment size
Land use
0.74***
Water quality
R² = 0.15
WQ × Sub
-0.30***
Shannon diversity
Geology
0.36***
Substrate coarseness
-0.26**
Slope
0.49***
Habitat complexity
0.49***
(b)
Catchment size
Land use
0.74***
Water quality
R² = 0.17
WQ × Sub
-0.28***
Simpson diversity
Geology
0.36***
Substrate coarseness
-0.24***
Slope
0.49***
Habitat complexity
0.51***
(c)
Catchment size
0.54***
Land use
0.74***
Water quality
R² = 0.30
Species richness
WQ × Sub
Geology
0.36***
Substrate coarseness
Slope
0.49***
Habitat complexity
0.51***
(d)
Catchment size
-0.27*
Land use
0.74***
Water quality
R² = 0.26
Evenness
WQ × Sub
-0.26***
Geology
0.36***
Substrate coarseness
-0.32***
Slope
0.49***
Habitat complexity
0.48***

Figure 5

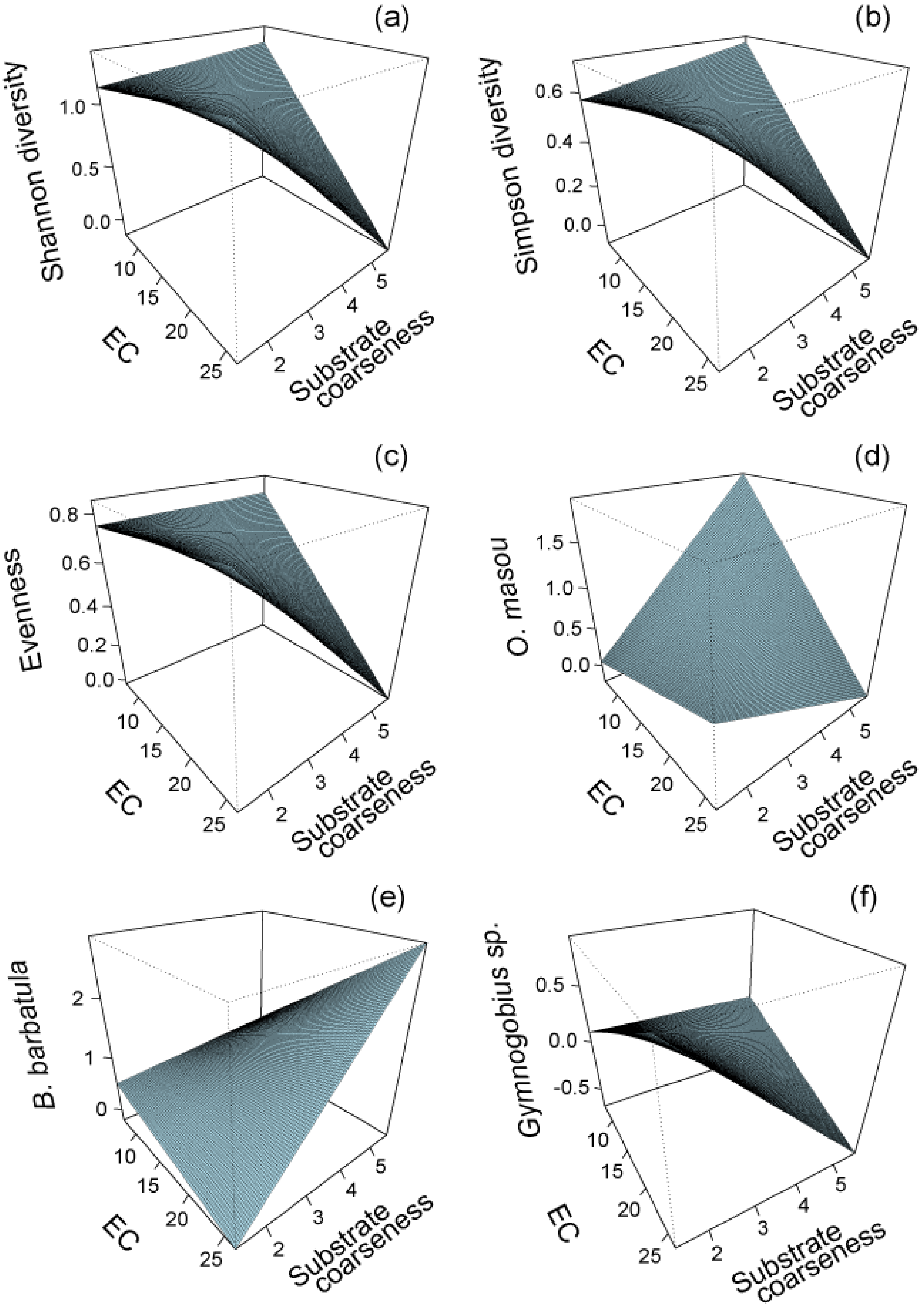
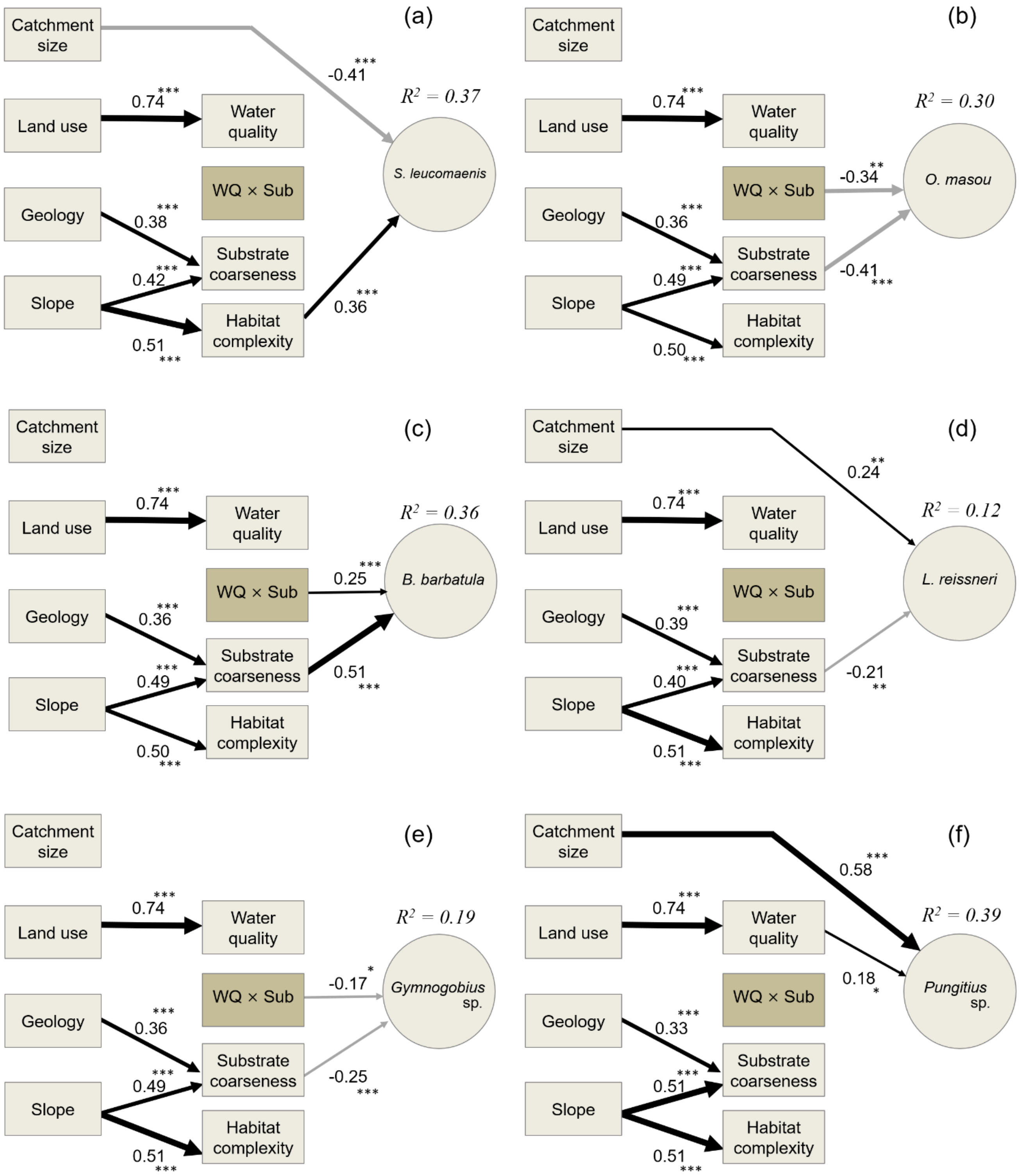

(a)
Shannon diversity
1.0
0.5
0.0
EC
10
15
20
25
Substrate coarseness
2
3
4
5
(b)
Simpson diversity
0.6
0.4
0.2
0.0
EC
10
15
20
25
Substrate coarseness
2
3
4
5
(c)
Evenness
0.8
0.6
0.4
0.2
0.0
EC
10
15
20
25
Substrate coarseness
2
3
4
5
(d)
O. masou
1.5
1.0
0.5
0.0
EC
10
15
20
25
Substrate coarseness
2
3
4
5
(e)
B. barbatula
2
1
0
EC
10
15
20
25
Substrate coarseness
2
3
4
5
(f)
Gymnogobius sp.
0.5
0.0
-0.5
EC
10
15
20
25
Substrate coarseness
2
3
4
5

Figure 6


(a)
Catchment size
Land use
Water quality
WQ × Sub
Geology
Substrate coarseness
Slope
Habitat complexity
S. leucomaenis
R² = 0.37
-0.41***
0.74***
0.38***
0.42***
0.51***
0.36***
(b)
Catchment size
Land use
Water quality
WQ × Sub
Geology
Substrate coarseness
Slope
Habitat complexity
O. masou
R² = 0.30
0.74***
0.36***
0.49***
0.50***
-0.34**
-0.41***
(c)
Catchment size
Land use
Water quality
WQ × Sub
Geology
Substrate coarseness
Slope
Habitat complexity
B. barbatula
R² = 0.36
0.74***
0.36***
0.49***
0.50***
0.25***
0.51***
(d)
Catchment size
Land use
Water quality
WQ × Sub
Geology
Substrate coarseness
Slope
Habitat complexity
L. reissneri
R² = 0.12
0.24**
0.74***
0.39***
0.40***
0.51***
-0.21**
(e)
Catchment size
Land use
Water quality
WQ × Sub
Geology
Substrate coarseness
Slope
Habitat complexity
Gymnogobius sp.
R² = 0.19
0.74***
0.36***
0.49***
0.51***
-0.17*
-0.25***
(f)
Catchment size
Land use
Water quality
WQ × Sub
Geology
Substrate coarseness
Slope
Habitat complexity
Pungitius sp.
R² = 0.39
0.58***
0.74***
0.18*
0.33***
0.51***
0.51***