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Rice paddy irrigation seasonally impacts stream benthic macroinvertebrate diversity at the catchment level

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Abstract. Agriculture is one of the most critical anthropogenic disturbances to freshwater ecosystems globally. In monsoon Asia, rice paddies provide habitats for aquatic species, but how their associated irrigation systems can affect downstream ecosystems is poorly understood. Here, we used structural equation modeling (SEM) to estimate seasonal variations in benthic macroinvertebrate diversity and environments and quantified indirect effects of land use, especially of rice paddy areas, on benthic macroinvertebrate diversity through local environmental alteration. Our study site was the Yasu River tributary of Lake Biwa, Japan, and we performed our investigation during both irrigation and nonirrigation periods, representing different seasons. Seasonal variations in physical and chemical variables and diversity were observed. Seasonal particulate phosphorus concentrations to a large extent determined the abundance and community composition of benthic macroinvertebrates. SEM revealed that the proportions of forest, urban, and rice paddy areas in the catchment had significant indirect effects on biodiversity indices of local benthic macroinvertebrate communities. The proportion of forest area had robust negative effects on water temperature, but the overall indirect effects on the macroinvertebrate diversity contrasted between the two seasonal periods. The proportion of rice paddy area had a strongly negative indirect effect on the diversity through increased particulate phosphorous loading during the irrigation period, while the proportion of urban area had a significantly negative indirect effect during the nonirrigation period only. The seasonal negative impacts of rice paddy irrigation on benthic macroinvertebrate communities were possibly due to siltation arising from rice paddy soils. Our results have implications for environmental restoration and biodiversity conservation in catchment management.

Key words: benthic macroinvertebrates; catchment and watershed management; land use; rice paddy; structural equation modeling.

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Introduction

Sixty-five percentage of freshwater ecosystems worldwide are currently estimated to be under environmental threat (Vörösmarty et al. 2010). Population declines in freshwater species are among the most serious of any wildlife, with an average decrease in the Living Planet Index of 76% since 1970 (McRae et al. 2014). Exploring human impacts on freshwater communities is a fundamental but complex aspect of biodiversity conservation that requires combined insights relating to the hydrosphere, biosphere, and anthroposphere (Cooper et al. 2017). In particular, landscape changes to accommodate population growth and economic development exert strong impacts on river and stream environments and biodiversity (Allen 2004). A key driver of landscape changes common to every watershed is agriculture. Agricultural land use not only causes water quality to deteriorate through inputs of sediment, nutrients, and pesticides but also causes habitat loss and fragmentation, both of which can lead to the loss of stream biodiversity (Corbacho et al. 2003, Allen 2004, Gimene 2015, de Castro et al. 2016).

Rice paddies, which represent one of the major uses of agricultural land in monsoon Asia, have attracted both ecological attention and economic attention because they are simultaneously important for biodiversity conservation and food production (Bignal and McCracken 1996, Lawler 2001). With regard to their ecological importance, rice paddies that have been reclaimed from natural wetlands partly maintain their wetland nature and serve as alternative habitats for wetland species (Bonells and Zavagl 2011). For example, more than 5000 species have been recorded in rice paddy areas in the Japanese archipelago biodiversity hot spots (Kiritani 2010). However, agricultural modernization over the last half-century, including agrochemical application, irrigation management, and farmland consolidation, has caused biodiversity losses in rice paddy ecosystems, as well as affecting subsequent stream and/or lake ecosystems (Washitani 2007, Natuhara 2013, Yamamuro et al. 2019). Previous studies have also shown that rice paddy irrigation causes eutrophication and siltation in receiving river and coastal waters through dissolved and particulate nutrient loading of wastewater (Sakai et al. 2013, Okano et al. 2018, Ishida et al. 2020). In many developed countries, where domestic nutrient loading has been substantially reduced by the installation of wastewater treatment plants (WWTPs), agricultural wastewater has increasingly been regarded as the major nonpoint source of nutrient loading within watersheds (LDEQ 2000, Poudel and Jeong 2009, Poudel et al. 2020). However, detecting any impacts of such nonpoint agricultural loading on stream biodiversity is difficult, because other human activities in a catchment, such as deforestation, dam construction, and residential land development, can simultaneously subject freshwater communities to multiple environmental stressors (Piggott et al. 2012, 2015).

A tool for identifying anthropogenic impacts on the habitats and biodiversity of streams and rivers would help local governments practice watershed management for environmental restoration and biodiversity conservation in watershed ecosystems. Field experiments are one possible way to understand the mechanisms of agricultural impacts on stream communities at the local level (Piggott et al. 2012). However, extrapolating experimental results to the watershed level can be difficult because of the complex relationships between causes and effects in a social–ecological watershed system. To consider the direct and indirect effects of human activities on the biodiversity of freshwater ecosystems, a better mechanistic understanding can be achieved by disentangling the intricate relationships between anthropogenic drivers and different aspects of stream and river environments within a watershed system, such as the physical, chemical, and biological components.

Structural equation modeling (SEM), so-called path analysis, is a less frequently used technique, which can quantify both direct and indirect effects (Shipley 2002, Grace 2006). This includes mechanisms to explore how independent variables can affect a response variable when it is mediated through a third set of variables. The applicability of SEM to test a wide range of ecological and evolutionary hypotheses has been demonstrated, from simple individual responses to environmental factors to complex multilevel interactions in food webs and/or communities (Scott 1973, Mitchell 1992, Arhonditsis et al. 2006, Shipley 2009). SEM has also provided new knowledge about the responses of aquatic communities and ecosystems to anthropogenic disturbances (Smith and Mather 2013, Olson et al. 2016, Fernandes et al. 2018, Hitchman et al. 2018, Harvey and Altermatt 2019).

Stream benthic macroinvertebrates, which are sensitive to environmental changes and serve as a useful indicator of water quality and habitat degradation, not only have important influence on nutrient cycles, primary productivity, decomposition, and translocation of materials, but also constitute an important source of food for fish in freshwater ecosystems (Wallace and Webster 1996, Ogbeibu and Oribhabor 2002). Studies have demonstrated the influence of environmental factors, including physical, biological, and chemical, on the distribution, abundance, and community composition structure of benthic macroinvertebrates and, consequently, leading to a certain change in benthic macroinvertebrate diversity (Rousi et al. 2011, Ko et al. 2019). For example, low water temperature but high DO formed suitable environments for high diversity and abundance of benthic macroinvertebrates in the Baltic Sea. Water temperature and chlorophyll *a* (Chl-*a*) concentrations significantly contributed to benthic macroinvertebrate diversity among watersheds with different levels of habitat transformation in Japan and in the Philippines (Ko et al. 2019, Peralta et al. 2020). Moreover, benthic macroinvertebrate communities may shift functional diversity during forest maturation or when experiencing deforestation (Stone and Wallace 1998, Kobayashi et al. 2010, Ishikawa et al. 2016). Although these environmental influences on freshwater ecosystems are widely recognized, previous studies have not assessed and compared these interrelated impacts on benthic macroinvertebrate communities.

Herein, we aimed to understand (1) spatiotemporal patterns of benthic macroinvertebrate diversity and the influence of environmental variables during both irrigation and nonirrigation periods, representing different seasons, and (2) the causal relationships between human activities, specifically agricultural activities, and stream benthic macroinvertebrate diversity, at catchment level. In the Lake Biwa watershed, rapidly modernized irrigation systems have been established since 1972, when a comprehensive lake development program was implemented. Although such an infrastructure-oriented approach substantially improved crop production efficiency, it also caused eutrophication and sedimentation in coastal waters due to dissolved and particulate nutrient loading from croplands (Sakai et al. 2013, Li et al. 2017, Nishino et al. 2017). This led to further alterations in benthic macroinvertebrate diversity and trophic energy flows in food webs (Karube et al. 2010, Okano et al. 2018). We therefore hypothesized that the presence or absence of rice paddies in a given area would seasonally impact stream benthic macroinvertebrate communities. Finally, we further discuss the implications of our analytical results for environmental restoration and biodiversity conservation in catchment and watershed management.

Methods

Study area and synoptic surveys

The Yasu River, approximately 65 km in length, originates from the Suzuka Mountains and drains into the north basin of Lake Biwa, which is the largest lake in Japan (surface area = 670.3 km^2, maximum depth = 103.6 m, average depth = 41.2 m). Its catchment area begins 377.42 km^2 upstream of the Yasu gauging station, and water resources in the catchment are heavily utilized for irrigation, domestic water supply, and industrial activities. Land use in the Yasu River catchment mainly includes forest, followed by cropland and urban areas (57.7%, 22.5%, and 6.5% of the catchment area, respectively; Fig. 1). A total of 91% of the cropland area is occupied by rice paddies. Rice paddy irrigation is carried out from April to August, and then, paddy fields are desiccated for harvesting and left to lie fallow from September. The paddy fields therefore alternate between wetlands and barrens during the irrigation and nonirrigation periods, providing habitats for aquatic and terrestrial communities, respectively. During the irrigation period, much of the wastewater is discharged from the rice paddies to the Lake's tributaries, before ultimately being transported to the lake basin.

Synoptic surveys were repeatedly conducted at multiple sites throughout the entire catchment

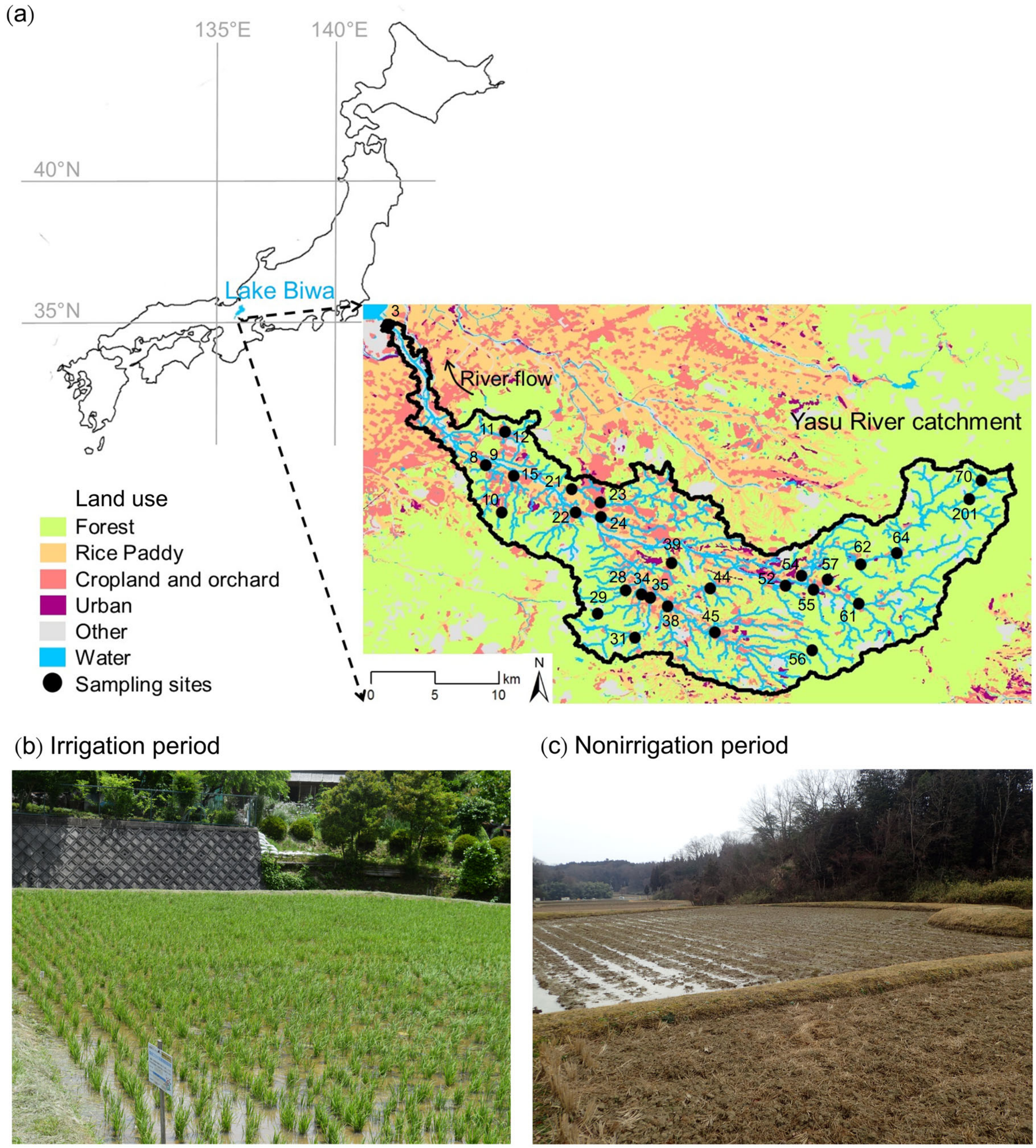

Fig. 1. (a) A map of land-use types in the entire Yasu River catchment (back solid line) of the Lake Biwa watershed, Japan. Black spots represent 30 sampling sites for the repeated synoptic surveys during the irrigation and nonirrigation periods. The site numbers refer to species and environmental information listed in Appendix S1: Tables S1, S2). Photographs of rice paddies during (b) irrigation and (c) nonirrigation periods.

of the Yasu River watershed during October 2012 (i.e., the nonirrigation period) and May 2016 (i.e., the irrigation period). Taking into account spatial variations in land use and stream order, 30 sampling sites were selected. One site in 2012 was not sampled because the riverbeds were disturbed by flooding, just before sampling was to take place.

Benthic and environmental data

Benthic macroinvertebrates were collected in duplicate at each sampling site, using a Surber sampler (30 × 30 cm, 475-μm mesh). The dissimilarities of community composition of benthic macroinvertebrates between the duplicate samples within a site were lower than those between a pair of two different sites from all combination of sampling sites, that is, 29 in 2012 and 30 in 2016, indicating the representativeness of the duplicate samples in this study (Appendix S1: Fig. S1). After sorting the benthic macroinvertebrates in the laboratory, they were identified to the species level, except for water mites (Acarina), under a microscope, and the number of each species was counted (Data S1).

Environmental parameters, including three physical, one biological, and seven chemical variables, were measured at each sampling site during each sampling period (Data S1). For the physical variables, dissolved oxygen (DO, mg/L) and pH were recorded using a DO meter (HQ40d; Hach, Loveland, Colorado, USA) and a pH meter (Orion3-Star; Thermo Scientific, Chelmsford, Massachusetts, USA), respectively. Water temperature (°C) measurements were taken using data loggers (Thermochron G; KN Laboratories, Fridley, Minnesota, USA), and the daily average over the three-week monitoring period was calculated.

For the biological variable, five cobbles were randomly extracted from the riffle at each sampling site to estimate epilithic biomass, using Chl-*a* concentration as a proxy for primary productivity. The epilithon was first scraped from a 6 × 6-cm area on the surface of individual cobbles using a toothbrush. It was then filtered through a 150-μm mesh net to remove any benthic animals and coarse particulate organic matter, and finally collected using GF/F glass fiber filters. Chl-*a* was extracted from the epilithic samples in a 90% acetone solution, and its concentration was measured using a spectrophotometer (UVmini-1240; Shimadzu, Kyoto, Japan), according to the SCOR/UNESCO method (SCOR/UNESCO 1966).

Surface river water samples were collected from each sampling site by gently sinking a 4L-PE bucket, and the following chemical measurements were made. The concentrations of four dissolved and three particulate nutrients were measured. The former included dissolved inorganic nitrogen (DIN), that is, concentrations of nitrite (NO_2^-), nitrate (NO_3^-), and ammonium (NH_4^+), and dissolved inorganic phosphate (PO_4^{3-}), while the latter allowed elemental analyses for concentrations of particulate carbon (PC), nitrogen (PN), and phosphorus (PP). For the DIN measurements, water samples were first filtered through a 1-mm nylon mesh to remove any coarse particles, followed by filtration through pre-combusted GF/F glass fiber filters (pore size 0.7 μm; Whatman plc., Maidstone, UK). The concentrations of NO_2^-, NO_3^-, and NH_4^+ in samples collected in 2012 were then analyzed using a second-derivative ultraviolet spectrophotometric method (NO_2^- and NO_3^-; Crumpton et al. 1992) and quantified spectrophotometrically using the indophenol method (NH_4^+; Solórzano 1969), while those of the 2016 samples were all analyzed using ion chromatography (Dionex ICS-3000; Thermo Fisher Scientific, Waltham, Massachusetts, USA). Water samples were filtered through a 0.2-μm membrane filter (DISMIC, 13HP020AN; Advantec, Toyo Roshi Kaisha, Japan) and used to measure soluble reactive phosphorus (SRP), representing PO_4^{3-} concentration, which was then quantified spectrophotometrically using the molybdenum blue method (Murphy and Riley 1962) with a microplate spectrophotometer (Multiskan GO; Thermo Fisher Scientific).

For the measurement of particulate nutrients, the residues on the aforementioned glass filters (GF/F, 0.7 μm; Whatman) were desiccated. The residues were collected by thoroughly scratching the filter surface using a spatula. Both the PC and PN concentrations were measured using an elemental analyzer (Flash EA 1112 connected to a Delta V Advantage via ConFlo III; Thermo Fisher Scientific). For the PP measurement, the filter samples were oxidized by adding potassium peroxodisulfate and then heated in an autoclave (Platt and Sathyendranath 1993, Marra 2002). Finally, the PP concentrations in the solution were measured using the same methods as for SRP.

Remote sensing for the detection of land-use patterns

The land-use types in the catchment area of each sampling site in the Yasu River watershed were classified into seven categories, including forest, rice paddy, urban, orchard, cropland, water, and other. The proportions of these land-use types were determined from a 1:50,000 digitized 2012 vegetation map, obtained from the Biodiversity Center of Japan, using a geographic information system (ArcGIS 10.2; ESRI, Tokyo, Japan).

SEM construction and statistical analyses

Species richness, the Shannon diversity index, H', and evenness were calculated to evaluate the diversity of local benthic macroinvertebrate communities at each sampling site, according to the definition of Patil and Taillie (1982). Richness is the total number of species found at a site on the basis of presence–absence data; species found in any of the duplicate samples from each site in this study were counted as present. The Shannon H' index reflects both the number of species and the relative abundance of each species in a local community; the abundance of individual species at each site in this study was calculated as the average number of individuals in the duplicate samples. Evenness refers to how close each species is to other species in terms of their numbers in the local community, ranging from zero (no evenness) to one (complete evenness); the site-level species richness and Shannon H' values were used to calculated species evenness.

To minimize multicollinearity among the explanatory variables, including the 11 environmental and seven land-use variables, and to maximize the parsimony of the hypothetical model, we first performed univariate analysis, by which the relationships of individual variables to each other were evaluated (Appendix S1: Table S1). Eight explanatory variables were then selected and screened for the construction of the hypothetical model.

The hypothesized paths, in which environmental and land-use variables had direct and indirect effects on benthic macroinvertebrate diversity, respectively, are summarized in Fig. 2.

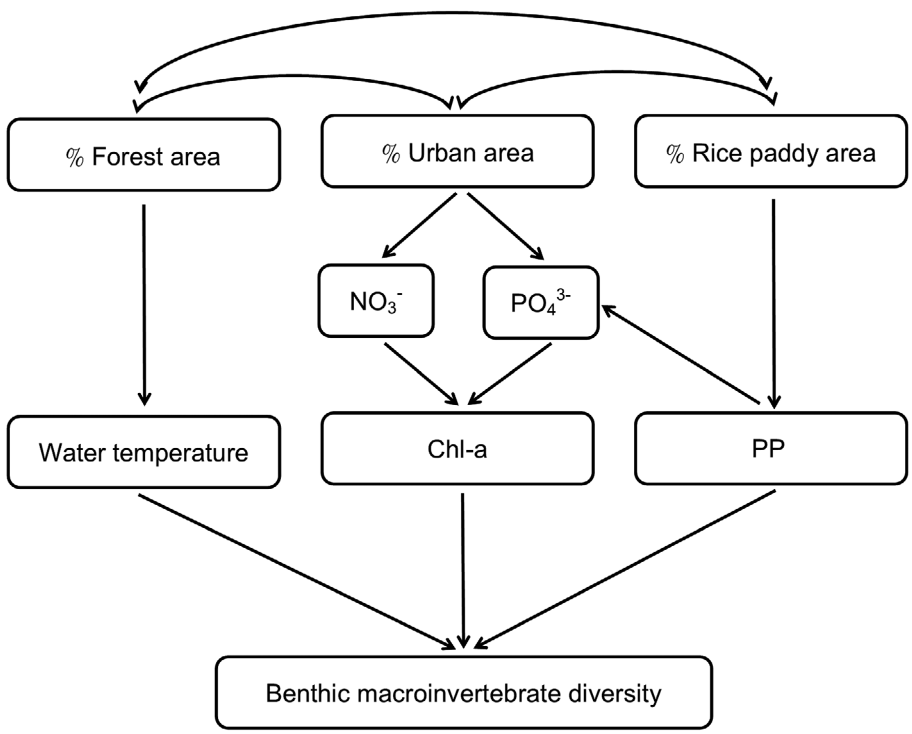

Fig. 2. A priori path model showing hypothetical paths of causal relationships between land-use and environmental variables and benthic macroinvertebrate diversity, based on repeated synoptic surveys in the entire Yasu River catchment. Unidirectional arrows indicate a causal effect, and double-headed arrows indicate an interactive effect. See text for the abbreviation of each variable.

In this model, the first path dictated that forest area could affect benthic macroinvertebrate diversity via the direct effect of water temperature, which is critical for these ectotherms. The second path dictated that urban area could affect benthic macroinvertebrate diversity via direct effects of Chl-*a* concentration responding to nitrate and/or phosphate concentrations. This assumed that the epilithic biomass indicated by the Chl-*a* concentration serves as a food source for macroinvertebrate communities (i.e., bottom-up trophic cascading effect) or alters the oxic/redox condition of their epilithic habitat through algal photosynthesis and respiration. The third path dictated that rice paddy area could affect benthic macroinvertebrate diversity via direct effects of PP concentration, causing siltation of their epilithic habitat. An SEM with a multiple group analysis was ultimately performed to contrast selected models between the irrigation and nonirrigation periods, as well as to determine the relative importance of each path in the model selected for each period. Here, the datasets from the irrigation and nonirrigation periods were regarded as two independent groups, based on the assumption that samples were repeatedly collected from each sampling site during the two temporal snapshots. A random effect of block was also incorporated into the model by linking multiple linear mixed models (with piecewise SEM).

A paired t test was used to determine differences in the benthic macroinvertebrate diversity and environments at each sampling site between the irrigation and nonirrigation periods. Redundancy analysis (RDA) was used to explore seasonal environmental influences on abundance and community composition of benthic macroinvertebrates. This constrained ordination technique is analogous to a multivariate multiple regression and performs well with nonorthogonal and collinear gradient data (McGarigal et al. 2000). The proportions of variances in the abundance and community composition of benthic macroinvertebrates accounted for by these explanatory variables, and their combined effects were further determined using variation partitioning analysis. The significance of the individual path coefficients was also considered using the t test. All differences among comparisons with $P < 0.05$ and $P < 0.1$ were considered significant and marginally significant, respectively. Computations were performed in R 3.6.2 (R Studio Team 2016).

Results

Seasonal variations in environments and biodiversity

Chemical and physical variables showed seasonal variations, but there were no seasonal variations in the biological variable, that is, Chl-*a* (Table 1). The concentrations of dissolved inorganic nutrients, that is, NO_3^- and PO_4^{3-}, and the water temperature were significantly or marginally higher during the nonirrigation period than during the irrigation period, whereas the concentration of PP was significantly higher during the irrigation period. Species richness of benthic macroinvertebrates was higher during the irrigation period than during the nonirrigation period, whereas species evenness showed the opposite

Table 1. Comparisons of environmental variables and diversity indices for each sampling site between the irrigation and nonirrigation periods, representing the spring and autumn seasons, respectively.

Environmental variable and diversity index	Period		t	P
	Irrigation	Nonirrigation		
Water temperature (°C)	17.7 ± 3.5 (11.7–24.7)	18.7 ± 2.0 (13.8–21.9)	2.020	0.036
Chl-*a* (mg/m^2)	18.34 ± 14.70 (0.31–46.43)	19.55 ± 27.53 (0.29–105.00)	0.292	0.772
NO_3^- (μmol/L)	25.29 ± 22.87 (0.32–98.13)	49.03 ± 30.78 (12.69–135.83)	5.018	<0.001
PO_4^{3-} (μmol/L)	0.43 ± 0.61 (0.01–2.85)	1.05 ± 1.69 (0.10–5.99)	1.868	0.073
PP (μg/L)	15.97 ± 19.80 (0.22–74.62)	5.17 ± 6.02 (0.12–23.27)	−3.532	0.001
Richness	31.86 ± 11.47 (6–61)	19.76 ± 8.16 (8–44)	−4.934	<0.001
Shannon H'	2.48 ± 0.66 (0.26–3.39)	2.32 ± 0.51 (0.80–2.89)	−1.393	0.175
Evenness	0.73 ± 0.16 (0.11–0.94)	0.80 ± 0.16 (0.33–0.98)	2.185	0.037

Notes: Chl-*a*, chlorophyll *a*; NO_3^-, nitrate; PO_4^{3-}, phosphate; PP, particulate phosphorus. Means and standard deviations (SD) are shown, with ranges in parentheses.

pattern, with significantly lower values during the irrigation period than during the nonirrigation period (Table 1). There were no consistent upstream and downstream spatial distributions of benthic macroinvertebrate diversity during either the irrigation or the nonirrigation periods (Fig. 3), implying that the spatial patterns of diversity indices might not be determined by connectivity among river networks.

When using RDA to evaluate whether chemical, physical, and biological variables affected benthic macroinvertebrates, these variables contributed 18.4% of the variation with the significant first axis of RDA ($P = 0.001$) in abundance composition during the irrigation period and 18.1% with the significant first two axes of RDA ($P = 0.001$ and 0.005 for RDA1 and RDA2, respectively) during the nonirrigation period (Fig. 4a, c). During the irrigation period, community species were primarily influenced by water temperature and PP, whereas four environmental variables, with the exception of NO_3^-, equally affected

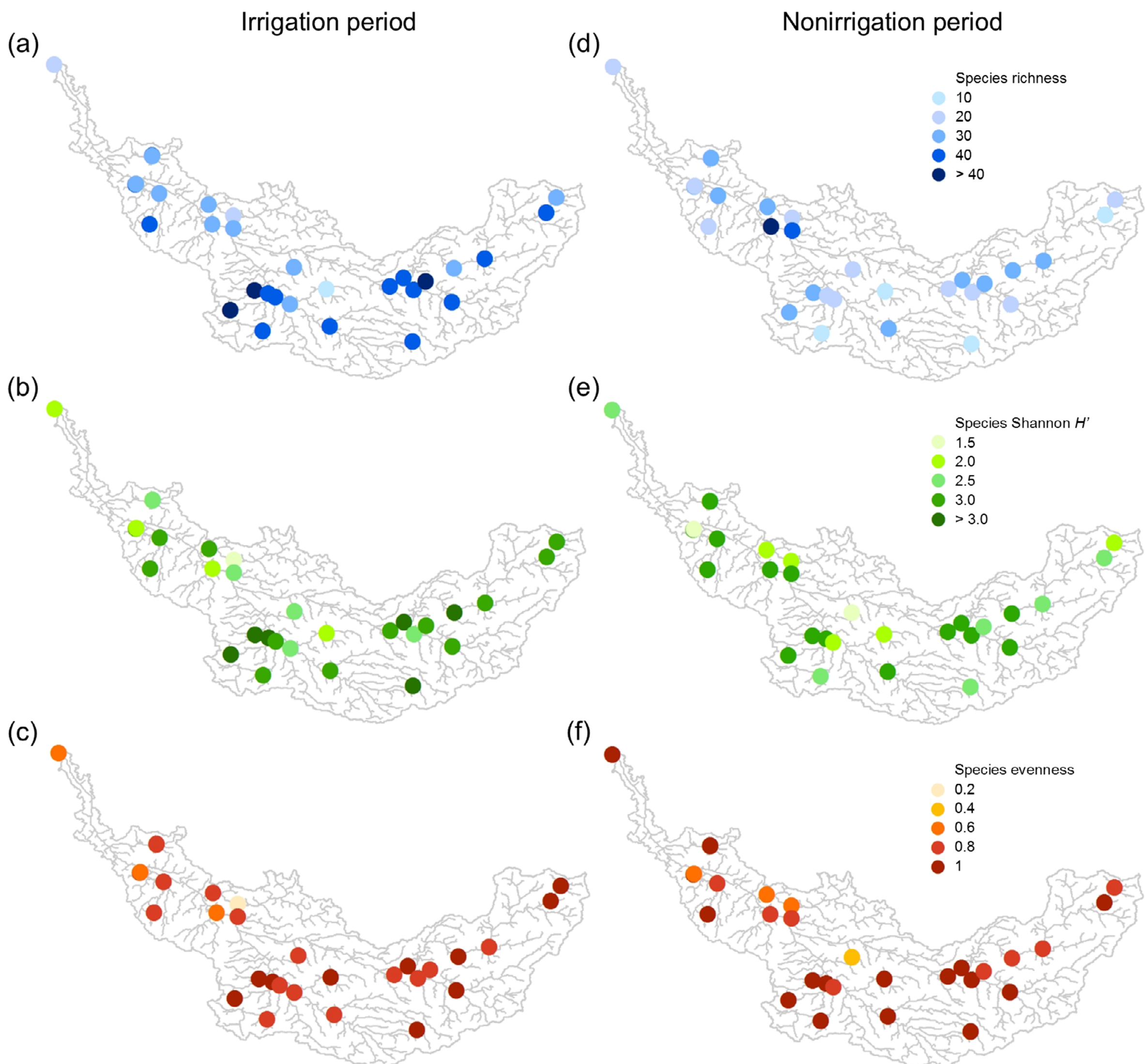

Fig. 3. Spatiotemporal distributions of benthic macroinvertebrate diversity, indicated by species richness (a, d), Shannon H' (b, e), and evenness (c, f), during the irrigation (a–c) and nonirrigation (d–f) periods.

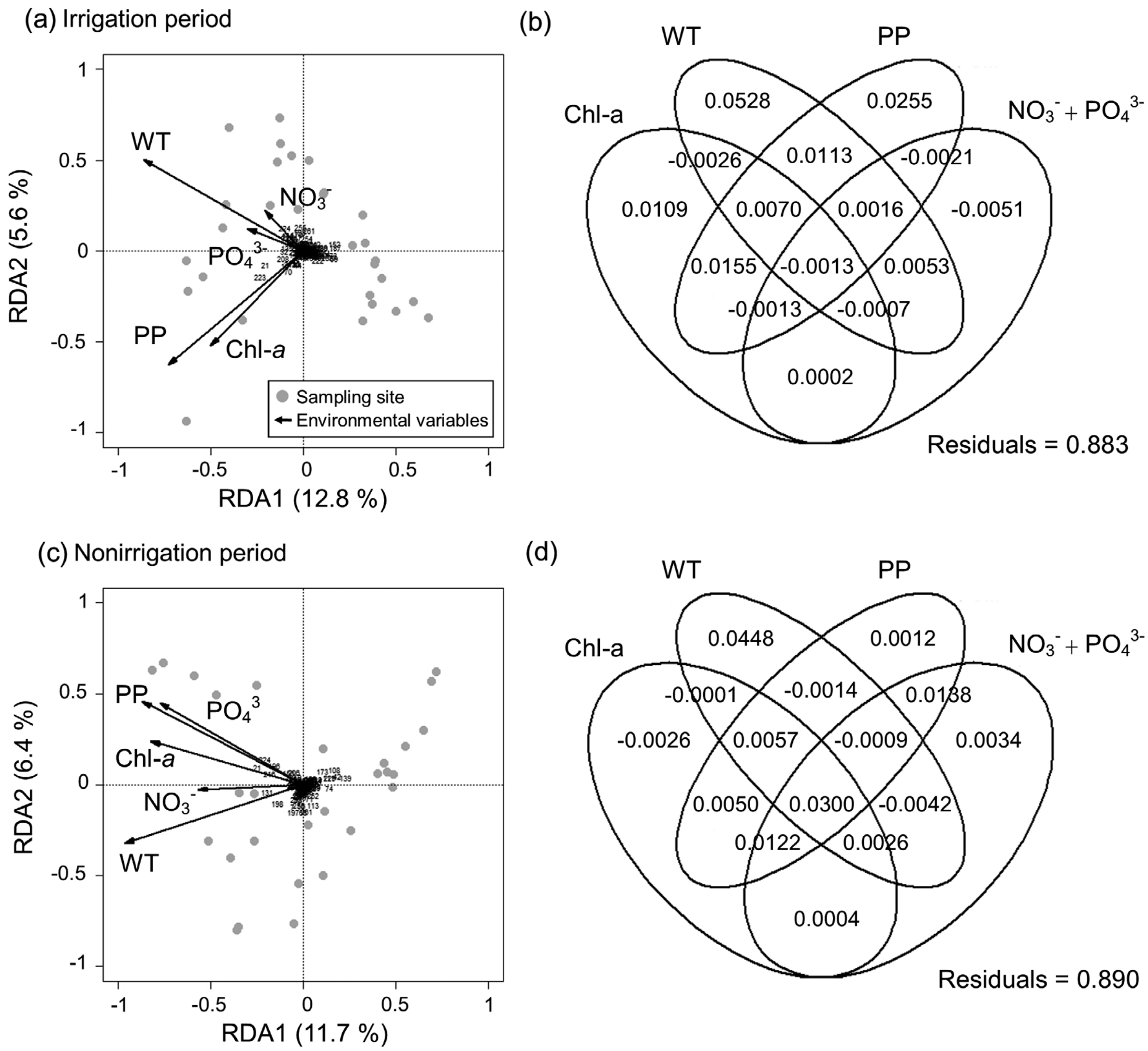

Fig. 4. Plots of redundancy analysis (RDA) and variation partitioning analysis showing the spatial and temporal relationships between the benthic macroinvertebrate communities and the environmental variables at the sampling sites during the (a, b) irrigation and (c, d) nonirrigation periods. Individual species are shown by different numbers, with detailed information shown in Appendix S1: Table S1, Fig. S1. Gray circles are sampling sites. Environmental variables are represented by black arrows. Abbreviations are WT, water temperature; Chl-*a*, chlorophyll *a*; NO_3^-, nitrate; PO_4^{3-}, phosphate; PP, particulate phosphorus.

community species during the nonirrigation period. This suggested that water temperature and PP had stronger environmental effects on the abundance and community composition of benthic macroinvertebrates. Some species, such as worms (Naididae gen. spp., No. 21, and *Branchiura sowerbyi*, No. 16) and Chironomidae (Stictochironomus sp., No. 223, Chironomus sp., No. 196, Microtendipes sp., No. 208, and Pagastia sp., No. 212), were frequently observed, predominantly in eutrophic streams (Appendix S1: Fig. S2 and Data S1). Their abundance markedly increased along the PP ordination, especially during the irrigation period, also potentially leading to the aforementioned low evenness. The variance partitioning analyses demonstrated that water temperature was consistently the main variable shaping the abundance and community composition of

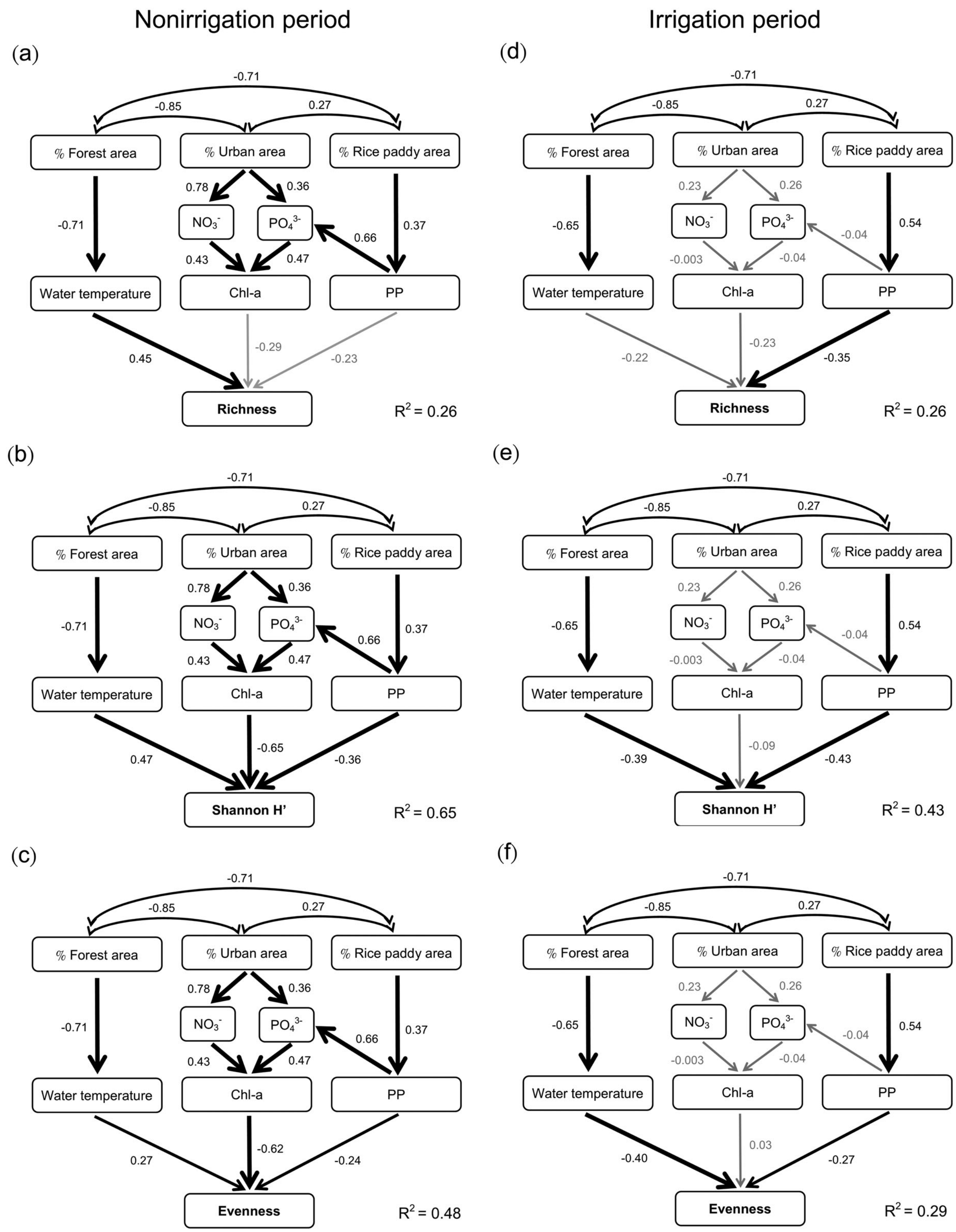

Fig. 5. Structural equation modeling to account for site variations in benthic macroinvertebrate diversity, indicated by (a) richness, (b) Shannon H', and (c) evenness during the nonirrigation (a–c) and irrigation (d–f) periods.

(Fig. 5. *Continued*)
The hypothetical framework is the same as that in Fig. 2. Thick black, thin black, and thin gray arrows are significant ($P < 0.05$), marginally significant ($P < 0.1$), and nonsignificant ($P \geq 0.1$) paths, respectively. Standardized path coefficients are shown for individual paths. Variation (R^2) of the benthic macroinvertebrate diversity indicates the overall effects for selected models.

benthic macroinvertebrates in the Yasu River. However, PP increased in importance during the irrigation period, while the interactive effects of all variables explained the second largest portion of the variance in the benthic macroinvertebrate data during the nonirrigation period (Fig. 4b, d).

Causal mechanisms for benthic macroinvertebrate diversity

Our SEM models accounted for 26–65% of the overall variation caused by the land-use and environmental variables (Fig. 5). During the nonirrigation period, all land-use variables had strong indirect effects on benthic macroinvertebrate diversity, except for richness (Fig. 5a–c). In particular, the indirect effect of percentage forest area was robust for all diversity indices, that is, it had a positive indirect effect on benthic macroinvertebrate diversity through its negative direct effect on water temperature. The percentage urban area had negative indirect effects on the Shannon H' index and evenness of benthic macroinvertebrate communities through increases in dissolved nutrient (NO_3^- and PO_4^{3-}) loading. This negative effect was mediated by nutrient enrichment effects on Chl-*a*. The percentage rice paddy area also had negative indirect effects on the Shannon H' index and evenness through increases in PP loading.

In contrast, during the irrigation period, the indirect effect of percentage forest area via water temperature was reversed, especially for the Shannon H' index and evenness (Fig. 5d–f). The negative indirect effect of percentage urban area disappeared, whereas the negative effect of percentage rice paddy area was robust for all diversity indices, with a stronger positive impact on PP loading.

Discussion

Our results showed that environmental variables affected seasonal benthic macroinvertebrate communities regardless of whether rice paddy irrigation was implemented. These results also highlighted the importance of land-use-associated processes for the multiple diversity of benthic macroinvertebrate communities in the Yasu River, Japan. Land uses, immediate substrates of physical, chemical, and biological availability, were important factors governing the abundance and distributions of benthic macroinvertebrates. It is, therefore, desirable to identify the underlying causal mechanisms that structure benthic macroinvertebrate communities in a given catchment. However, frameworks for habitat conservation and decisions relating to human land-use activity networks rarely take a catchment perspective into account, and limited information relating to biodiversity during different periods often means that freshwater habitats are not given the attention they deserve.

Effects of land use on benthic macroinvertebrate diversity

We demonstrated that benthic macroinvertebrate diversity decreased with increasing proportions of rice paddy area in the catchment, via increased PP inputs. We also showed that such indirect effects became more prominent during the irrigation period. This negative impact may be associated with seasonal activities in rice paddy operations. For example, prior to the rainy season, puddling and planting activities are carried out, and then silted wastewater is discharged into streams during the irrigation period. This wastewater contains many extremely fine mineral particles derived from phosphorous-rich rice paddy soils, as indicated by the PP concentration (Ishida et al. 2020); therefore, rice paddy irrigation results in the seasonal silting of riverbeds (Vromant and Chau 2005). In the Lake Biwa watershed, rice paddy irrigation is also the primary factor leading to increased turbidity of receiving lagoon waters, in which benthic macroinvertebrates are depauperated (Okano et al. 2018). Previous studies have also reported that agricultural activities cause soil erosion and subsequent siltation downstream, which has a negative impact on feeding functional diversity, especially on epilithic grazers and filter feeders, such as mayflies and caddis flies, of stream and coastal benthic macroinvertebrates (Lenat 1984, Cover et al. 2008, Okano et al. 2018). In the Yasu River ecosystem, Ishikawa et al. (2017) reported that the integrated trophic position, defined as the average number of steps involved in biomass transfer of all the animals in a food web, varied with the diversity of benthic macroinvertebrate communities. Therefore, our results suggest that human land use in this catchment, especially agricultural activities, can have a cascade effect on ecosystem functioning via biodiversity loss in the watershed ecosystem.

The SEM also showed that the rice paddy weakly but significantly increased PP loading in stream waters, even during the nonirrigation period. An approaching typhoon led to a flooding event in this watershed, just before the synoptic survey was carried out. Therefore, rice paddy soils may have been discharged into streams and deposited on the riverbed prior to sampling during the nonirrigation period. This may explain why the rice paddy effect on benthic macroinvertebrate diversity was detected even during the nonirrigation period, although it should be less important. Additionally, based on field observations, rice paddy soil accumulated in irrigation water channels and on agricultural riverbeds during the nonirrigation period, suggesting the soil was a possible source of particulate matter found in the river (T. Ishida, *personal communication*).

In contrast, we found that residential activity had a limited indirect effect on benthic macroinvertebrate diversity during the nonirrigation period, through domestic nutrient loading and resultant increases in epilithic biomass. In developing countries, urbanization is the most critical factor leading to decreased stream biodiversity in watershed ecosystems (Peralta et al. 2019, 2020). The possible mechanism is that domestic nutrient loading from residential areas decreases dissolved oxygen in stream habitats via epilithic microbial respiration that is enhanced by cultural eutrophication (Peralta et al. 2020). We also found a negative path from epilithic biomass, that is, Chl-a, to benthic macroinvertebrate diversity, rejecting the possibility of a bottom-up trophic cascading effect on stream biodiversity. For some taxa, it is well known that diversity indices increase with ecosystem productivity, as a macroecological pattern (Mittelbach et al. 2001, Fraser et al. 2015, Brun et al. 2019). However, whether the diversity–productivity relationship is positive, negative, or null depends on the range of productivity. In the Yasu River ecosystem, nutrient levels are generally low (Table 1), and most streams show higher DO (mean $\pm$ standard deviation: 9.38 ± 0.62 mg/L) than the criterion for stream water quality (7.5 mg/L) designated by the Ministry of Environment in Japan. Thus, unlike streams in developing countries (Peralta et al. 2020), it is less likely that eutrophication-induced oxygen depletion decreases benthic macroinvertebrate diversity in the Yasu River. An alternative explanation may be a decrease in the diversity of food sources for consumers under nutrient enrichment conditions. Among diverse functional feeding groups, such as grazers, shredders, filter feeders, collector gatherers, and predators, algal-rich habitats may select for the grazers, leading to the overwhelming dominance of algal grazers and/or omnivores shifting to algal grazing. The increased abundances of these groups decrease functional diversity rather than species diversity of benthic macroinvertebrate communities.

Notably, the urbanization effect disappeared during the irrigation period. In the entire Lake Biwa watershed, domestic phosphorous and nitrogen loading from point sources are estimated to be 15.9% and 6.3%, respectively, which are comparable to those from nonpoint agricultural sources (16.2% for phosphorous and 13.7% for nitrogen; Lake Biwa Environmental Research Institute 2011). In the Yasu River, which has the most advanced sanitation system in the Lake Biwa watershed, most urbanized areas in the lower catchment (89.7% of the population) are covered by a central WWTP (Shiga Prefecture Department of Lake Biwa and the Environment 2017), whose wastewater is not discharged directly into the main river but into the south basin of Lake Biwa. In contrast, in the upstream areas, domestic waste from rural communities is treated in small-scale local WWTPs and discharged directly into streams. The proportion of the population of the catchment area in rural communities with local WWTPs is just 2.1%. Therefore, the negative impact of domestic loading is relatively small and could be masked by the stronger impact of PP loading from rice paddies during the irrigation period.

More interestingly, both NO_3^- and PO_4^{3-} concentrations measured in individual streams in the Yasu River catchment were lower during the irrigation period than during the nonirrigation period, despite the fact that rice paddy irrigation discharged many nutrients into the streams. In parallel with the present study, our research team conducted nutrient spiral metrics to measure the in-stream metabolic turnover of phosphorous and nitrogen throughout the whole Yasu River catchment. These metrics revealed that phosphorous and nitrogen uptake rates might be higher during the irrigation period than during the nonirrigation period (T. Iwata, *unpublished data*). Considering there was no difference in epilithic biomass between these two periods in this catchment area, a much higher proportion of epilithic biomass might have been trophically transferred to consumers in stream food webs during the more productive irrigation period (N. Ishikawa, *unpublished data*). Our results, therefore, support previous research into food webs conducted in the Yasu River ecosystem during the nonirrigation period (Ishikawa et al. 2017). Another explanation for these lower nutrient concentrations may be the adsorption of NO_3^- and PO_4^{3-} on particulate matter (Huang et al. 2011). Soil particles can adsorb these anions, decreasing dissolved inorganic nutrient concentrations.

In addition to the effects of rice paddy and urban areas, forest areas were found to have a robust negative effect on stream water temperature in this study; this is reasonable because stream surfaces are shaded by riparian vegetation in the forest areas. For aquatic ectotherms, it is known that water temperature has a positive effect on their diversity, mainly via a productivity effect with increased energy availability and food-web complexity (Gaston 2000, Smol et al. 2005, Dallas 2007, Brucet et al. 2013). However, in the Yasu River, the water temperature effect on benthic macroinvertebrate diversity was inconsistent between the irrigation and nonirrigation periods, that is, negative for the former and positive for the latter. We speculate that, although water temperature is a critical factor to determine the phenology of hatching and emergence of aquatic benthic macroinvertebrates, the direction of the temperature effect on the frequency of their appearance is both season- and species-specific (Cayrou and Cereghino 2005, Fontanarrosa et al. 2009, Moore and Schindler 2010, Glazaczow et al. 2016). This makes the temperature dependency of stream biodiversity patterns more complicated.

Implications for environmental restoration and biodiversity conservation

The results of our SEM, which aimed to unravel complicated causal mechanisms for how land use can affect stream communities, also have some implications for environmental restoration and biodiversity conservation in watershed management. First, deforestation may not always decrease stream biodiversity, because forests can have contrasting effects on benthic macroinvertebrate diversity between two seasons, as shown in this study. However, deforestation-driven warming can change the broad-scale distribution and community composition of stream species, such as benthic macroinvertebrates and fishes (Lorion and Kennedy 2009, Castello and Macedo 2016, Ilha et al. 2018). Our study supported the findings of Scrine et al. (2017), who combined experimental manipulation of habitat complexity with a natural stream temperature gradient to identify increases in benthic macroinvertebrate abundance, body mass, and biomass in the warmest streams of high-latitude Iceland, even though this is not the case for the temperature effects on its biodiversity.

Deforestation may have other possible impacts on stream biodiversity. Forests can provide a variety of food sources for stream benthic macroinvertebrates, through the transportation of dissolved and particulate organic matter, increasing the diversity of feeding functional groups (Ishikawa et al. 2016). In the watersheds of developing countries, riparian deforestation is considered to be a secondary critical factor, behind urbanization, in decreasing the EPT index, which is defined as the species richness or density of the disturbance-sensitive insect orders, Ephemeroptera, Plecoptera, and Trichoptera, which have diverse feeding functions (Peralta et al. 2020). Although we did not explicitly explore the feeding functions of benthic macroinvertebrate communities in this study, special attention should be paid to the impact on functional diversity in stream ecosystems whenever deforestation occurs, as proposed by researchers who performed studies in Southeast Asia and Madagascar (Benstead et al. 2003, Benstead and Pringle 2004, Wilkinson et al. 2018).

Second, in the Yasu River catchment, in which most cropland areas are occupied by rice paddies, rice paddy irrigation is regarded as a straightforward anthropogenic driver of biodiversity loss. However, we should note that the number of rice paddies has been gradually decreasing in the Yasu River catchment because of declining agriculture, while benthic macroinvertebrate diversity has historically been decreasing in receiving shallow coastal waters, from the late 1960s to the present (Shibata et al. 2014). In the Lake Biwa watershed, a comprehensive lake development program was implemented in 1972 for multiple purposes and to develop and conserve the entire watershed system. Irrigation systems were drastically modified, with the construction of dams and pumping stations to improve irrigation efficiency and crop productivity, to speed up economic development. Following the establishment of modern irrigation systems, however, the sedimentation rate increased in shallow coastal waters (Nishino et al. 2017), possibly due to increased particulate loading from the rice paddies (Sakai et al. 2013). This increased particulate loading could account for the decreasing trend in coastal benthic macroinvertebrate diversity in Lake Biwa (Shibata et al. 2014). We therefore conclude that the modernization of irrigation systems, rather than the rice paddies themselves, may be a driver of stream biodiversity loss.

To mitigate the aforementioned agricultural impacts due to modern irrigation systems, we performed action research using a social–cultural approach to empower farming communities to adopt eco-friendly farming practices using traditional irrigation systems. The aim was to conserve familiar nature, defined as nature that was meaningful for individual farming communities in the context of their lives and livelihoods (Asano et al. 2018). In fact, a field experiment had demonstrated that eco-friendly farming could reduce phosphorous loadings during the irrigation period, on average by 26%, compared with conventional farming practices using modern irrigation techniques (Ishida et al. 2020). If such a governance approach can promote eco-friendly farming using traditional irrigation techniques throughout the whole Yasu River catchment, it would be expected to increase benthic macroinvertebrate diversity at the watershed level through reductions in PP loading during the irrigation period.

Finally, our seasonal/periodical comparison showed that species richness was on average higher during the irrigation period than during the nonirrigation period. This may be just a short-term periodical and/or seasonal variation in the hatching and emergence of aquatic benthic macroinvertebrates. More importantly, the evenness of local communities was lower during the irrigation period than during the nonirrigation period, suggesting higher β-diversity among the former. When comparing spatial patterns of benthic macroinvertebrate communities between the moderately disturbed Yasu River and the less disturbed Ado River within the Lake Biwa watershed, Ko et al. (2019) found that the β-diversity was higher for the former, despite the lower species richness. The Yasu River has a different pattern of land-use types in its catchment (i.e., 57.7%, 22.5%, and 6.5% for forest, cropland, and urban land use, respectively) compared with that of the Ado River (91.5%, 3.7%, and 0.7%, respectively); thus, there is higher spatial heterogeneity of local stream environments in the former catchment. The same is true for seasonal comparisons within the Yasu River catchment. A larger proportion of between-stream variation in abundance and community composition of benthic macroinvertebrates was accounted for by environmental components during the irrigation period, compared with that during the nonirrigation period, consequently resulting in higher diversity of benthic macroinvertebrates.

Our study revealed that rice paddy irrigation could magnify environmental spatial heterogeneity through increases in PP. This may preferentially sort eutrophication-resistant species, such as worms and Chironomidae, suggesting a predominance of species sorting in meta-community processes. In the Yasu River catchment, seasonal agricultural activities decreased the α-diversity of stream communities, while it might increase γ-diversity in the entire catchment through increased habitat heterogeneity. As another meta-community process, mass effect might play a key role in determining diversity patterns through river networks that can facilitate upward–downward dispersal (Clarke et al. 2008, Altermatt et al. 2013). To further understand how land-use activities in a catchment can affect the γ-diversity of stream communities, more sophisticated statistical approaches will be necessary in the future.

Conclusions

Seasonal variations in the Yasu River were associated with distinct changes, in both the diversity of benthic macroinvertebrates and site-level environments. SEM with multiple group analysis in this study revealed that each land-use type in the catchment had different indirect effects on stream benthic macroinvertebrate diversity, through alterations in local environments within the entire Yasu River catchment. The SEM also highlighted seasonal negative impacts of rice paddy irrigation on local benthic macroinvertebrate communities, possibly through siltation due to increased loading of particulate nutrients derived from rice paddy soils. Such structural spatial statistics based on a causal mechanistic model can be a powerful tool for biodiversity conservation in freshwater ecosystems. They can also provide useful information for watershed management, helping make decisions about what is prioritized to mitigate environmental stressors of stream communities. Finally, our findings suggest that the relative impacts of different land-use types on stream benthic macroinvertebrate diversity can vary seasonally and/or periodically, and may consequently not be given sufficient weight in conservation policy and management at the catchment level.

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3468/full