Received: 10 October 2018 | Accepted: 3 November 2018
DOI: 10.1111/1365-2664.13316

RESEARCH ARTICLE

Journal of Applied Ecology | BRITISH ECOLOGICAL SOCIETY

Catch diversification provides multiple benefits in inland fisheries

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Funding information
JSPS KAKENHI, Grant/Award Number: 15H02380 and 18K11734; Environmental Restoration and Conservation Agency, Grant/Award Number: 4-1705

Handling Editor: Robert Arlinghaus

Abstract

1. Diversification of fisheries and agroecosystems can increase and stabilize production and revenue, despite unpredictable changes in ecosystems and markets. Recent work suggests that diversification can provide multiple benefits simultaneously, but empirical evidence of relationships between catch or crop diversification and the provision of multiple benefits is scarce. The effect of diversification on multiple benefits may vary temporally and among systems.
2. Using long-term (11–54 years) capture fishery statistics from five Japanese lakes, we examined whether catch diversity increased multiple benefits, including revenue, nitrogen and phosphorus removal, and seasonal commercial species diversity. We also assessed whether catch species diversity increased the stability of each benefit via a portfolio effect (PE).
3. Our study revealed positive relationships between catch diversity and the bundle of benefits (the mean of all normalized benefits; i.e., the provisioning of multiple benefits) in all five lakes, even after controlling for the total catch. The effects of catch diversity on individual benefits were positive or insignificant and differed among the study lakes. These differences were likely caused by the range and variation of functional characteristics among catch species. The influence of the annual mean price on revenue suggested that market forces did have an effect.
4. We also found that aggregated revenue as well as N and P removal were 1.6–2.1 times (four lakes), 1.5–2.2 times (four lakes), and 1.4–2.2 times (all five lakes) more stable, respectively, than would be expected if only a single species were harvested. This greater stability suggests that maintaining catch species diversity may increase the stability of multiple benefits through PEs.
5. *Synthesis and applications*. Our analysis suggests that catch diversification has great potential to increase the magnitude and stability of multiple benefits. Although total catch alone was sufficient to provide multiple benefits, a goal of maximization with specialization may decrease stability and deplete resources. Under fluctuating environmental and economic conditions, diversification strategies promise to be a potential management option for achieving resilient and sustainable inland fisheries.

KEYWORDS
catch diversity, ecosystem services, fishery management, lake ecosystem, multifunctionality, nutrient management, specialization, sustainability

1 | INTRODUCTION

Both crop diversification (i.e., mixed planting or crop rotation) and catch diversification (i.e., catching multiple fisheries species) have been touted as a means to maintain yields and revenue in agroecosystems and fisheries despite large and abrupt changes in environmental and market conditions (Anderson et al., 2017; Binder, Isbell, Polasky, Catford, & Tilman, 2018; Holland et al., 2017; Isbell, 2015; Isbell, Adler, et al., 2017). Therefore, there is considerable interest in designing and developing diversification strategies for these systems. Recent analyses on crop diversification strategies have used complementarity, selection effects, and other aspects of biodiversity–ecosystem functioning to demonstrate that diversification can increase total production or revenue in agricultural systems (Allan et al., 2015; Isbell, Adler, et al., 2017; Knoke et al., 2016; Kremen & Miles, 2012; Van Huylenbroeck, Vandermeulen, Mettepenningen, & Verspecht, 2007). Furthermore, other studies have shown that intentional crop diversification may provide multiple simultaneous benefits, which not only include increased production but also pollination, pest suppression, and carbon storage (Binder et al., 2018; Blesh, 2018; Isbell, Adler, et al., 2017). However, the relationship between catch or crop diversification and the provision of multiple benefits may vary temporally and among ecosystems. Moreover, the consistency of this relationship remains unexplored. Unlike agroecosystems, fisheries exploit natural ecosystems, and fish stocks are selectively harvested to advance the goals of the fishery. Therefore, the framework of biodiversity–ecosystem functioning does not necessarily apply to catch diversification in fisheries. More empirical evidence is needed to enable the broad implementation of diversification strategies in socio-ecological systems.

Commercial capture fisheries are especially vulnerable to abrupt environmental perturbations and unexpected shifts in market conditions (Anderson et al., 2017; Cline, Schindler, & Hilborn, 2017; Holland et al., 2017). There is a critical need to explore resilient management strategies that are robust to uncertainties and regime shifts in fisheries resources and markets. Recent studies have revealed that catch diversification can increase catch or revenue (Cline et al., 2017; Dee et al., 2016; Holland et al., 2017; Steneck et al., 2011). Creating and maintaining flexibility in fishing opportunities could be one mechanism to make the benefits derived from exploitation of fish stocks more resilient to perturbation (Cline et al., 2017). In addition, catch diversity has been reported to stabilize total catch or revenue through portfolio effects (PEs; i.e., the statistical averaging of multiple species or populations) and asynchrony (Anderson et al., 2017; Nesbitt & Moore, 2016; Ward et al., 2017). The biodiversity–ecosystem functioning framework may help elucidate the mechanisms responsible for this enhanced stability. However, catch diversification strategies may not only be important for the enhancement of catch or revenue, but for the provision of other benefits as well (Brummett, Beveridge, & Cowx, 2013). For example, fisheries can remove a substantial amount of nutrients from aquatic ecosystems (Allgeier, Valdivia, Cox, & Layman, 2016; Maranger, Caraco, Duhamel, & Amyot, 2008), as reported by Hjerne and Hansson (2002), who found that harvesting removes 1.4% and 7% of the total anthropogenic nitrogen (N) and phosphorus (P) loads to the Baltic Sea, respectively. Allgeier, Layman, Mumby, and Rosemond (2014) demonstrated that the richness and diversity of fish communities influence the amount of nutrients stored in community biomass. Although these studies suggest that catch diversity can enhance other benefits in addition to revenue, few studies to date have addressed the relationships between catch diversity and the provision of multiple benefits.

Earlier studies on catch diversification strategies have focused on marine fisheries, but it remains a challenge to inland fisheries (Cline et al., 2017). In Japan, lake capture fisheries face severe ecological and social challenges. First, fishery stocks have suffered the impact of multiple anthropogenic drivers, including shore development, water level alteration, and exotic piscivores invasions (Matsuzaki & Kadoya, 2015; Nishizawa, Kurokawa, & Yabe, 2006; Yamamoto, Kohmatsu, & Yuma, 2006). Second, unlike in developing countries, in Japan there has been a dramatic decline in the market demand for inland fishery resources because of changes in people's lifestyles associated with globalization and modernization (i.e., low demand for protein from freshwater fish and invertebrates). Third, the ageing of the current generation of fishers, and a shortage of successors, is also a serious concern. As a consequence, fishers and markets have increasingly concentrated on a few commercial species. For example, the dependence on high-valued species such as ayu (*Plecoglossus altivelis*) and Japanese clam (*Corbicula japonica*) has increased substantially in Lake Biwa and Lake Ogawara, respectively (Katano, Hakoyama, & Matsuzaki, 2015; Kawanabe, Nishino, & Maehata, 2012). This lack of catch diversity may heighten the risk of ecological and economic disruption (Cline et al., 2017; Ward et al., 2017). Furthermore, in the event of such disruptions, managers are unlikely to invest in the restoration of lake capture fisheries, because their value and function have seldom been evaluated or recognized (Beard et al., 2011). Therefore, a comprehensive assessment of the multiple benefits of catch diversification is necessary to facilitate the use of diversification strategies in ecosystem-based fishery management.

In this study, we examined whether higher catch diversity leads to simultaneous increases in revenue and other benefits, and whether catch diversity increases the stability of these benefits. We used unique long-term commercial fishery datasets collected over 11–54 years from five Japanese lakes with different commercial fish and invertebrate species compositions. We evaluated four potential benefits: revenue, N removal, P removal, and seasonal species diversity (diversity in the peak season of individual commercial species). Seasonality is an important aspect of traditional culture of Japan, which experiences four distinct seasons because of its temperate climate; seasonal ingredients have also long been valued in Japanese cuisine (Kawanabe et al., 2012; Shimomura, 2016). Consumers enjoy seasonal fish, shrimp, and shellfish at times during the year when they are freshest and most flavourful. Higher diversity among seasonal species is expected to create a more stable supply chain for consumers and thereby help to maintain traditional Japanese

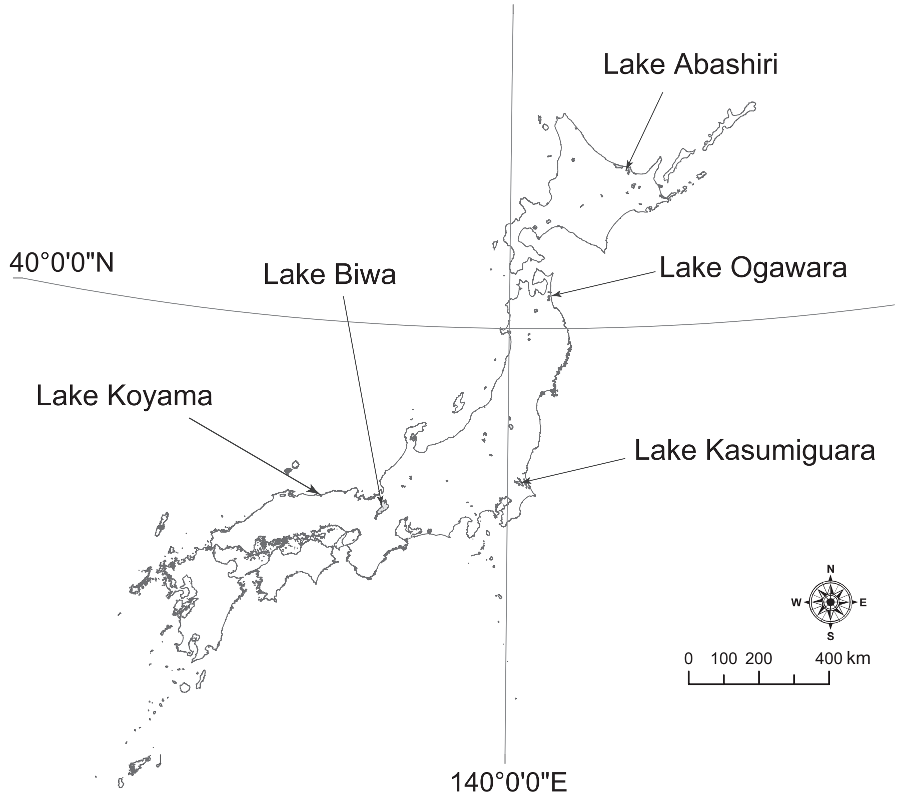

FIGURE 1 Map of the five Japanese lakes examined in this study. All five lakes support important inland fisheries

culinary culture. We calculated the mean of all normalized benefits and defined this as a "bundle of benefits" (Isbell, Gonzalez, et al., 2017) provided by inland fisheries. We expected that high catch diversity would maximize the bundle of benefits after controlling for the effect of total catch. We also examined whether catch diversification increases the stability of revenue and N and P removal through PEs.

2 | MATERIALS AND METHODS

2.1 | Study lakes

We examined five Japanese lakes—Lake Abashiri, Lake Ogawara, Lake Kasumigaura, Lake Biwa and Lake Koyama (Figure 1)—where long-term revenue data were available. The morphological characteristics and trophic statuses of the lakes, and the corresponding commercial species compositions, are shown in Supporting Information Tables S1 and S2, respectively.

2.2 | Fishery data and catch diversity

Although it is generally difficult to collect revenue data because of privacy concerns, we were able to collect species-specific catch and revenue data for all five of our study lakes. We successfully obtained species-specific annual catch and revenue data from our five study lakes (Figure 2). The data for Lake Abashiri were gathered from the fisheries statistics of Abashiri City (1962–2015). The data for Lake Ogawara were obtained from the annual reports of Lake Ogawara's fishery cooperative association (1977–2016). The data for Lake Kasumigaura were gathered from the Lake Kasumigaura-Kitaura Fishery Statistics by Ibaraki Prefecture (1962–2006). The data for Lake Biwa were collected from annual reports of statistics on agriculture, forestry, and fisheries in Shiga Prefecture, which are produced by the Ministry of Agriculture, Forestry and Fisheries (MAFF) of Japan (1963–2006). The data for Lake Koyama were taken from the annual reports of the fishery cooperative association of Lake Koyama (2001–2011).

These fishery data were originally collected and compiled for each lake by local fisheries cooperative associations. Annual catch surveys were conducted once per year using the methods described in the reports of the MAFF. Local fisheries cooperative associations compiled the total annual catch of each commercial species caught by various gear types, including trawl nets, gill nets, longlines, stationary nets, and rakes. The MAFF or prefectures gathered data through reporting surveys or interviews and published the results in the Annual Statistics of Fishery and Aquaculture Production. The fisheries cooperative associations of the five study lakes compiled revenue data following a procedure identical to the procedure used for the catch data. We adjusted all revenue data for inflation using the consumer price index time series (category: fishery products) for 2016.

We calculated the compositional diversity of the fisheries catch in terms of catch rather than revenue (Dee et al., 2016; Steneck et al., 2011). We used the Shannon–Wiener index (H') because this index is more sensitive to rare species whereas the Simpson index is more sensitive to dominant species (Magurran & Dornelas, 2010). The

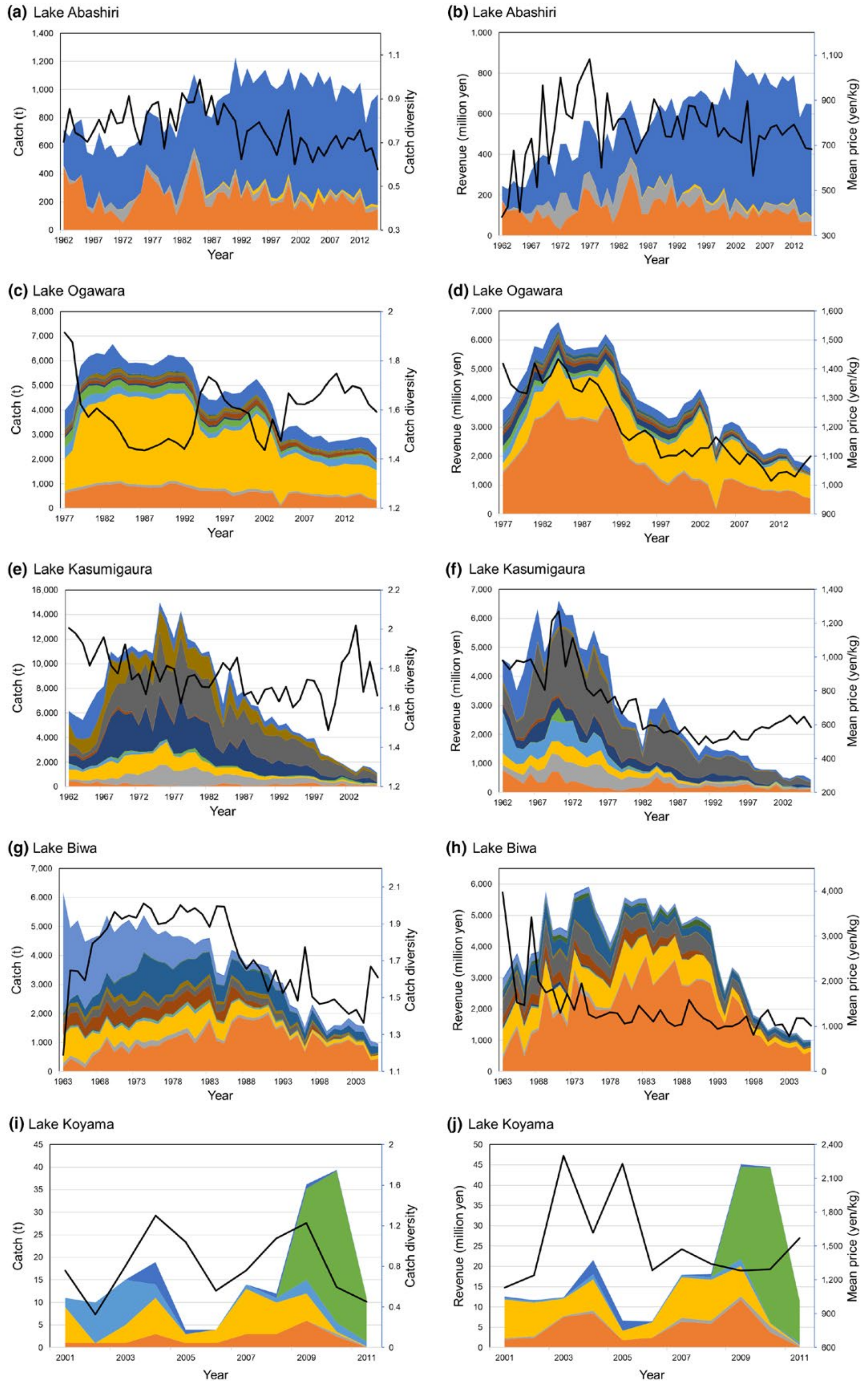

FIGURE 2 Left-hand panels show long-term trends in the catch of commercial fish or invertebrates (colours indicate different species) and catch diversity (Shannon–Wiener index, black line) in five Japanese lakes (a, c, e, g, and i). Right-hand panels show long-term trends in revenue (colours indicate different species) and mean price per weight (b, d, f, h, and j)

Shannon–Wiener index was calculated using $H = -\Sigma_{i=1}^{k} \ln(p_i)p_i$, where p_i is the proportional catch of the species *i*th and *k* is the number of species. Because evenness is an important dimension of diversity, we calculated Pielou's evenness index, which is H' divided by the ln-transformed catch species richness. However, Pielou's evenness index was highly and positively correlated with the Shannon–Wiener index in all five study lakes (Lake Abashiri; r^2 = 0.76, Lake Ogawara; r^2 = 0.99, Lake Kasumigaura; r^2 = 0.99, Lake Biwa; r^2 = 0.99, Lake Koyama; r^2 = 0.56), probably because catch species richness did not change much over time. We therefore focused on the effect of catch diversity on multiple benefits. These diversity indices were calculated using the VEGAN package (Oksanen et al., 2007) in R. All statistical analyses were performed in R version 3.2.3.

2.3 | N and P removal throughout harvesting

In lake ecosystems, nutrient removal via harvesting could be important for the maintenance of water quality. Some previous studies have only considered the N and P contents of the edible portions of harvested fish (i.e., the muscles), and therefore underestimated the amounts of nutrients removed through harvesting. To more accurately quantify the total amounts of N and P removal through harvesting, we used whole-body N and P contents (i.e., including bones) of fish and invertebrates.

We gathered data on measured whole-body N and P contents from the literature (Supporting Information Table S3, Hayakawa, Tsujimura, Jiao, Ishikawa, & Ishikawa, 2010; Kojima, Sato, Yoshinaka, & Ikeda, 1986a, 1986b; Kumamaru, 1998; Mikami et al., 2001; Nakamura & Mori, 1998). For species for which data were not available (nine fish species), we measured whole-body N and P contents ourselves. We captured three to eight individuals of *Hypomesus nipponensis*, *Salangichthys microdon*, *Cyprinus carpio*, *Carassius* spp., Bitterlings (*Rhodeus ocellatus*), *Hyporhamphus intermedius*, *Mugil cephalus*, and *Anguilla japonica* with a stationary net in Lake Kasumigaura. We also captured three individuals of *Platichthys stellatus* with a stationary net in the coastal area of Hachinohe near Lake Ogawara.

We dried whole fish samples at 55°C for 2 or 3 days and ground them to a fine powder with a high-speed vibrating mill (TI-200, CMT Co., Ltd., Japan). For N analysis, we measured subsamples (2 mg) of fish powder using a CN elemental analyser (Micro Coder JM10, J-Science Lab Co., Ltd., Japan). For P analysis, we ashed 60 mg of fish powder at 550°C for a minimum of 96 hr (Hendrixson, Sterner, & Kay, 2007). After hydrochloric acid digestion with 1 mol/L HCl to convert all P to soluble reactive P (for 20 hr), the extracts were filtered through a membrane filter (0.45 μm, PVDF; Millipore) and diluted by a factor of 1,000. We analysed P using the molybdenum blue method (Murphy & Riley, 1962) using a spectrophotometer (UV2500PC; Shimadzu, Japan). The minimum detection limit (3σ of 20 blanks) for this method was approximately 2.0 μg P/L.

To determine the species-specific N and P removed through harvesting, we multiplied species-specific N and P content by the annual catch of each species at a given lake. The sums of these values for each species harvested were taken as the total amounts of N and P removed through harvesting.

2.4 | Seasonal species diversity

We evaluated seasonal species diversity by calculating an abundance-weighted functional diversity index. We identified the peak season (spring, summer, autumn, and winter) for all fish and invertebrate species based on published monographs and books. For each species, their peak season(s) were scored as 1, whereas the remaining seasons were scored as 0. Using this species and peak season matrix, we calculated Rao's quadratic entropy (Rao's *Q*), a measure of functional diversity that considers relative species abundances (Mouillot, Graham, Villeger, Mason, & Bellwood, 2013). Rao's *Q* is the sum of pairwise functional distances between species weighted by their relative abundance (here, using catch data). We calculated pairwise functional distances using the Gower distance, which is appropriate for binary data. Calculations of Rao's *Q* were performed using the FD package (Laliberté, Legendre, Shipley, & Laliberté, 2014) in R.

2.5 | Bundle of benefits

We calculated the bundle of benefits, that is, the simultaneous provision of multiple benefits, by averaging the normalized magnitudes of multiple benefits into a single index. This approach is widely used to calculate multifunctionality (Byrnes, Gamfeldt, et al., 2014; Fanin et al., 2018). Each of the four benefits was normalized to a scale of 0–1 by dividing by the maximum observed value. We then calculated the arithmetic mean of these normalized values across all individual benefits. This approach requires the absence of any trade-offs between benefits (Byrnes, Gamfeldt, et al., 2014), but we confirmed that there were no significant negative correlations among the four functions used in this study (Supporting Information Table S4).

2.6 | Statistical analysis

We employed a generalized least squares (GLS) multiple regression model that corrects for a first-order autoregressive process (AR1) to simultaneously examine the effects of catch diversity and total catch on single benefits or the bundle of benefits. For revenue, we included the mean price per weight in the model as an explanatory variable, because prices reflect fluctuations in market demand and therefore potentially influence revenue (McClanahan, 2010). The mean price per weight (kg) of each catch species was estimated by dividing total revenue by total catch. Those means were averaged to calculate the mean price per weight of all species (Figure 2). We used the Nagelkerke pseudo R^2, which measures the proportion of variance explained by the model, as a measure of the goodness-of-fit. The GLS models were analysed using the *gls*() function in the NLME package (Pinheiro, Bates, DebRoy, & Sarkar, 2014) in R. The Nagelkerke pseudo R^2 was calculated using the package PIECEWISESEM in R.

To examine whether catch diversification stabilizes gross revenue, and N and P removal, we quantified the PE, the degree to which diversity (here, the number of species caught) increases stability. PE in population ecology can be calculated simply by comparing the temporal coefficient of variation (CV) of an aggregate population with the average CV of all the subpopulations, which is known as the "average-CV PE" (Anderson, Cooper, & Dulvy, 2013; Schindler et al., 2010). Using the ECOFOLIO package (Anderson et al., 2013) in R, we estimated the average-CV PE using the following formula:

$$\text{Average-CV PE} = \frac{CV_{sp1} + CV_{sp2} + \ldots + CV_{spN}/N}{CV_{total}}$$

where CV_{sp} is the CV of catch for a given species, N is the total number of commercial species, and CV_{total} is the CV of total catch. Average-CV PE values greater than 1 indicate stabilizing effects. Following the method of Anderson et al. (2013), we sampled the species from all species 1,000 times by bootstrap and estimated 95% confidence intervals (CI) of average-CV PE.

3 | RESULTS

3.1 | Long-term trends in catch, catch diversity, revenue, and mean price

Long-term trends in total catch and catch diversity differed among the five lakes (Figure 2). Total catch increased significantly over time in Lake Abashiri, whereas it decreased significantly in Lake Biwa and declined after the late 1980s in Lakes Ogawara and Kasumigaura. Catch diversity decreased significantly in Lakes Abashiri and Kasumigaura, but it increased slightly after the year 2000 in Lake Kasumigaura. In Lake Biwa, catch diversity tended upward until 1980 and has declined since then. Catch diversity in Lake Ogawara was highly variable. There were no significant trends in total catch or catch diversity in Lake Koyama, probably due to the short time series.

Gross revenue tended to increase over time in Lakes Abashiri and Koyama, whereas it decreased in Lakes Ogawara, Kasumigaura, and Biwa after the late 1980s (Figure 2). Mean price tended to decline after the 1970s in all lakes except Lake Koyama, and it decreased after the mid-2000s in Lake Koyama.

3.2 | Effects of catch diversity on the magnitude of single benefits and bundles of benefits

The GLS multiple regression results showed that gross revenue increased significantly with catch diversity as well as with total catch in all five lakes (Table 1, Supporting Information Figure S1). Mean price also affected revenues in four of the five lakes. In Lakes Abashiri, Ogawara, and Kasumigaura, there were significant positive relationships between revenue and mean price, but in Lake Koyama, revenue was negatively correlated with mean price. N and P removal increased significantly with catch diversity in four and three of lakes, respectively (Table 1, Supporting Information Figures S2 and S3). Both N and P removal increased with catch diversity, but not total catch, in Lake Koyama, whereas they increased with total catch, but not catch diversity, in Lake Kasumigaura. There were also significant positive relationships between catch diversity and seasonal species diversity in all lakes except Lake Kasumigaura (Table 1, Supporting Information Figure S4). Although seasonal species diversity of Lake Ogawara and Lake Biwa did not increase with total catch, there were significant positive relationships between catch diversity and seasonal species diversity. The bundle of benefits was significantly positively related to catch diversity in all lakes (Table 1, Figure 3).

3.3 | Effects of catch diversity on the stability of multiple benefits

Higher catch species richness substantially increased the stability of revenue and nutrient removal. Excluding Lake Ogawara, aggregate revenue and N removal amounts were 1.6–2.1 and 1.5–2.2 times more stable, respectively, than those that would be expected from a single species (Figure 4). In Lake Ogawara, however, the 95% CIs of the average-CV PEs slightly overlapped with 1, indicating that there were marginally significant PEs. Average-CV PEs were greater than 1 for P removal amounts in all lakes. Aggregate P removal amounts were 1.4–2.2 times more stable than those that would be expected from a single species.

4 | DISCUSSION

Overall, our comprehensive synthesis of long-term data clearly demonstrates that catch diversity provides multiple benefits, and furthermore, that it increases the stability of those benefits (Figures 3 and 4, Table 1). Although this supports recent agroecosystem research suggesting that crop diversification can not only boost total production or revenue but also provide multiple benefits (Finney & Kaye, 2017; Isbell, 2015), to our knowledge, our study is the first study to examine the relationships between catch diversification and the provision of multiple benefits. Catch diversification may be required to maintain and stabilize fisheries benefits in an increasingly unpredictable environmental and market context. Because the benefits that we considered benefit consumers and ecosystems as well as fishers, our findings suggest that catch diversification strategies could play an important role in boosting both inland fishery sustainability and human well-being.

Total catch increased individual benefits and the provision of multiple benefits, depending on the lakes (Table 1), suggesting that increasing total catch alone, even with one or several species, could be sufficient to provide multiple benefits. However, a higher catch does not always guarantee more benefits for the following reasons. First, maximizing catch by targeting one or a few species (i.e., specialization) can pose long-term risks if environmental and market conditions change rapidly and unexpectedly (Anderson et al., 2017; Dee et al., 2016; Ward et al., 2017). For example, Alaskan fishing communities that had high catch diversity or were able to opportunistically shift the species composition of their catch experienced small or negligible changes in revenue following major ocean

TABLE 1 Summary of the generalized least squares (GLS) multiple regression models for testing the effects of catch diversity and total catch on gross revenue, nitrogen and phosphorus removal, seasonal species diversity, and bundle of benefits in five Japanese lakes. For gross revenue, the models included the effect of mean price. Significant coefficients (p < 0.05) are indicated with bold text. R^2: Nagelkerke pseudo-R^2

	Catch diversity				Total catch				Mean price per weight				
Response variables	Coefficient	*SE*	*Z*-value	*p*	Coefficient	*SE*	*Z*-value	*p*	Coefficient	*SE*	*Z*-value	*p*	R^2
Gross revenue													
Abashiri	**276.1**	**66.6**	**4.1**	<0.001	**0.44**	**0.06**	**7.8**	<0.001	**0.181**	**0.039**	**4.6**	<0.001	0.40
Ogawara	**1,516.0**	**654.5**	**2.3**	0.026	**3.83**	**1.01**	**3.8**	<0.001	**0.938**	**0.107**	**8.8**	<0.001	0.92
Kasumigaura	**2,000.7**	**847.0**	**2.4**	0.023	**0.14**	**0.07**	**2.0**	0.047	**1.862**	**0.889**	**2.1**	0.042	0.38
Biwa	**2,291.1**	**644.5**	**3.6**	0.001	**0.74**	**0.14**	**5.2**	<0.001	−0.272	0.169	−1.6	0.115	0.77
Koyama	**5.3**	**2.1**	**2.5**	0.039	**1.08**	**0.06**	**18.6**	<0.001	**−0.004**	**0.002**	**−2.6**	0.037	0.99
N removal													
Abashiri	**3.0**	**1.3**	**2.4**	0.022	**0.020**	**0.0011**	**18.1**	<0.001	–	–	–	–	0.67
Ogawara	**42.7**	**2.5**	**17**	<0.001	**0.013**	**0.0003**	**38.9**	<0.001	–	–	–	–	0.99
Kasumigaura	−4.8	3.2	−1.5	0.136	**0.024**	**0.0001**	**260.9**	<0.001	–	–	–	–	0.99
Biwa	**18.6**	**7.4**	**2.5**	0.016	**0.021**	**0.002**	**10.4**	<0.001	–	–	–	–	0.84
Koyama	**0.3**	**0.1**	**2.5**	0.039	0.007	0.003	2.2	0.062	–	–	–	–	0.65
P removal													
Abashiri	0.21	0.27	0.8	0.433	**0.0035**	**0.0002**	**15.3**	<0.001	–	–	–	–	0.60
Ogawara	**6.18**	**0.72**	**8.6**	<0.001	**0.0016**	**0.0001**	**12.7**	<0.001	–	–	–	–	0.90
Kasumigaura	−0.35	2.03	−0.2	0.866	**0.0048**	**0.0001**	**75.7**	<0.001	–	–	–	–	0.99
Biwa	**4.22**	**1.31**	**3.2**	0.003	**0.0034**	**0.0003**	**9.8**	<0.001	–	–	–	–	0.89
Koyama	**0.04**	**0.01**	**2.6**	0.031	0.0005	0.0004	1.4	0.19	–	–	–	–	0.59
Seasonal species diversity													
Abashiri	**0.08**	**0.01**	**6.5**	<0.001	**6.4.E-05**	**1.0.E-05**	**6.4**	<0.001	–	–	–	–	0.32
Ogawara	**0.04**	**0.01**	**5.8**	<0.001	1.1.E-06	6.0.E-07	1.9	0.071	–	–	–	–	0.52
Kasumigaura	0.03	0.02	1.5	0.145	**2.6.E-06**	**5.9.E-07**	**4.5**	<0.0001	–	–	–	–	0.40
Biwa	**0.03**	**0.01**	**3.7**	<0.001	−2.5.E-06	2.4.E-06	−1.0	0.308	–	–	–	–	0.11
Koyama	**0.06**	**0.02**	**2.8**	0.025	**1.7.E-03**	**5.4.E-04**	**3.1**	0.014	–	–	–	–	0.67
Bundle of benefits													
Abashiri	**0.28**	**0.06**	**4.9**	<0.001	**8.5.E-04**	**4.8.E-05**	**17.6**	<0.001	–	–	–	–	0.74
Ogawara	**0.44**	**0.03**	**14**	<0.001	**1.2.E-04**	**4.0.E-06**	**29.2**	<0.001	–	–	–	–	0.98
Kasumigaura	**0.18**	**0.05**	**3.8**	<0.001	**4.7.E-05**	**3.1.E-06**	**15.1**	<0.001	–	–	–	–	0.94
Biwa	**0.25**	**0.06**	**4.3**	<0.001	**1.1.E-04**	**1.6.E-05**	**7.3**	<0.001	–	–	–	–	0.76
Koyama	**0.37**	**0.1**	**3.6**	0.007	**1.3.E-02**	**2.8.E-03**	**4.7**	0.002	–	–	–	–	0.86

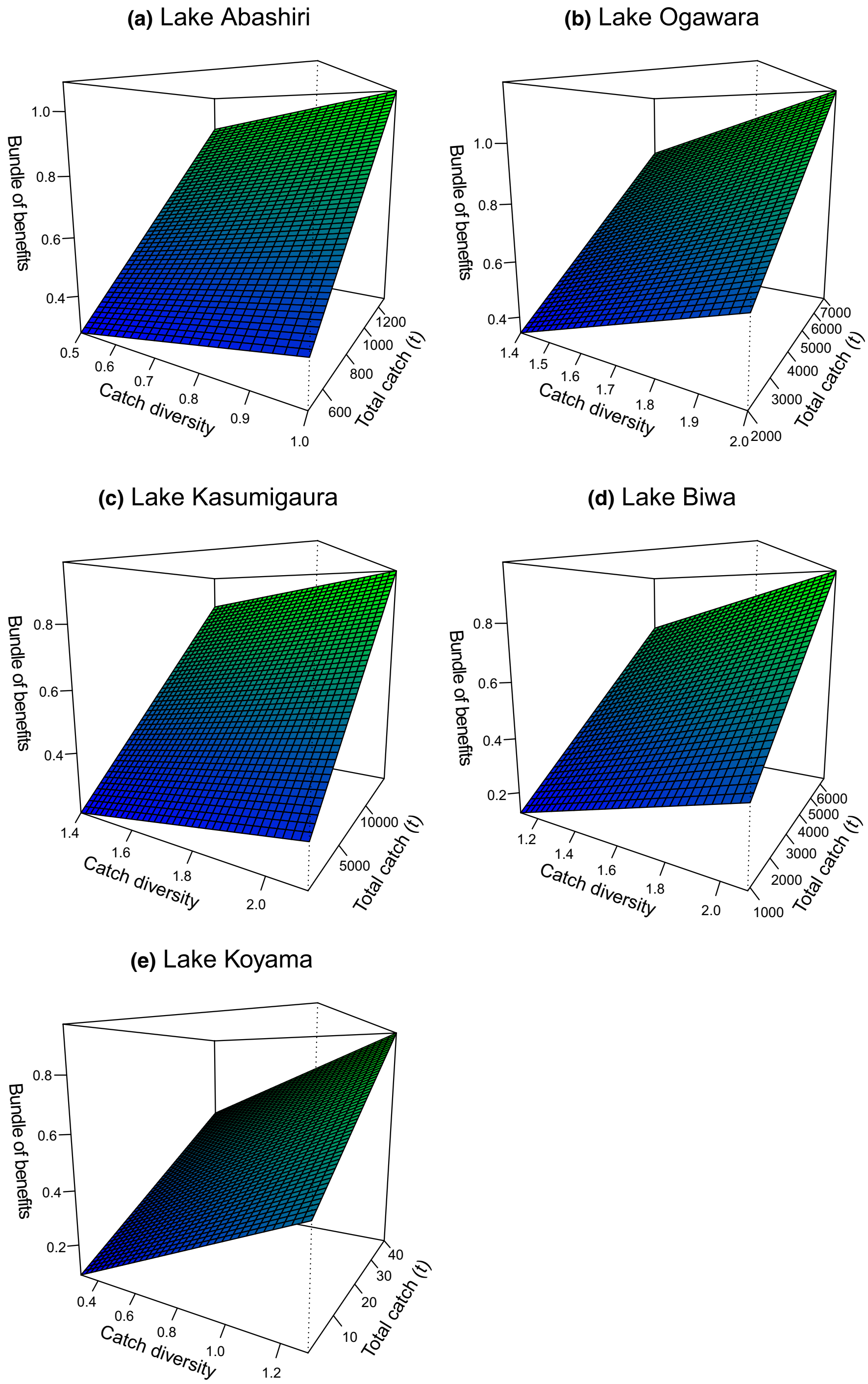

FIGURE 3 3D wireframes of the bundle of benefits (the mean of four normalized benefits; see main text) plotted against catch diversity (Shannon–Wiener index) and total catch in the five Japanese lakes ([a] Lake Abashiri, [b] Lake Ogawara, [c] Lake Kasumigaura, [d] Lake Biwa, and [e] Lake Koyama). Wireframes were generated using coefficients obtained from generalized least squares (GLS) models

and market regime shifts that occurred in 1989 (Cline et al., 2017). Our results also suggest that increasing catch by specialization may decrease the stability of multiple benefits (Figure 4). Second, maximizing catch can lead to overexploitation. In addition to commercial harvesting, other anthropogenic drives, including invasive species and climate change, can further decrease fishery resources. To improve the sustainability of Japanese inland fisheries, it is therefore essential to maximize catch diversity at sustainable harvest levels.

Although we demonstrated the positive contribution of catch diversity to the bundle of benefits in all lakes, such positive effects were not necessarily observed for all individual benefits (Table 1). This may be due to trade-offs among benefits, because a multifunctionality index (here, the bundle of benefits) does not imply that all benefits are positively correlated (Byrnes, Gamfeldt, et al., 2014; Byrnes, Lefcheck, et al., 2014; Mori et al., 2016). However, there were no significant negative relationships among the four benefits we examined (Supporting Information Table S4). Instead, individual benefits may have responded differently to change in catch diversity in the five lakes, because of differences in functional characteristics and in abundance levels among catch species (Cline et al., 2017). Since each

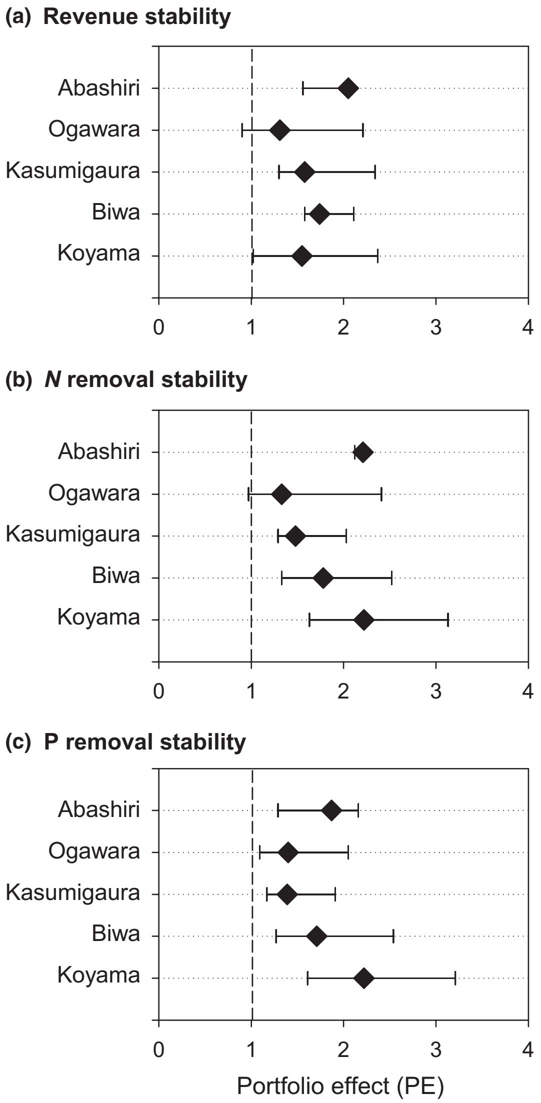

FIGURE 4 Portfolio effects (PEs) for (a) revenue, (b) N removal, and (c) P removal in five lakes. Filled diamonds show average-CV PEs and lines indicate 95% confidence intervals. Average-CV PEs >1 represent stabilizing effects

species has different functional characteristics (i.e., the value and range of price, N and P content, and seasonality), the magnitude of a benefit can differ even at the same level of catch diversity. In contrast, if functional characteristics are overlapped among species, the magnitude of a benefit may remain constant or change due to the difference in abundance. Further study is needed to understand how the functional composition can effectively maximize the bundle of benefits.

Although revenue can be maximized even at a very low level of catch diversity if the harvested species are highly valuable, we did not find such a pattern over time. One possible reason is the temporal changes in market price. The importance of mean price as one of the determinants of revenue in four of the lakes (Table 1) suggests that supply and demand relationships can substantially affect revenue (Cline et al., 2017). The decline of revenue in Lakes Abashiri, Ogawara, and Kasumigaura may be associated with the decline in demand for inland fishery species. Thus, diversifying and increasing the demand for inland fish and invertebrates are necessary components of catch diversification strategies.

The efficiency of harvesting as a means of nutrient removal is noteworthy in the context of eutrophication. We compared the annual amount of N or P removed by harvesting with the annual external N or P loading and estimated the removal efficiency based on the most recent annual data available for each lake (Supporting Information Table S5). Our estimates suggest that the removal efficiency of N and P varied greatly among the five studied lakes. Those efficiencies were similar to efficiencies reported in previous studies (Hjerne & Hansson, 2002), although Lake Ogawara had much higher N and P removal efficiencies than the other lakes. Whereas Lake Ogawara is a mesotrophic lake, its total catch was the highest among the lakes (close to 3,000 t), and it maintains high catch diversity. Our analysis of P removal efficiency included measurements of whole-body P contents (i.e., including bones), in contrast to previous studies. This analysis revealed that removal efficiency was greater for P than N in all lakes. Our results thus suggest that fisheries might play a greater role in improving water quality in mesotrophic and/or P-limited lakes. Considering that water treatment plants have already spent enormous amounts of money to remove nutrients, we believe that nutrient removal by harvesting should be reevaluated as a win-win management option for water quality improvement and fisheries restoration.

Whereas earlier studies have examined the effect of catch diversification on the stability of total catch or revenue (e.g., Anderson et al., 2017), few studies have focused on the stabilizing effect of catch diversity on nutrient removal. Twining, Palkovacs, Friedman, Hasselman, and Post (2017) examined the impact of catch diversity on the stability of total fish-derived nutrient inputs to fresh waters, although the effect was only marginally significant. Our results show that catch diversity not only increased revenue stability but also stabilized N and P removal amounts in all lakes except Lake Ogawara (Figure 4). Interestingly, Lake Ogawara also had the second highest catch species richness out of our five study lakes (Supporting Information Table S2). This result suggests the need to consider other mechanisms, such as the negative covariance among species and the effect of dominant species (Sasaki & Lauenroth, 2011), and it indicates that the relative importance of different mechanisms might differ among lakes.

Although we only evaluated the effect of commercial capture fisheries on multiple benefits, recreational fisheries can also increase the cultural and educational value of inland fisheries. Importantly, they may not only provide income from fishing fees but also contribute to nutrient removal and thereby enhance the benefits from commercial fisheries. Unfortunately, the magnitude of these benefits cannot be evaluated due to a paucity of data on the number of anglers, species-specific catch volumes, and other parameters (Katano et al., 2015). The linkage between recreational fisheries and commercial fisheries could be important in terms of diversification strategies.

4.1 | Management implications

Japanese lakes and fishery resources have suffered from multiple anthropogenic stressors and demand for inland fish and invertebrates has declined (Katano et al., 2015). These conditions can increase environmental and market uncertainties. Our findings underscore the potential need to implement catch diversification strategies in lake fishery management. However, as discussed in previous studies (Anderson et al., 2017; Cline et al., 2017), there are at last two key steps that must be taken to implement catch diversification strategies in Japanese fisheries.

First, it is important to explicitly link catch diversity strategies to stock assessments. Because catch diversity is not calculated based on the stock of each species, promoting catch diversification can result in overexploitation and trigger ecosystem changes. Intensive multispecies fisheries may initially deplete larger and higher-trophic-level species, followed by a gradual shift to smaller and lower-trophic-level species (known as "fishing down the food web," Welcomme, 1999). Furthermore, indiscriminate multispecies fisheries, which target all species and size classes, can deplete stocks (McCann et al., 2016). Monitoring the statuses and trends of individual stocks can increase opportunities to switch among target species (Garcia et al., 2012; Katsukawa & Matsuda, 2003). Link (2017) has suggested that the aggregate-level stock rather than individual stocks should be estimated to manage a diverse portfolio of catch species. Stock-by-stock assessment is constrained by logistical and financial considerations. The use of aggregate-level stock information and the development of new, cost-effective methods (e.g., environmental DNA; Lacoursière-Roussel, Côté, Leclerc, & Bernatchez, 2016) may help establish a safe limit and support harvest regulation. Importantly, diversification strategy and stock assessment should be complemented by an adaptive management scheme, whereby new knowledge continually informs and improves management and policy decisions.

An additional step might be to increase demand for inland fishery species. Average price influences revenue (Table 1), and demand is currently concentrated on few species. These market forces can restrict diversification opportunities and promote specialization (Anderson et al., 2017). Although it is quite difficult to change market forces, there is a need to first increase awareness among dealers and buyers that diversification strategies are a powerful way to buffer risk. Specifically, management strategies should aim to encourage the seasonal supply of multiple species and the production of high-value or new value-added fishery products, and to create new opportunities to use low-value or unutilized species (David, Özkundakci, Pingram, Bergin, & Bergin, 2018). An example of the latter involves invasive species. Because exotic piscivorous fish are considered a shared driver that affects the stocks of multiple commercial species in Japanese lakes (Matsuzaki & Kadoya, 2015), removing and converting these fish into beneficial products, such as fertilizers and livestock feeds, could be one solution for addressing the constraints on diversification.

The five lakes included in our analysis are located across Japan and differ widely in their characteristics and commercial species compositions. Although our study demonstrates that catch diversification can increase and stabilize multiple benefits, a more extensive multi-lake comparative analysis would improve understanding of what levels of catch diversification are needed to maximize and stabilize multiple benefits. Whereas, we limited the scope of our investigation to four distinct and important benefits, future studies could add other benefits, such as recreational services and trophic diversity/structure, and explicitly incorporate trade-offs between functions (Byrnes, Gamfeldt, et al., 2014). This would provide a more detailed understanding of the effects of catch diversity on the simultaneous provision of multiple benefits.

ACKNOWLEDGEMENTS

We are grateful to Kumiko Kobayashi, Masayasu Nagasaki, Toshinori Fukui and Akihiro Mori for providing fishery statistics data. We also thank Megumi Nakagawa, Junko Hirama and Megumi Yoshiba for help with fish nutrient analyses and data compilation. The manuscript was greatly improved by thoughtful comments from Taku Kadoya, Robert Arlinghaus, and three reviewers. This study was supported by JSPS KAKENHI (nos 15H02380 and 18K11734) and the Environment Research and Technology Development Fund of the Environmental Restoration and Conservation Agency (no. 4-1705).

AUTHORS' CONTRIBUTIONS

S.S.M. and T.S. led the research design. S.S.M. collected the data. S.S.M., K.U., and T.S. analysed the data. R.S. conducted chemical analyses. All authors interpreted the results. S.S.M. led the writing of the manuscript. All authors significantly contributed to the final version of the manuscript and gave final approval for publication.

DATA ACCESSIBILITY

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.mv59665 (Matsuzaki, Shinohara, Uchida, & Sasaki, 2018).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: Matsuzaki SS, Shinohara R, Uchida K, Sasaki T. Catch diversification provides multiple benefits in inland fisheries. *J Appl Ecol*. 2019;56:843–854. https://doi.org/10.1111/1365-2664.13316