**ECOSPHERE** 



# Role of wetlands in mitigating the trade-off between crop production and water quality in agricultural landscapes

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Abstract. Agriculture faces the great challenge of developing strategies to maintain production while simultaneously reducing environmental impacts. The trade-off between crop production and water quality services is one of the most serious issues facing agriculture, and interest in achieving win-win outcomes through management of ecosystem services is growing. Although wetlands can reduce nitrogen loads, it is unclear whether maintaining and restoring wetlands can ameliorate the trade-off between crop production and water quality and thereby increase the likelihood of win-win outcomes. We defined the orthogonal residuals from the regression line relating the trade-offs between two conflicting services as the degree to which the trade-off was mitigated (mitigation effectiveness score). The more positive the residual, the higher mitigation effectiveness score, and the greater the potential to mitigate the trade-off. We measured nitrate concentrations, as an indicator of water quality, five times during summer and winter across 49 sub-watersheds of the watershed of Lake Kasumigaura, which is highly nitrogen-loaded by agriculture. We quantified the mitigation effectiveness score from the trade-off relationships between cropland area and nitrate concentrations, and we also identified landscape and environmental factors that affected these scores. Some sub-watersheds in our study had high cropland cover but low nitrate concentrations. Overall, we found that mitigation effectiveness scores were positively associated with wetland cover at all sampling times. Other factors, including covers of paddy rice fields, abandoned rice fields, and impervious surfaces, and dissolved organic carbon concentrations, had no significant effects on mitigation effectiveness scores, although these factors were considered to increase nitrogen removal. Our findings suggest that maintaining and restoring wetlands might mitigate the trade-off between crop production and water quality and thereby enhance the likelihood of win-win outcomes in agricultural landscapes. Because wetland area has decreased, flooding or ponding abandoned rice fields may be an important alternative management option. The nitrate concentrations we observed met the water quality standard for drinking water, but the

fact that they sometimes exceeded the nitrogen environmental target adopted within Lake Kasumigaura in terms of eutrophication suggests that simultaneous reduction of croplands and fertilizer inputs should still be encouraged.

**Key words:** abandonment; agricultural ponds; croplands; ecosystem services; landscape composition; mitigation; nitrogen loading; restoration; trade-off; watershed; wetlands; win—win outcomes.

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#### INTRODUCTION

Agricultural systems provide humans with food, forage, and bioenergy, and they are essential to human well-being (Power 2010, Foley et al. 2011). Whereas increasing population and consumption placing unprecedented are demands on agriculture, the intensification of agriculture has resulted in the degradation of many other ecosystem services, including water supply and quality, carbon storage, and habitats for biodiversity (Raudsepp-Hearne et al. 2010, Iverson et al. 2014). The great challenge for agricultural management is therefore to develop strategies that maintain social and economic benefits while simultaneously reducing environmental impacts (Foley et al. 2005, 2011). Enhancing win-win opportunities for farmers and ecosystems is important for the development of more productive and sustainable agricultural systems and is a powerful means of creating a more positive relationship between people and nature (DeFries et al. 2004, Qiu and Turner 2013, Iverson et al. 2014, Karp et al. 2018).

The trade-off between crop production and water quality is one of the most serious and challenging issues in agricultural landscapes (Bennett et al. 2009). High rates of fertilizer use on croplands have led to substantial increases of nitrate levels in surface water and groundwater (non-point nitrogen pollution) that have eventually caused diverse problems, including toxic algal blooms, loss of oxygen, fish kills, and loss of biodiversity in limnetic and coastal ecosystems (Carpenter et al. 1998, Scavia et al. 2017). However, because nitrogen can be permanently removed from surface water via denitrification (Jordan et al. 2003, Craig et al. 2008,

Roley et al. 2012), much recent attention has focused on the question of whether watershed management may reduce downstream nitrate export without loss of agricultural function (Craig et al. 2008). Some studies have suggested the possibility of ameliorating the trade-off between crop production and water quality by enhancing buffering capacity, including maintenance and restoration of wetlands, which remove nitrate effectively (Zedler 2003, Qiu and Turner 2015, Doody et al. 2016, Hansen et al. 2018).

Previous studies have suggested that wetlands can reduce the nutrient loads at a watershed scale, although the nitrogen removal efficiency of wetlands can vary considerably as a function of environmental conditions and water residence time (Jordan et al. 2011, Powers et al. 2015). Nevertheless, it has sometimes been questioned whether wetlands can significantly reduce nitrogen loads in areas of high cropland cover (Verhoeven et al. 2006). It is therefore still unclear whether wetlands can mitigate the trade-off between crop production and water quality and whether win-win outcomes can be achieved. Qiu and Turner (2013) have explored the occurrence of win-win exceptions to the trade-off between crop production and water quality and have demonstrated that the exceptions are associated with the extent of wetland cover. However, their analysis was not quantitative and was based on cutoff values for the upper and lower 20th percentiles to define win-win exceptions. To foster win-win strategies in an agricultural landscape management, more effort is required to quantify the degree to which trade-offs can be mitigated and whether the likelihood of win-win outcomes can be increased (Qiu and Turner 2013).

Here, we develop a simple but quantitative metric (hereafter called the "mitigation effectiveness score") to quantify the degree to which the trade-off between crop production and water quality can be mitigated in agricultural landscapes. The mitigation effectiveness score is represented by orthogonal residuals from the regression line between two services across watersheds (Fig. 1). Watersheds where good water quality is maintained despite high crop production tend to have higher positive residuals, which are interpreted to reflect more effective mitigation of trade-offs (blue arrows in Fig. 1). In contrast, the negative residuals for other watersheds reflect less effective mitigation of trade-offs (red arrows in Fig. 1) and a decrease of both services (lose-lose outcomes). Although nutrient removal efficiency may be affected by various environmental and land use factors and can change seasonally, this quantitative approach enables prioritization of restoration sites and more direct identification of the factors that could be managed in a way that would increase the likelihood of win-win outcomes.

We applied this approach to examine the trade-off between crop production and water quality across 49 sub-watersheds in the watershed of Lake Kasumigaura, Japan. This watershed is highly nitrogen-loaded by agriculture (Matsumori and Itahashi 2009, Shindo et al. 2009), and Matsuzaki et al. (2018) have recently reported that the primary production of Lake Kasumigaura is controlled by nitrogen. There is thus a need to reduce nitrogen inputs to the lake while maintaining crop production in the watershed. We conducted repeated and simultaneous water quality observations in each sub-watershed to quantify the effectiveness of mitigation. Because the focus of our study was on nitrogen removal, we used nitrate (NO<sub>3</sub><sup>-</sup>) concentrations as indicators of water quality service. Furthermore, we identified the landscape and environmental factors that affected the mitigation effectiveness score. We included the areas covered by wetlands, rice fields, and abandoned rice fields among the landscape factors that might reduce nitrate concentration. Rice fields in Asian countries are known to have high denitrification rates similar to those of wetlands (Kato 2005, Takeda and Fukushima 2006). Spring water from upland fields (dominated by cropland) has

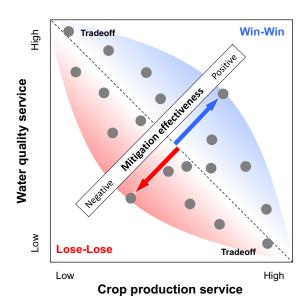


Fig. 1. Diagram illustrating hypothetical win–win outcomes to a trade-off between crop production and water quality services (each gray circle indicates an individual sub-watershed). The mitigation effectiveness score of each sub-watershed is defined as the orthogonal residuals from the best-fit line of a Deming regression that accounts for error in both ecosystem services (broken line). Positive scores indicate the degree to which the trade-off can be mitigated or transitioned to win–win outcomes (blue arrow). In contrast, negative scores indicate the degree to which the trade-off can be intensified or transitioned to lose–lose outcomes (red arrow).

been used for irrigation in the rice fields in the summer, and nitrogen included in water is removed by denitrification (Nakasone and Kuroda 1999, Kato 2005). In Japan, however, rice fields have been dramatically modernized by installation of pumps and taps to facilitate more efficient irrigation (Fujioka and Lane 1997). In modern rice fields, it is likely that nitratecontaminated spring water from upland areas flows directly downstream without passing through the rice fields. Furthermore, a significant number of rice fields have recently been abandoned (Osawa et al. 2015, 2016). Although these modernized and abandoned rice fields may not contribute to nitrate removal at a watershed scale, restoration of these rice fields to wetlands is expected to improve downstream water quality.

We also examined the effects of impervious surface area (ISA) and dissolved organic carbon (DOC) concentrations, which can potentially influence nitrogen transport or removal. Impervious surface area is well known to be an indicator of the degree of urbanization (Arnold and Gibbons 1996). Increased availability of DOC can enhance denitrification rates (Bernhardt and Likens 2002, Craig et al. 2008, Hansen et al. 2016). Finally, we proposed practical management strategies to increase the likelihood of winwin outcomes in agricultural landscapes.

#### **M**ETHODS

#### Study area

Lake Kasumigaura is located in the southern part of Ibaraki Prefecture ~60 km northeast of Tokyo, Japan. This lake is the second largest lake in Japan (surface area of 172 km²). It is shallow (mean depth of 4 m, maximum depth of 7 m) and has a watershed area of 1426 km² (29 inflows and one major outflow; Takamura 2012). The watershed of Lake Kasumigaura is dominated largely by agricultural landscapes (paddy

fields, 25.8%; plowed fields, 21.2%; Matsushita et al. 2006). Ibaraki Prefecture, which includes the Lake Kasumigaura watershed, is the top producer of some vegetables in Japan. Although these agricultural activities have supported farming livelihoods and the local economy, they have resulted in the eutrophication of Lake Kasumigaura, which is currently hypereutrophic (Takamura 2012, Matsuzaki et al. 2018).

We targeted the entire watershed of Lake Kasumigaura (Fig. 2). To classify sub-watersheds, we used the Lake Kasumigaura field-checked basin map (LKBM) developed by the Geospatial Information Authority of Japan (2003). The LKBM includes approximately 180 sub-watersheds that have been identified as geographically meaningful units based on a 1:25,000 topographical map and a digital elevation model with 50-m resolution. We did not address the sub-watersheds adjacent to the lake, because their water quality can be greatly affected by lake water, and those areas are too flat to define a sub-watersheds accurately (Geospatial Information Authority of Japan 2003). Finally, we divided the whole watershed of Lake Kasumigaura without those areas into 49

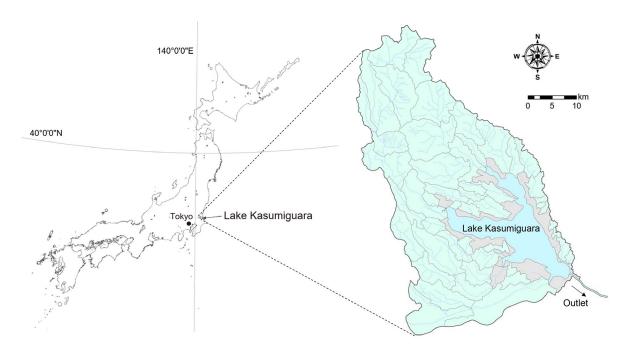


Fig. 2. Maps of the study watershed within Japan (left map) and the 49 sub-watersheds of Lake Kasumigaura (right map). We did not target sub-watersheds along the lake (shown in gray), because their water quality is largely affected by lake water.

sub-watersheds (Fig. 2). The delineation of the sub-watersheds and subsequent geographic analyses were conducted using ArcGIS 10.4.1. (ESRI, Redlands, California, USA).

### Water sample collection and laboratory analysis

We collected water samples to measure nitrate and DOC concentrations during July 2016, January 2017, August 2017, January 2018, and August 2018 (total of five times), at each outlet of the 49 sub-watersheds (Appendix S1: Table S1). A total of 245 water samples were collected during normal baseflow conditions, but only the samples collected during August 2017 were associated with precipitation (8.5 mm of cumulative precipitation) during the 2 d prior to the sampling date (Appendix S1: Fig. S1). Each set of samples was collected within a timeframe of 1–2 d.

We collected water samples with acid-washed polypropylene bottles that had been rinsed with site water prior to sample collection. During July 2016 and January 2017, water samples were transported back to the laboratory in the dark and under ice-cooled conditions. They were immediately filtered through Whatman GF/F filters, which have a pore size of 0.7 µm. In August 2017, January 2018, and August 2018, water samples were filtered in the field with Whatman GF/F filters and transported on ice. All filtered water samples were frozen until analysis. The nitrate concentrations were determined via ion chromatography (ICS-2100; DIONEX, Tokyo, Japan). The detection limit was 5.1 μg/L for nitrate-nitrogen. Dissolved organic carbon concentrations were measured as non-purgeable organic carbon with a Shimadzu TOC-5000 total organic carbon analyzer equipped with a Pt catalyst on quartz wool. Potassium hydrogen phthalate (Kanto Chemical, Tokyo, Japan) was used as a DOC standard. At least three measurements were made on each sample, and the analytical precision was typically less than  $\pm 2\%$ .

#### Land cover

We used the percentage of land under crop cultivation as an indicator of crop production, because crop yield data were not available at a sub-watershed scale. We used data on the distributions of cropland, rice fields, and abandoned rice fields from the Census for Agriculture,

Forestry, and Fisheries (CAFF) dataset (Ministry of Agriculture Forestry, and Fisheries [MAFF], 2008). This census is conducted every 5 yr by the MAFF. We used data released in 2005 because the more recent CAFF 2010 data contain large amounts of data that were masked to protect personal information. The CAFF dataset was summarized statistically using old municipality units, which are irregularly shaped. To convert the municipality units into the sub-watershed units, we assigned the municipality-based data to small 100-m mesh (i.e., 1-ha unit) using 1-ha unit land use data (cropland, rice fields, and abandonment rice fields) available from the 2009 National Land Numerical Information download service (Osawa et al. 2015, 2016). We used 1-ha mesh units as the smallest units for accuracy because the smallest municipality unit was 1.27 km<sup>2</sup> in the MAFF dataset, and larger-mesh units (e.g., 1- or 10-km mesh) did not meet our accuracy requirements. We assumed that cropland, rice fields, and abandoned rice fields were distributed equally in the 1-ha units within the same municipality. Subsequently, we calculated the total area of cropland, rice fields, and abandoned rice fields within sub-watershed.

We calculated the fraction of ISA in each subwatershed of Lake Kasumigaura using a ISA distribution map, which we obtained from a Landsat-5 TM image acquired on 16 August 2007 (Yang et al. 2010). For wetland cover, we used the nation-scale Geographic Information System (GIS) database on the spatial distribution and abundance of small lentic waterbodies (Kizuka et al. 2016). Kizuka et al. (2016) have used the shore line data of the GSI Digital Map 25,000 (2001-2007) developed by the Geographical Survey Institute of Japan, and we extracted small lentic waterbodies, including agricultural ponds, mire pools, floodplain pools, oxbow lakes, and lagoons, by excluding natural rivers and lakes, dams, industrial water bodies, water treatment plants, and golf course water hazards that are depicted on topographical maps with a scale size of 1/25,000. We designated these small lentic water bodies as wetlands and calculated the percentage of wetland cover and the density of wetlands in each sub-watershed.

We calculated Spearman's rank correlation coefficients to compare the spatial distribution of

all five land use data (Appendix S1: Table S2). Pairwise Spearman rank correlation coefficients were not high (Appendix S1: Table S3). In the following analysis, we used the coverages of cropland, paddy fields, abandoned rice fields, ISA, and wetland as the percentage of upstream watershed area contributing river flow to the sampled location (Hansen et al. 2018). Contributing sub-watershed areas ranged from 1.85 to 355.0 km² across all sites.

# Seasonal and temporal variations in nitrate concentrations

We conducted two statistical analyses to examine seasonal and temporal differences in nitrate concentrations. First, we pooled the nitrate data of the five sampling dates and analyzed the effect of season (summer vs. winter) on nitrate concentrations using a generalized linear model (GLM). We also calculated Spearman rank correlation coefficients to explore the degree of congruence of nitrate concentrations between sampling years in summer or winter.

#### Mitigation effectiveness score calculation

We multiplied nitrate concentrations by -1(i.e., lower nitrate concentrations indicate higher water quality) so that the results were consistent with Fig. 1, where crop production service and water quality service were negatively correlated. We analyzed the relationship between cropland cover and water quality using a Deming regression (Therneau 2014), which accounts for the errors in both the X and Y components. Prior to the Deming regression, we standardized both variables so that they had means of 0 and variances of 1. We calculated the orthogonal residuals on each sub-watershed from the best-fit line of a Deming regression. We defined each residual as a mitigation effectiveness score, because a higher positive score (i.e., to the upper right corner in Fig. 1) indicated a higher likelihood of mitigating the trade-off between crop production and water quality and a higher likelihood of a win-win outcome. This analysis was conducted separately during each season (i.e., sampling date).

In the watershed of Lake Kasumigaura, various crop species, mainly vegetables, are cultivated throughout the year. Chemical fertilizer and manure are applied to croplands, but the

amounts can differ among crop species. Thus, fertilizer inputs and crop productivity can vary for the same cropland cover and can influence the value of the mitigation effectiveness score. Although we could not obtain direct evidence relating fertilizer inputs and productivity at a sub-watershed scale because quantitative data were not available, we used groundwater nitrate concentration data as indirect evidence and assumed that fertilizer inputs and productivity increased proportionally with increasing cropland cover. The nitrate concentrations in groundwater are directly influenced by nitrogen fertilizer inputs and the amount of nitrogen not absorbed by crops. We collected groundwater nitrate concentration data from the Water Quality Survey of Public Water Areas (Ibaraki Prefecture 2018) database and investigated the relationship between cropland cover and groundwater nitrate concentrations at a sub-watershed scale (Appendix S2). There was a significant positive linear relationship between cropland cover and the nitrate + nitrite concentrations of groundwater (Appendix S2: Fig. S1), although the groundwater survey could be biased by well selection and the fact that samples were collected in different years. Moreover, the nitrate concentrations in groundwater were highest in sub-watershed No. 30, which had the highest mitigation effectiveness score but the highest cropland cover. These results suggest that fertilizer inputs and productivity can increase proportionally with increasing cropland cover. We believe that the differences in nitrogen fertilizer inputs and productivities per unit cropland area probably had little impact on the value of the mitigation effectiveness scores in the study watershed.

#### Factor analysis of mitigation effectiveness scores

We explored how wetland cover, rice field cover, abandoned rice fields, and DOC influenced the mitigation effectiveness scores using a GLM with a Gaussian distribution. In the models, we controlled for the effect of sub-watershed area on the mitigation effectiveness scores. We applied a multi-model inference framework to account for the uncertainty in the procedure of model selection (Burnham and Anderson 2003). We compared and ranked all possible subset models based on Akaike's information criterion corrected for small sample size (AIC<sub>c</sub>).

Model-averaged estimates of the intercept and model coefficient were obtained as weighted-average estimates in each model, and the models were weighted with their Akaike weight. We determined the relative importance of each variable (relative variable importance [RVI]) by summing the Akaike weights of each model containing that factor (Burnham and Anderson 2003). We also compared the AIC<sub>c</sub> between the models with wetland cover (%) and wetland density (no. per km²) as explanatory variables to investigate the effects of wetland composition and configuration on the mitigation effectiveness scores.

All statistical analyses were performed in R version 3.2.3. The Deming regression and model averaging were conducted using the deming and MuMIN packages, respectively.

## **R**ESULTS

Nitrate concentrations were significantly lower in summer than winter (Fig. 3, P < 0.001). Nitrate concentrations were highly correlated between the sampling years in both summer and winter (Appendix S1: Table S4). All Spearman correlation coefficients between summer and winter exceeded 0.76.

The Deming regressions showed significant negative relationships between cropland cover and water quality in July 2016 (slope  $\pm$  standard error [SE] =  $-1.00\pm0.39$ ), January 2017 (slope  $\pm$  SE. =  $-1.00\pm0.19$ ), January 2018 (slope  $\pm$  SE =  $-1.00\pm0.17$ ), and August 2018 (slope  $\pm$  SE =  $-1.00\pm0.40$ ), but the relationship in August 2017 was only marginally significant (slope  $\pm$  SE =  $-1.00\pm0.53$ ; Fig. 4). Despite these trade-offs between cropland production and water quality, there were some sub-watersheds within which both cropland cover and water quality were high on all sampling dates and some sub-watersheds within which both were low.

The model-averaging analyses revealed that wetland cover had the largest RVI at all sampling times (Table 1). The mitigation effectiveness scores were positively associated with wetland cover (Fig. 5). The models with wetland cover had substantially lower AIC<sub>c</sub> than models with wetland density on all sampling dates (Appendix S1: Table S5). During January 2018, rice fields cover had a relatively large RVI value and

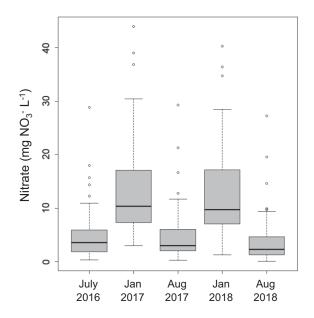


Fig. 3. Boxplot showing the seasonal changes of nitrate concentrations throughout the five sampling dates. The dark horizontal lines represent the median, the box encloses the 25th and 75th percentiles, the whiskers represent the 5th and 95th percentiles, and circles represent the outliers.

influenced mitigation effectiveness scores positively, albeit weakly. The effects of abandoned rice fields, ISA, and DOC concentrations were relatively weak on all sampling dates.

#### DISCUSSION

Accumulating evidence of the trade-offs between crop production and water quality in agricultural landscapes has led to a growing interest in alleviating this conflict and producing win-win situations (DeFries et al. 2004, Doody et al. 2016). By shedding light on the orthogonal residuals from a trade-off relationship (Fig. 1), we attempted to quantify the potential for mitigating the trade-off between crop production and water quality (i.e., mitigation effectiveness score) in 49 sub-watersheds in the watershed of Lake Kasumigaura, which has been adversely impacted by high rates of nitrogen loading. Overall, wetland cover explained most of the variations of the mitigation effectiveness scores, despite seasonal variability (Fig. 5, Table 1). Our findings suggested that maintaining and

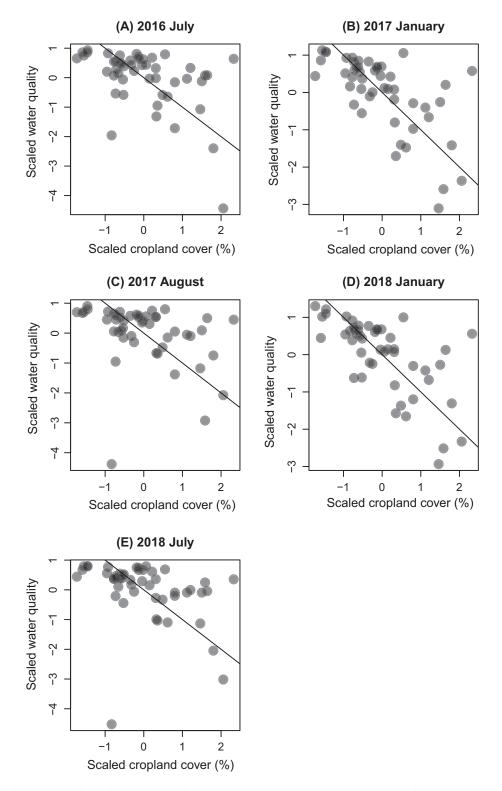


Fig. 4. The relationships between cropland cover and water quality service (the nitrate concentration [mg  $NO_3^-/L$ ] was multiplied by -1) on five sampling dates: July 2016 (A); January 2017 (B); August 2017 (C); January 2018 (D); July 2018 (E). Note that the regression line was obtained from the orthogonal linear regression between the two scaled variables.

Table 1. Model-averaged results (estimate  $\pm$  standard error [SE]) for the effects of wetland cover, rice field cover, abandoned rice field cover, impervious surface area (ISA), and dissolved organic carbon (DOC) concentrations on mitigation effectiveness scores in the watershed of Lake Kasumigaura.

Factors	Year	Month	Estimate	SE	Z	RVI
Wetland (%)	2016	July	2.25	0.55	4.01	1.00
	2017	January	2.12	0.38	5.37	1.00
		August	1.89	0.68	2.70	0.92
	2018	January	2.15	0.39	5.38	1.00
		July	2.05	0.61	3.26	0.97
Rice fields (%)	2016	July	0.01	0.02	0.71	0.29
	2017	January	0.02	0.02	1.24	0.44
		August	-0.01	0.02	0.61	0.27
	2018	January	0.03	0.01	1.78	0.66
		July	-0.01	0.02	0.50	0.26
Abandoned rice fields (%)	2016	July	0.19	0.15	1.25	0.43
	2017	January	-0.10	0.10	0.96	0.33
		August	-0.04	0.15	0.24	0.23
	2018	January	-0.06	0.10	0.57	0.26
		July	0.18	0.16	1.11	0.37
ISA (%)	2016	July	0.00	0.01	0.28	0.23
	2017	January	0.00	0.01	0.37	0.26
		August	0.00	0.02	0.06	0.22
	2018	January	0.00	0.01	0.25	0.27
		July	0.00	0.02	0.08	0.22
DOC (mg C/L)	2016	July	-0.25	0.26	0.93	0.33
	2017	January	-0.27	0.21	1.23	0.43
		August	0.47	0.27	1.72	0.62
	2018	January	-0.32	0.20	1.57	0.56
		July	0.20	0.20	1.01	0.34
Sub-	2016	July	0.00	0.00	0.89	0.32
watershed area (%)	2017	January	0.00	0.00	0.72	0.28
		August	0.00	0.00	0.68	0.27
	2018	January	0.00	0.00	0.57	0.26
		July	0.00	0.00	1.12	0.38

*Note:* Results with Z-values >2.0 are shown in bold. RVI, relative variable importance.

restoring wetlands may increase buffering capacity substantially and contribute to increasing the likelihood of win–win outcomes in agricultural landscapes.

Although the importance of wetlands in reducing nitrate concentrations and nitrogen loading has been reported (Kovacic et al. 2000, Zedler 2003, Ardon et al. 2010, Jordan et al. 2011), whether wetlands remove significant amounts of nitrogen in areas with high cropland cover has been debated. Although some studies have used multiple regression analysis to consider the simultaneous effects of both cropland cover and

wetlands on water quality (Qiu and Turner 2015, Hansen et al. 2016, 2018), this approach does not make it possible to explicitly examine whether high water quality can be maintained when crop cover is high. Qiu and Turner (2013) have addressed this issue and identified win-win exceptions to the trade-off between crop yield and water quality; the occurrence of win-win exceptions was associated with wetland cover. The results of our study were consistent with this earlier work, but our quantitative approach evaluated the potential to mitigate the trade-off within each of the sub-watersheds and explored the factors that could be managed to increase the likelihood of win-win outcomes. Our approach is a general and useful tool for helping conservation and restoration efforts to mitigate the tradeoff between crop production and water quality.

The positive relationships between wetland cover and mitigation effectiveness scores seemed to be driven by two influential sub-watersheds with very high wetland cover (Fig. 5). However, even after removing these two sub-watersheds, the simple regressions revealed that those positive relationships were still significant or marginally significant, except during January 2018 (July 2016; P = 0.079, January 2017; P = 0.086, August 2017; P = 0.092, January 2018; P = 0.109, July 2018; P = 0.025). Wetlands have a significant role in improving water quality, but wetland coverage of at least 2-7% of the total watershed is needed to effect a significant increase of water quality at the watershed scale (Verhoeven et al. 2006). The two influential sub-watersheds had wetland coverage of 2.3% and 3.3%. Our findings suggest that the trade-off between crop production and water quality can be greatly mitigated, but only beyond some threshold percentage of wetland cover.

Although our temporal resolution of water sampling was coarse, nitrate concentrations differed between summer and winter (Fig. 3). Because some processes associated with nitrogen removal, including denitrification, microbial immobilization, and plant uptake, can increase with higher temperatures (Herrman et al. 2008, Roley et al. 2012), nitrate removal by wetlands is likely to be higher in summer than in winter. However, the relationships between wetland cover and mitigation effectiveness scores were significant even in winter, though the estimated

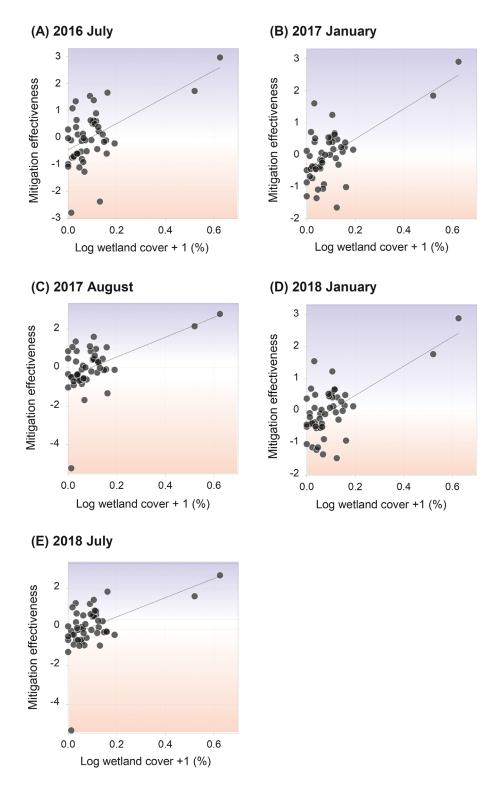


Fig. 5. The relationships between wetland cover and the mitigation effectiveness scores on each of five sampling times. Positive and negative scores are represented by increasing gradients of blue and red, respectively. Note that wetland cover is log-transformed.

coefficients were lower in winter than in summer (Table 1). Spatial congruences of nitrate concentrations between years as well as between seasons were high (Appendix S1: Table S4). Although we did not explicitly incorporate uncertainty in the estimates of mitigation effectiveness score, these results suggest that our estimates of mitigation effectiveness scores were robust, at least during baseflow conditions. Our study also underscores the importance of wetlands in mitigating trade-offs throughout the year.

Recent evidence has suggested that the spatial position and configuration of wetlands may affect the nutrient removal capacity of wetlands within a watershed (Qiu and Turner 2015, Hansen et al. 2018). Qiu and Turner (2015) have demonstrated that the contribution of wetland cover to water quality is greater than that of wetland patch density. In contrast, Cheng and Basu (2017) have shown that given the same loss in wetland area, the nutrient removal potential lost is larger when smaller wetlands are lost from the landscape. In accord with the results of Qiu and Turner (2015), the relative abundance of wetland cover was more important in the study watershed (Appendix S1: Table S5). We also identified some characteristics of wetlands in the subwatersheds with relatively high mitigation effectiveness scores. First, agricultural ponds may be the wetlands that most efficaciously increase mitigation effectiveness scores. Because agricultural ponds have been constructed to facilitate irrigation of lowland rice fields with water from uplands (where crops are cultivated), these ponds can play an important role in effectively collecting and purifying spring water containing high concentrations of nitrogen from croplands (Nakasone and Kuroda 1999, Yamamoto et al. 2005). Second, two sub-watersheds with relatively high mitigation effectiveness scores included a multi-pond system that consisted of several connected agricultural ponds. These systems have a large capacity to retain nutrients (Verhoeven et al. 2006, Schmadel et al. 2018). Third, the mean size of agricultural ponds relative to the sub-watershed area might help to explain additional variability in mitigation effectiveness scores. For example, even though the sub-watersheds No. 34 and No. 46 had similar wetland cover, the mean size of the agricultural ponds in the latter sub-watershed was higher and that watershed had positive mitigation effectiveness scores on all sampling dates. A similar difference was apparent in the comparison between sub-watershed No. 23 and No. 29. Although we could not assess the effects of spatial wetland position in stream networks (Hansen et al. 2018), our results suggest that the abundance, size, and connection of agricultural ponds within sub-watersheds can be important to the enhancement of buffering capacity.

Despite much evidence that rice fields are effective at removing nitrate (Kuroda et al. 2005, Takeda and Fukushima 2006, Matsumori and Itahashi 2009), both rice fields and abandoned rice fields did not influence mitigation effectiveness scores at a watershed scale in this study. Before modernization, rice fields in the watershed of Lake Kasumigaura were directly irrigated with spring water from uplands. Spring water was thereby effectively purified in the rice fields (Fujioka and Lane 1997). However, with the current irrigation system, water is supplied from Lake Kasumigaura through underground pipes via taps and is drained into ditches with concrete-side. Nitrate-contaminated waters from croplands are therefore likely to flow downstream without removal of nitrate in rice fields. Although there was a marginally positive relationship between rice field cover and mitigation effectiveness scores in January 2018, our results suggest that the current rice field system has a low probability of mitigating the trade-off between crop production and water quality. Abandoned rice fields that have not been modernized may have the potential to remove nitrate, but some of those fields have already been dried and converted to dry grassland and shrubs (Matsumori and Itahashi 2009, Kidera et al. 2018). Our results suggest that maintaining current conditions in abandoned rice fields has low potential to mitigate the trade-off between crop production and water quality.

Several studies have reported that nitrogen removal through denitrification can be enhanced by making carbon such as DOC available at reach and watershed scales as well as at channel and ditch scales (Bernhardt and Likens 2002, Kaushal et al. 2014, Hansen et al. 2016). Interest in increasing carbon supply and promoting organic matter storage to increase nitrogen

removal is therefore growing (Craig et al. 2008). However, DOC did not affect the mitigation effectiveness scores in this study. Hansen et al. (2016) have demonstrated that wetlands can be sources of DOC in agricultural landscapes and that the balance between DOC concentrations and nitrate supplies can influence denitrification rates. However, the ratio of DOC to nitrate concentrations was unrelated to the mitigation effectiveness scores in both summer and winter. These results suggest that increasing the water residence time by increasing wetland cover may be a more effective way to increase the potential for denitrification and nitrogen removal than enhancing DOC availability in the Lake Kasumigaura watershed. Note that we did not consider the availability of sediment organic carbon, which has been reported to increase denitrification potentials in channels and ditches (Roley et al. 2012, Webster et al. 2018). However, the evaluation at a watershed scale would be challenging, because denitrification rates are known to be spatially quite variable (Groffman et al. 2009).

# Management implications

Our findings clearly underscored the need to conserve and restore wetlands, and in particular to maintain and even increase the relative abundance of wetlands, to ameliorate the trade-off between crop production and water quality services at a watershed scale. This management strategy could simultaneously enhance other ecosystem services, such as habitat creation, water storage, climate regulation, and flood control by promoting multifunctional green infrastructure in urbanizing agricultural watersheds (Zedler 2003). Whereas crop production has been maintained at a high level in the watershed of Lake Kasumigaura, the area of wetlands, including agricultural ponds, has declined mainly because of urban and agricultural land developments, and the conditions of wetlands have deteriorated because of their abandonment (Matsumori and Itahashi 2009). Creating new ponds and wetlands may not be a feasible management option, and indeed, there are no or few wetlands in some sub-watersheds. Given the fact that abandonment of rice fields is expected to further accelerate (Osawa et al. 2016), active utilization of abandoned rice fields as wetlands

may have considerable potential as a management option. Several field experimental studies have demonstrated that flooding or ponding abandoned rice fields can remove nitrate and improve water quality (Tabuchi et al. 2001). We encourage future studies to determine whether these treatments are effective in achieving win—win outcomes at a watershed scale and to compare the effectiveness of flooded, abandoned rice fields vs. agricultural ponds.

We caution that even if the sub-watersheds have the same mitigation effectiveness score, the extent to which the trade-off is mitigated will depend on societal goals for both services and the ranges of acceptability for both. Service values beyond ecologically or socially accepted thresholds are not beneficial to management in a way that produces win-win outcomes (Qiu and Turner 2013). In this study, it would be important that the nitrate level of the sub-watersheds with high mitigation effectiveness scores does not exceed local water quality standards (Verhoeven et al. 2006). The fact that the nitrate concentrations (mean: 8.4 mg NO<sub>3</sub>/L, range: 0.07-44.0 mg NO<sub>3</sub>/L) in the 49 sub-watersheds averaged over five sampling times was lower than the water quality standards for drinking water (10 mg N/L [44.3 mg NO<sub>3</sub>/L]) suggests that the trade-off between crop production and water quality might be ameliorated in some subwatersheds. However, the observed nitrate concentration did not meet the environmental water quality target for total nitrogen (0.4 mg/L [1.77 mg NO<sub>3</sub>/L]) that has been adopted within Lake Kasumigaura to avoid eutrophication problems. To meet health and environmental standards, more effort to reduce nitrogen loads from the watershed by reducing fertilizer inputs as well as maintenance and restoration of wetlands and abandoned rice fields may be required (Doody et al. 2016).

Watershed-scale nutrient management is going to become increasingly important in the context of climate change. Although we sampled water during baseflow conditions, nitrogen loads from croplands can increase during heavy rainfall events or floods (Baron et al. 2013) and nitrogen removal can be affected by temperature (Hansen et al. 2016). Recent work has suggested that adaptation to climate change is possible if management of local stressors reduces the risk of

climate change-induced ecosystem collapse (i.e., the uncontrollable aspects of climate change) by enhancing ecosystem resilience (Scheffer et al. 2015). We underscore the importance of future studies to examine whether a trade-off between crop production and water quality can be achieved through the maintenance and restoration of wetlands and abandoned rice fields despite climate-driven extreme events.

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# LITERATURE CITED

- Ardon, M., J. L. Morse, M. W. Doyle, and E. S. Bernhardt. 2010. The water quality consequences of restoring wetland hydrology to a large agricultural watershed in the southeastern coastal plain. Ecosystems 13:1060–1078.
- Arnold Jr., C. L., and C. J. Gibbons. 1996. Impervious surface coverage: the emergence of a key environmental indicator. Journal of the American planning Association 62:243–258.
- Baron, J. S., E. K. Hall, B. T. Nolan, J. C. Finlay, E. S. Bernhardt, J. A. Harrison, F. Chan, and E. W. Boyer. 2013. The interactive effects of excess reactive nitrogen and climate change on aquatic ecosystems and water resources of the United States. Biogeochemistry 114:71–92.
- Bennett, E. M., G. D. Peterson, and L. J. Gordon. 2009. Understanding relationships among multiple ecosystem services. Ecology Letters 12:1394–1404.
- Bernhardt, E. S., and G. E. Likens. 2002. Dissolved organic carbon enrichment alters nitrogen dynamics in a forest stream. Ecology 83:1689–1700.
- Burnham, K. P., and D. R. Anderson. 2003. Model selection and multimodel inference: a practical information-theoretic approach. Springer Science & Business Media, New York, New York, USA.

- Carpenter, S. R., N. F. Caraco, D. L. Correll, R. W. Howarth, A. N. Sharpley, and V. H. Smith. 1998. Nonpoint pollution of surface waters with phosphorus and nitrogen. Ecological Applications 8:559–568.
- Cheng, F. Y., and N. B. Basu. 2017. Biogeochemical hotspots: role of small water bodies in landscape nutrient processing. Water Resources Research 53:5038–5056.
- Craig, L. S., et al. 2008. Stream restoration strategies for reducing river nitrogen loads. Frontiers in Ecology and the Environment 6:529–538.
- DeFries, R. S., J. A. Foley, and G. P. Asner. 2004. Landuse choices: balancing human needs and ecosystem function. Frontiers in Ecology and the Environment 2:249–257.
- Doody, D. G., P. J. A. Withers, R. M. Dils, R. W. McDowell, V. Smith, Y. R. McElarney, M. Dunbar, and D. Daly. 2016. Optimizing land use for the delivery of catchment ecosystem services. Frontiers in Ecology and the Environment 14:325–332.
- Foley, J. A., et al. 2005. Global consequences of land use. Science 309:570–574.
- Foley, J. A., et al. 2011. Solutions for a cultivated planet. Nature 478:337–342.
- Fujioka, M., and S. J. Lane. 1997. The impact of changing irrigation practices in rice fields on frog populations of the Kanto Plain, central Japan. Ecological Research 12:101–108.
- Geospatial Information Authority of Japan. 2003. Lake Kasumigaura Wateshed GIS Data. https://www. gsi.go.jp/ [In Japanese.]
- Groffman, P. M., K. Butterbach-Bahl, R. W. Fulweiler, A. J. Gold, J. L. Morse, E. K. Stander, C. Tague, C. Tonitto, and P. Vidon. 2009. Challenges to incorporating spatially and temporally explicit phenomena (hotspots and hot moments) in denitrification models. Biogeochemistry 93:49–77.
- Hansen, A. T., C. L. Dolph, and J. C. Finlay. 2016. Do wetlands enhance downstream denitrification in agricultural landscapes? Ecosphere 7:e01516.
- Hansen, A. T., C. L. Dolph, E. Foufoula-Georgiou, and J. C. Finlay. 2018. Contribution of wetlands to nitrate removal at the watershed scale. Nature Geoscience 11:127–132.
- Herrman, K. S., V. Bouchard, and R. H. Moore. 2008. An assessment of nitrogen removal from headwater streams in an agricultural watershed, northeast Ohio, USA. Limnology and Oceanography 53:2573–2582.
- Ibaraki Prefecture. 2018. Groundwater water quality results of the Water Quality Survey of Public Water Areas. http://www.pref.ibaraki.jp/seikatsukankyo/kantai/suishitsu/water/chikasui.html [in Japanese.]
- Iverson, A. L., L. E. Marin, K. K. Ennis, D. J. Gonthier, B. T. Connor-Barrie, J. L. Remfert, B. J. Cardinale, and I. Perfecto. 2014. Do polycultures promote

- win-wins or trade-offs in agricultural ecosystem services? A meta-analysis. Journal of Applied Ecology 51:1593–1602.
- Jordan, S. J., J. Stoffer, and J. A. Nestlerode. 2011. Wetlands as sinks for reactive nitrogen at continental and global scales: a meta-analysis. Ecosystems 14:144–155.
- Jordan, T. E., D. F. Whigham, K. H. Hofmockel, and M. A. Pittek. 2003. Nutrient and sediment removal by a restored wetland receiving agricultural runoff. Journal of Environmental Quality 32:1534–1547.
- Karp, D. S., et al. 2018. Crop pests and predators exhibit inconsistent responses to surrounding land-scape composition. Proceedings of the National Academy of Sciences USA 115:E7863–E7870.
- Kato, T. 2005. Development of a water quality tank model classified by land use for nitrogen load reduction scenarios. Paddy and Water Environment 3:21–27.
- Kaushal, S. S., K. Delaney-Newcomb, S. E. G. Findlay, T. A. Newcomer, S. W. Duan, M. J. Pennino, G. M. Sivirichi, A. M. Sides-Raley, M. R. Walbridge, and K. T. Belt. 2014. Longitudinal patterns in carbon and nitrogen fluxes and stream metabolism along an urban watershed continuum. Biogeochemistry 121:23–44.
- Kidera, N., T. Kadoya, H. Yamano, N. Takamura, D. Ogano, T. Wakabayashi, M. Takezawa, and M. Hasegawa. 2018. Hydrological effects of paddy improvement and abandonment on amphibian populations; long-term trends of the Japanese brown frog, *Rana japonica*. Biological Conservation 219:96–104.
- Kizuka, T., S. Ishida, T. Kadoya, M. Akasaka, and N. Takamura. 2016. Distribution and abundance of small lentic water bodies for wildlife habitats throughout Japan inferred from geospatial data. Japanese Journal of Conservation Ecology 21:181–192.
- Kovacic, D. A., M. B. David, L. E. Gentry, K. M. Starks, and R. A. Cooke. 2000. Effectiveness of constructed wetlands in reducing nitrogen and phosphorus export from agricultural tile drainage. Journal of Environmental Quality 29:1262–1274.
- Kuroda, H., T. Kato, and H. Nakasone. 2005. The nitrate nitrogen pollution and the nitrogen removal by paddy field in agricultural area. Journal of Water and Environment Technology 3:165–168.
- Matsumori, K., and S. Itahashi. 2009. Changes of nitrogen concentration in Branch River of Lake Kasumigaura and their causes. Technical Report of the National Institute for Rural Engineering 210:61–73.
- Matsushita, B., M. Xu, and T. Fukushima. 2006. Characterizing the changes in landscape structure in the Lake Kasumigaura Basin, Japan using a high-quality GIS dataset. Landscape and Urban Planning 78:241–250.

- Matsuzaki, S. S., K. Suzuki, T. Kadoya, M. Nakagawa, and N. Takamura. 2018. Bottom-up linkages between primary production, zooplankton, and fish in a shallow, hypereutrophic lake. Ecology 99:2025–2036.
- Ministry of Agriculture Forestry, and Fisheries [MAFF]. 2008. Census for agriculture, forestry, and fisheries. http://www.maff.go.jp/j/tokei/census/afc/ [In Japanese.]
- Nakasone, H., and H. Kuroda. 1999. Relationship between water quality in irrigation reservoirs and land use of the watershed. Lakes & Reservoirs: Research & Management 4:135–141.
- Osawa, T., T. Kadoya, and K. Kohyama. 2015. 5- and 10-km mesh datasets of agricultural land use based on governmental statistics for 1970–2005. Ecological Research 30:757–757.
- Osawa, T., K. Kohyama, and H. Mitsuhashi. 2016. Multiple factors drive regional agricultural abandonment. Science of the Total Environment 542:478–483.
- Power, A. G. 2010. Ecosystem services and agriculture: tradeoffs and synergies. Philosophical Transactions of the Royal Society B-Biological Sciences 365:2959–2971.
- Powers, S. M., J. L. Tank, and D. M. Robertson. 2015. Control of nitrogen and phosphorus transport by reservoirs in agricultural landscapes. Biogeochemistry 124:417–439.
- Qiu, J. X., and M. G. Turner. 2013. Spatial interactions among ecosystem services in an urbanizing agricultural watershed. Proceedings of the National Academy of Sciences USA 110:12149–12154.
- Qiu, J. X., and M. G. Turner. 2015. Importance of landscape heterogeneity in sustaining hydrologic ecosystem services in an agricultural watershed. Ecosphere 6:1–19.
- Raudsepp-Hearne, C., G. D. Peterson, and E. M. Bennett. 2010. Ecosystem service bundles for analyzing tradeoffs in diverse landscapes. Proceedings of the National Academy of Sciences USA 107:5242–5247.
- Roley, S. S., J. L. Tank, M. L. Stephen, L. T. Johnson, J. J. Beaulieu, and J. D. Witter. 2012. Floodplain restoration enhances denitrification and reach-scale nitrogen removal in an agricultural stream. Ecological Applications 22:281–297.
- Scavia, D., et al. 2017. Multiple models guide strategies for agricultural nutrient reductions. Frontiers in Ecology and the Environment 15:126–132.
- Scheffer, M., et al. 2015. Creating a safe operating space for iconic ecosystems. Science 347:1317–1319.
- Schmadel, N. M., J. W. Harvey, R. B. Alexander, G. E. Schwarz, R. B. Moore, K. Eng, J. D. Gomez-Velez, E. W. Boyer, and D. Scott. 2018. Thresholds of lake and reservoir connectivity in river networks

- control nitrogen removal. Nature Communications 9:2779.
- Shindo, J., K. Okamoto, H. Kawashima, and E. Konohira. 2009. Nitrogen flow associated with food production and consumption and its effect on water quality in Japan from 1961 to 2005. Soil Science and Plant Nutrition 55:532–545.
- Tabuchi, T., H. Kuroda, and M. Shimura. 2001. Experiment on the nitrate removal in the flooded paddy field. Journal of the Japanese Society Soil Physics 87:27–36.
- Takamura, N. 2012. Status of biodiversity loss in lakes and ponds in Japan. Pages 133–148. *In* The biodiversity observation network in the Asia-Pacific region. Springer, Berlin, Germany.
- Takeda, I., and A. Fukushima. 2006. Long-term changes in pollutant load outflows and purification function in a paddy field watershed using a circular irrigation system. Water Research 40:569–578.
- Therneau, T. 2014. Deming: Deming, Thiel-Sen and Passing-Bablock Regression. R Package Version:1.0-1. https://cran.r-project.org/web/packages/deming/index.html

- Verhoeven, J. T. A., B. Arheimer, C. Q. Yin, and M. M. Hefting. 2006. Regional and global concerns over wetlands and water quality. Trends in Ecology & Evolution 21:96–103.
- Webster, A. J., P. M. Groffman, and M. L. Cadenasso. 2018. Controls on denitrification potential in nitrate-rich waterways and riparian zones of an irrigated agricultural setting. Ecological Applications 28:1055–1067.
- Yamamoto, T. N., H. Nakasone, Y. Matsusawa, H. Kuroda, and T. Kato. 2005. Removal effect of runoff loads in an irrigation reservoir. Journal of Japan Society on Water Environment 28:29–36.
- Yang, F., B. Matsushita, and T. Fukushima. 2010. A pre-screened and normalized multiple endmember spectral mixture analysis for mapping impervious surface area in Lake Kasumigaura Basin, Japan. ISPRS Journal of Photogrammetry and Remote Sensing 65:479–490.
- Zedler, J. B. 2003. Wetlands at your service: reducing impacts of agriculture at the watershed scale. Frontiers in Ecology and the Environment 1: 65–72.

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