Journal of
Water & Climate Change

Journal of Water and Climate Change Vol 14 No 2, 387 doi: 10.2166/wcc.2023.274

Nitrous oxide emission from a flooded tropical wetland across a vegetation and land use gradient

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ABSTRACT

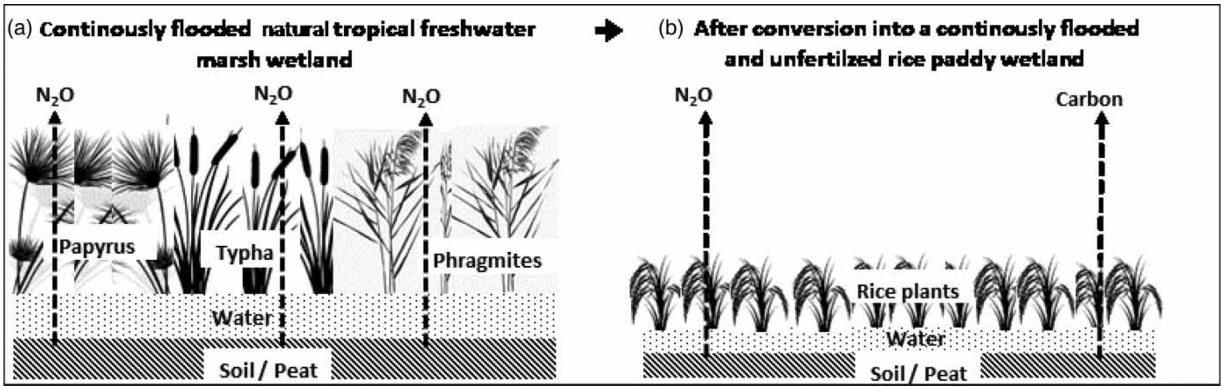
This study investigated, using the closed chamber method, the impact of (1) vegetation community type (*Typha latifolia, Cyperus papyrus* and *Phragmites mauritianus*) in a natural tropical freshwater marsh wetland (marsh) and (2) conversion of a natural tropical freshwater marsh into a rice paddy wetland (rice paddy), on nitrous oxide (N_2O) emission. Both the marsh and the rice paddy were continuously flooded, while the rice paddy was unfertilized. Average N_2O emission from the marsh did not vary significantly ($p > 0.05$) among the vegetation communities, ranging from 0.5 to 0.6 $\mu g\ m^{-2}\ h^{-1}$. Similarly, these N_2O emission rates were not significantly different ($p > 0.05$) from those recorded in the rice paddy (0.7 $\pm$ 2.8 [SE] $\mu g\ m^{-2}\ h^{-1}$). There was no significant correlation ($p > 0.05$) between environmental parameters and N_2O emission. We concluded that vegetation community type does not affect N_2O emission from natural tropical freshwater marshes under continuous flooding. Further, converting natural tropical freshwater marshes into continuously flooded and unfertilized rice paddies does not affect N_2O emission but instead enhances carbon emission, as was depicted by the significantly lower ($p > 0.05$) soil organic carbon content in the rice paddy. In view of climate change mitigation, therefore, wetland management should give priority to the conservation/protection of natural wetlands.

Key words: climate change, freshwater marshes, greenhouse gases, N_2O, rice paddy, Uganda

HIGHLIGHTS

- Vegetation community type does not affect N_2O emission from continuously flooded natural tropical wetlands.
- Continuously flooded and unfertilized rice paddies are not N_2O emission hotspots but are significant carbon sources.
- N_2O emission from continuously flooded tropical wetlands is not affected by seasonal changes.
- Conserving natural wetlands, rather than converting them into rice paddies, enhances climate change mitigation.

GRAPHICAL ABSTRACT



1. INTRODUCTION

Climate change is currently one of the most critical global environmental concerns, which science-based evidence attributes to the increasing emission of greenhouse gases (GHGs) into the atmosphere. Addressing climate change and its impacts is currently no longer an option but a must for the survival of humanity and ecosystems. According to the IPCC (2013), the main GHGs implicated in climate change are carbon dioxide (CO_2), methane (CH_4) and nitrous oxide (N_2O), which account for close to 90% (WMO 2019) of the radiative forcing by long-lived GHGs. However, even though N_2O has the least atmospheric concentration among the three GHGs, its global warming potential (GWP) is 265 times that of CO_2 (Liu *et al.* 2020), far higher than that of CH_4, whose GWP is only 28 times that of CO_2 on a 100-year timescale (IPCC 2014). This makes N_2O an important greenhouse gas in the global climate change equation and has since captured the attention of climate change scientists and policy makers worldwide.

Wetlands are recognized by the Millennium Ecosystem Assessment (2005) as vital ecosystems due to their various ecosystem services. They are among the most important natural ecosystems in climate change mitigation through carbon capture and storage. Natural wetlands, in an undisturbed state, are vital carbon sinks, where their photosynthetic CO_2 uptake through primary production exceeds CO_2 losses due to ecosystem respiration (Mitsch *et al.* 2013; Were *et al.* 2019). However, despite being carbon sinks, a number of studies indicate that wetlands are also important sources of N_2O emitted into the atmosphere (Wu *et al.* 2009; Liengaard *et al.* 2013; Audet *et al.* 2014; Yang *et al.* 2019).

Unlike CO_2, N_2O is primarily biogenic (IPCC 2007), with denitrifiers and nitrifiers being key players in the regulation of its global sinks and sources. Denitrification and nitrification processes in wetland soils are affected by changes in environmental conditions, which can occur either naturally due to temporal (e.g., diurnal and seasonal) variations, or due to wetland management practices (Ajwang'Ondiek *et al.* 2021). Intermittent wetting and drying cycles in wetlands in relation to natural changes in hydrological regimes or due to soil and water management practices (such as in rice paddies) alter soil parameters which regulate denitrification and nitrification processes (Liengaard *et al.* 2013). These parameters are even expected to vary more under future climate scenarios, due to alterations of temperature, rainfall and nutrient regimes (Tian *et al.* 2015). Besides, environmental conditions in wetlands also vary spatially since soil conditions, vegetation characteristics and soil and water management practices change even at small spatial scales (Butterbach-Bahl *et al.* 2016). Consequently, N_2O emission can also vary across small spatial scales, necessitating measurements in all wetlands situated across different climatic and geographic locations, and under different management practices, e.g., natural, agricultural and wastewater treatment wetlands.

Although there has been an increase in knowledge of the sinks and sources of N_2O, the global N_2O budget remains less understood (IPCC 2007; Liengaard *et al.* 2013). Tropical ecosystems are vital in understanding global N_2O balance because several studies have indicated that the high productivity of these ecosystems is likely to translate into rates of accumulation, recycling and loss of nitrogen far higher than those of temperate ecosystems (Hedin *et al.* 2009; Liengaard *et al.* 2013; Pärn *et al.* 2018; Liu *et al.* 2020). Further, with a coverage of about 30% of the global wetland area (Marín-Muñiz *et al.* 2015), tropical wetlands have a substantial influence on the global atmospheric N_2O budget. Despite these, studies on N_2O emission from wetlands have mainly focused on temperate wetlands (Liengaard *et al.* 2013; Ajwang'Ondiek *et al.* 2021). This has limited a proper understanding of the magnitudes and controlling factors of N_2O emission from tropical wetlands, hence hindering their inclusion in global climate models. Indeed, recent studies by Butterbach-Bahl *et al.* (2016) and Boateng *et al.* (2017) have noted with concern the reliance of field measurements and estimation of GHG fluxes from tropical wetlands using emission factors calibrated from temperate wetlands, despite significant differences between the two climate types. Further, with specific reference to Uganda, whereas a few studies have investigated controls and magnitudes of GHG fluxes from the country's wetlands (e.g., Were *et al.* 2021a, 2021b), they have mainly focused on CO_2 and CH_4, at the expense of N_2O.

The aims of this study were to investigate the impact of: (1) vegetation community type in a natural tropical freshwater marsh wetland on N_2O emission, and (2) converting a natural tropical freshwater marsh wetland into a rice paddy wetland, on N_2O emission. We hypothesized that N_2O emission in a natural tropical freshwater marsh wetland varies based on the type of vegetation community, and that conversion of the wetland into a rice paddy wetland enhances N_2O emission.

2. MATERIALS AND METHODS

2.1. Study area

This study was conducted on Naigombwa wetland, a freshwater wetland which forms part of the complex and interconnected wetland systems of the Lake Kyoga basin in Eastern Uganda (Figure 1). This extensive wetland has natural and altered

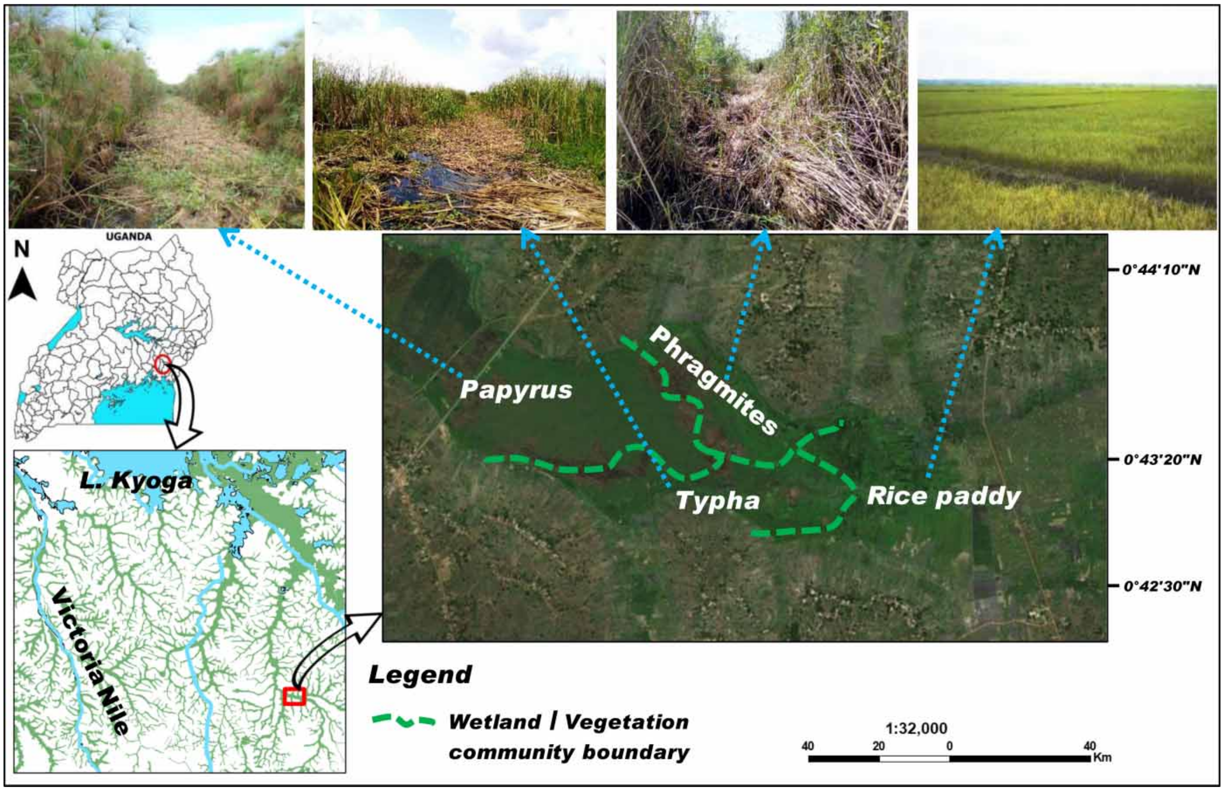


Figure 1 | Location of the study wetland. The study area was zoomed and geo-referenced from Google Earth.

sections, and thus, based on land use, the wetland can be subdivided into two different wetland subcategories: natural wetland and rice paddy wetland.

The natural wetland can be categorized as a marsh and exhibits unaltered hydrology and vegetation characteristics dominated by perennial sedge and grass communities. In view of the dominant vegetation community types, the wetland can be further subdivided into three different sections: *Typha latifolia* (Typha), *Phragmites mauritianus* (Phragmites) and *Cyperus papyrus* (Papyrus). The Papyrus vegetation community occurs downstream of the Typha and Phragmites vegetation communities, and its morphology displays two growth forms; emergent and floating (Were *et al.* 2020a), unlike the Typha and Phragmites vegetation communities that grow only emergent.

The rice paddy wetland was previously part of the natural wetland, with similar conditions as described above for the natural wetland, before it was altered to enable the cultivation of rice. Rice is cultivated on a seasonal basis because it relies on natural flooding, which itself is dependent on seasonal rainfall. The cultivation is done on smallholder scales, where rice is planted through the broadcasting of rice seeds by hand into the fields or by transplanting rice seedlings from nursery beds into the main fields. There is no standard planting density, and therefore, plant density varies from field to field. Rice cultivation is done under no fertilization conditions but rather depends on the natural fertility of the soil.

Surface and ground water level dynamics in these wetlands and their riparian areas have been described by Kayendeke *et al.* (2018). Seasonal flooding and drying cycles have been reported at wetland edges of the natural wetland in relation to the wet and dry seasons, respectively. However, wetland areas away from the edges are usually flooded throughout the year, but the flooding level varies seasonally. In the rice paddy wetland, intermittent flooding and drying cycles also occur with respect to the wet and dry seasons. However, compared to the natural wetland, both the flooding level and duration in the rice paddy wetland are manually regulated depending on the rice growth/cultivation stage. During the entire sampling course for this study, both the natural and rice paddy wetlands were continuously flooded (with water above the soil surface).

The study area temperature can generally be described as warm. Air temperature data for the study area during the sampling period were obtained from the Uganda National Meteorological Authority (UNMA) and showed wet season air temperature of 21.3 ± 0.2 °C (mean ± standard error; SE), in comparison to 23.4 ± 0.1 °C during the dry season.

2.2. Gas sampling and analysis

Soil-atmosphere N_2O exchange was measured in each of the wetlands/vegetation community types described in section 2.1. Gas samples were collected using steady-state flux chambers (Minamikawa *et al.* 2015). The chamber technique is preferred and has been widely applied in the measurement of gas fluxes from wetlands because it is less costly and allows for measurements at fine scales (Butterbach-Bahl *et al.* 2016).

Chambers included the following components: a thermometer to monitor internal air temperature, a vent tube to stabilize inside air pressure, and a gas sampling port, which allowed for manual extraction of the gas samples from the chambers using a syringe and a needle (Minamikawa *et al.* 2015). Because of the strong solar radiation that increases the heating up of the chambers during daytime sampling (the study area is located along the equator), white-coloured chambers were used whose external surfaces were further covered with a reflective aluminum tape. Chamber bases were sunk up to 10 cm into the soil (Butterbach-Bahl *et al.* 2016), onto which chamber lids were firmly fixed to provide a gas-tight enclosure. The headspace of the chambers had the following average dimensions: height = 25 cm and basal area = 490.63 cm^2, amounting to a volume of 10 L.

In each sampling area, three chambers were deployed and sampled consecutively to increase the spatial representativeness (Minamikawa *et al.* 2015; Butterbach-Bahl *et al.* 2016). To minimize artificial gas ebullition associated with physical soil disturbance during gas sampling, wooden walking platforms were installed. The wooden walking platforms also eased movement during sampling in these usually waterlogged environments. However, for the floating growth form of the Papyrus vegetation community, it was realized that the walking platforms could not control shaking and artificial gas ebullition during sampling due to the suspended nature of the root mat over the water column. This occurrence was noticed from preliminary measurements that showed abnormally high gas concentrations. Consequently, the final sampling plan considered only the emergent growth form of the Papyrus vegetation community.

Sampling was done over a period of 12 months, as follows: Dry season; February, March and April 2019, and February, March and April 2021; and Wet season; August, September and October 2019, and August, September and October 2021. During each sampling event, the duration of gas sampling for each chamber was limited to 30 min, at intervals of 10 min, i.e., 0, 10, 20 and 30 min (Butterbach-Bahl *et al.* 2016). Further, prior to the start of each sampling event, ambient air samples outside the chamber were collected for quality control (Butterbach-Bahl *et al.* 2016). Gas samples in the chambers were collected using 60 mL luer lockable syringes attached to needles. The collected gas samples were stored in 10 mL glass vials under high pressure, after being evacuated using 40 mL of the syringe gas volume. Vial tops were covered with parafilms to prevent contamination of samples prior to analysis. The frequency of sampling in each wetland/vegetation community type was twice a month, on a fortnightly basis. Gas samples were analyzed by gas chromatography (SRI 8610C gas chromatograph, USA), at the International Livestock Research Institute (ILRI) in Nairobi, Kenya.

Nitrous oxide (N_2O) flux, f ($\mu\text{g m}^{-2}\text{ h}^{-1}$) was calculated as in Equation (1) (Butterbach-Bahl *et al.* 2011). N_2O flux was computed as linear only if $R^2 \geq 0.70$ (Rochette *et al.* 2008).

$$f = S \times \frac{V_c}{A_c} \times \frac{M}{V_m} \times \frac{273.15}{273.15 + T} \times P \times 60 \tag{1}$$

where S is the slope (ppbv min^{-1}), V_c is the volume of the chamber (cm^3), A is the basal area of the chamber (cm^2), M is the molar weight of N_2O (which is 28 g mol^{-1}), V_m is the molar volume of N_2O ($\text{m}^3\text{ mol}^{-1}$), T is the average chamber temperature during sampling (°C), P is the pressure at the time of sampling (atm) and 60 is used to convert minutes to an hour.

2.3. Measurement of environmental parameters

Environmental (soil and hydrological) parameters were measured during the sampling period. In each wetland/vegetation community type, soil samples at the top (0–10 cm) soil layer (Inglett *et al.* 2012) were collected, from which soil physicochemical characteristics; salinity, pH, total nitrogen (TN) and organic carbon (OC) were determined. Soil temperature was also measured *in situ,* using a digital soil thermometer. Soil moisture content was not investigated since the wetlands were under continuous flooding throughout the sampling period.

Composite soil samples that were obtained after mixing three samples in each sampling plot were placed in labeled ziploc bags and transported for analysis at the Soil Science Laboratory, Makerere University, Kampala, Uganda. Soil samples were air dried at room temperature in the laboratory for 21 days, ground and sieved through a 2 mm nylon sieve.

Soil OC was obtained from soil organic matter, following the loss on ignition procedure and using van Bemmelen's index of 0.58 as in Were *et al.* (2020a). Soil TN content was determined following the Kjeldahl digestion procedure. Soil pH and salinity were obtained using a portable multi-parameter meter (CyberScan PC 300), after mixing soil and deionized water using a soil : water ratio of 1 : 5 (Were *et al.* 2021a, 2021b).

The wetland hydrological parameter considered in this study was water level, and specifically surface water level since the water was above the soil surface for the entire sampling period. Surface water level was measured at the gas sampling location during each sampling event, using a cm-marked wooden stick.

2.4. Data analysis

Data were sorted and statistically analyzed using the Microsoft Excel (2016) and R programming software (version 4.0.5). The data were first tested for normal distribution and homogeneity of variance. Whereas data for soil and surface water level showed normal distribution, N_2O flux data did not satisfy conditions for normal distribution. Consequently, parametric one-way ANOVA alongside the Tukey HSD *post hoc* tests were used to examine the significance of mean values of soil and water level characteristics between the wetlands/vegetation community types and seasons, at $p < 0.05$ significance. On the other hand, the Kruskal–Wallis *H* test was used to examine the significance of mean N_2O fluxes between the wetlands/vegetation community types and seasons, at $p < 0.05$ significance. The effect of environmental conditions on N_2O fluxes was investigated by determining the Spearman's rank-order correlations between soil and surface water level characteristics and N_2O flux, at $p < 0.05$ significance. Unless stated otherwise, all values presented from the analysis are mean ± SE.

3. RESULTS

3.1. Soil physico-chemical and water level characteristics

Soil physico-chemical characteristics did not vary significantly either between the wetlands/among vegetation community types or between seasons, except OC and C: N ratio (Table 1). Whereas mean OC contents of the three vegetation communities did not differ significantly ($p > 0.05$) during both the dry and wet seasons, they were over two-fold higher than was recorded in the rice paddy wetland. Mean C:N ratios of the Typha vegetation community (dry season = 33.2:1 and wet season = 33.3:1) were significantly higher ($p < 0.05$) than those measured in the other two vegetation communities of the natural wetland and rice paddy wetland. Mean pH values during the wet and dry seasons in both wetlands were slightly acidic, ranging from 5.98 to 6.54 and 6.00 to 6.87 during the wet and dry seasons, respectively. Temperature had mean values in both wetlands ranging from 26.3 to 26.9 and 26.6 to 27.0 during the wet and dry seasons, respectively.

Water was above the soil surface even during the dry season and rapidly increased significantly during the wet season (Figure 2). Comparing the two wetlands, surface water levels in the three vegetation communities of the natural wetland during the dry (Typha = 7.1 ± 5.0 cm Phragmites 1.9 ± 1.3 = cm and Papyrus = 7.5 ± 5.5 cm) and wet (Typha = 29.1 ± 6.0 cm, Phragmites = 21.0 ± 5.2 cm and Papyrus = 31.5 ± 6.1 cm) seasons were significantly higher ($p < 0.05$) than those recorded in the rice paddy wetland (dry season = 0.4 ± 0.1 cm and wet season = 10.9 ± 1.7 cm).

3.2. Nitrous oxide emission

Generally, fluxes of N_2O from both the natural and rice paddy wetlands were very low (close to zero) during the two sampling seasons. Considering the impact of vegetation community type (in the natural wetland) on N_2O fluxes, no significant variation ($p > 0.05$) in N_2O flux was noted among the three vegetation communities during both seasons (Table 2). Mean N_2O fluxes from the three vegetation communities of the natural wetland ranged from 0.5 to 0.6 $\mu g\ m^{-2}\ h^{-1}$ during the dry season, and from 0.4 to 0.5 $\mu g\ m^{-2}\ h^{-1}$ during the wet season.

In view of the impact of land use change (from natural to rice paddy wetland) on N_2O fluxes, the difference between N_2O fluxes from the natural and rice paddy wetlands was insignificant ($p > 0.05$), with the latter recording an average flux value of 0.7 $\mu g\ m^{-2}\ h^{-1}$. Further, in both wetlands, seasonal changes (dry vs wet) did not affect N_2O fluxes significantly ($p > 0.05$). Cumulatively, mean annual N_2O fluxes from the natural and rice paddy wetlands ranged from 4.4 to 6.1 $mg\ m^{-2}\ yr^{-1}$, with annual carbon dioxide equivalents (CO_2e) ranging from 1.2 to 1.6 $g\ m^{-2}\ yr^{-1}$ (Table 2).

Whereas mean N_2O fluxes did not vary significantly between wetlands, and between seasons, individual fluxes showed great variations even within the same wetland/vegetation community type and season. However, the variations were much more pronounced in the rice paddy wetland, as can be shown by the extent of whiskers on the box plots in Figures 3 and 4. For instance, during the dry season, individual N_2O fluxes varied from −5.2 to 5.5, −4.9 to 6.3 and

Table 1 | Soil physico-chemical characteristics in the natural and rice paddy wetlands ($n = 36$)

Soil/hydrological parameter	**Wetland**	**Season**	
pH	Natural	Dry	Wet
	Typha	6.23 ± 0.01	6.24 ± 0.02
	Phragmites	6.06 ± 0.01	6.20 ± 0.01
	Papyrus	6.00 ± 0.01	5.98 ± 0.01
	Rice paddy	6.87 ± 0.03	6.54 ± 0.02
Temperature (°C)	Natural		
	Typha	26.9 ± 0.1	26.8 ± 0.1
	Phragmites	26.6 ± 0.1	26.5 ± 0.1
	Papyrus	26.6 ± 0.0	26.3 ± 0.0
	Rice paddy	27.0 ± 0.1	26.9 ± 0.1
TN (%)	Natural		
	Typha	0.4 ± 0.0	0.4 ± 0.0
	Phragmites	0.5 ± 0.0	0.5 ± 0.0
	Papyrus	0.7 ± 0.0	0.8 ± 0.0
	Rice paddy	0.4 ± 0.0	0.4 ± 0.0
OC (%)	Natural		
	Typha	12.9 ± 0.1	13.3 ± 0.2
	Phragmites	12.1.0 ± 0.1	12.7 ± 0.1
	Papyrus	15.0 ± 0.1	16.3 ± 0.0
	Rice paddy	6.00 ± 0.1*	6.2 ± 0.0*
C:N	Natural		
	Typha	32.3 ± 0.0*	33.3:1 ± 0.0*
	Phragmites	20.0 ± 0.0	23.4 ± 0.0
	Papyrus	21.4 ± 0.0	20.4 ± 0.0
	Rice paddy	20.0 ± 0.0	21.7 ± 0.0
Salinity (mS m^{-1})	Natural		
	Typha	129.2 ± 2.4	125.9 ± 1.7
	Phragmites	118.6 ± 2.5	91.3 ± 1.4
	Papyrus	132.8 ± 4.9	128.7 ± 3.8
	Rice paddy	102.9 ± 5.8	91.1 ± 2.2

*Significant ($p < 0.05$) within the same season, OC, Organic carbon; TN, Total nitrogen.

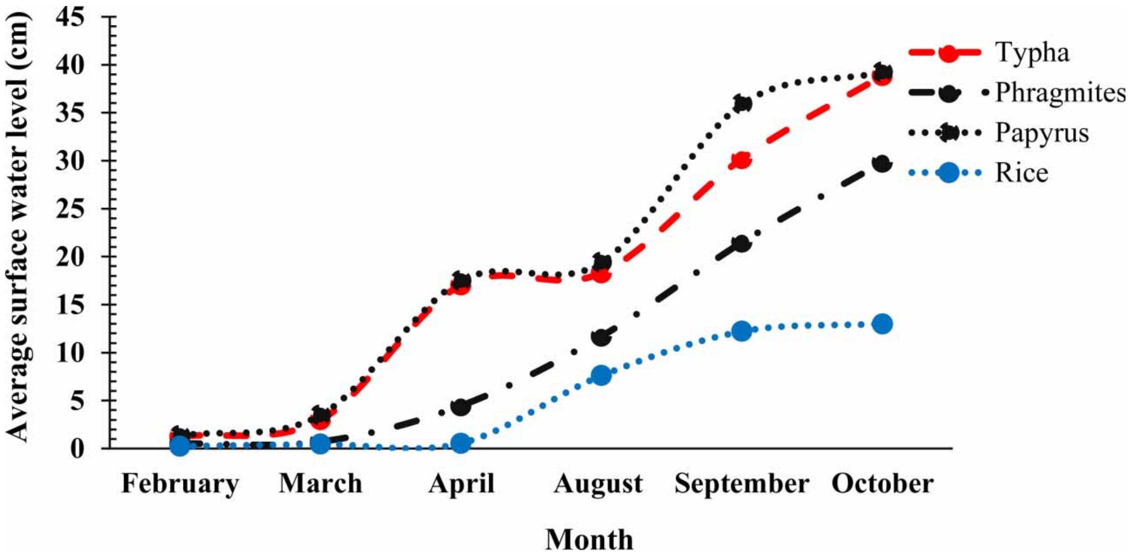


Figure 2 | Variation of surface water level in the natural (Typha, Phragmites and Papyrus) and rice paddy (Rice) wetlands during the dry (February, March and April) and wet (August, September and October) seasons.

Table 2 | Average nitrous oxide (N_2O) fluxes from the natural and rice paddy wetlands and their carbon dioxide equivalents (CO_2e; $n = 72$)

Wetland	**N_2O ($\mu g\ m^{-2}\ h^{-1}$)**					
Natural	**Wet season**	**Dry season**	**Average**	**N_2O ($\mu g\ m^{-2}\ d^{-1}$)**	**N_2O ($mg\ m^{-2}\ yr^{-1}$)**	**CO_2e* ($g\ m^{-2}\ yr^{-1}$)**
Typha	0.5 ± 1.4	0.6 ± 1.6	0.6 ± 1.5	14.4 ± 36.0	5.3 ± 13.1	1.4 ± 3.5
Phragmites	0.4 ± 1.5	0.5 ± 1.7	0.5 ± 1.6	12.0 ± 38.4	4.4 ± 14.0	1.2 ± 3.7
Papyrus	0.5 ± 1.5	0.5 ± 1.3	0.5 ± 1.4	12.0 ± 33.6	4.4 ± 12.3	1.2 ± 3.2
Average	0.5 ± 1.5	0.5 ± 1.5	0.5 ± 1.5	12.0 ± 36.0	4.4 ± 13.1	1.2 ± 3.5
Rice paddy	0.6 ± 2.7	0.7 ± 2.8	0.7 ± 2.8	16.8 ± 48.8	6.1 ± 17.8	1.6 ± 4.7

*CO_2e calculated considering a N_2O GWP of 265 times that of CO_2 (IPCC 2014), and considering 365 days in a year.

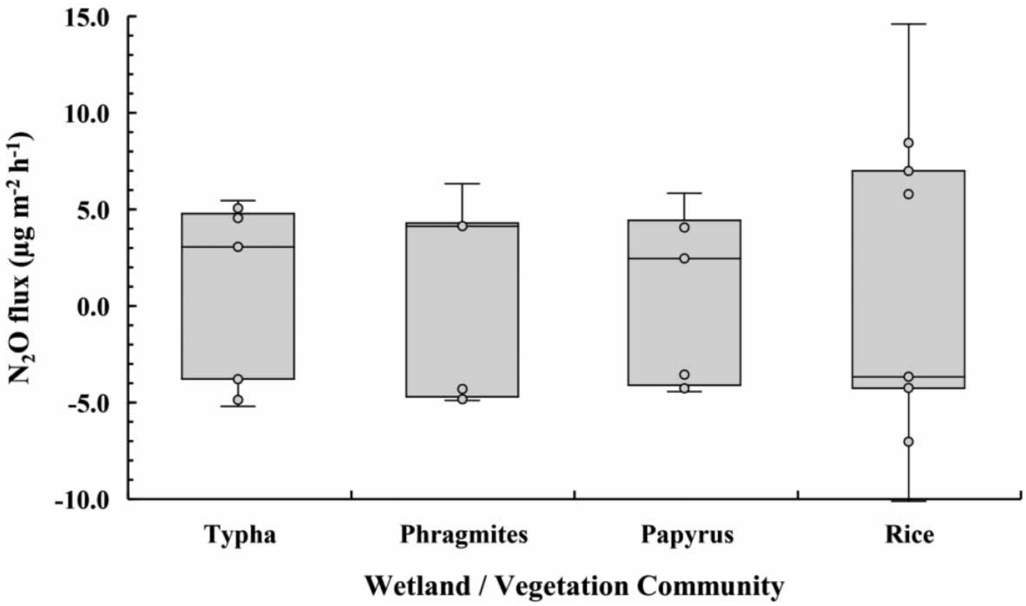


Figure 3 | Comparison of N_2O fluxes from the natural (Papyrus, Typha and Phragmites) and rice paddy (Rice) wetlands during the dry season. Box lines show upper and lower quartiles, while horizontal lines within boxes show median values ($n = 72$). Whiskers extend to the minimum and maximum values. Mean values are not significant across wetlands/vegetation community types ($p > 0.05$).

−4.4 to 5.8 $\mu g\ m^{-2}\ h^{-1}$ with respect to the Typha, Phragmites and Papyrus vegetation communities of the natural wetland, compared to −10.1 to 14 $\mu g\ m^{-2}\ h^{-1}$ from the rice paddy wetland. During the wet season, individual N_2O fluxes ranged from −4.4 to 5.2, −4.5 to 4.7, −4.7 to 4.9 $\mu g\ m^{-2}\ h^{-1}$ from Typha, Phragmites and Papyrus respectively, compared to −7.5 to 11.8 $\mu g\ m^{-2}\ h^{-1}$ from the rice paddy wetland. This can explain the big divergence of the mean and median N_2O flux values in both wetlands during the two sampling seasons (Figures 3 and 4).

3.3. Effect of soil physico-chemical and water level characteristics on nitrous oxide emission

The relationship between soil physico-chemical and surface water level characteristics and N_2O fluxes from the wetlands is depicted in Table 3. As shown by the Spearman's rank-order correlation coefficients, soil physico-chemical parameters temperature, pH and TN positively correlated with N_2O flux, unlike OC, salinity and C: N that showed negative correlations. Similarly, the correlation between surface water level and N_2O flux was negative. In terms of the magnitude of the correlations, neither soil physico-chemical characteristics nor surface water level significantly correlated ($p > 0.05$) with N_2O.

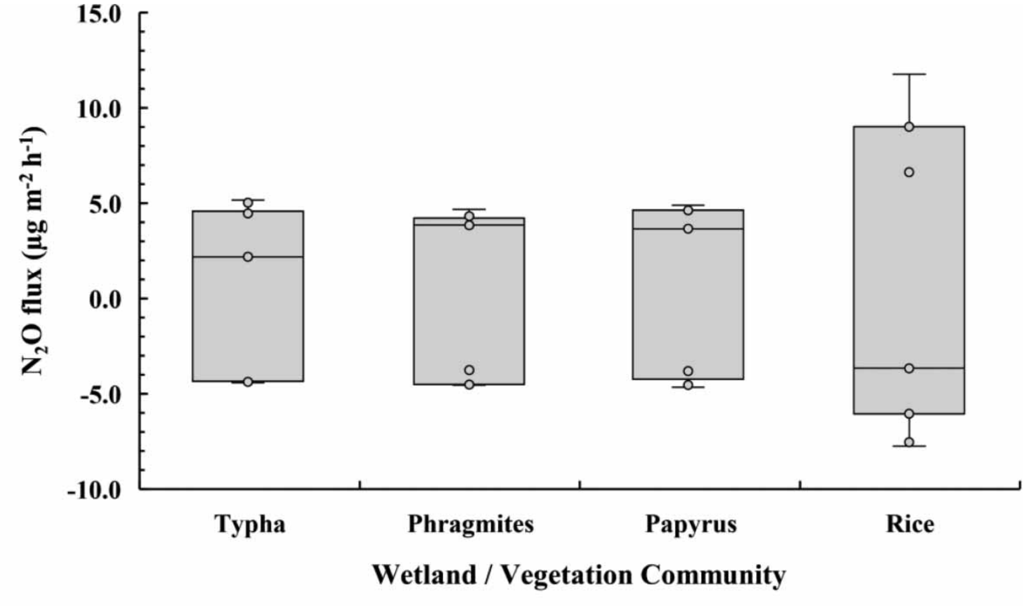


Figure 4 | Comparison of N_2O fluxes from the natural (Papyrus, Typha and Phragmites) and rice paddy (Rice) wetlands during the wet season. Box lines show upper and lower quartiles, while horizontal lines within boxes show median values ($n = 72$). Whiskers extend to the minimum and maximum values. Mean values are not significant across wetlands/vegetation community types ($p > 0.05$).

Table 3 | Correlation between N_2O flux and soil temperature, pH, nitrogen, organic carbon, salinity, carbon to nitrogen ratio and surface water level ($n = 36$)

	N_2O	Temp	pH	N	OC	Salinity	C:N	S. water level
N_2O	1.00							
Temp	0.26	1.00						
pH	0.03	0.19	1.00					
TN	0.28	−0.21	−0.29	1.00				
OC	−0.05	−0.34*	−0.10	−0.46*	1.00			
Sal	−0.06	0.07	−0.03	0.24	−0.16	1.00		
C:N	−0.21	0.17	−0.23	−0.21	0.25	0.09	1.00	
S. water level	−0.26	−0.55	−0.40	0.42	0.37	0.35	0.32	1.00

*Significant at $p < 0.05$; Temp, temperature; N, nitrogen; OC, organic carbon; S. water level, surface water level.

4. DISCUSSION

4.1. Nitrous oxide emission from the natural and rice paddy wetlands

Emission of N_2O did not vary significantly among the vegetation community types in the natural section of the wetland. In natural wetlands, OC and nitrogen are some of the most important factors controlling the production of N_2O, which are influenced by the type of plant communities (Marín-Muñiz *et al.* 2015). Detailed discussions on these factors have been made by Maucieri *et al.* (2017) and Smith *et al.* (2018), while Huang *et al.* (2013) discussed in detail the mechanisms of N_2O emission from wetlands. OC in soils is important for N_2O emission since it provides electrons for heterotrophic denitrification (Marín-Muñiz *et al.* 2015), while organic nitrogen is a substrate for nitrification and denitrification processes. Most of the greenhouse gas production in wetland soils occurs in the top 5 cm (Were *et al.* 2021a), and it is in this layer where accumulation of aboveground residues from plants occurs. Therefore, the observation of no significant difference in N_2O emission among the three different vegetation communities in this study could be explained by the fact that OC and nitrogen contents did not differ significantly among the vegetation communities (Table 1). These findings are consistent with those of other studies. Marín-Muñiz *et al.* (2015) reported no significant difference in N_2O emission from swamp and marsh wetlands with varying vegetation community types in Mexico. In Canada, Baskerville *et al.* (2021) reported similar N_2O emission rates across different vegetation communities in riparian zones along the Washington Creek.

However, several other studies have reported different results. Liu *et al.* (2014) showed that emissions of N_2O from two vegetated coastal wetland zones, one dominated by *Spatina* spp. and the other dominated by *Phragmites* spp., differed significantly, with the *Phragmites* spp. zone showing higher N_2O flux. This observation was explained by differences in biomass productivity, which affected the resultant organic matter and nitrogen input into the soil. Similarly, Piñeiro-Guerra *et al.* (2019), who studied several wetland sites across Argentina, showed that N_2O emission increased with biomass productivity. Wang *et al.* (2008) while investigating the impact of plant species on N_2O emission noted significantly higher N_2O fluxes from a *Zizania latifolia*-dominated wetland compared to those dominated by *Phragmites australis* and *Typha latifolia*. They attributed the results to differences in the root structure of the plant species, where the root structure of *Zizania latifolia* was favored by ammonia-oxidizing bacteria for N_2O formation.

This study found no significant difference in N_2O emission between the natural and rice paddy wetlands. However, it had been expected that N_2O emission would be higher in the rice paddy wetland compared to the natural wetland. Conversion of a wetland from its natural state into a rice paddy wetland enhances N_2O emission mainly due to: (i) water table drawdown through drainage favors oxygen availability, thus increasing the mineralization of soil organic nitrogen (Liengaard *et al.* 2013; Ajwang'Ondiek *et al.* 2021), and (ii) fertilizer application in rice paddies increases nitrogen availability in soil. Liengaard *et al.* (2013) reported that partial soil wetting in a tropical South American freshwater wetland resulted in high N_2O emission compared to long-term soil waterlogging following heavy rain. Kritee *et al.* (2018) established that intermittently flooded Indian rice paddies emitted 30–40% more N_2O than those under continuous flooding. In China, Yang *et al.* (2013) observed that N_2O emission from a natural marsh wetland increased by 120% as the water level reduced from +14 to −11 cm (below the soil surface). A study on European peatlands by Liu *et al.* (2020) has reported a N_2O emission factor of 19.3 kg N ha^{-1} $year^{-1}$ in agriculture-drained peatlands, higher than in grasslands (17.4 kg N ha^{-1} $year^{-1}$) and forests (3.4 kg N ha^{-1} $year^{-1}$). The study further recommended that rewetting of all drained European peatlands could cut the cumulative N_2O emissions by 70%. Similarly, a recent synthesis of several studies on the effect of soil moisture content (as affected by water table depth) on N_2O emission from freshwater sediments has reported N_2O pulses following sediment drying and rewetting events, with exposed sediments being active spots for N_2O emissions during dry phases (Pinto *et al.* 2021). In view of the impact of fertilization, nitrogen addition into rice paddies enhances N_2O emission. Owino *et al.* (2020) reported that the conversion of Papyrus wetlands into nitrogen-fertilized rice paddies in Kenya significantly increased N_2O emission (4.37 ± 3.18 μg m^{-2} h^{-1} from the fertilized fields against -3.59 ± 2.56 18 μg m^{-2} h^{-1} from the unfertilized fields). Zhang *et al.* (2014) also reported a positive correlation between the amount of fertilizer application and N_2O emissions from rice paddies, irrespective of the rice growth stage. Therefore, in this study, the lack of a significant difference in N_2O fluxes between the natural and rice paddy wetlands could be explained as follows: (i) both the natural and rice paddy wetlands were continuously flooded throughout the sampling period, so the influence of water level on N_2O fluxes was similar across both wetlands, and (ii) artificial fertilization of the studied rice paddy fields was not being done, as rice cultivation was only reliant on the natural fertility of the soil. Undoubtedly, the soil nitrogen contents in the natural and rice paddy wetlands were not different, as was seen in Table 1.

Seasonal variations showed no impact on N_2O emission during this study, in both wetlands. The influence of seasonal changes on N_2O emissions from wetlands has been previously reported, especially in temperate wetlands (Czóbel *et al.* 2010; Jørgensen & Elberling 2012). Warmer soil temperatures during summer seasons enhance microbial activities, resulting in increased mineralization of organic nitrogen in soils. In tropical regions, however, Sjögersten *et al.* (2014) indicated that temperature is unlikely to exert a significant control on GHGs fluxes from wetlands because temperatures are relatively stable, irrespective of season. Bernal & Mitsch (2013) instead showed that seasonal fluxes of N_2O from tropical wetlands are more likely to be driven by changes in water table depth (or soil moisture content). In the present study, seasonal changes (dry vs wet) were not associated with drying and wetting cycles as water level was above the soil surface in both seasons, and neither did soil temperature significantly vary between the dry and wet seasons (Table 1). These, thus, could explain why N_2O emissions did not vary between the dry and wet seasons.

The average N_2O emissions measured in this study were generally low, about four times lower than the average emission reported for tropical wetland systems (van Lent *et al.* 2015). However, it was noted that the average N_2O emission reported by van Lent *et al.* (2015) included fertilized wetland systems, and those under different degrees of disturbance, which could have accounted for the high N_2O flux value. This study's average N_2O flux values are within the range reported for undisturbed natural tropical systems (Matson & Vitousek 1987; Marín-Muñiz *et al.* 2015) and unfertilized rice paddy wetlands (Owino *et al.* 2020).

This study showed great variations in individual N_2O fluxes even within the same wetland/vegetation community type or season, with values ranging from negative (indicating N_2O consumption) to positive (indicating N_2O emission) (Figures 3 and 4). This has also been reported by other studies (Audet *et al.* 2014; Owino *et al.* 2020; Ajwang'Ondiek *et al.* 2021), where it is attributed to wetland soils acting as both N_2O sinks and sources. Wu *et al.* (2013) explained that soils act as sinks of N_2O when N_2O is consumed during either nitrification or denitrification, largely under conditions of limited nitrate (NO_3^-). However, in most cases, as has been reported from instantaneous and annual estimates, soils act as net sources of N_2O (Schlesinger 2013). Indeed, a review by Chapuis-Lardy *et al.* (2007) on soil N_2O uptake made a conclusion that most field values were small and unlikely to contribute to a large N_2O sink globally, while Schlesinger (2013) has suggested that soil N_2O uptake is as low as 5% of the estimates of global net flux from soils to the atmosphere. In this study, N_2O emission and uptake could be attributed to soil oxygen level, with anoxic soil conditions favoring N_2O emission, while suboxic soil conditions enhancing N_2O consumption (Schlesinger 2013). This is supported by the fact that there was an inverse relationship between N_2O flux and water level (Table 3), and the water table also displays an inverse correlation with soil oxygen content (Bernal & Mitsch 2013).

In Uganda, no study has evaluated the totality of N_2O emissions from the country's natural and rice paddy wetlands. Therefore, to provide a basis for future studies, we used our study findings to roughly estimate total annual N_2O emissions from Uganda's natural and rice paddy wetlands. To achieve this, we made a simple assumption that other natural and rice paddy wetlands in the country present more or less similar conditions to our study wetland. Natural wetlands in Uganda cover about 26,165 km^2, compared to 150 km^2 occupied by rice paddy wetlands (Were *et al.* 2021b). We obtained mean annual N_2O emission from the natural and rice paddy wetlands as 4.4 ± 13.1 and 6.1 ± 17.8 mg m^{-2} yr^{-1} (Table 2). Therefore, total N_2O emissions from Uganda's natural and rice paddy wetlands are estimated at 115.1 ± 342.8 T yr^{-1} ($CO_2e = 30{,}501.5 \pm 90{,}842$ T yr^{-1}) and 0.9 ± 2.7 T yr^{-1} ($CO_2e = 242.5 \pm 707.6$ T yr^{-1}), respectively. However, due to the rapid rate of conversion of natural wetlands into rice paddy wetlands, rice paddy wetlands are expected to be the main sources of N_2O emitted from the country's wetlands in the near future.

4.2. Implication of rice cultivation under permanent flooding and no fertilizer application on climate change mitigation

To mitigate climate change and its impacts, the IPCC (2014) has emphasized increasing carbon sequestration while at the same time minimizing the emission of GHGs into the atmosphere. Some of the suggested measures to increase carbon sequestration include protection and conservation of natural ecosystems such as wetlands, forests and grasslands. Wetlands are unique ecosystems, where water is the terminal parameter that influences the development of soil and plant characteristics that are different from other ecosystems. These unique characteristics have a great influence on carbon and nitrogen cycling in these ecosystems (Mitsch *et al.* 2013). Several studies have acknowledged that conversion of natural wetlands into farmed wetlands compromises climate change mitigation by enhancing carbon and nitrogen emission (Owino *et al.* 2020; Were *et al.* 2020b; Ajwang'Ondiek *et al.* 2021). As earlier explained, water drawdown in rice paddy induces carbon and nitrogen emissions from wetlands (Were *et al.* 2019; Owino *et al.* 2020), with fertilized rice paddies being hotspots for N2O emission (Owino *et al.* 2020).

With the increasing human population globally, increased food demand implies that natural tropical freshwater wetlands will remain under high pressure for conversion into rice paddies. Indeed, Davidson & Finlayson (2018) have reported an average increase in global rice paddy acreage of 0.62% per year. As result, there is need to a strike a balance between rice production and climate change. This would involve exploring ways of optimizing carbon sequestration while minimizing emission of other GHGs such as N_2O from rice paddy wetlands.

In this study, it was noted that N_2O emission from the rice paddy wetland was not significantly higher than that emitted from the natural wetland, an indication that rice cultivation under continuous flooding and without fertilizer application can minimize N_2O emissions associated with rice paddies, hence enhancing climate change mitigation. However, this finding may be limited due to several factors:

(a) It was observed that SOC content in the rice paddy wetland was less than half that obtained in any of the three vegetation communities of the natural wetland (Table 1). This indicates that the conversion of the natural wetland into the rice paddy wetland resulted in the decomposition of organic matter, and the consequent release of carbon (either as CO_2 or CH_4)

into the atmosphere. Certainly, in the same wetland, Were *et al.* (2021b) reported significantly high carbon dioxide emission in the wetland section under rice cultivation, compared to the natural section. Therefore, whereas undertaking rice cultivation under continuous flooding and no fertilization may minimize N_2O emission associated with rice paddies, it enhances the release of soil carbon into the atmosphere.

(b) Different rice varieties have differing water requirements, with some requiring drying and wetting cycles. As a result, continuous flooding may not be feasibly applied across all rice paddies due to differences in rice varieties grown. Indeed, studies have found higher rice yields in rice cropping systems subjected to intermittent flooding (Pascual & Wang 2016; Isnawan *et al.* 2022). Yet, intermittently flooded systems have also been reported to be hotspots for N_2O emission (Liengaard *et al.* 2013).

(c) In agricultural systems such as rice paddies, soil fertility decreases as the period of crop cultivation increases, implying that unfertilized rice cultivation may not be sustainable in the long run. Long-term studies show that nitrogen fertilization in rice farms significantly increases rice yields ranging from 81.9 to 92.3% (Liao *et al.* 2010; Lu *et al.* 2015). As a result, in a bid to maintain or increase rice yields, the application of fertilizers in rice paddies may be inevitable as a response to declining soil fertility.

Based on these factors, rice cultivation under continuous flooding and no fertilizer application is not a sustainable option for enhancing climate change mitigation in the long run. Therefore, wetland management, in view of climate change mitigation should give priority to the conservation/protection of existing natural wetlands. It has already been shown that undrained wetlands represent net carbon (Mitsch *et al.* 2013) and nitrogen (Tangen & Bansal 2022) sinks. Alongside climate change mitigation, wetland conservation/protection will guarantee the availability of several other ecosystem services that are necessary for adaptation to climate change impacts.

5. CONCLUSIONS

In a continuously flooded natural tropical freshwater marsh wetland, N_2O emission does not vary spatially based on changes in the type of vegetation community. Further, it was also found that N_2O emission did not vary between the natural and rice paddy wetlands. Therefore, the conversion of tropical freshwater marsh wetlands into continuously flooded and unfertilized rice paddy wetlands does not affect N_2O emission. Nevertheless, the observation of significantly lower SOC content in the rice paddy wetland (less than half that measured in the natural wetland) implies that rice paddy wetlands even under continuous flooding and no fertilizer application can be significant sources of carbon. This, therefore, calls for prioritizing the conservation/protection of existing natural wetlands to enhance climate change mitigation by wetlands.

Temporal variations, due to changes in season (dry vs wet) have no effect on N_2O emission from continuously flooded tropical wetlands. Environmental parameters showed no significant correlation with N_2O flux from the wetlands, indicating that N_2O emission in flooded tropical wetlands is controlled by an interplay between several factors, with no single factor exerting a dominant influence.

ACKNOWLEDGEMENT

We thank the University of Natural Resources and Life Sciences (BOKU), Vienna, Austria, and the International Foundation for Science (IFS) for the financial support during this study. We also acknowledge the immense support rendered by the local community members in the study area during the period of field sampling.

FUNDING

This work was supported by the University of Natural Resources and Life Sciences (BOKU), Vienna, Austria, through Mag. Gerold Winkler and Prof. Thomas Hein, and the International Foundation for Science (IFS).

AUTHORS' CONTRIBUTIONS

The study was conceptualized and designed by DW. DW carried out data collection and analysis, and wrote, edited and reviewed the first draft manuscript. TH and FK edited, reviewed and contributed to the discussion of the manuscript. Funding acquisition was by TH and DW. The study was supervised by TH and FK. All authors read and approved the final manuscript.

DATA AVAILABILITY STATEMENT

All relevant data are included in the paper or its Supplementary Information.

CONFLICT OF INTEREST

The authors declare there is no conflict.

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First received 28 July 2022; accepted in revised form 12 January 2023. Available online 23 January 2023