



Original Articles

Interactive effects of land-use intensity, grazing and fire on decomposition of subtropical seasonal wetlands

Yuxi Guo^a, Elizabeth H. Boughton^b, Jiangxiao Qiu^{a,*}^a School of Forest, Fisheries, and Geomatics Sciences, Fort Lauderdale Research and Education Center, University of Florida, 3205 College Ave, Davie, FL 33314, USA^b Archbold Biological Station, Buck Island Ranch, 300 Buck Island Ranch Road, Lake Placid, FL 33852, USA

ARTICLE INFO

Keywords:

Agricultural practice
Grazing
Fire
Land-use intensity
Wetland management
Carbon cycling
Decomposition indicator

ABSTRACT

Understanding how global change drivers and their interactions affect decomposition in wetlands embedded in agricultural landscapes remains challenging, especially in tropical and subtropical biomes, which are disproportionately important for global carbon cycling yet with high uncertainties. In a long-term whole-ecosystem experiment, we used a widely-adopted indicator of decomposition, the Teabag Index (TBI), to investigate individual and interactive effects of surrounding land-use intensity, cattle grazing, and prescribed fire on seasonal wetland decomposition (i.e., decay rate k , and stabilization factor S) in an exemplar subtropical landscape in central-south Florida, USA. We ask: (1) How do land-use intensity and management practices affect the decomposition in seasonal wetlands? (2) How does wetland decomposition vary with hydrological gradient and seasonal climatic condition? (3) What are the dominant direct and indirect pathways through which land-use intensity and management practices affect wetland decomposition? Our results showed that, overall, surrounding land-use intensity exerted much stronger effects on litter decomposition compared to grazing and prescribed fire, and cattle grazing reduced decomposition rate k . There was a complex three-way interaction among land-use intensity, grazing and fire on the stabilization factor S – a proxy related to carbon sequestration potential. Grazing-fire interactive effects on S only existed in wetlands embedded in intensively-managed landscapes, where grazing reduced S in burned wetlands but did not affect S in unburned wetlands. Decay rate k showed profound temporal variation primarily driven by seasonal climatic conditions (especially precipitation), whereas S varied spatially along the hydrological gradient. Our structural equation modeling (SEM) analyses further revealed that effects on k were also indirectly manifested through changes on soil C/N, C/P, and pH, while effects on S were manifested through alterations in soil C/P ratio, pH, soil nutrients and water content. Our TBI results suggest that anthropogenic environmental changes, including land-use intensification, livestock introduction and fire suppression, could compromise carbon sequestration potential in tropical and subtropical seasonal wetlands. Our research highlights the importance of considering landscape context in wetland management and demonstrates the use of TBI as an indicator to quantify and inform combinations of land management and agricultural practices could conserve wetlands and sustain their vital functions and services, especially from the lens of promoting carbon storage and nutrient retention services.

1. Introduction

Organic matter decomposition is one of the most fundamental processes underlying a range of ecosystem functions and services. For example, decomposition regulates biogeochemical cycling, maintains primary production, contributes to soil formation, and affects greenhouse gas (GHG) emissions (Chapin et al., 2002; Swift et al., 1979; Zhang et al., 2008). However, global change drivers (e.g., land-use intensification and altered disturbance regimes) (Steffen et al., 2006)

have substantially modified the rates and controlling factors of decomposition, including physicochemical properties of the environment, plant functional traits, and decomposer communities (Solly et al., 2014; Wang et al., 2015). Hence, it is critical to investigate the response of decomposition to global change drivers, and explore key mechanisms for quantitative assessments of consequences for carbon and nutrient cycling and associated ecosystem services underpinned by decomposition.

It has been acknowledged that the relative controls on

* Corresponding author.

E-mail address: qiu@ufl.edu (J. Qiu).<https://doi.org/10.1016/j.ecolind.2021.108301>

Received 10 March 2021; Received in revised form 25 September 2021; Accepted 17 October 2021

Available online 19 October 2021

1470-160X/© 2021 The Authors.

Published by Elsevier Ltd.

This is an open access article under the CC BY-NC-ND license

[\(http://creativecommons.org/licenses/by-nc-nd/4.0/\)](http://creativecommons.org/licenses/by-nc-nd/4.0/).

decomposition and its responses to environmental changes are likely ecosystem- or context-dependent (Swift et al., 1979). Prior research has thoroughly studied litter decomposition across an array of terrestrial and aquatic ecosystems (Chapin et al., 2002; Zhang et al., 2008). However, less is known about decomposition in transitional systems, such as seasonal freshwater wetlands. Inland seasonal or intermittently inundated wetlands have often been lumped into surrounding uplands, presumably due to their small size, embedment in landscape mosaics, and inundation dynamics (Kollmann et al., 2016; Reis et al., 2017). Yet these ecosystems are disproportionately important, given their: (1) large global presence (i.e., 10.6×10^6 km², or 62% of total global wetland extents) (Fluet-Chouinard et al., 2015; Davidson et al., 2018); and (2) social-ecological value because they support high biodiversity and productivity (Brinson et al., 1981), (3) regulation of GHG and global carbon budget (Raymond et al., 2013), and (4) provision of diverse ecosystem services, such as water purification and erosion control (Qiu & Turner, 2013; Qiu et al., 2018).

Compared to permanently inundated wetlands or aquatic ecosystems, hydrologic pulses in seasonal wetlands could enhance primary productivity (Gomez-Casanovas et al., 2020; Odum et al., 1995), particularly in tropical/subtropical biomes (Aselmann & Crutzen, 1989), leading to greater litter inputs and therefore a larger carbon sink. On the other hand, sediment exposure during dry periods in seasonal wetlands could accelerate decomposition and may then switch seasonal wetlands to a carbon source (Moura et al., 2008), although the net carbon effect remains inconclusive due to large uncertainties (Raymond et al., 2013). In addition, during wet seasons, compared to permanently inundated wetlands, seasonal wetlands tend to have shallower water levels and thus less vertical stratification, which makes their physicochemical conditions more sensitive to external environmental changes that further affect wetland litter decomposition (McLatchey & Reddy, 1998). In central Florida, for example, many shallow seasonal wetlands are embedded in managed grasslands and thus highly susceptible to agricultural management, including fertilization, lime application, water pumping and ditch construction (Boughton et al., 2010; Boughton et al., 2016). Furthermore, livestock grazing and prescribed fire are two additional typical yet essential management factors and disturbances that may also exert significant impacts on litter decomposition in seasonal wetlands (Steffen et al., 2006).

Prior research has demonstrated that land-use intensification, livestock grazing and prescribed fire have exerted individual and sometimes interactive effects on soil properties, water quantities and qualities, methane fluxes, and plant communities in seasonal wetlands (Bohlen & Gathumbi, 2007; Boughton et al., 2016; DeLucia et al., 2019; Ho et al., 2018; Jansen et al., 2019). Yet whether and how these drivers affect wetland decomposition, either directly, indirectly, or interactively, remains largely unclear. For instance, decomposition could be directly affected by cattle trampling, or indirectly affected via higher available soil nutrients from cattle dung and fertilization inputs from surrounding grasslands. Fire-grazing interactions have also been demonstrated to affect wetland plant productivity, leaf nutrient content and water nutrients (Jansen et al., 2019; Sonnier et al. 2020), which could also further affect organic matter decomposition in wetlands. Hence, a key step is to unravel the effects of these land management practices and their interactions, as well as the relative contributions of direct or indirect pathways through which decomposition is shaped in seasonal wetlands. Such knowledge is vital to informing management of seasonal wetlands embedded in agricultural landscapes to sustain their essential functions and services given accelerating anthropogenic environmental changes.

To address these knowledge gaps, we focus on decomposition in subtropical wetlands – a biome less well understood in the literature but largely represented in global seasonal wetlands (Davidson et al., 2018; Prigent et al., 2007). We used the Tea Bag Index (TBI) to quantify decomposition processes that include decay rate k and stabilization factor S , because (1) TBI allows multiple measurements across time, and

(2) enables comparisons across ecosystems and geographic regions by standardizing litter quality (Petraglia et al., 2019). We ask: (1) How do land-use intensity and management practices (i.e., cattle grazing and prescribed fire) interact to affect seasonal wetland decomposition? (2) How does wetland decomposition vary with hydrological gradient and seasonal climatic condition? (3) What are the dominant direct and indirect pathways through which land-use intensity and management practices affect wetland decomposition? To answer these questions, we measured decomposition in a whole wetland field experiment in central-south Florida, USA (Boughton et al., 2016; Ho et al., 2018) that manipulated presence/absence of grazing and fire in wetlands embedded in upland grasslands managed at two levels of land-use intensity (i.e., high vs. low) (Fig. 1). We hypothesized that land-use intensity would exert greater effects than grazing and prescribed fire, due to strong modifications of hydrologic regimes and soil properties. However, the direction of the land-use intensity effect is uncertain, because under intensified land-use, neutral pH resulting from upland lime application may stimulate microbial activities and accelerate decomposition, but N-enrichment from upland fertilization may inhibit labile organic matter decomposition (Li et al., 2016). We also hypothesized that grazing and fire were more likely to show interactive effects on organic matter decomposition in wetlands embedded within high-intensity upland grasslands, considering wetland soil nutrients were only interactively modified by grazing and fire under high-intensity land-uses (Ho et al., 2018).

2. Materials and methods

2.1. Study area

Our study took place at Archbold Biological Station's Buck Island Ranch (BIR) in central-south Florida, USA (Fig. 1). BIR is a working ranch (4,336 ha) with commercial-scale cow-calf operations (~3,000 cows) for research purposes. BIR is part of the Archbold Biological Station-University of Florida USDA Long-term Agroecosystem Research (LTAR) site. This is one of 18 sites forming a nationwide network designed to assess strategies for sustainable intensification of agriculture at the national scale (Kleinman et al., 2018; Spiegel et al., 2018). BIR contains two pasture (or grassland) types representing typical land-use intensities for this region (Fig. 1): intensively managed (IM) vs. semi-natural (SN). IM pastures are heavily drained, planted with non-native bahiagrass (*Paspalum notatum*), and are intensively grazed by cattle during wet seasons (June-October). IM pastures were also regularly limed, N-fertilized every 1–2 years, and were historically fertilized with P and K until 1987. SN pastures were never fertilized (Swain et al., 2007), composed of mixed non-native bahiagrass and native grasses, and are grazed primarily during dry seasons (November-May). Average animal use days per hectare for IM and SN pastures are 391.2 and 177.7, respectively (data from 2014 to 2019).

Isolated seasonal wetlands are an important feature of tropical/subtropical landscapes that are embedded within and thus influenced by surrounding upland pastures (Fig. 1). In BIR, there are >600 wetlands (~comprising of 12% of the area) (Boughton et al., 2010) with hydroperiods ranging 2–10 months and size between 0.007 and 41.9 ha. Plant communities of wetlands within SN pastures are diverse and dominated by native and perennial species, such as *Panicum hemitomon*, *Rhynchospora inundata*, *Diodia virginiana*, *Sagittaria lancifolia*, *Pontedaria cordata*. However, in wetlands within IM pastures, plant communities have lower richness, more exotic and annual species, and are often dominated by *Juncus effusus* var. *solutus*, *Persicaria punctata*, and *Pontedaria cordata* (Boughton et al., 2011a). Cattle grazing and prescribed fires are the two most common grassland management actions in this region and elsewhere, which also have shown significant effects on wetland vegetation. For example, grazed wetlands tended to have greater abundance of short graminoids and forbs, such as *Luziola fluitans*, *Eleocharis vivipara* and *Bacopa caroliniana*, than ungrazed wetlands, which were dominated by

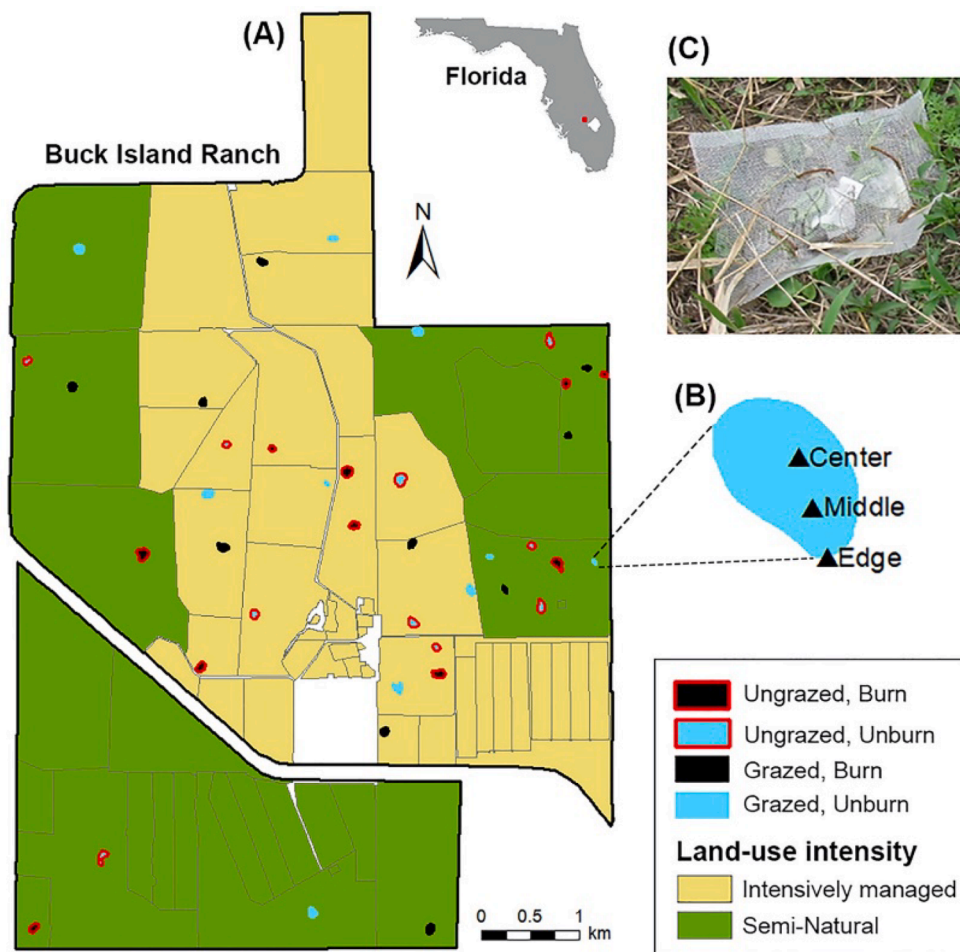


Fig. 1. (A) Map of the 40 wetlands in a whole-ecosystem experiment at Archbold Biological Station's Buck Island Ranch. Intensively managed (IM) pastures are shown in yellow, and semi-natural (SN) pastures are shown in green. Fenced (ungrazed) wetlands are illustrated with red outlines, and grazed wetlands with no outlines. Burned wetlands are shown in black color, and unburned wetlands are filled with light blue color. (B) Each wetland has three sampling sites – center, middle, and edge – to capture the spatial variation along the hydrological gradient. (C) Photo is shown as an example of tea bag deployment in the field. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

taller species such as *P. hemitomom* and *Sacciolepis striata* (Boughton et al., 2011b; Boughton et al., 2016). Moreover, fire interacted with grazing that increased shrubs in ungrazed wetlands but showed no effect on shrubs in grazed wetlands (Boughton et al., 2016). In addition, wetland edges typically have greater diversity and more variable plant composition compared to wetland centers which are lower in diversity and primarily dominated by broadleaf emergent vegetation (*P. cordata* and *Sagittaria lancifolia*) (Boughton et al., 2019; Boughton et al., 2021). Please refer to SI for more details on study region.

2.2. Experimental design

Our research was conducted in a long-term whole-ecosystem wetland experiment initialized in 2008 with a randomized complete block design. Details in experimental design can be found in Boughton et al. (2016) and Ho et al. (2018). In brief, forty similar-size wetlands (0.5–1.5 ha, Fig. 1A) were selected across the BIR and organized into five blocks. In each block, the crossed presence/absence of grazing and fire treatments were implemented in wetlands within IM and SN pastures (i. e., $2 \times 2 \times 2$ factorials). For ungrazed treatment, cattle exclosures were installed in 2007; for grazed treatment, cattle use (stocking rate typical of the local region) activities were tracked for pastures in which wetlands were embedded (number of cattle and days in and out). Prescribed fire treatment was imposed to 5 random wetlands in each combination of pasture type \times grazing treatment during dry seasons of 2008, 2011, 2013–2014, and 2020 mimicking local return intervals. Standard drip torch and overlapping strip lines were used to ignite fires and ensure that $> 80\%$ of the wetland was burned. Such a whole-ecosystem and

long-term manipulative experiment allows us to tease apart effects of different factors of environmental changes in real-world settings.

Given our design, three sites (i.e., center, middle, and edge) were selected per wetland that vary along the hydrological gradient to measure aboveground decomposition (Fig. 1B). The center site is the lowest point of the wetland; the edge site is determined by the longest distance between the center and wetland margin where transitions in vegetation normally occur along the hydrological gradient; the middle site is the midpoint with equal distances to the center and edge sites. Our selection of three sites per wetland not only captured local variation in wetland decomposition, but also can be aggregated to obtain the representative wetland-level estimates (see Table S1 in SI).

2.3. Tea bag Index approach

TBI uses two standardized materials – labile (Lipton green tea) and recalcitrant (Lipton rooibos tea) litter (Fig. 1C) – to assess decay rate k and stabilization factor S within a single incubation (Keuskamp et al., 2013). K quantifies mass loss rate that reflects short-term litter decomposition dynamics (Eq. (1), 2), with higher values indicating faster decomposition of labile organic components. S measures the amount of hydrolysable compounds turning recalcitrant (Eq. (3)) and reflects completeness of decomposition. Thus, high S values suggest inhibition of litter decomposition, likely due to factors such as anoxia or low pH, leading to high carbon sequestration potential (Keuskamp et al., 2013). As an effective and standardized method, TBI has been widely tested to study decomposition across diverse ecosystems globally, including montane and lowland forests (Elumeeva et al., 2018; Fujii et al., 2017),

temperate grasslands and lakes (Petraglia et al., 2019; Seelen et al., 2019), peatlands (MacDonald et al., 2018), and subarctic wetlands (Whigham et al., 2017).

Before deployment, all tea bags were weighed (± 0.001 -g) and labelled. A pair of tea bags (one green-EAN:8714100770542 and one rooibos-EAN:8722700188438) were deployed at each sampling site in January and March 2019, then retrieved in March and June 2019, respectively. These two deployments were intended to capture effects of intra-annual climatic variations during dry season (January to March) and dry-wet season transitions (March to June). We did not measure decomposition during wet seasons because of high water level, logistic constraints, and high risks of losing tea bags. Hence, a total of 240 pairs of tea bags were deployed in all wetlands (i.e., 40 wetlands \times 3 sites \times 2 incubations). To capture aboveground litter decomposition (i.e., where most decomposition occurs in wetlands) (Brinson et al., 1981), we placed tea bags on the sediment surface and secured them using meshed nylon net and landscape pins (Fig. 1C). The retrieval times of tea bags (i.e., incubation period) were within 60–90 days after deployments, according to Keuskamp et al. (2013) for the tropical/subtropical biome. At the end of each incubation, we retrieved tea bags and transported them to the lab, removed adhering sediments, and oven-dried tea bags at 60 °C for at least 48 h until constant weight. Since the weights of bag, cord, and label of each teabag are initially consistent and provided by Keuskamp et al. (2013), after the incubation, we only weighed dried tea materials that were carefully taken out of each bag to avoid the confounding effect of weight changes in bag, cord, and label.

2.4. TBI calculation

Based on our measurements, decomposition rate k was calculated by the rooibos tea mass loss W after incubation time t , following a negative double exponential regression describing the breakdown of decomposable fraction a_r at the beginning, and then gradually slowing down, with the recalcitrant fraction $(1-a_r)$ left over time (Equation (1)):

$$W(t) = a_r e^{-kt} + (1 - a_r) \quad (1)$$

The decomposable fraction of rooibos tea (a_r) was determined by its hydrolysable fraction H_r and stabilization factor S (Equation (2)):

$$a_r = H_r(1 - S) \quad (2)$$

The stabilization factor S was calculated based on decomposable fraction a_g and hydrolysable fraction H_g of green tea (Equation (3)):

$$S = 1 - \frac{a_g}{H_g} \quad (3)$$

Hydrolysable fractions of rooibos tea (H_r) and green tea (H_g) were provided in Keuskamp et al., (2013).

2.5. Environmental variables collection

At each site per wetland, three soil cores (5-cm depth \times 10-cm diameter) were taken in March and June 2019 (in synchrony with tea bag retrieval times) to measure soil properties. Top 5-cm soils were sampled because they exert most influences on aboveground decomposition. All soil samples were sieved (with 2-mm mesh) and then used to measure water content, pH, organic matter, total C and N, and plant-available P, K, Ca, Mg, all of which could affect decomposition (Chapin et al., 2002; Zhang et al., 2008). Gravimetric soil water content was measured by weight loss after oven drying in 105 °C for 72-hr, and soil pH was measured by a hand-held HANNA pH meter (Hanna Instruments, CA) (Thomas, 1996). Soil organic matter was measured by mass loss after 4-hr high-temperature oxidation in a 450 °C muffle furnace (Schulte & Hopkins, 2015). Soil C and N content were measured using LECO CN628 C/N Determinator (LECO Corporation, MI) (Bremner, 2018). Plant-available P, K, Ca and Mg were extracted with Mehlich-3 solution (Mehlich, 1984), and analyzed using inductively coupled

plasma atomic emission spectrometry technique (Soltanpour et al., 2018) with the Perkin Elmer Avio 200 (Perkin-Elmer, CT).

Meteorological data over the two incubations were collected by the main BIR weather station, including daily temperature (°C) and precipitation (mm). Daily average temperature and precipitation were calculated based on the timing and duration over which the tea bags were incubated in each experimental wetland. Elevations of wetlands (i.e., a variable that could affect wetland hydrology) were extracted from their geographic locations and the Light Detection and Ranging (LiDAR) by Optech 1233 Airborne Laser Terrain Mapper system in 2006, and averaged by their extents.

2.6. Statistical analyses

To determine individual and interactive effects of land-use intensity and management factors on wetland decomposition ($Q1$), and how it varies across hydrological gradient (i.e., sampling sites) and climatic conditions (i.e., incubation period) ($Q2$), we performed linear mixed-effects models separately for k and S . In the model specification, wetland management (i.e., land-use intensity, grazing, and prescribed fire), sampling site (center, middle, and edge), and incubation period (January through March, and March through June) were treated as fixed factors, and block as a random factor. Residual plots were assessed to check assumptions of normality and homogeneity of variance; no violations were detected. P -values were estimated using Type III Sums of Squares, due to multiple specified non-sequential variables and their interactions. We conducted our analyses at both site and aggregated whole-wetland levels (Table S1) and found that the significant factors in determining k and S were consistent.

To disentangle the direct and indirect pathways through which management practices affected decomposition (i.e., $Q3$), we performed structural equation modeling (SEM) (Hooper et al., 2008). First, we reduced dimensions of soil properties using principal component analysis (PCA), because of high levels of collinearities among soil variables (Fig. S1). We used the derived first three components in our subsequent analyses, which together accounted for 82% of total variance. In addition, we performed multiple linear regressions as exploratory analyses to determine which principal components affected the decay rate k and stabilization factor S (Table 2). Based on these analyses and system knowledge, we constructed hypothesized path diagrams (Fig. S5) before fitting empirical data, along with other covariates that were hypothesized to affect decomposition (Figs. 5 and 6). Given that land-use intensity, grazing, and fire treatments were categorical variables, we evaluated their effects using χ^2 likelihood ratio tests. We also performed post-hoc Tukey tests to determine significance of differences in categorical variables within each grouping (Bowen et al., 2017). Linear mixed-effect models, PCA, and SEM were performed in R 3.6.1 using “lme4”, “pls”, and “piecewiseSEM” packages, respectively (Bates et al., 2015; Lefcheck, 2016; Wehrens & Mevik, 2007).

3. Results

Land-use intensity, cattle grazing, and prescribed fire showed significant individual and interactive effects on decomposition rate k and stabilization factor S . For k , cattle grazing overall reduced k (Table 1); in addition, under fire treatment, wetlands embedded in IM pastures also showed marginally lower k than those in SN pastures (Table 1). For S , a significant three-way interaction among land-use intensity, grazing, and fire was detected (Table 1). Specifically, wetlands embedded in IM pastures tended to have lower S than those in SN pastures across most combinations of grazing and fire treatments, except for grazed and unburned wetlands (Fig. 2B). In addition, grazing and fire only showed significant interactive effects in IM wetlands, where grazing increased S in unburned wetland but did not affect S in burned wetlands (Fig. 2B).

Substantial temporal and spatial variation in wetland decomposition were also revealed, presumably associated with climatic conditions and

Table 1

Linear mixed-effects model results on wetland decomposition rate k ($\text{mg}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$) and stabilization factor S (%) in response to management factors and environmental covariates (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, • $p < 0.10$). Significant variables are highlighted in bold font.

Explanatory variable	Estimate	SE	<i>P</i> -value
Decomposition rate k			
Pasture (IM)	0.0004	0.0017	0.128
Grazing (Grazed)	-0.0014	0.0017	0.022*
Fire (Burned)	0.0032	0.0016	0.437
Site (M)	-0.0101	0.0008	0.140
Site (C)	0.0018	0.0010	0.140
Period (March-June)	0.0002	0.0010	<0.001***
IM × Grazed	-0.0003	0.0024	0.391
IM × Burned	-0.0046	0.0024	0.083.
Grazed × Burned	-0.0022	0.0023	0.724
IM × Grazed × Burned	0.0034	0.0033	0.304
Stabilization factor S			
Pasture (IM)	-0.159	0.026	<0.001***
Grazing (Grazed)	-0.032	0.025	0.897
Fire (Burned)	0.013	0.025	0.393
Site (M)	-0.017	0.013	<0.001***
Site (C)	-0.077	0.015	<0.001***
Period (March-June)	-0.133	0.015	0.169
IM × Grazed	0.146	0.036	0.003**
IM × Burned	0.080	0.036	0.717
Grazed × Burned	-0.011	0.035	0.002**
IM × Grazed × Burned	-0.139	0.050	0.005**

Table 2

Multiple linear regression estimates of wetland decomposition rate k ($\text{mg}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$) and stabilization factor S (%) using the first three principal components (PC) from the principal component analysis (PCA).

PCs	Estimate	SE	<i>P</i> -value
Decomposition rate k			
PC1	0	0.0002	0.993
PC2	-0.0015	0.0005	0.002**
PC3	0.0002	0.0005	0.597
Stabilization factor S			
PC1	0.023	0.003	<0.001***
PC2	0.006	0.006	0.335
PC3	-0.019	0.006	0.003**

hydrological gradient, respectively. The teabags incubated from January-March 2019 had significantly higher k than those from March-June 2019 (Table 1, Fig. 3A). In addition, spatial variation was more pronounced for S along the hydrologic gradient, where wetland edge sites had higher S than centers (Table 1, Fig. 3B).

Direct and indirect pathways on how land-use intensity and management affected decomposition were also revealed. Our SEM of k (Fisher's $C = 4.74$, $p = 0.58$) showed that k was directly affected by land-use intensity and grazing (Fig. 5), yet stronger effects of land-use intensity were indirectly manifested through PC2 of soil attributes (indicated by soil C/N, C/P and pH, Fig. 4), which negatively associated with k ($p = 0.017$). In addition, effects of sampling site and wetland elevation were also manifested via PC2 (Fig. 5). Daily precipitation directly affected k ($p < 0.001$), but also indirectly through altering soil conditions (i.e., PC2).

SEM of S (Fisher's $C = 6.24$, $p = 0.40$) showed that S was directly affected by land-use intensity, sampling site, and daily average temperature ($p < 0.05$, effect size = -0.01) (Fig. 6). Effects of land-use intensity and daily temperature were also manifested through PC3 (indicated by soil C/P and pH, Fig. 4), which negatively associated with S ($p < 0.05$, effect size = -0.02). Effects of geographic location and wetland elevation on S were also manifested through PC1 (defined by soil nutrients and water content, Fig. 4), which positively associated with S ($p < 0.001$, effect size = 0.01).

4. Discussion

Our research demonstrated that wetland decomposition was affected by land-use intensity, management, geographical features, and seasonal climate, either directly or indirectly through altering soil properties. Among all factors considered, land-use intensity was the most influential driver of wetland decomposition (Table 1), with complex interactions among grazing and fire disturbances. Specifically, our results highlighted that: (1) grazing slowed down decomposition (Figs. 2, 5), and intensified land-use also reduced decomposition rate, but only when wetlands were burned; (2) intensified land-use reduced plant litter stabilization and thus carbon sequestration potentials (Fig. 6); fire increased litter stabilization when wetlands were ungrazed but showed no effects in grazed wetlands, and such fire-grazing interactions only occurred in intensively-managed pastures (Fig. 3); (3) substantial spatial variation in S from wetland edge to center were revealed, likely reflecting its sensitivity to hydrological gradient (Figs. 3, 5); and (4) significant temporal variation in k were detected, indicating its sensitivity to seasonal climate conditions (Figs. 3, 6). Findings from this research have important implications for managing tropical/subtropical seasonal wetlands to sustain their crucial ecosystem functions and services in the context of global environmental changes.

4.1. Interactive effects of land-use intensity and management practices on wetland decomposition

Intensified land-uses could slow down decomposition of labile components in plant litter (Fig. 5), consistent with previous studies (e.g., Solly et al., 2014; Violita et al., 2016). The primary mechanism could be that when mineral N nutrients are adequate through runoff from surrounding upland fertilized pastures, soil microbes are provided sufficient amounts of easily digested nutrient, hence, lowering the microbial nutrient demands and delaying the associated N mineralization (Fog, 1988). Such inhibitory effects of N enrichment on decomposition rate have also been observed in other studies (Entry, 2000; Hobbie, 2008; Tao et al., 2013; Li et al., 2016; Song et al., 2017). However, another seemingly 'contradictory' theory posits that nutrient addition may stimulate decomposers' activities, thereby facilitating decomposition (Swift et al., 1979). Yet as a matter of fact, this facilitation refers to decomposition completeness (i.e., reducing S), rather than the rate of initial decomposition (i.e., increasing k), because nutrient enrichment tends to enhance fungal growth that are the major decomposers of recalcitrant organic compounds (Ferreira & Chauvet, 2011). A recent molecular study confirmed this explanation by showing that N-induced inhibition only existed on labile litter components (e.g., cellulose) but not on complex macromolecules (e.g. lignin) (Chen et al., 2019). Therefore, in tandem, both mechanisms explain why wetlands in IM pastures had lower k and meanwhile lower S than those embedded in SN pastures (Fig. 2). Such results also highlighted the importance of investigating decomposition processes of different litter components and their dominant actors and mechanisms.

Moreover, in IM wetlands, increased soil pH was also found to decrease S (Fig. 6), which could be another mechanism related to land-use intensity, which concurs with findings from Elumeeva et al. (2018). The lime applied in IM pastures contributed to a more pH-neutral environment in wetlands (Fig. S2), which may favor microbial diversity and activities (Paul, 2014) and then promote decomposition completeness. However, the specific effects of microbial composition and diversity on organic matter stabilization need to be further explored.

Grazing decreased k and S , especially in SN wetlands (Figs. 2, 5, 6). Similar to effects of intensified land-uses on k , cattle grazing could return nutrients to wetlands and lead to N inhibitory effect on labile material decomposition, because much of animal-excreted N was in readily available urea or dung forms to decomposers (Wang et al., 2015). In addition to animal waste nutrient inputs, grazing reduced vegetation

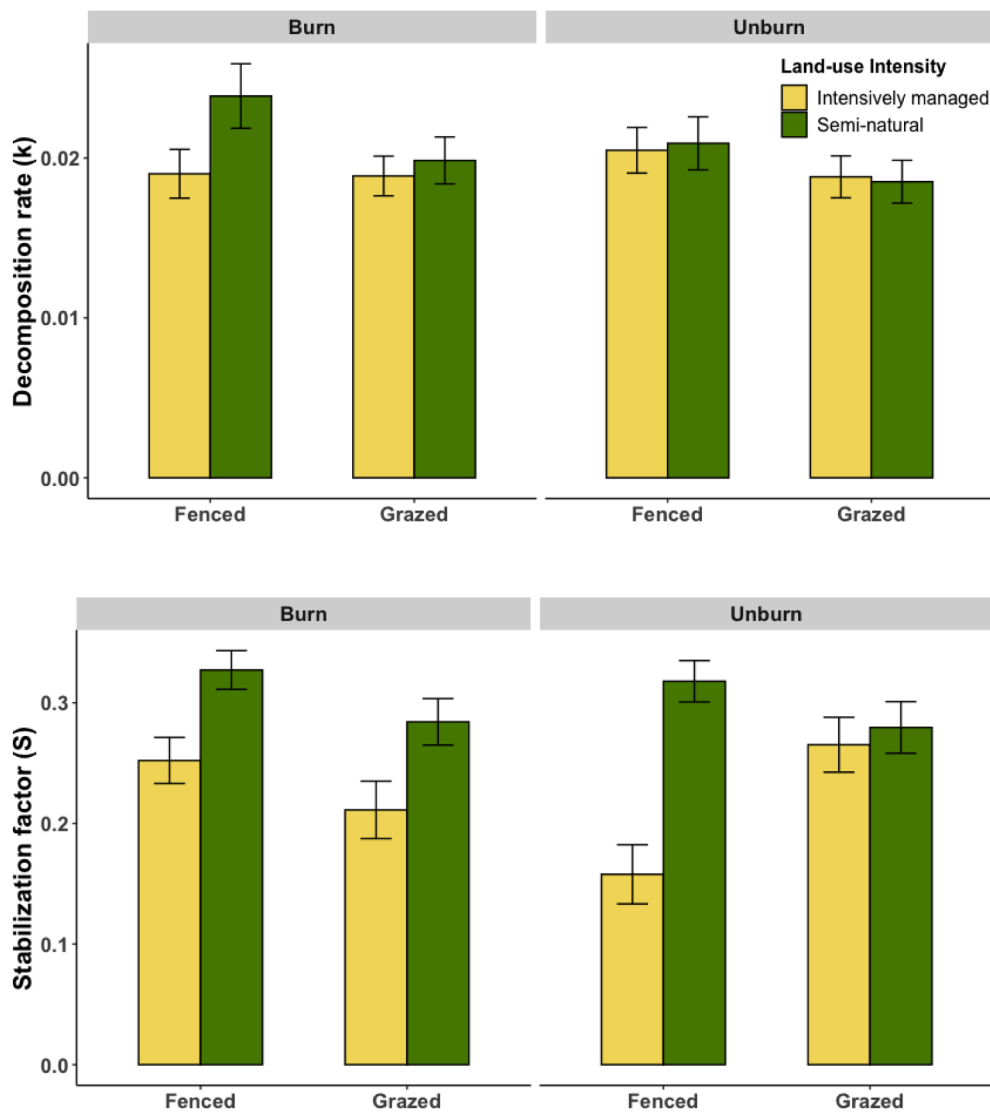


Fig. 2. Differences in teabag decomposition rate k (A) and stabilization factor S (B) across wetland treatments (from embedded in intensively managed and semi-natural pastures, grazed and fenced (ungrazed) wetlands, burned and unburned wetlands). Error bars represent SEs. Full results of model fitting are shown in Table 1.

canopy and promoted the abundance of short graminoids and forbs from foraging activities (Boughton et al., 2016; Ho et al., 2018), which could increase exposure of underlying plant litter to the solar radiation, increase the surface temperature and enable photodegradation that consequently enhances decomposition completeness (i.e., S) (Austin et al., 2016). Grazing effects on k and S were more profound in SN wetlands, probably because intensified land-uses had the same directional effects as grazing, and the magnitude of land-use intensity effects through nutrient enrichment might already saturate for wetland decomposition in IM wetlands (Chapin et al., 2002).

Individual effects of prescribed fire on decomposition were much weaker as compared to land-use intensity and grazing, perhaps due to its infrequent occurrence and pulse dynamics that resulted in no stable or persistent impacts over time, coupled with weak lag effects. Overall, in IM wetlands, fire tended to increase S where wetlands were released from grazing but did not affect S in grazed wetlands (Fig. 2B), while fire had no effect on S in SN wetlands. The interactive fire-grazing effect on litter decomposition might result from complex plant-soil-microbe interactions that vary with grazing regimes (Churchland & Grayston, 2014). Fire had been found to reduce overall N stocks in wetland soils (Ho et al., 2018), which might have positive effects on litter stabilization (Fig. 6). However, cattle grazing could add soil nutrients through

excrement and reduce nutrient loss by favoring growth of unpalatable and slow-growing wetland plants and associated decomposers (Boughton et al., 2016), which counteracted fire effects on S . Moreover, burned and ungrazed wetlands had more non-native plants (Boughton et al., 2016). Invasive plants might release phenolic acids that suppress microbial respiration (Jones et al., 2019) and thereby increase litter stabilization.

4.2. Spatial and temporal variations in wetland decomposition

Substantial spatial variation in wetland litter stabilization S (Table 1, Fig. 3B) suggested that in the lowest and wettest point of a wetland there was lower litter stabilization. This trend is consistent with MacDonald et al. (2018) that found wetter sites in peatlands were associated with lower S . Indeed, our SEM results (Fig. 6) corroborated this finding by showing that sampling site (i.e., center, middle, edge) affected S through changes in soil water content and nutrient levels. Given the relationships among soil properties where higher water contents were associated with higher soil nutrients (Fig. S1), we argue that the completeness of litter decomposition could be enhanced by higher soil moisture and nutrient concentrations and associated decomposers activities.

Our results also showed significant temporal variation in

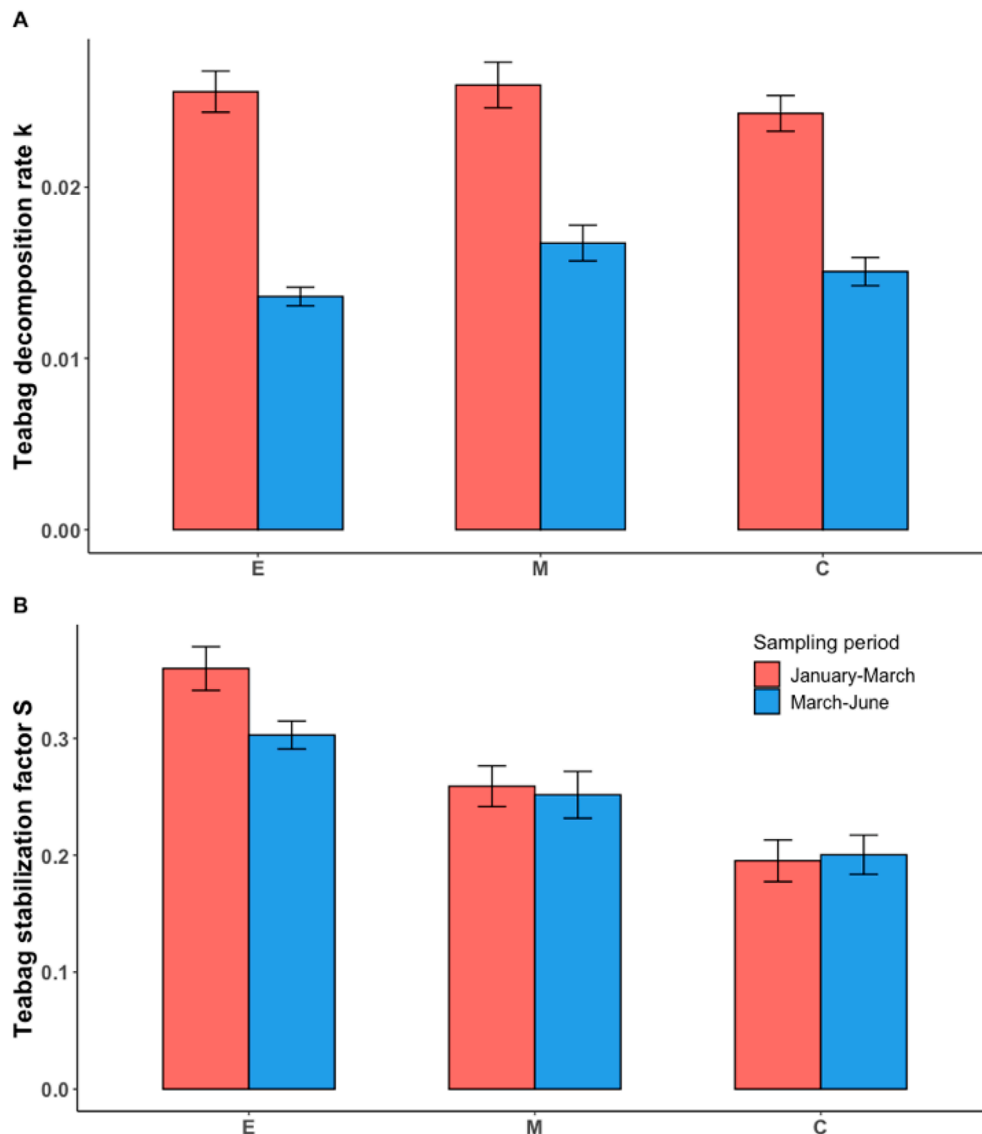


Fig. 3. Differences in teabag decomposition rate k (A) and stabilization factor S (B) across three wetland sampling sites (edge, middle and center) and incubation periods (January to March, and March to June). Error bars represent SEs.

decomposition rate k (Table 1, Fig. 3A), likely resulting from influences of seasonal climatic conditions (Zhang et al., 2008). Two teabag incubation periods had significantly different meteorological characteristics (Fig. S4). The second incubation from March through June 2019 had higher temperature and less precipitation than the first incubation, which led to lower soil water content during the second incubation (Fig. S3). Based on the SEM results (Fig. 5), we infer that increased precipitation during dry seasons could accelerate decomposition rate by increasing soil moisture and pH, as well as associated decreased soil C/N and C/P ratio.

4.3. Management implications

Our findings have important implications for wetland management in landscapes dominated by agriculture. Our observation of decomposition variability along the hydrological gradient within wetlands is relevant to understanding effects of ongoing water retention and hydrologic restoration measures (i.e., for providing flooding control and nutrient retention services). As water retention in the headwaters of the Florida Everglades – i.e., one of the world’s largest and most diverse wetlands – garners more attention for controlling downstream

eutrophication, the consequences of water retention need to be fully evaluated (Boughton et al., 2019; Sonnier et al., 2018). For example, water retention could increase wetland water table and depth, and extend hydroperiods, making future wetland edge/middle sites more similar to current center sites. Hence, hydrological restoration in this region might lead to lower litter stabilization (Fig. 3), and thus less carbon sequestration potential (Chamberlain et al., 2017). This possible water-carbon tradeoff in seasonal wetlands due to water retention measures requires further testing in future studies.

Land-use intensification, grazing introduction and fire suppression are all typical anthropogenic management and disturbances in subtropical/tropical wetlands and marshes. Taking ungrazed, burned wetlands embedded in SN as the historical benchmark for a “natural” reference, we found that all types of human disturbances tend to lower litter stabilization and therefore carbon sequestration potentials of seasonal wetlands (Fig. 2). Across all factors examined, intensified land-use of pastures had the strongest adverse impact on wetland decomposition, highlighting the importance of landscape context in wetland management, as well as the need of avoiding land-use intensification surrounding subtropical/tropical seasonal wetlands. Moreover, if pastures must be managed under intensified land-use (e.g., for achieving

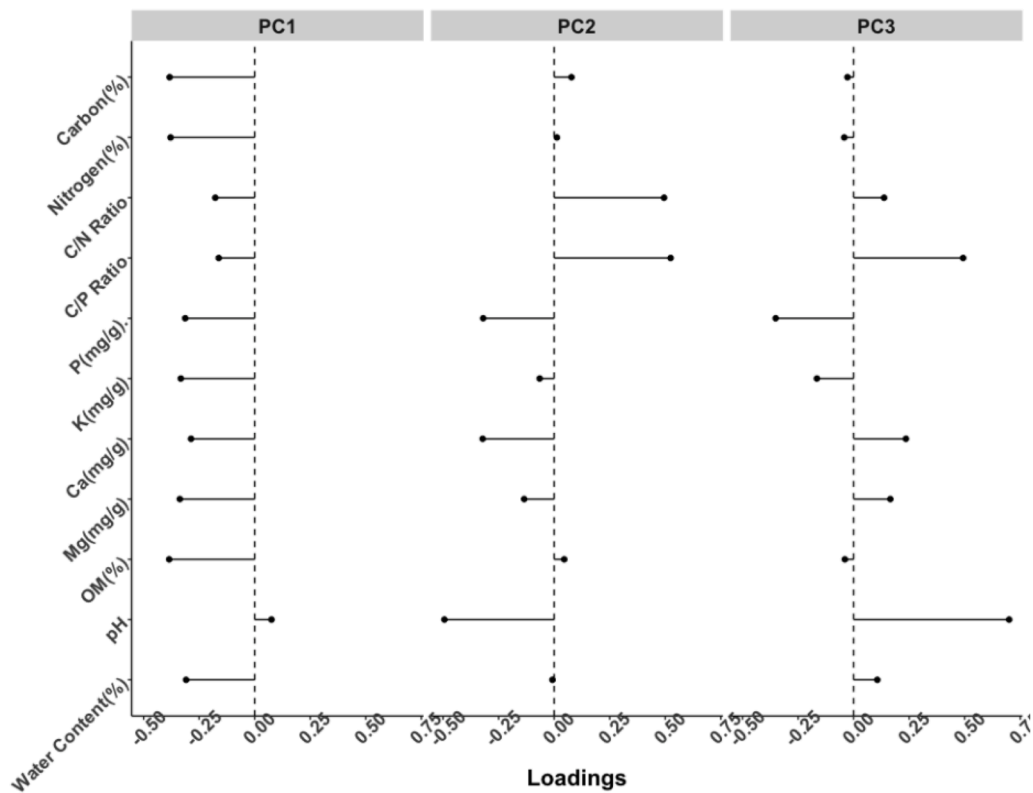


Fig. 4. Loadings of predictor variables from the soil physical-chemistry properties principal component analysis (PCA). Resulting principal component (PC) 1, PC2 and PC3 altogether account for 81.5% of the total variation.

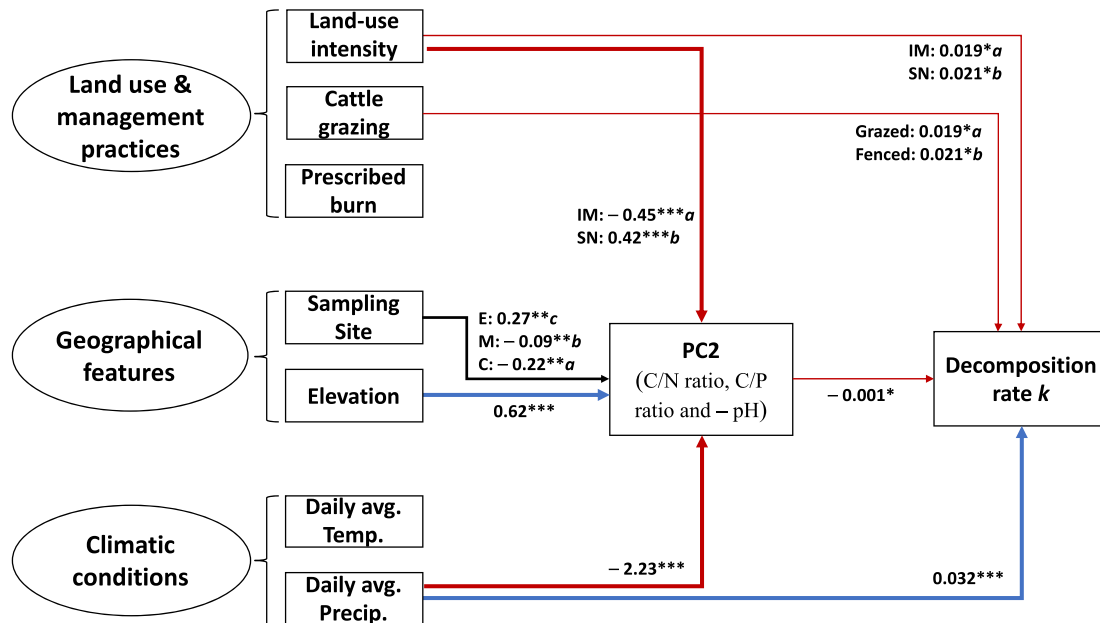


Fig. 5. Structural equation modeling results for decomposition rate k . PC2 represents the second principal component of PCA on soil properties that is primarily defined by soil C/N ratio, C/P ratio and pH. Blue and red arrows represented each significant path (* indicates $p < 0.05$; ** indicates $p < 0.01$; *** indicates $p < 0.001$), with blue and red colors indicate positive and negative treatment effects/relationships, respectively. Nonsignificant treatment effects or relationships ($p > 0.05$) are omitted in the figure for clarity. The thickness of the arrow is proportional to the magnitude of effect size. Post-hoc tests (denoted as letters a, b and c) were performed to denote the level of significance within each group of categorical variables. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

sufficient forage productivity for livestock), it is critical to avoid the combined practices of cattle exclusion and fire suppression. Further, in agricultural areas with focus on cattle production, management under

low-intensities and with periodically prescribed fires could help counteract the potential negative grazing effects on long-term carbon sequestration and nutrients retention in seasonal wetlands.

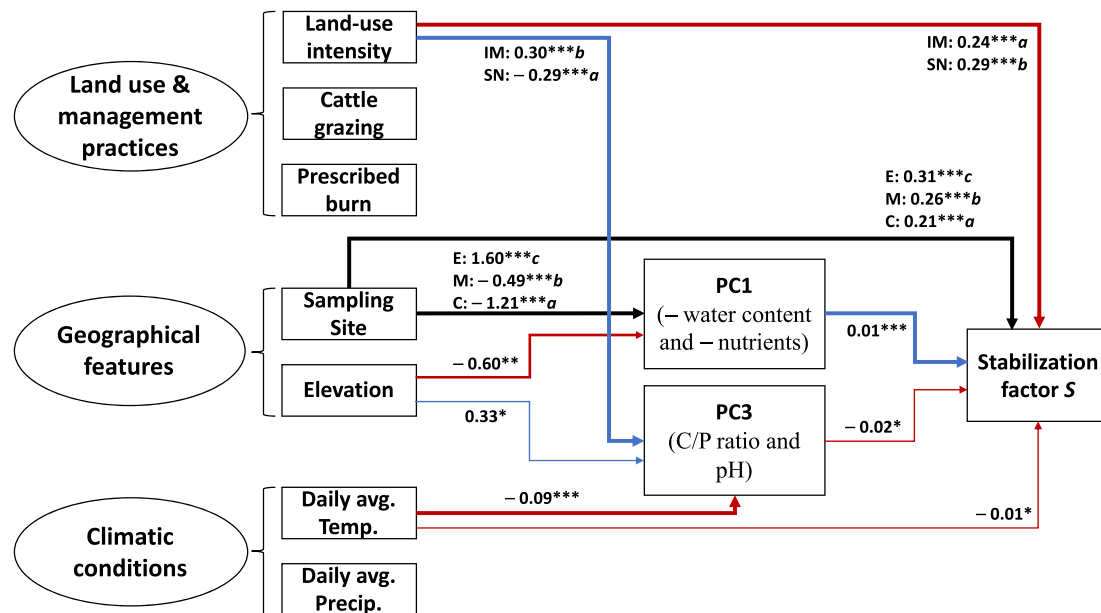


Fig. 6. Structural equation models for stabilization factor S. PC1 represents the first principal component of PCA on soil properties that is primarily defined by soil nutrients and water content, while PC3 is primarily defined by soil C/P ratio and pH. Blue and red arrows indicate positive and negative treatment effects/relationships, respectively (* indicates $p < 0.05$; ** indicates $p < 0.01$; *** indicates $p < 0.001$). Nonsignificant relationships ($p > 0.05$) have been omitted for clarity. The thickness of the arrow is proportional to the magnitude of effect size. Post-hoc tests (denoted as letters a, b and c) were performed to denote the level of significance within each group of categorical variables. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

4.4. Methodological considerations

Several methodological limitations in our study are worth discussion. Human activities and external environmental changes could alter plant stoichiometry, and the structure and composition of plant communities (Boughton et al., 2010, 2016). Our TBI approach cannot capture those indirect effects through vegetational changes, litter quality and local plant-soil-microbe interactions, if any. One example of such plant-microbe interactions is that if certain wetlands are dominated by plants with inherently high lignin content, their local microbial communities are likely to be better adapted and “primed” to process lignin-rich organic matter in the tea bags. Hence, our results primarily reflect how human activities and other induced abiotic factors influence decomposition processes and potentials. Uncovering these complex plant-microbial interactions in wetland decomposition would be a fruitful avenue for future research (e.g., using controlled laboratory experiments). Another potential limitation is that we did not measure wetland decomposition before the initial implementation of management treatments that occurred over a decade ago. Nevertheless, our randomized block design can to some extent control the effects of differences in initial conditions that may confound treatment effects.

5. Conclusion

Our research demonstrates that anthropogenic management practices and disturbances could reduce wetland organic matter decomposition rate and stabilization. If a management goal is to promote carbon sequestration and nutrient retention ecosystem services in wetlands, our results highlight the need to maintain low-intensity land-use on surrounding upland areas and avoid fire suppression especially when cattle are excluded within the wetlands. Estimates from our research fill a key empirical data gap of wetland decomposition in the tropical/subtropical biome, which could help inform earth system models to quantify and predict anthropogenic effects on regional and global carbon and nitrogen cycling in an underrepresented ecosystem. Combining decomposition results with other ecosystem functions and services is a necessary

next step to holistically assess synergies and tradeoffs among diverse management goals and achieve multifunctional agricultural landscapes.

CRediT authorship contribution statement

Yuxi Guo: Conceptualization, Data curation, Formal analysis, Investigation, Visualization, Writing – original draft. **Elizabeth H. Boughton:** Conceptualization, Methodology, Resources, Writing – review & editing. **Jiangxiao Qiu:** Conceptualization, Methodology, Funding acquisition, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank Chase O’Neil, Gregory Sonnier and Steffan Pierre for their assistance with the field fence construction that was used to protect our deployed teabags in grazed wetlands. We thank Dr. Edzard van Santen and Simon Riley from IFAS Statistical Consulting Unit in the University of Florida for their help in the specification of linear mixed-effects models. Funding support of this work comes from USDA National Institute of Food and Agriculture, Hatch (FLA-FTL-005640), McIntire-Stennis (FLA-FTL-005673) and AFRI Foundational and Applied Science Program (GRANT13070634) projects. The initial set-up of the experiment was funded by the United States Department of Agriculture CSREES [#2006-35101-17204], which provided initial funding to set up the experiment and data collection for 4 yr (2006-2009). We thank Laurent Lollis and Gene Lollis for implementing prescribed fires and managing wetland fences for this project. This research is a contribution of the Long-term Agroecosystem Research Network. The LTAR is supported by the United States Department of Agriculture.

Author Contributions

Yuxi Guo: Conceptualization, Data curation, Formal analysis, Investigation, Visualization, Writing - original draft. Elizabeth H. Boughton: Conceptualization, Resources, Methodology, Writing - review & editing. Jiangxiao Qiu: Conceptualization, Methodology, Funding acquisition, Writing - review & editing.

Data Statement

Data and associated codes will be permanently archived in the publicly accessible repository of Dryad if the manuscript is accepted for publication.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2021.108301>.

References

- Aselmann, I., Crutzen, P.J., 1989. Global distribution of natural freshwater wetlands and rice paddies, their net primary productivity, seasonality and possible methane emissions. *J. Atmos. Chem.* 8 (4), 307–358. <https://doi.org/10.1007/BF00052709>.
- Austin, A.T., Méndez, M.S., Ballaré, C.L., 2016. Photodegradation alleviates the lignin bottleneck for carbon turnover in terrestrial ecosystems. *Proc. Natl. Acad. Sci.* 113 (16), 4392–4397. <https://doi.org/10.1073/pnas.1516157113>.
- Bates, D., Maechler, M., Bolker, B., Walker, S., Christensen, R.H.B., Singmann, H., Dai, B., Grothendieck, G., Green, P., Bolker, M.B., 2015. Package 'lme4'. *Convergence* 12 (1), 2.
- Bohlen, P.J., Gathumbi, S.M., 2007. Nitrogen cycling in seasonal wetlands in subtropical cattle pastures. *Soil Sci. Soc. Am. J.* 71 (3), 1058–1065.
- Boughton, E.H., Quintana-Ascencio, P.F., Bohlen, P.J., Fauth, J.E., Jenkins, D.G., Pärt, T., 2016. Interactive effects of pasture management intensity, release from grazing and prescribed fire on forty subtropical wetland plant assemblages. *J. Appl. Ecol.* 53 (1), 159–170.
- Boughton, E.H., Quintana-Ascencio, P.F., Bohlen, P.J., Jenkins, D.G., Pickert, R., 2010. Land-use and isolation interact to affect wetland plant assemblages. *Ecography*. <https://doi.org/10.1111/j.1600-0587.2009.06010.x>.
- Boughton, E.H., Quintana-Ascencio, P.F., Jenkins, D.G., Bohlen, P.J., Fauth, J.E., Engel, A., Shukla, S., Kiker, G., Hendricks, G., Swain, H.M., 2019. Trade-offs and synergies in a payment-for-ecosystem services program on ranchlands in the Everglades headwaters. *Ecosphere* 10 (5), e02728. <https://doi.org/10.1002/ecs2.2728>.
- Boughton, E.H., Quintana-Ascencio, P.F., Nickerson, D., Bohlen, P.J., 2011a. Management intensity affects the relationship between non-native and native species in subtropical wetlands. *Appl. Veg. Sci.* 14 (2), 210–220.
- Boughton, E.H., Quintana-Ascencio, P.F., Bohlen, P.J., 2011b. Refuge effects of *Juncus effusus* in grazed, subtropical wetland plant communities. *Plant Ecol.* 212 (3), 451–460.
- Boughton, E.H., Quintana-Ascencio, P.F., Bohlen, P.J., Michalet, R., 2021. Grazing and microhabitat interact to affect plant-plant interactions in subtropical seasonal wetlands. *J. Veg. Sci.* 32 (1) <https://doi.org/10.1111/jvs.v32.110.1111/jvs.12962>.
- Bowen, J.L., Kearns, P.J., Byrnes, J.E.K., Wigginton, S., Allen, W.J., Greenwood, M., Tran, K., Yu, J., Cronin, J.T., Meyerson, L.A., 2017. Lineage overwheals environmental conditions in determining rhizosphere bacterial community structure in a cosmopolitan invasive plant. *Nat. Commun.* 8 (1), 433. <https://doi.org/10.1038/s41467-017-00626-0>.
- Bremner, J. M. (2018). Nitrogen-Total. In *Methods of Soil Analysis* (pp. 1085–1121). John Wiley & Sons, Ltd. <https://doi.org/10.2136/sssabookser5.3.c37>.
- Brinson, M.M., Lugo, A.E., Brown, S., 1981. Primary productivity, decomposition and consumer activity in freshwater wetlands. *Annu. Rev. Ecol. Syst.* 12 (1), 123–161.
- Chamberlain, S.D., Groffman, P.M., Boughton, E.H., Gomez-Casanovas, N., DeLucia, E. H., Bernacchi, C.J., Sparks, J.P., 2017. The impact of water management practices on subtropical pasture methane emissions and ecosystem service payments. *Ecol. Appl.* 27 (4), 1199–1209.
- Chapin, F.S., Matson, P.A., Mooney, H.A., 2002. *Terrestrial decomposition*. Springer.
- Chen, Z., Xu, Y., Cusack, D.F., Castellano, M.J., Ding, W., 2019. Molecular insights into the inhibitory effect of nitrogen fertilization on manure decomposition. *Geoderma* 353, 104–115. <https://doi.org/10.1016/j.geoderma.2019.06.034>.
- Churchland, C., Grayston, S.J., 2014. Specificity of plant-microbe interactions in the tree mycorrhizosphere biome and consequences for soil C cycling. *Front. Microbiol.* 5 <https://doi.org/10.3389/fmicb.2014.00261>.
- Davidson, N.C., Fluet-Chouinard, E., Finlayson, C.M., 2018. Global extent and distribution of wetlands: trends and issues. *Mar. Freshw. Res.* 69, 620–627.
- DeLucia, N.J., Gomez-Casanovas, N., Boughton, E.H., Bernacchi, C.J., 2019. The role of management on methane emissions from subtropical wetlands embedded in agricultural ecosystems. *J. Geophys. Res. Biogeosci.* 124 (9), 2694–2708.
- Elumeeva, T.G., Onipchenko, V.G., Akhmetzhanova, A.A., Makarov, M.I., Keuskamp, J. A., 2018. Stabilization versus decomposition in alpine ecosystems of the Northwestern Caucasus: The results of a tea bag burial experiment. *Journal of Mountain Science* 15 (8), 1633–1641. <https://doi.org/10.1007/s11629-018-4960-z>.
- Entry, J.A., 2000. Influence of nitrogen on cellulose and lignin mineralization in blackwater and redwater forested wetland soils. *Biol. Fertil. Soils* 31 (5), 436–440.
- Fluet-Chouinard, E., Lehner, B., Rebelo, L.-M., Papa, F., Hamilton, S.K., 2015. Development of a global inundation map at high spatial resolution from topographic downscaling of coarse-scale remote sensing data. *Remote Sens. Environ.* 158, 348–361.
- Ferreira, V., Chauvet, E., 2011. Synergistic effects of water temperature and dissolved nutrients on litter decomposition and associated fungi. *Glob. Change Biol.* 17 (1), 551–564.
- FOG, KÅRE, 1988. The Effect of Added Nitrogen on the Rate of Decomposition of Organic Matter. *Biol. Rev.* 63 (3), 433–462. <https://doi.org/10.1111/brv.1988.63.issue-310.1111/j.1469-185X.1988.tb00725.x>.
- Fujii, S., Mori, A.S., Koide, D., Makoto, K., Matsuoka, S., Osono, T., Isbell, F., Cadotte, M., 2017. Disentangling relationships between plant diversity and decomposition processes under forest restoration. *J. Appl. Ecol.* 54 (1), 80–90. <https://doi.org/10.1111/1365-2664.12733>.
- N. Gomez-Casanovas N.J. DeLucia E.H. DeLucia E. Blanc-Betes E.H. Boughton J. Sparks C.J. Bernacchi Seasonal controls of CO2 and CH4 dynamics in a temporarily flooded subtropical wetland. *Journal of Geophysical Research Biogeosciences* 125 3 2020 e2019JG005257.
- Ho, J., Boughton, E.H., Jenkins, D.G., Sonnier, G., Bohlen, P.J., Chambers, L.G., 2018. Ranching practices interactively affect soil nutrients in subtropical wetlands. *Agric. Ecosyst. Environ.* 254, 130–137. <https://doi.org/10.1016/j.agee.2017.11.031>.
- Hobbie, S.E., 2008. Nitrogen Effects on Decomposition: A Five-Year Experiment in Eight Temperate Sites. *Ecology* 89 (9), 2633–2644. <https://doi.org/10.1890/07-1119.1>.
- Hooper, D., Coughlan, J., Mullen, M.R., 2008. Structural equation modelling: Guidelines for determining model fit. *Electronic Journal of Business Research Methods* 6 (1), 53–60.
- Jansen, L.S., Pierre, S., Boughton, E.H., 2019. Interactions of fire, grazing and pasture management: Short-term and long-term responses of water quality to management regimes in subtropical isolated wetlands. *Agric. Ecosyst. Environ.* 280, 102–113. <https://doi.org/10.1016/j.agee.2019.04.026>.
- Jones, G.L., Scullion, J., Worgan, H., Gwynn-Jones, D., 2019. Litter of the invasive shrub *Rhododendron ponticum* (Ericaceae) modifies the decomposition rate of native UK woodland litter. *Ecol. Ind.* 107, 105597. <https://doi.org/10.1016/j.ecolind.2019.105597>.
- Keuskamp, J.A., Dingemans, B.J.J., Lehtinen, T., Sarneel, J.M., Hefting, M.M., Muller-Landau, H., 2013. Tea Bag Index: A novel approach to collect uniform decomposition data across ecosystems. *Methods Ecol. Evol.* 4 (11), 1070–1075. <https://doi.org/10.1111/2041-210X.12097>.
- Kleinman, P.J.A., Spiegel, S., Rigby, J.R., Goslee, S.C., Baker, J.M., Bestelmeyer, B.T., Boughton, R.K., Bryant, R.B., Cavignelli, M.A., Derner, J.D., Duncan, E.W., Goodrich, D.C., Huggins, D.R., King, K.W., Liebigh, M.A., Locke, M.A., Mirsky, S.B., Moglen, G.E., Moorman, T.B., Pierson, F.B., Robertson, G.P., Sadler, E.J., Shortle, J. S., Steiner, J.L., Strickland, T.C., Swain, H.M., Tsegaye, T., Williams, M.R., Walthall, C.L., 2018. Advancing the sustainability of US agriculture through long-term research. *J. Environ. Qual.* 47 (6), 1412–1425.
- Kollmann, J., Meyer, S.T., Bateman, R., Conradi, T., Gossner, M.M., de Souza Mendonça, M., Fernandes, G.W., Hermann, J.-M., Koch, C., Müller, S.C., Oki, Y., Overbeck, G.E., Paterno, G.B., Rosenfield, M.F., Toma, T.S.P., Weisser, W.W., 2016. Integrating ecosystem functions into restoration ecology—Recent advances and future directions. *Restor. Ecol.* 24 (6), 722–730.
- Lefcheck, J.S., 2016. piecewiseSEM: Piecewise structural equation modelling in R for ecology, evolution, and systematics. *Methods Ecol. Evol.* 7 (5), 573–579.
- Li, Y., Ning, Z., Cui, D., Mao, W., Bi, J., Zhao, X., Hui, D., 2016. Litter Decomposition in a Semiarid Dune Grassland: Neutral Effect of Water Supply and Inhibitory Effect of Nitrogen Addition. *PLoS ONE* 11 (9), e0162663. <https://doi.org/10.1371/journal.pone.0162663>.
- MacDonald, E., Brummell, M.E., Bieniada, A., Elliott, J., Engering, A., Gauthier, T.-L., Saraswati, S., Touchette, S., Turmel-Courchesne, L., Strack, M., 2018. Using the Tea Bag Index to characterize decomposition rates in restored peatlands. *Boreal Environ. Res.* 23 (221–235).
- McLatchey, G.P., Reddy, K.R., 1998. Regulation of organic matter decomposition and nutrient release in a wetland soil. *J. Environ. Qual.* 27 (5), 1268–1274.
- Mehlich, A., 1984. Mehlich 3 soil test extractant: A modification of Mehlich 2 extractant. *Commun. Soil Sci. Plant Anal.* 15 (12), 1409–1416.
- Sousa Moura, J.M., Martens, C.S., Moreira, M.Z., Lima, R.L., Sampaio, I.C.G., Mendlovitz, H.P., Menton, M.C., 2008. Spatial and seasonal variations in the stable carbon isotopic composition of methane in stream sediments of eastern Amazonia. *Tellus B: Chemical and Physical Meteorology* 60 (1), 21–31. <https://doi.org/10.1111/j.1600-0889.2007.00322.x>.
- Odum, W.E., Odum, E.P., Odum, H.T., 1995. Nature's pulsing paradigm. *Estuaries* 18 (4), 547. <https://doi.org/10.2307/1352375>.
- Paul, E., 2014. *Soil microbiology, ecology and biochemistry*. Academic press.
- Petraglia, A., Cacciatori, C., Chelli, S., Fenu, G., Calderisi, G., Gargano, D., Abeli, T., Orsenigo, S., Carbognani, M., 2019. Litter decomposition: Effects of temperature driven by soil moisture and vegetation type. *Plant Soil* 435 (1), 187–200. <https://doi.org/10.1007/s11104-018-3889-x>.
- C. Prigent F. Papa F. Aires W.B. Rossow E. Matthews 112 D12 2007 10.1029/2006JD007847.
- Qiu, J., Turner, M.G., 2013. Spatial interactions among ecosystem services in an urbanizing agricultural watershed. *Proc. Natl. Acad. Sci.* 110 (29), 12149–12154. <https://doi.org/10.1073/pnas.1310539110>.

- Qiu, J., Carpenter, S.R., Booth, E.G., Motew, M., Zipper, S.C., Kucharik, C.J., Chen, X.i., Loheide, S.P., Seifert, J., Turner, M.G., 2018. Scenarios reveal pathways to sustain future ecosystem services in an agricultural landscape. *Ecol. Appl.* 28 (1), 119–134.
- Raymond, P.A., Hartmann, J., Lauerwald, R., Sobek, S., McDonald, C., Hoover, M., Butman, D., Striegl, R., Mayorga, E., Humborg, C., Kortelainen, P., Dürr, H., Meybeck, M., Ciais, P., Guth, P., 2013. Global carbon dioxide emissions from inland waters. *Nature* 503 (7476), 355–359. <https://doi.org/10.1038/nature12760>.
- Reis, V., Hermoso, V., Hamilton, S.K., Ward, D., Fluet-Chouinard, E., Lehner, B., Linke, S., 2017. A Global Assessment of Inland Wetland Conservation Status. *Bioscience* 67 (6), 523–533. <https://doi.org/10.1093/biosci/bix045>.
- Schulte, E.E., Hopkins, B.G., 2015. Estimation of Soil Organic Matter by Weight Loss-On-Ignition. In: *Soil Organic Matter: Analysis and Interpretation*. John Wiley & Sons, Ltd, pp. 21–31. <https://doi.org/10.2136/sssaspepub46.c3>.
- Seelen, L.M.S., Flaim, G., Keuskamp, J., Teurlincx, S., Arias Font, R., Tolunay, D., Fránková, M., Šumberová, K., Temponeras, M., Lenhardt, M., Jennings, E., de Senerpont Domis, L.N., 2019. An affordable and reliable assessment of aquatic decomposition: Tailoring the Tea Bag Index to surface waters. *Water Res.* 151, 31–43. <https://doi.org/10.1016/j.watres.2018.11.081>.
- Solly, E.F., Schöning, I., Boch, S., Kandeler, E., Marhan, S., Michalzik, B., Müller, J., Zscheischler, J., Trumbore, S.E., Schrumpp, M., 2014. Factors controlling decomposition rates of fine root litter in temperate forests and grasslands. *Plant Soil* 382 (1), 203–218. <https://doi.org/10.1007/s11104-014-2151-4>.
- Soltanpour, P.N., Johnson, G.W., Workman, S.M., Jones, J.B., Miller, R.O., 2018. Inductively Coupled Plasma Emission Spectrometry and Inductively Coupled Plasma-Mass Spectrometry. In: *Methods of Soil Analysis*. John Wiley & Sons, Ltd, pp. 91–139. <https://doi.org/10.2136/sssabookser5.3.c5>.
- Song, X., Li, Q., Gu, H., 2017. Effect of nitrogen deposition and management practices on fine root decomposition in Moso bamboo plantations. *Plant Soil* 410 (1–2), 207–215.
- Sonnier, G., Bohlen, P.J., Swain, H.M., Orzell, S.L., Bridges, E.L., Boughton, E.H., Zang, RunGuo, 2018. Assessing the success of hydrological restoration in two conservation easements within Central Florida ranchland. *PLoS ONE* 13 (7), e0199333. <https://doi.org/10.1371/journal.pone.0199333>.
- Sonnier, G., Quintana-Ascencio, P.F., Bohlen, P.J., Fauth, J.E., Jenkins, D.G., Boughton, E.H., 2020. Pasture management, grazing, and fire interact to determine wetland provisioning in a subtropical agroecosystem. *Ecosphere* 11 (8). <https://doi.org/10.1002/ecs2.v11.810.1002/ecs2.3209>.
- Spiegel, S., Bestelmeyer, B.T., Archer, D.W., Augustine, D.J., Boughton, E.H., Boughton, R.K., Cavigelli, M.A., Clark, P.E., Derner, J.D., Duncan, E.W., Hapeman, C. J., Harmel, R.D., Heilman, P., Holly, M.A., Huggins, D.R., King, K., Kleinman, P.J.A., Liebig, M.A., Locke, M.A., McCarty, G.W., Millar, N., Mirsky, S.B., Moorman, T.B., Pierson, F.B., Rigby, J.R., Robertson, G.P., Steiner, J.L., Strickland, T.C., Swain, H. M., Wienhold, B.J., Wulfhorst, J.D., Yost, M.A., Walthall, C.L., 2018. Evaluating strategies for sustainable intensification of US agriculture through the Long-Term Agroecosystem Research network. *Environ. Res. Lett.* 13 (3), 034031. <https://doi.org/10.1088/1748-9326/aaa779>.
- Steffen, W., Sanderson, R.A., Tyson, P.D., Jäger, J., Matson, P.A., Moore III, B., Oldfield, F., Richardson, K., Schellnhuber, H.-J., Turner, B.L., 2006. *Global change and the earth system: A planet under pressure*. Springer Science & Business Media.
- Swain, H.M., Bohlen, P.J., Campbell, K.L., Lollis, L.O., Steinman, A.D., 2007. Integrated ecological and economic analysis of ranch management systems: an example from South Central Florida. *Rangeland Ecol. Manage.* 60 (1), 1–11.
- Swift, M.J., Heal, O.W., Anderson, J.M., Anderson, J.M., 1979. *Decomposition in Terrestrial Ecosystems*. University of California Press.
- Tao, B., Song, C., Guo, Y., 2013. Short-term effects of nitrogen additions and increased temperature on wetland soil respiration, Sanjiang Plain, China. *Wetlands* 33 (4), 727–736.
- Thomas, G.W., 1996. Soil pH and soil acidity. *Methods of Soil Analysis: Part 3 Chemical Methods* 5, 475–490.
- Violita, V., Triadiati, T., Anas, I., Miftahudin, M., 2016. Fine Root Production and Decomposition in Lowland Rainforest and Oil Palm Plantations in Sumatra, Indonesia. *HAYATI Journal of Biosciences* 23 (1), 7–12. <https://doi.org/10.1016/j.hjb.2015.10.008>.
- Wang, Y., Gong, J.-R., Liu, M., Luo, Q., Xu, S., Pan, Y., Zhai, Z., 2015. Effects of land use and precipitation on above- and below-ground litter decomposition in a semi-arid temperate steppe in Inner Mongolia, China. *Appl. Soil Ecol.* 96, 183–191. <https://doi.org/10.1016/j.apsoil.2015.07.010>.
- R. Wehrens B.-H. Mevik The pls package: Principal component and partial least squares regression in R 2007.
- Whigham, D.F., Walker, C.M., Maurer, J., King, R.S., Hauser, W., Baird, S., Keuskamp, J. A., Neale, P.J., 2017. Watershed influences on the structure and function of riparian wetlands associated with headwater streams – Kenai Peninsula, Alaska. *Sci. Total Environ.* 599–600, 124–134. <https://doi.org/10.1016/j.scitotenv.2017.03.290>.
- Zhang, D., Hui, D., Luo, Y., Zhou, G., 2008. Rates of litter decomposition in terrestrial ecosystems: Global patterns and controlling factors. *Journal of Plant Ecology* 1 (2), 85–93. <https://doi.org/10.1093/jpe/rtn002>.