


# Wetland soil carbon storage exceeds uplands in an urban natural area (Florida, USA)

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## ABSTRACT

**Context.** Urban greenspaces and natural areas are often recognised for their cultural services, but may also provide ecological services, including carbon (C) sequestration and storage. **Aims.** This study investigated the strength of the relationship between easily discernible ecosystem characteristics (e.g. topographic position, vegetation, and soil type) and soil C storage, and evaluated common conversion factors and methodologies used in soil C inventories. **Methods.** Sixty-seven full-depth (up to 5 m) soil cores were collected across nine community types in University of Central Florida's Arboretum (Orlando, Florida, USA) and were analysed for bulk density, organic matter (OM) content, total C, and total nitrogen (N). **Key results.** Wetlands stored an average of 16 times more C than uplands and C density increased with soil depth. A 70% underestimation of soil C stocks would have occurred if sampling stopped at 50 cm. A strong linear relationship between soil C and OM supports the use of a 0.56 (C:OM) conversion factor for estimating soil organic C. **Conclusions.** The presence of wetlands is the key predictor of soil C and N storage, but the magnitude of storage varies widely among wetlands. Overall, the 225-ha study area stored  $85\,482 \pm 3365$  Mg of soil C. **Implications.** Urban natural areas should be evaluated for their ecosystem services separately from their surrounding developed land use/land cover with consideration for C storage potential. Leveraging topographic position, a site-specific soil OM conversion factor, and depth to refusal testing can increase the accuracy and cost-effectiveness of soil C inventories.

**Keywords:** biogeochemistry, carbon inventory, climate change, soil carbon, soil type, uplands, urbanization, wetlands.

## Core ideas

- Topographic position is the most robust predictor of soil C and N stocks and densities
- Wetlands averaged 16 times greater soil C content (per m<sup>2</sup>) than uplands
- Soil organic matter content can be used to predict organic C with a 0.56 conversion factor
- Wetland soil C stocks would be underestimated by 70% if sampled only to 50 cm
- Urban natural areas can serve as significant C sinks

## Introduction

Soil carbon (C) quantification studies have become increasingly common due to the relevance to global climate change (e.g. [Chmura \*et al.\* 2003](#); [Heimann and Reichstein 2008](#); [Ausseil \*et al.\* 2015](#); [Petrescu \*et al.\* 2015](#)) and the acknowledgement that soil often represents a larger and longer-term reservoir for C than vegetative biomass ([Reddy and DeLaune 2008](#); [Ontl and Schulte 2012](#)). As a key component of the global C cycle, the soil C reservoir can serve as a natural climate solution through the preservation and restoration of natural soil C sinks ([Bossio \*et al.\* 2020](#)), but additional data are needed from diverse ecosystems and locations to better inform land-based climate mitigation strategies ([Malhotra \*et al.\* 2019](#)).

In the past, scientific research related to soil C often focused on how agriculture and land management practices affect organic matter (OM) quantity and quality, and thus soil

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C storage (e.g. Barnwell *et al.* 1992; McLauchlan 2006; Abbas *et al.* 2020; Kumar *et al.* 2020). As human population and urban expansion progress world-wide (WWT Consulting 2018; United Nations, Department of Economic and Social Affairs, and Population Division 2019), additional research is warranted to better understand the factors influencing soil C storage in urban landscapes. For example, soil grading, excavating, and filling have been shown to influence soil properties, including C storage (Herrmann *et al.* 2020). Urbanisation (e.g. infrastructure development, alteration of hydrology, and fire suppression) can accelerate soil erosion (Myers and Ewel 1990; Dahl 2000; Reiss 2006), diminish vegetation coverage (McDonald 2008; McKinney 2008; Hutryra *et al.* 2011; Seto *et al.* 2012), and reduce overall soil C storage (Lal 2003; Roose *et al.* 2006; Ito 2007). Habitat fragmentation often results from urbanisation (Myers and Ewel 1990), leaving only small pockets of natural areas (defined here as undeveloped lands managed to promote native flora, fauna, and ecosystem processes) or greenspaces (defined here as open areas and parks containing vegetation) within a matrix of infrastructure development. Under traditional ecosystem service evaluations, natural areas and greenspaces within an urban matrix would often be lumped together under the categorisation 'urban' and considered to have no or negligible ecosystem services (Costanza *et al.* 1997; Zang *et al.* 2011). This contradicts numerous studies documenting that development buffers around sensitive aquatic ecosystems (e.g. wetlands and rivers) and the preservation of urban natural areas and greenspaces (e.g. semi-natural ecosystems, parks, and arboretums), can indeed provide many ecosystem services (Alberti *et al.* 2003; Groffman *et al.* 2004; Fuller *et al.* 2007; Niemelä *et al.* 2010; Jenerette *et al.* 2011; Ahn and Schmidt 2019). Therefore, it is important to provide additional quantification of the ecosystem services that urban natural areas provide, particularly in relation to a current knowledge gap regarding their ability to function as a soil C sink.

The capacity of soils to store C is highly variable and can be influenced by any factor that affects the balance between C inputs (photosynthesis and deposition) and C outputs (decomposition and export). On large spatial scales, latitude and climate are the primary determinants of soil C storage (Hobbie *et al.* 2000; Schuur *et al.* 2001; Davidson and Janssens 2006; Ontl and Schulte 2012), while hydrology (Carvalhais *et al.* 2014), soil type (Morisada *et al.* 2004; Conforti *et al.* 2016; Paz *et al.* 2016), vegetation composition (Jobbágy and Jackson 2000), and natural disturbances (O'Donnell *et al.* 2011; Richards *et al.* 2011; Griffiths and Mitsch 2021) can account for much of the local and regional spatial and temporal variation in soil C. On an ecosystem scale, wetlands have been shown to store a disproportionately high amount of soil C relative to their land area due to the combination of high primary production and anaerobic soil conditions that slow the decomposition of OM (Heimann and Reichstein 2008; Reddy and DeLaune 2008). However, the quality and coverage

of wetlands tends to decrease as the natural hydrology is replaced with the engineered ditches, drains, and retention ponds that often accompany urbanisation (Myers and Ewel 1990; Kuhn *et al.* 1999; Portnoy 1999). While there is significant research on wetland soil C storage, much of this work has focused on 'blue carbon' wetlands (e.g. seagrass beds, salt marshes, and mangroves; Sanders *et al.* 2010; McLeod *et al.* 2011; Ouyang and Lee 2014; Alongi 2018; Breithaupt *et al.* 2020), with estimates that salt marsh and mangrove wetlands store up to 10 000 Tg C globally (Chmura *et al.* 2003). However, freshwater wetlands cover significantly more area than coastal wetlands, e.g. 95% of all wetlands in the US are freshwater (Dahl 2011), and are therefore estimated to hold 12 times more total soil C than saline wetlands (Nahlik and Fennessy 2016). In addition to wetland area, the depth of the organic soil layer (e.g. peat layer) must also be considered. Many studies quantifying soil C only collect the top 50 or 100 cm of the soil (e.g. Chmura *et al.* 2003; Duarte *et al.* 2013; Davila and Bohlen 2021; Dayathilake *et al.* 2021), despite peat thickness being known to exceed 8 m in some regions of the world (Page *et al.* 2011). Therefore, the loss or conversion of wetlands during urbanisation, particularly deep peat-forming wetlands (i.e. histosol soils), can have far greater impacts on the local and regional C balance than the alteration of other habitat types.

Identifying and conserving areas of high soil C storage could be incorporated into urban development planning that strives for environmental sustainability. The destruction of soil C hotspots (i.e. areas that serve as significantly greater net C sinks than the surrounding lands) not only causes the direct release of soil C as greenhouse gases (e.g. CO<sub>2</sub> and CH<sub>4</sub>), but also results in an opportunity cost for all the future atmospheric C that the natural ecosystem could have sequestered had they been conserved (Friedlingstein *et al.* 2006; McLeod *et al.* 2011; Ausseil *et al.* 2015). These ecological services would be further enhanced by recognising and targeting areas of high soil C storage, such as pockets of wetlands in urbanised landscapes, which provide the additional benefits of C off-sets, nutrient burial [including total nitrogen (N) storage], and biogeochemical cycling (Reddy and DeLaune 2008; Dayathilake *et al.* 2021).

Soil C inventories, or the quantitative assessment of the soil C density (mass per volume) or soil C stock (mass per area), could be leveraged as a tool for identifying ideal areas for development buffers, greenspaces, and natural areas. However, landscape-scale soil C quantification can be costly and time consuming, often requiring specific equipment and expertise, making proxies for estimating soil C a desirable alternative. Using soil OM content to estimate soil organic C content is one of the most widely used proxies, with the understanding that organic C and total C are comparable in carbonate-free soils (henceforth referred to simply as C) (Craft *et al.* 1991; Dayathilake *et al.* 2021). The benefit of this approach is that soil OM content can be quantified by loss on ignition (LOI), a straight-forward, fast, and economical

method compared to total C analysis, which requires an elemental analyser. However, conversion factors for soil OM to C can range from 0.22 to 0.60; clay content, unrecognised carbonate content, and soil age have all been cited as possible causes for this variability (Craft *et al.* 1991). Additionally, soil OM content, latitude, soil depth, and dominant vegetation have been shown to alter C:OM (Craft *et al.* 1991; Fourqurean *et al.* 2014; Ouyang and Lee 2020), suggesting that a unique conversion factor for different soil or ecosystem types may be needed, particularly when considering a landscape mosaic. These uncertainties warrant additional research to improve the accuracy of C:OM conversion factors and determine if easily discernible ecosystem characteristics (e.g. upland vs wetland, woody vs herbaceous plants, and vegetation community type) or existing data [e.g. Natural Resource Conservation Service (NRCS) soil classification] may serve as a predictor of soil C storage. Leveraging empirical predictors of soil C could allow land managers and urban planners to easily incorporate soil C as a decision-making tool, with little or no need for direct soil analysis. This study sought to fill this knowledge gap by determining which data or ecosystem characteristics are the most robust predictors of soil C. By quantifying total soil N, in addition to C, the study also examined soil N storage and the soil C:N ratio as an indicator of soil quality and degradability (Franzluebbers 2002; Adebeye *et al.* 2011), which may differ based on soil or ecosystem characteristics.

The goal of this study was to quantify soil C storage (encompassing both stock and density) in an urban natural area located within Orlando, Florida, USA to determine its contribution as a potential soil C sink, while also evaluating the existence of large-scale transferable trends between soil C storage and (1) topographic position (upland and wetland), (2) vegetation morphology (woody and herbaceous), (3) vegetation community type, (4) NRCS soil type, and (5) soil depth. Secondly, this study sought to add to the body of knowledge about the relationships between different soil properties (i.e. C:N, C:OM, and N:OM) to determine both the strength of the relationship, and how they may differ based on the above-mentioned ecosystem characteristics. Finally, methodology for sampling deep histosols in freshwater wetlands is evaluated, including the use of full-depth coring (to refusal) and the accuracy of data interpolation between depth subsamples.

## Methods

### Site description

This study took place on the main campus of the University of Central Florida (UCF), the largest university in Florida and second largest university in the USA, based on enrolment (UCF 2020). Located on the eastern edge of the Greater Orlando metropolitan area, a region of over 2.6 million, the

area around UCF is characterised by a steady increase in infrastructure development, following guidelines designed to conserve critical natural areas (Municipal Code Corporation and the City of Orlando, Florida 2021). Within the boundaries of the 567-ha campus, 324 ha are natural lands of various habitats (i.e. multiple types of upland flatwoods, hammock, and sandhill, as well as diverse wetlands, such as basin and dome swamp, baygall, and marsh) and in a range of ecological conditions. This natural area was dedicated to the UCF Arboretum in 1983 and is actively managed using prescribed fire and invasive species removal (UCF Arboretum 2021). The study site is located at 28.6006°N and 81.1968°W, has an elevation 25 m above sea level, and is characterised by a hot rainy season (approximately June–October) and a cooler dry season (approximately November–May); mean monthly temperature range is 22–33°C and mean annual precipitation is 132 cm (Weather and Climate 2020). Although the UCF Arboretum itself is already under conservation with limited development pressure, it is an ideal case study for the types and diversity of ecosystems in the surrounding natural landscape that are under increasing development pressure. This diversity of habitat and soil types also allows for a robust evaluation of patterns and relationships that will be transferable to other regions.

### Field site selection and sampling

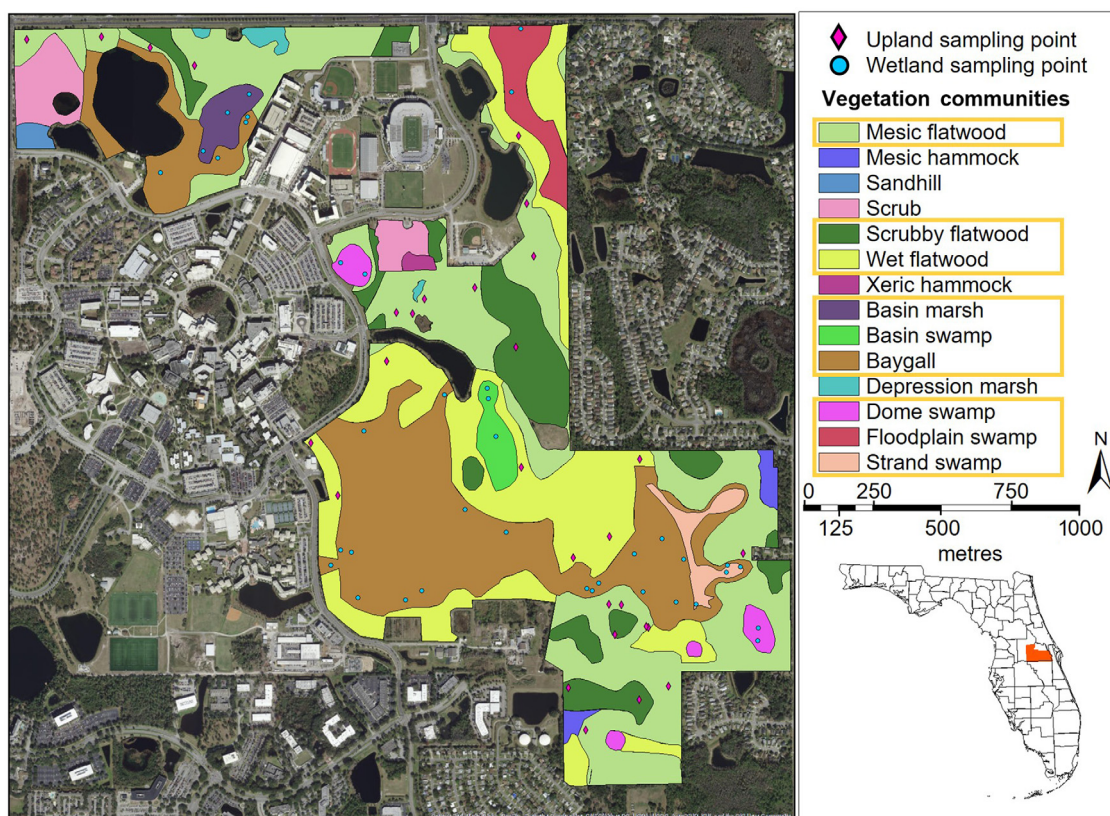
An existing habitat shapefile developed by the Florida Natural Areas Inventory (FNAI 2019) was leveraged in ArcMap (ver. 10.6.1) to categorise the campus natural lands into two broad ecosystem types, upland and freshwater wetland, and further into 14 unique vegetation community types. The nine dominant vegetation community types (encompassing 225 ha of the 324 ha) were chosen for this study to ensure adequate replication was possible within each community type (Table 1).

Using the projection NAD\_1983\_HARN\_UTM\_Zone\_17N for the basemap and importing land cover and soil type shapefiles, sampling points for each community type were proportioned by dividing community type by the total study area. After using a fishnet tool to create a sampling grid, a 10 m buffer in the study area was generated to ensure sampling points were not too close to another community type or the edge of the arboretum. Stratified random sampling in ArcMap distributed 67 points within the sampling grid that were both within the sampling area and proportioned to distribute 38 points in wetland sites and 29 points in upland sites within nine of the 14 vegetation community types present in the study area (Fig. 1). This weighting between wetland and upland sites was chosen using our ecological knowledge that the average wetland stores more soil C than the average upland, but with more spatial variability. Therefore, to increase the accuracy of our site-wide soil C storage inventory we sought a slightly larger sampling effort in wetland habitats. Sampling points were imported from ArcMap to a handheld GPS (Garmin Montana 650 t; Olathe,

**Table 1.** Distribution of sampling points by vegetation community type and associated ecosystem characteristics.

Community type	Wetland <i>n</i>	Upland <i>n</i>	Total area ha	Areal cover %	Soil type	Vegetation morphology
Basin marsh	3		4	1.8	Bas	He
Basin swamp	3		4	1.8	Bas	Wo
Baygall	22		64	28.4	Bas; Sam; San; Smy	Wo
Dome swamp	4		2	0.9	Bas; San	Wo
Floodplain swamp	2		7	3.1	Fel; Smy	Wo
Strand swamp	4		4	1.8	Sam; Smy	Wo
Mesic flatwood		17	67	29.8	Bas; Smy; Zol	Wo; He
Scrubby flatwood		4	23	10.2	Pom	Wo; He
Wet flatwood		8	50	22.2	Fel; Smy	Wo
Total	38	29	225	100		

Bas, basinger fine sand; Fel, felda fine sand; Pom, pomello fine sand; Sam, samsula-hontoon-basinger; San, sanibel muck; Smy, smyrna fine sand; Zol, zolfo fine sand; He, herbaceous plant dominated; Wo, woody plant dominated.



**Fig. 1.** Site map of vegetation community type and sampling point distribution located in the UCF Arboretum, FL, USA. Land cover shapefiles were provided by Florida Natural Areas Inventory (FNAI 2019). Sampling areas were ground-truthed; thus, some locations were altered in ArcMap (10.6.1). Gold boxes represent sampled vegetation communities.

KS, USA) to navigate to the field locations. Soil sampling occurred over a period of 20 days from 30 May to 15 July 2019. Field observations on dominant plant species, vegetation density, and other relevant site information were noted at each point to confirm that the point characteristics matched the

mapped community type on the FNAI shapefile. The NRCS Soil Survey Geographic Database (SSURGO) was used to determine the spatial distribution of soil types across the study area.

Three soil sampling tools were employed for the study, based on the soil conditions at each sampling point. For all

upland points ( $n = 29$ ) a gouge auger (50 cm horseshoe-shaped sampling chamber with an area of 4.60 cm<sup>2</sup>; Eijkelkamp Soil and Water, Netherlands) was used to collect the top 0–20 cm of soil. Due to the resistance provided by the sand that dominated the upland points, it was not possible to extract samples deeper than 20 cm. If a duff layer (a layer of identifiable decomposing OM above the A horizon) was present at the upland points, its depth was recorded, the duff layer removed, and the soil surface (0 cm) considered to be directly below the duff layer. At the wetland points ( $n = 38$ ) the above-mentioned gouge auger, a Russian peat borer [50 cm long half-circle (5.2 cm diameter) sampling chamber with an area of 9.8 cm<sup>2</sup>; with up to 10 1-m long extensions; Eijkelkamp Soil and Water] or a polycarbonate core tube bevelled on the bottom edge [1 m long circle (7 cm diameter) with an area of 38.48 cm<sup>2</sup>] were used. The choice of collection instrument was determined through trial and error, with the final decision based on which instrument was able to collect an intact column of soil without visible compaction of the surface, or loss of material upon extraction from the ground. At each sampling point, the instrument was noted and the subsequent bulk density calculations based on the appropriate core tube volume. For each wetland point, a 20 cm sample was taken every 100 cm (e.g. 0–20, 100–120, 200–220 cm depth, etc.) until refusal, which was indicated by stratigraphic change occurring from high OM peat to underlying sand or bedrock. For samples that reached stratigraphic change in-between a sampling interval, a sample was collected from the deepest 20 cm before the change occurred. All samples were immediately sealed in polyethylene bags, stored on ice, and transported back to the laboratory for analysis.

### Soil physicochemical properties

Bulk soil samples ( $n = 107$ ) were immediately weighed upon return to the laboratory, then homogenised by hand. Soil moisture content (%) was determined by weighing a 40–50 g subsample of each soil into an aluminium weigh dish, drying at 70°C in a gravity oven (ThermoFisher Scientific, Waltham, MA, USA) until constant weight (minimum of 3 days), and reweighing for gravimetric water content. Bulk density (g cm<sup>-3</sup>) was calculated as the total dry mass of the sample divided by the volume of the 20-cm section of the core instrument used to collect that sample. Following drying, samples were ground using a mortar and pestle and transferred to 20-mL scintillation vials. One ceramic mill ball was added to the sample vial and it was placed on a Spex 8000 mixer/mill (Spex Sample Prep, Metuchen, NJ, USA) for up to 5 min, until ground to individual particle size. A subsample of 0.3–0.4 g of soil was weighed in a 50-mL glass beaker and ashed in a muffle furnace (ThermoFisher Scientific) at 550°C for 4 h. Soil OM content was calculated as the difference in mass before and after ashing, following the LOI method (Dean 1974). To confirm inorganic C was not present in our soils and total C

was indicative of organic C content, 10 randomly selected soil samples (including five upland and five wetland sites) were burned in the muffle furnace (as described above for LOI) and only the remaining inorganic ash analysed for total C. Total C and total N content were determined for each sample using a dried ground subsample (4.8–5.4 mg) with a MicroVario CN Analyser (Elementar Americas, Inc., Ronkonkoma, NY, USA). The C:N was calculated on a per mole basis as total C/12:total N/14.

### Calculations

Soil C storage was calculated on an area-basis (stock) and a concentration-basis (density) basis. First, percent (%) C, as determined by elemental analysis (Elementar Americas, Inc., Ronkonkoma, NY), was converted to g C kg<sup>-1</sup> using Eqn 1. This is referred to as C density.

$$\% \text{ C} = \frac{\text{gC}}{100 \text{ g}} \times \frac{1000 \text{ g}}{1 \text{ kg}} = \frac{\text{gC}}{\text{kg}} \quad (1)$$

Then, dry bulk density (g cm<sup>-3</sup>) and the depth of the soil for that sample (cm) were used to calculate soil C by area (g cm<sup>-2</sup>), followed by a unit conversion to Mg ha<sup>-1</sup>, using Eqn 2. This is referred to as C stock.

$$\begin{aligned} \frac{\text{gC}}{\text{kg}} \times \frac{\text{g}}{\text{cm}^3} \times \frac{0.001 \text{ kg}}{1 \text{ g}} \times \text{cm} \\ = \frac{\text{gC}}{\text{cm}^2} \times \frac{100\,000\,000 \text{ cm}^2}{1 \text{ ha}} \times \frac{1 \text{ Mg}}{1\,000\,000 \text{ g}} = \frac{\text{MgC}}{\text{ha}} \quad (2) \end{aligned}$$

For deep cores (>20 cm), C content for missing depth segments was estimated by interpolating the total C content of the adjacent soil segments using weighted averages based on the distance to a known sample concentration. This resulted in a representative C density value for the following depth segments in deep cores: 0–20, 20–50, 50–100, 100–200, 200–300, 300–400, and 400–500 cm, as applicable to each core based on the depth to refusal. Stock (Mg ha<sup>-1</sup> for the full depth of the soil) was calculated as the sum of total C in the entire soil core, surface (0 cm) to refusal depth. Soil N density and N stocks (Mg N ha<sup>-1</sup>) were calculated in the same manner as C stocks.

This method of weighted interpolation used to estimate the soil C and N density for unsampled depth segments was validated by collecting triplicate cores at the deep representative wetland point and analysing total C and N in every 10-cm depth segment within 0–460 cm deep (refusal depth for this sampling point). These analytical values were then compared to those collected using the above-described method (i.e. collecting one 20-cm sample every 100 cm and using weighted interpolation to estimate the soil properties for the unsampled depths). Relative standard deviation (RSD) was then calculated to compare the true (analytical)

C content ( $\text{g kg}^{-1}$ ) for each 10-cm depth interval and composited depth interval to the interpolated (calculated) value.

Landscape-scale C storage was calculated by multiplying the arithmetic mean C stock ( $\text{Mg ha}^{-1}$ ) for the site descriptor of interest by the area it occupied within the study area (ha). A depth-weighted mean C stock was also calculated for wetland soils only. Wetland soil stocks were binned based on the maximum depth of the peat deposit (i.e. depth to refusal, such as 20, 50, and 100 cm), and mean C stock calculated for each bin. This mean was then multiplied by the proportion of wetland area found to contain this depth of peat and summed to estimate total wetland soil C.

## Data analysis

Statistical analyses were conducted using R ver. 4.0.4 in R Studio (ver. 1.4.1103; R Foundation for Statistical Computing, Vienna, Austria). First, all datasets were tested to see if the parametric assumptions of normality (Shapiro–Wilk test) and homogeneity of variance (Levene’s test) were met; significance was set at  $\alpha = 0.05$  for all tests. The data violated both assumptions, so the nonparametric tests of Mann–Whitney U (only two groups) and Kruskal–Wallis H (more than two groups) were performed using the untransformed data. A Dunn’s *post hoc* rank sum comparison was performed following the Kruskal–Wallis H test (using the `kruskalmc` function) to identify significant differences between multiple groups. Soil C:OM ratios were determined based on the slope ( $b$ ) of the line, using the formula:  $Y = bX + a$ . Where  $Y = \% \text{ total C or total N}$ ,  $X = \% \text{ OM}$  (obtained via LOI), and  $a = y\text{-intercept}$ . Only direct field-derived data were used in regressions.

## Results

### Method validation

The representative deep wetland core used to validate the use of weighted-average interpolation data for unsampled soil depth segments had total C ( $\text{g kg}^{-1}$ ) RSD values for every 10-cm soil depth increment (to 460 cm) in the range of 0.12–5.08 (mean = 2.05; median = 1.69). The RSDs by 10-cm segments for soil N ranged within 0.33–21.3 (mean = 8.98; median = 8.82; Fig. 2). For both total C and total N, the RSDs for the composited depth segments (e.g. 0–20, 20–50, 50–100 cm, etc.) were lower than when calculated on a 10-cm depth increment basis (means = 1.59 and 6.50, for total C and total N, respectively).

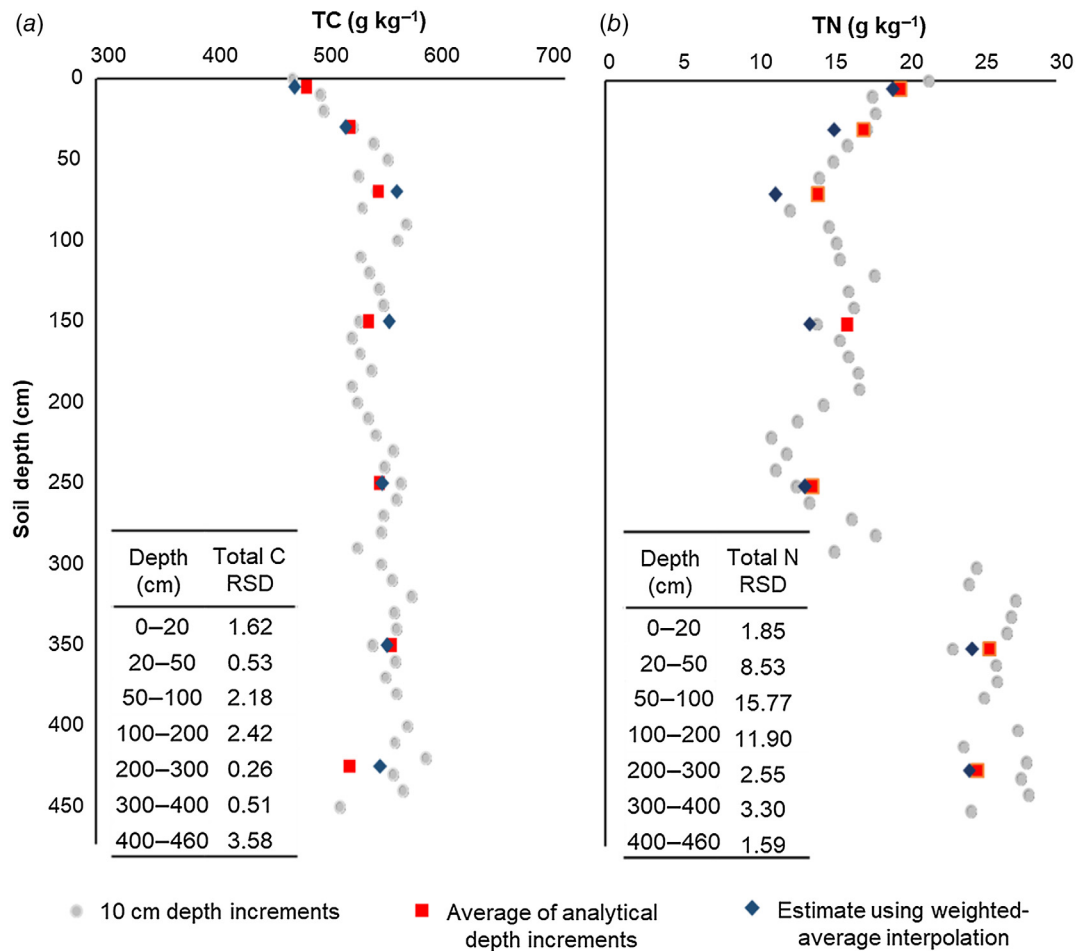
The 10 randomly selected soil samples, used to confirm that there was negligible carbonate content at the research site, spanned the entire geographic area of the site; total C content was in the range of 7.5–483  $\text{g kg}^{-1}$  C. Following application of the LOI method, the same samples had

inorganic C contents of range 0.48–0.76  $\text{g kg}^{-1}$  C. The area under the curve for the C chromatographs of the inorganic C samples was  $80.7 \pm 6.0$ , which was lower than the area under the curve for seven blanks (empty tins) run in the same analytical run ( $87.3 \pm 31.2$ ), indicating that inorganic C content was below the lower detection limit of the instrument. Henceforth, all C data are presented as simply ‘C,’ which can be considered equivalent to both total C and organic C at this study site.

### Soil C inventory

Both soil C stock [Mann–Whitney test statistic ( $U$ ) = 63,  $P < 0.001$ ] and soil C density ( $U = 46$ ,  $P < 0.001$ ) differed significantly based on topographic position. Specifically, wetland soils averaged 16 times more C stock ( $940 \pm 158 \text{ Mg ha}^{-1}$ ) and eight times greater C density ( $270 \pm 27 \text{ g kg}^{-1}$ ) than upland soils ( $58 \pm 7 \text{ Mg ha}^{-1}$  and  $32 \pm 4 \text{ g kg}^{-1}$ , respectively, Fig. 3a, b). Soil C stocks did not differ by dominant plant morphology (woody vs herbaceous), but soil C density was slightly higher at woody-dominated sites ( $187 \pm 24 \text{ g kg}^{-1}$ ) compared to herbaceous sites ( $65 \pm 22 \text{ g kg}^{-1}$ ;  $U = 188$ ;  $P = 0.04$ ; Fig. 3c, d). Vegetation community type was a significant predictor of soil C stock [Kruskal–Wallis test statistic ( $H$ ) = 43,  $P < 0.001$ ] and soil C density ( $H = 47$ ,  $P < 0.001$ ; Fig. 3e, f). The strand swamp community had the maximum C stock in the study ( $3461 \text{ Mg ha}^{-1}$ ), but also the greatest variation among the community types ( $1527 \pm 736 \text{ Mg ha}^{-1}$ ;  $n = 4$ ; Fig. 3e). Strand swamp C stocks were greater than scrubby flatwoods ( $19 \pm 4 \text{ Mg ha}^{-1}$ ;  $n = 4$ ), while baygall swamp ( $999 \pm 213 \text{ Mg ha}^{-1}$ ;  $n = 22$ ) was greater than both scrubby flatwoods and mesic flatwoods ( $55 \pm 9 \text{ Mg ha}^{-1}$ ;  $n = 17$ ). Average soil C density was greatest in the baygall swamp ( $314 \pm 68 \text{ g kg}^{-1}$ ), which was significantly different to the scrubby flatwoods ( $9.0 \pm 1.9 \text{ g kg}^{-1}$ ) and wet flatwoods ( $49 \pm 8 \text{ g kg}^{-1}$ ;  $n = 8$ ).

Seven NRCS soil types were found within the study area and showed differences in both C stocks ( $H = 33$ ,  $P < 0.001$ ) and C density ( $H = 33$ ,  $P < 0.001$ ; Fig. 3g, h). Smyrna fine sand was the most common soil classification ( $n = 26$ ), with 81% of points within this classification being within the mesic or wet flatwoods communities and having a relatively uniform soil C stock ( $68 \pm 8 \text{ Mg ha}^{-1}$ ). However, the final five points classified as smyrna fine sand were wetland points, [baygall swamp (1), basin swamp (1), stand swamp (2), and floodplain swamp (1)], which added significant variance to this soil type, moving the mean from 68 to  $211 \pm 131 \text{ Mg ha}^{-1}$ . Samsula–hontoon–basinger ( $n = 14$ ) had the highest soil C stock ( $1234 \pm 258 \text{ Mg ha}^{-1}$ ) and was found only in baygall swamp (12 of 14) and strand swamp (2 of 14) communities. Sanibel muck ( $n = 10$ ) was also found in only two community types [baygall swamp (8) and dome swamp (2)] and averaged  $611 \pm 288 \text{ Mg ha}^{-1}$ .



**Fig. 2.** Soil total carbon (TC) density (a) and total nitrogen (TN) density (b) with depth for a representative deep wetland soil core. Grey circles represent the analytical concentration of a composited triplicate core by 10-cm depth increments. Red squares represent the averages of these analytical samples binned by the depth segments used in this study. Blue diamonds represent actual study data from a nearby core where only a 20-cm segment was collected and analysed for every 100 cm of soil, then a weighted-average was calculated to interpolate the concentrations in the missing/unsampled depth segments. The relative standard deviation (RSD) tables display the difference between the analytical average and the interpolated average.

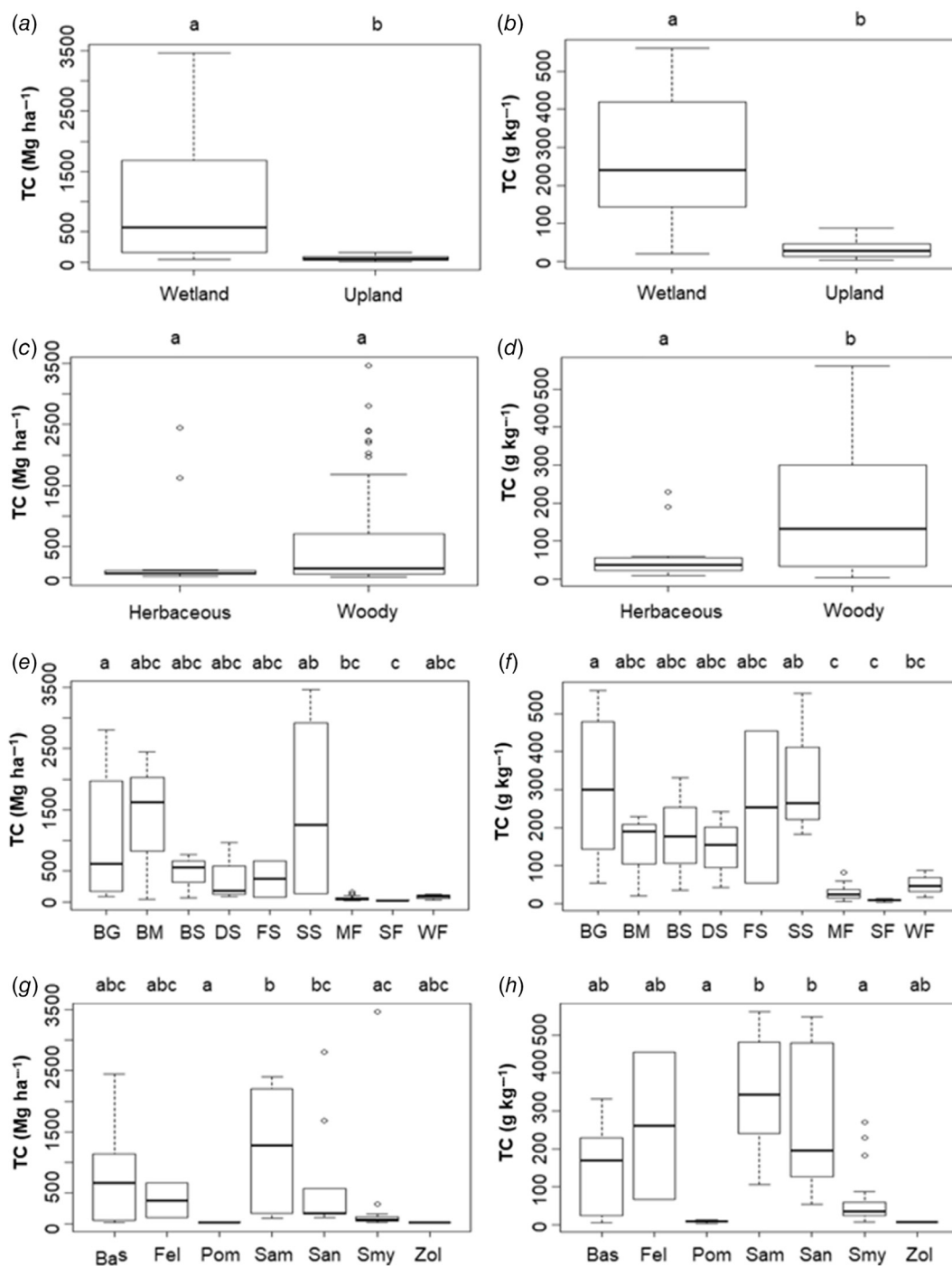
### Soil N content and C:N ratios

Similar to soil C, soil N stocks differed significantly by topographic position and were 23 times higher in wetland soils ( $28.9 \pm 5.2 \text{ Mg ha}^{-1}$ ) than upland soils ( $1.25 \pm 0.2 \text{ Mg ha}^{-1}$ ;  $U = 29$ ,  $P < 0.001$ ; Fig. 4a). Soil N density was also 12 times higher in wetland soils ( $8.59 \pm 0.83 \text{ g kg}^{-1}$ ) than upland soils ( $0.70 \pm 0.12 \text{ g kg}^{-1}$ ;  $U = 28$ ,  $P < 0.001$ ; Fig. 4b). This resulted in an atomic C:N of  $58.0 \pm 2.7$  in upland soils and  $38.8 \pm 1.9$  in wetland soils ( $U = 907$ ,  $P < 0.001$ ; Fig. 4c). The density of soil N was slightly greater in soils dominated by woody vegetation ( $5.8 \pm 0.8 \text{ g kg}^{-1}$ ) relative to herbaceous-dominated soils ( $2.1 \pm 0.5 \text{ g kg}^{-1}$ ;  $U = 188$ ,  $P = 0.04$ ), but C:N did not differ between woody and herbaceous-dominated soils. Soil N stocks and densities also differed by vegetation community ( $H = 46$  and  $47$ , respectively, both  $P < 0.001$ ) and soil type ( $H = 33$  and  $37$ , respectively, both  $P < 0.001$ ),

mimicking the patterns for soil C stocks and densities. Dome swamp had the lowest soil C:N ( $26.4 \pm 1.4$ ) and was significantly less than mesic ( $57.8 \pm 2.5$ ) and wet ( $63.7 \pm 8.0$ ) flatwood communities ( $H = 34$ ,  $P < 0.001$ ). Soil C:N did not differ based on soil depth (Fig. 5c).

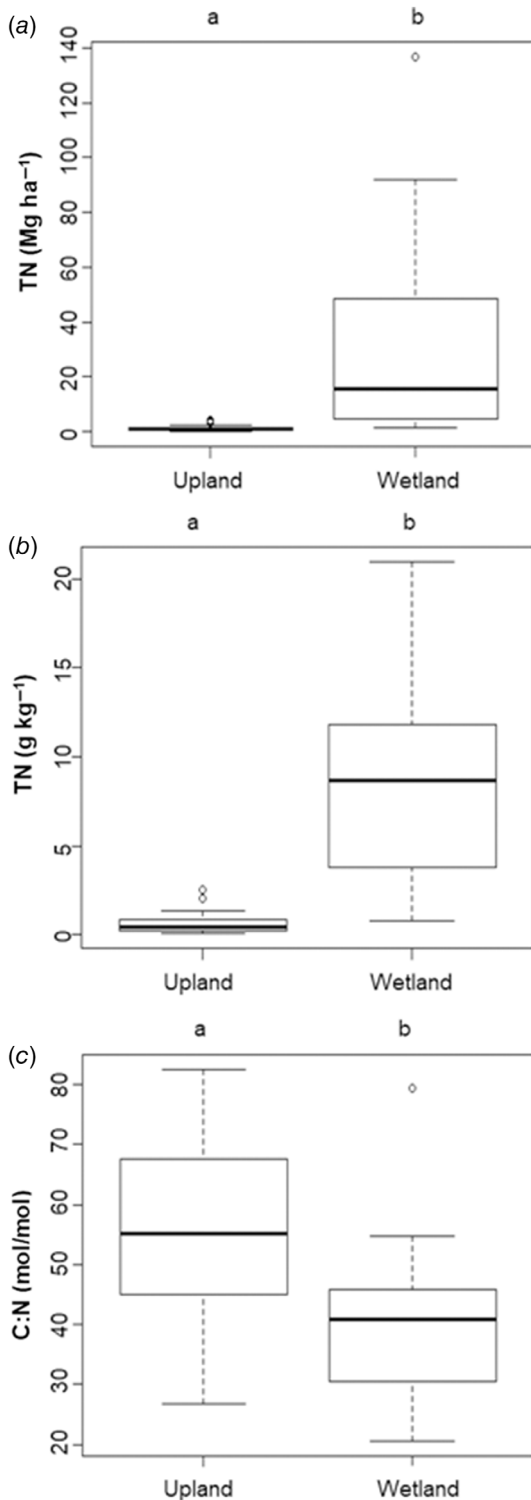
### Relationships with soil OM

Including all field samples, % total soil C (equivalent to organic C) showed a strong positive linear relationship with % soil OM ( $y = 0.56x + 0.96$ ,  $R^2 = 0.99$ ,  $n = 91$ ; Fig. 6a), indicating that C comprised ~56% of the soil OM. The use of a quadratic equation yielded similar results without significantly improving the model fit ( $y = -5.0 \times 10^{-4}x^2 + 0.60x + 0.54$ ,  $R^2 = 0.99$ ). Various predictors were tested to determine the effect on the strength of the relationship

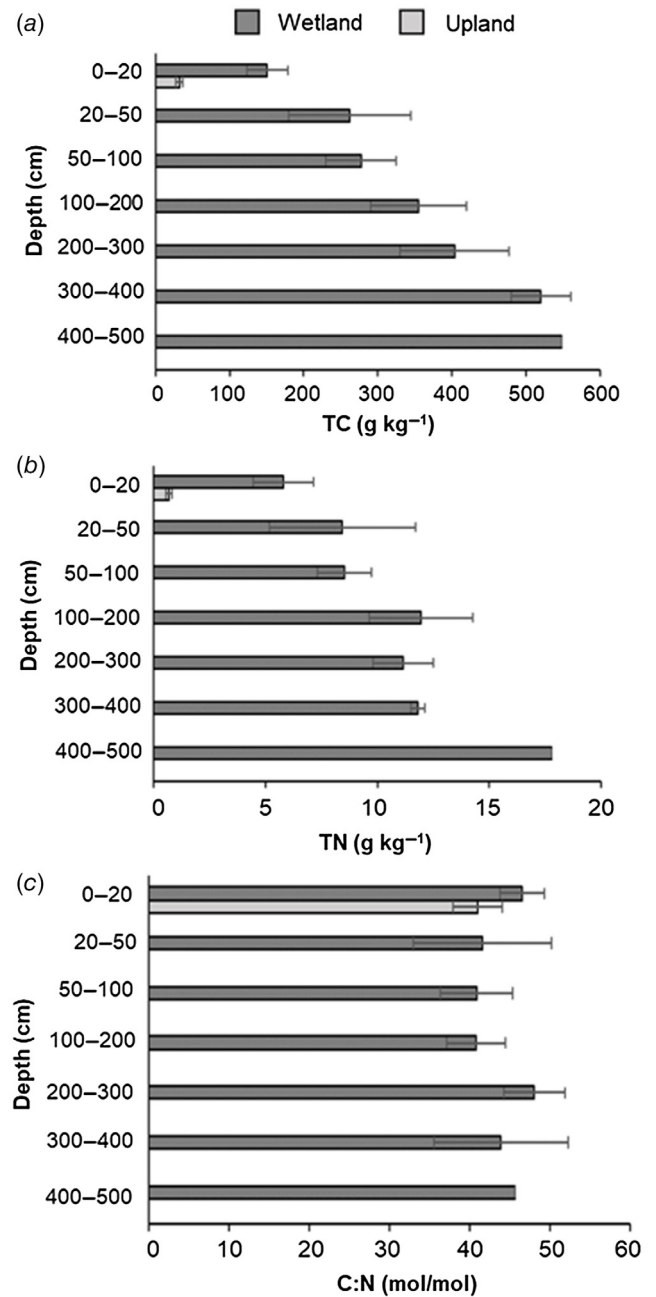


**Fig. 3.** Soil total carbon (TC) stocks (a, c, e, g) and concentrations (b, d, f, h) by sampling point characteristic: panels (a and b) topographic position, (c and d) vegetation morphology, (e and f) vegetation community type, and (g and h) soil type. Boxes represent median and interquartile range, error bars represent upper and lower extremes, and circles represent outliers (>1.5 times the interquartile range). Kruskal multiple comparison *post hoc* test results are denoted by the letters above the boxplots, where different letters indicate a significant difference ( $P < 0.05$ ). BG, baygall; BM, basin marsh; BS, basin swamp; DS, dome swamp; FS, floodplain swamp; SS, strand swamp; MF, mesic flatwood; SF, scrubby flatwood; WF, wet flatwood. Abbreviations for g and h: Bas, basinger fine sand; Fel, felda fine sand; Pom, pomello fine sand; Sam, samsula-hontoon-basinger; San, sanibel muck; Smy, smyrna fine sand; Zol, zolfo fine sand.



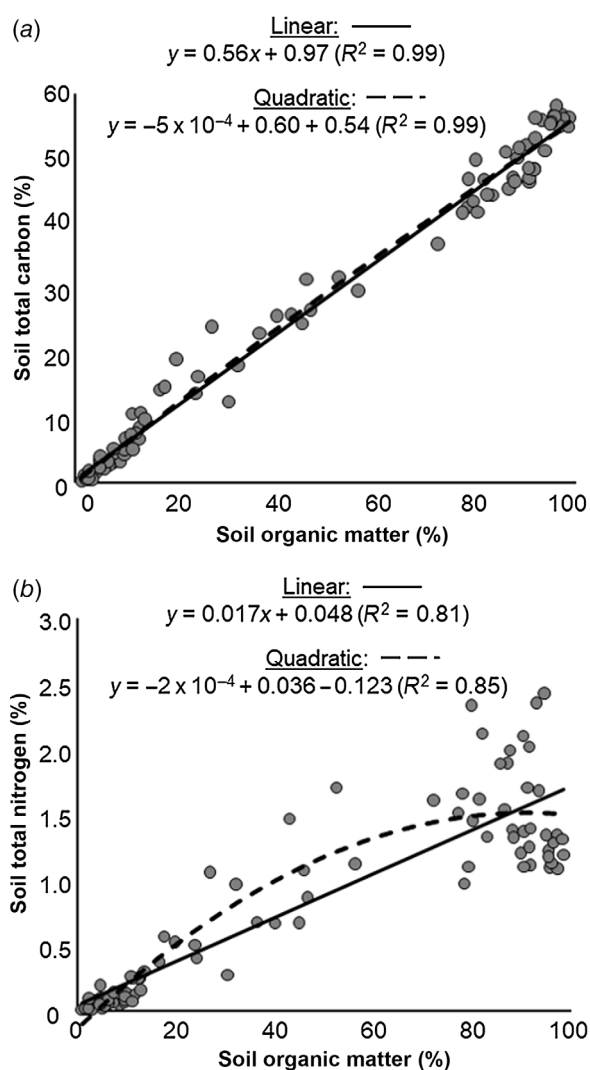


**Fig. 4.** Soil total nitrogen (TN) stock (a) and concentration (b) and molar ratio of total carbon to total nitrogen (C:N) (c) by topographic position. Boxes represent median and interquartile range, error bars represent upper and lower extremes, and circles represent outliers (>1.5 times the interquartile range). Kruskal multiple comparison *post hoc* test is denoted by the letters above the boxplots, where different letters indicate a significant difference ( $P < 0.05$ ).



**Fig. 5.** Concentrations (mean  $\pm$  s.e.) of total carbon (TC;  $n = 67$ ) (a), total nitrogen (TN;  $n = 67$ ) (b), and carbon to nitrogen ratio (C:N;  $n = 93$ ) (c) by sampling depth.

between C and soil OM (Table 2). Besides including all field data together, partitioning the data based on vegetation morphology and soil depth produced the highest  $R^2$  values ( $\geq 0.97$ ). These linear regressions suggest that soils in herbaceous-dominated communities had a slightly greater proportion of C within the soil OM (61%) compared to soils from woody-dominated communities (55% of the soil OM is C). The proportion of C in the soil OM ranged within 54–58%



**Fig. 6.** Linear regression of the relationship between soil organic matter content (%) and soil total carbon (a) and soil total nitrogen (b). Regression formulas for a linear best fit (solid line) and quadratic best fit (dashed line) also presented.

based on soil depth. Of all the predictors tested (Table 2), the highest % C was in soils with the lowest soil OM content (0–20% OM, 84% C,  $R^2 = 0.90$ ).

Soil OM content had a positive linear relationship with soil total N content ( $y = 0.017x + 0.048$ ,  $R^2 = 0.81$ ,  $n = 91$ ), which was slightly improved when a quadratic fit was applied ( $y = 2.0 \times 10^{-4}x^2 + 0.036x - 0.123$ ,  $R^2 = 0.85$ ; Fig. 6b). Therefore, N comprised  $\sim 1.7\%$  of the soil OM.

### Soil depth considerations

Seven wetland points had  $\geq 300$  cm of peat. Five of the seven deepest cores were collected in the baygall swamp community (including the only 500-cm core, both 400-cm cores, and two of the 300-cm cores), while the remaining two 300-cm deep cores were collected in the strand swamp community. Of all

**Table 2.** Linear regression equation terms obtained when soil organic matter (OM) content was used to predict soil total carbon content using different sampling site descriptors.

Descriptor	Category	n	Slope (m)	y-intercept (b)	$R^2$
All field data	All	91	0.56	0.96	0.99
Topographic position	Upland	25	0.59	-0.13	0.91
	Wetland	64	0.54	2.47	0.98
Vegetation morphology	Herbaceous	8	0.61	-0.15	0.99
	Woody	81	0.55	1.17	0.99
Soil OM content	0–20%	40	0.84	-1.14	0.90
	20–60%	11	0.51	3.94	0.73
	>60%	36	0.69	-11.03	0.77
Soil depth	0–20 cm	65	0.55	0.93	0.98
	20–100 cm	9	0.54	2.63	0.97
	100–500 cm	16	0.58	0.26	0.99

wetland points sampled, depth to refusal (i.e. depth of peat) was 20 cm (39%), 50 cm (8%), 100 cm (21%), 200 cm (13%), 300 cm (11%), 400 cm (5%), and 500 cm (3%). All upland points lacked an organic horizon and were collected to 20 cm. In general, soil C density increased linearly with depth (Fig. 5a), including an average C density increase from  $151 \pm 28$  g kg $^{-1}$  (0–20 cm) to  $548$  g kg $^{-1}$  (400–500 cm;  $n = 1$ ) in wetland soils. Soil total N also showed a general increase with depth (Fig. 5b).

To test the importance of sampling wetland sites all the way to refusal, rather than arbitrarily stopping at 50 or 100 cm, as has been done by others, final soil C estimates were compared for each scenario. The average C stock for all wetland sites when full-depth (to refusal) was evaluated as  $940 \pm 158$  Mg ha $^{-1}$ . If only the top 50 cm of soil were collected, the average would be  $283 \pm 27$  Mg ha $^{-1}$ , and  $493 \pm 61$  Mg ha $^{-1}$  if only the top 100 cm were collected. This demonstrated that the average wetland C stock would be underestimated by 70% if sampling stopped at 50 cm, and by 48% if sampling stopped at 100 cm at this study location.

### Landscape soil C estimates

Within the 225-ha study area, averaging all soil C stocks and multiplying by area produced a soil C stock estimate of  $125\,755 \pm 4345$  Mg C. However, C stocks differed significantly with topographic position and vegetation community type (Fig. 3). Averaging C stocks based on area coverage of these site descriptors revealed total C stock estimates of  $88\,105 \pm 2676$  Mg C when based on topographic position (wetland/upland), which was not significantly different than when averaged based on vegetation community type (i.e.  $89\,025 \pm 4390$  Mg C). Since much of the variability in wetland soil C stocks resulted from differences in the total depth of the peat deposit (Fig. 5), total stock was also

calculated using depth-weighted averages based on the estimated proportion of wetland area within each total maximum depth bin. This approach resulted in our most constrained site soil C estimate,  $85\,482 \pm 3365$  Mg C.

If soil % C were estimated from % OM using the standard conversion factor of 0.50 (Craft *et al.* 1991), rather than obtained through direct measurement, the total C stock based on topographic position would be underestimated by 12.6% ( $71\,955 \pm 1164$  Mg C) because the actual C:OM for this site was 0.56.

## Discussion

### Best indicators of soil C content

Soil C stocks (area basis) and densities (mass basis) differed most based on topographic position (i.e. wetland vs upland), with wetlands containing an average of  $\sim 1.2$  orders of magnitude greater soil C stocks than uplands. Other studies comparing wetland and upland soil C also found wetlands (e.g. riparian, forested, and peatlands) had higher C storage compared to uplands (e.g. upslope, forest, aspen-dominated, mixed hardwoods, and conifer-dominated; Table 3; Hazlett *et al.* 2005; Weishampel *et al.* 2009; Christiansen *et al.* 2012).

Wetlands are well known to serve as a disproportionately large sink for global soil C relative to their aerial extent (e.g. Lal 2008; Köchy *et al.* 2015; Nahlik and Fennessy 2016). Nahlik and Fennessy (2016) highlighted that freshwater wetlands in the USA contain greater soil C stores than coastal wetlands due to their greater areal extent and often deeper C reservoirs ( $>30$  cm). However, most inventories of wetland soil C are conducted in coastal (blue C) ecosystems (e.g. Marín-Muñiz *et al.* 2014; Adame *et al.* 2015; Alongi *et al.* 2016; Simpson *et al.* 2017; Gao *et al.* 2018; Radabaugh *et al.* 2018). These studies generally found that mangroves contain greater soil C than seagrass beds, swamps, and marshes (e.g. Alongi *et al.* 2016; Simpson *et al.* 2017; Gao *et al.* 2018; Radabaugh *et al.* 2018). Among freshwater wetlands, Ausseil *et al.* (2015) found bogs had greater C content than ephemeral systems, with soil type being the key driver; Davila and Bohlen (2021) found bay swamp (i.e. baygall) contained more soil C in the upper 50 cm than cypress swamp and marsh. Even small changes in soil moisture status (Amundson 2001) and slope (Conforti *et al.* 2016) can affect soil C storage, but most contend that multiple factors (e.g. vegetation type, productivity, wetland age and size, and site history) interact with water table depth and hydroperiod to control soil C accumulation in freshwater wetlands (Davila and Bohlen 2021).

Plant type was only differentiated at the level of morphology (woody vs herbaceous) and resulted in no differences in soil C stocks, but almost two times greater soil C density at woody sites. More detailed studies of plant effects on soil C suggest

forest soils tend to have a greater proportion of soil organic C in the upper 20 cm, followed by grasslands and shrublands (Jobbágy and Jackson 2000). Soil depth below the surface is an important consideration when evaluating the relationship between vegetation and soil C because the vertical distribution of belowground biomass tends to differ among plant functional types (Jackson *et al.* 2017; Jobbágy and Jackson 2000). In peat-accumulating wetlands, the relationship between current vegetation and soil C stores is further decoupled as soil age tends to increase with depth, and the nature of historic plant communities is often unknown.

Soil C content also varied by vegetation community type in this study, but closer evaluation suggests this relationship was significant due to the underlying co-variation with topographic position (i.e. no differences were observed between individual types of upland communities, or individual types of wetland communities, only wetland vs upland). Spatial heterogeneity of soil C within each vegetation community was high, particularly within the wetlands. For example, the strand swamp community contained one site with the highest measured C stock ( $3461$  Mg ha<sup>-1</sup>) and another site as low as  $130$  Mg ha<sup>-1</sup>. Others have studied pockets of freshwater wetlands within urban landscapes and found each individual wetland has a unique soil C stock (Dayathilake *et al.* 2021), suggesting that although differentiating wetlands from uplands is a good place to begin when conducting a landscape-scale soil C inventory, individual wetlands can vary greatly in the magnitude of the soil C reservoir and should be evaluated independently. Within a wetland, this study confirmed a general trend that peat deposits are deepest in the centre of a wetland and decrease with proximity to the upland margin (van Ardenne *et al.* 2018).

Soil type, as defined by SSURGO (USDA NRCS 2019), was a relatively weak indicator of differences in soil C stocks at our site, with statistical differentiation in soil C content found only between three individual soil types during pairwise comparisons, and large variability within soil types (Fig. 3g, h). While a soil taxonomic approach is often employed for calculating soil C storage on global scales (e.g. Bohn 1982; Eswaran *et al.* 1993; Amundson 2001), this study demonstrates that it may be inappropriate at the landscape scale, at least partially due to the rate of soil misclassification at finer scales. For example, Smyrna fine sand, the most common soil type at our study site, is classified as a Spodosol (Smyrna Series; USDA 1997), yet we found 29% of soil cores collected within this map unit would be better classified as Histosols. Previous studies evaluating the match between soil series field descriptions and SSURGO descriptions found an 80% match for most properties (Drohan *et al.* 2003).

### Soil N content and C:N ratios

As expected, soil total N stock and density followed the same general pattern as soil C content, with topographic position (wetland vs upland) serving as the most robust indicator of

**Table 3.** Published soil carbon (C) stock and density data from diverse global ecosystems.

Location	Study's focus	<i>n</i>	Depth (cm) <sup>A</sup>	Soil C Mean (s.e.)	Unit	Reference
Canada	Riparian	NA	0–75	35.6 (2.3)	Mg ha <sup>-1</sup>	Hazlett <i>et al.</i> (2005)
	Upslope			29.8 (2.6)		
China	Estuary	14	0–100	211 (19)	Mg ha <sup>-1</sup>	Gao <i>et al.</i> (2018)
	Muddy beach	9		243 (14)		
	Coastal saltwater lake	12		167 (22)		
	Mangrove	15		354 (31)		
	Delta	4		179 (10)		
	Seagrass bed	10		287 (21)		
China	Urban	233	0–20	21 (0.57)	g kg	Luo <i>et al.</i> (2014)
	Suburban	257		17 (0.48)		
China	Urban coniferous forest	69	0–30	8 (0.18)	g kg <sup>-1</sup>	Xu <i>et al.</i> (2021)
	Urban broadleaved forest	99		8 (0.16)		
Denmark	Forest upland	8	0–30 <sup>B</sup>	66 (5)	Mg ha <sup>-1</sup>	Christiansen <i>et al.</i> (2012)
	Forest hydromorphic	4		86 (6)		
Indonesia	Seagrass bed	32	0–100	130 (10)	Mg ha <sup>-1</sup>	Alongi <i>et al.</i> (2016) and references therein
	Mangrove forest	37		761 (74)		
Italy	Urban parks and non-parks	NA	0–40	7 (3)	Mg ha <sup>-1</sup>	Canedoli <i>et al.</i> (2020)
Italy	Beech forest	28	A	69 (25)	g kg <sup>-1</sup>	Conforti <i>et al.</i> (2016)
		13	AB	48 (15)		
		18	Bw	26 (9)		
		5	BC	14 (4)		
		16	Cr	5 (2)		
Mexico	Mangrove forest	7	0–150	506 (73)	Mg ha <sup>-1</sup>	Adame <i>et al.</i> (2015)
	Peat swamp	1		615 (86)		
	Marsh	1		298 (39)		
Mexico	Marsh	12	0–80	126 (3)	g kg <sup>-1</sup>	Marín-Muñiz <i>et al.</i> (2014)
	Swamp	12		116 (10)		
New Zealand	Bog	26	FD	1677 (266)	Mg ha <sup>-1</sup>	Ausseil <i>et al.</i> (2015)
	Fen	36		1331 (174)		
	Swamp	55		1397 (214)		
	Marsh	4		1516 (160)		
	Pakihi	2		179 <sup>C</sup>		
	Ephemeral	3		0–30		
Poland	Pine forest	292	0–100	85 (32)	Mg ha <sup>-1</sup>	Gruba and Socha (2019)
	Oak forest	41		100 (46)		
	Fir forest	48		109 (38)		
	Spruce forest	41		109 (46)		
	Beech forest	46		100 (39)		
Sri Lanka	Urban freshwater wetland	NA	0–60	504 (14)	Mg ha <sup>-1</sup>	Dayathilake <i>et al.</i> (2021)
	Urban freshwater wetland			550 (23)		
USA (FL)	Urban upland	29	0–20	58 (7)	Mg ha <sup>-1</sup>	This study
	Urban freshwater wetland	38	0–500	941 (158)		

(Continued on next page)

**Table 3.** (Continued).

Location	Study's focus	<i>n</i>	Depth (cm) <sup>A</sup>	Soil C Mean (s.e.)	Unit	Reference
USA	Tidal saline	967 <sup>D</sup>	0–120	340 <sup>C</sup>	Mg ha <sup>-1</sup>	Nahlik and Fennessy (2016)
	Coastal plains			198 (21)		
	East mountains and upper midwest			478 (58)		
	Interior plains			195 (25)		
	West			216 (30)		
USA (FL)	Mangrove	6	13–50	134 (13)	Mg ha <sup>-1</sup>	Radabaugh <i>et al.</i> (2018)
	Salt marsh	6	4–50	66 (25)		
	Salt barren	4	4–50	27 (8)		
USA (FL)	Fringe mangrove	NA	0–50	241 (31)	Mg ha <sup>-1</sup>	Simpson <i>et al.</i> (2017)
	Interior mangrove			320 (22)		
	Ecotonal mangrove			189 (23)		
	Salt marsh			123 (5)		
USA (MN)	Aspen upland	NA	0–40	60 (2)	Mg ha <sup>-1</sup>	Weishampel <i>et al.</i> (2009)
	Hardwood upland			57 (3)		
	Conifer upland			60 (3)		
	Non-forested upland			58 <sup>C</sup>		
	Open peatland			1506 (99)		
	Alder peatland			1199 (11)		
	Black spruce peatland			641 <sup>C</sup>		
USA (ME)	Salt marsh	NA		33 <sup>C</sup>	Mg ha <sup>-1</sup>	van Ardenne <i>et al.</i> (2018)

NA, not applicable; FD, full-depth; s.e., standard error.

<sup>A</sup>Sample depth in cm unless otherwise stated.

<sup>B</sup>0–100 cm sample depth for one forest upland and two forest hydromorphic study sites.

<sup>C</sup>No s.e. provided.

<sup>D</sup>Total number of study sampling points not separated by category.

variation across the study area. However, the differences in soil N content between wetland and upland communities was even greater than for soil C (~1.4 orders of magnitude), resulting in an average of a 31% higher C:N in upland compared to wetland soils. This suggests the upland soils are more N limited than the wetland soils, but both are poised for net N immobilisation (i.e. average C:N > 25; Reddy and DeLaune 2008). Soil C:N ratios are expected to decline over time and with depth as C is mineralised and the remaining OM more closely matches the C:N of microbial biomass (Melillo *et al.* 1989; Soong and Cotrufo 2015). In this study, an abrupt increase in soil N (decrease in C:N) was seen in our representative deep core (Fig. 2), which could be an artefact of a past shift in vegetation community (Marty *et al.* 2017). However, on the whole the soil C:N profiles of deep (wetland) soils in this study were nearly vertical (range 40–48, Fig. 5c), suggesting minimal microbial processing over time. A similar lack of a trend in C:N with soil depth has been observed in coastal mangrove peat, but the ratios were much lower (~19–24, Breithaupt *et al.* 2020).

### Controls on soil OM conversion factors

The relationship between soil C and OM content, as determined by elemental analysis and LOI, respectively, has been the topic of significant research (see Craft *et al.* 1991), particularly in blue C ecosystems (e.g. Howard *et al.* 2014). Calculated soil C conversion factors are based on the slope of the C:OM relationship and range within 0.22–0.87, with *R*<sup>2</sup> values being equally variable (e.g. 0.25–0.99, see Craft *et al.* 1991). Despite this variability, published conversion factors are routinely used to estimate soil C from LOI in the literature (e.g. van Ardenne *et al.* 2018; Dayathilake *et al.* 2021).

The C:OM found in this study when all field data were used (0.56) was within the range determined for coastal marsh soils of 0.40–0.60 by Craft *et al.* (1991) and 0.52 by Ouyang and Lee (2020), but slightly higher than 0.42 for mangrove soils (Kauffman *et al.* 2011) and 0.42 for seagrass soils (Fourqurean *et al.* 2014). Several studies indicate that soil OM content alters the C:OM ratio, such that soils with low OM (e.g. <5–20%) have a slightly lower C conversion factor than soils with higher OM contents (Craft *et al.* 1991;

Fourqurean *et al.* 2014; Ouyang and Lee 2020). The current study found the opposite trend, with the highest C conversion factor (0.84) in soils with low (<20%) soil OM (Table 2). It has been suggested that high C conversion factors result from 'aged,' or older, highly processed soils, and the accumulation of reduced organic compounds (Craft *et al.* 1991). If ageing is defined by post-depositional degradation, the unique inclusion of upland soils in our study (all were within the 0–20% soil OM content range) may represent the greatest degree of ageing, as this soil OM has persisted despite aerobic decomposition. In contrast, deep wetland peat may have been buried longer, but experienced less degradation overall due to the prevailing anaerobic conditions. Indeed, all upland soils had a slightly higher C conversion factor (0.59) than all wetland soils (0.51).

Only a small increase in C:OM was found in deep wetland soils (Table 2). The observed negative *y*-intercept for the soils with the highest (>60%) soil OM content has been observed previously; it may represent a methodological error where not all the water was successfully removed in the most organic soils (thus overestimating soil OM content) or could indicate that a quadratic fit is more appropriate for the highest soil OM content soils. The lack of consistently positive *y*-intercepts supports the assertion that the soils of this study contained negligible carbonate and that total C is an accurate proxy for organic C, as was also confirmed in our method validation. Finally, we found herbaceous soils had a slightly higher C conversion factor than woody soils.

The use of soil OM to predict total N is far less common in the literature, but others have found a strong ( $R^2 = 0.97$ ) quadratic relationship between these two variables, suggesting ~2% of soil OM is composed of N (Craft *et al.* 1991), which is similar to our finding of ~1.7%. Total N quantification does not discriminate between the forms of N, but organic N is typically assumed to comprise over 95% of total N, while the remaining (<5%) represents inorganic N (e.g.  $\text{NH}_4^+$  and  $\text{NO}_3^-$ ) or N in its most biologically reactive form (Reddy and DeLaune 2008). Knowledge of the size of the soil total N pool can be advantageous in predicting soil quality for support of vegetation and the potential role of soil N in contributing the eutrophication of local watersheds.

### Field sampling and depth considerations

A significant limitation to our current understanding of soil C stocks across landscapes is methodological. Specifically, most studies set a depth limit on sample collection, typically capturing only the top 50 or 100 cm of the soil profile (Chmura *et al.* 2003; Duarte *et al.* 2013; Dayathilake *et al.* 2021). Researchers have begun recognising the potential for significant underestimations of soil C with depth-limited sampling (Jobbágy and Jackson 2000), and advocate for an explicit measurement of the depth, particularly for peat deposits (Holmquist *et al.* 2018). In the first global assessment of deep (3 m) soil profile C stocks, Jobbágy and Jackson (2000) found

that the estimated soil organic C stock increased by 56% compared to the estimate when only 1 m was evaluated. The same study also discovered that including the second metre when evaluating histosols increased the soil C content by 180%. Similarly, van Ardenne *et al.* (2018) found limiting sampling to only 50 cm would lead to a 125% underestimation of soil C stock in salt marsh soils. The current study documents a 70% underestimation of the average wetland soil C stock if sampling ceased at 50 cm, and a 48% underestimation if only taken to 100 cm. Additionally, ~11% of wetland soil sites contained peat deposits of at least 300 cm in depth and these were mostly in baygall swamps, and secondarily strand swamps. In addition to missing soil C stocks when limiting the depth of collection, our data indicated that average soil C density increased by 72% from 0–20 to 400–500 cm depths in wetlands, similar to the trend found by Nahlik and Fennessy (2016). However, the importance of quantifying full-depth C stocks may be dependent on the local soil properties, land management, and the potential effect of land use change. Upland soils, for example, are less likely to have substantial deep C deposits, and surficial land use changes that maintain the natural hydrology may not affect deep soil C. These ideas should be considered when designing soil C inventory studies.

Logistically, we employed three different soil sampling devices that were chosen *ad hoc* at each sampling point based on which most successfully retained a complete soil core. *Post-hoc* analysis of sampling equipment revealed that the polycarbonate core tube (using the push core method with a wooden block and mallet) and the Russian peat borer were strictly used in wetland environments with soil moisture contents >84%, while the gouge auger was utilised in both landscape topographies, with moisture contents of range 5–90%. Anecdotally, the gouge auger resulted in the quickest soil core extraction, but the soil needed to have non-negligible amounts of minerals or only moderately decomposed peats (e.g. fibrist or hemist peat); saprist (mucky) peat required the use of the polycarbonate core tube (deposits <1 m) or the Russian peat borer (with extensions up to 10 m available).

### Implications for urban planning and sustainable development

Best estimates from this study suggest that the 225-ha natural lands study area contains  $85\,482 \pm 3365$  Mg of soil C. This equates to  $313\,719 \pm 6149$  Mg  $\text{CO}_2$  equivalents (using a conversion factor of 3.67, after Kauffman and Donato 2012). Assuming the average US passenger car emits 4.6 Mg of  $\text{CO}_2$  annually (U.S. Environmental Protection Agency 2018), the C storage in these urban natural area soils is equivalent to removing 68 200 US passenger cars from the roads for 1 year. Therefore, the preservation of this soil C pool, particularly by maintaining the site's natural hydrology to keep the wetland soils wet can promote the continued accumulation of soil C, potentially off-setting some local  $\text{CO}_2$  emissions to reduce

the C footprint of urban areas. The subtropical humid climate and flat topography of central Florida, coupled with a legacy of land management focused on the preservation of natural lands (UCF Arboretum 2021) likely contributed to the development of this soil C reservoir. Other studies have also found significant soil C pools in urbanised areas, with urban parks often having the greatest soil C when compared to non-park and suburban lands, and in several cases urban soil C pools are comparable to those of natural upland ecosystems (Vasenev *et al.* 2013; Luo *et al.* 2014; Canedoli *et al.* 2020). Incorporation of green spaces and natural areas into urban and suburban development can have compounding positive impacts because in addition to providing ecosystem services like C storage, residential property values in proximity to conservation areas can often be marketed at a higher value due to the desirability to live near natural lands (Ready and Abdalla 2003; Gies 2009; U.S. Environmental Protection Agency 2009; Chamblee *et al.* 2011; Delaware Valley Regional Planning Commission 2011; Mockrin *et al.* 2017).

To target green spaces with the highest C storage capacity, our findings highlight the importance of differentiating wetlands and uplands. Preservation of freshwater wetlands is already favoured because they are one of the most difficult landscape elements to develop due to the terrain, regulatory issues, and permitting requirements. Studies confirm that even urban wetlands can possess large C reservoirs (Dayathilake *et al.* 2021), but that some anthropogenic impacts can diminish urban wetland C stores. For example, Nahlik and Fennessy (2016) saw a ~42% reduction in mean soil C stock in highly disturbed freshwater wetlands compared to least disturbed wetlands. Avoiding both direct and indirect (e.g. hydrological disturbance) impacts to wetlands will help to conserve and promote C storage.

## Conclusions

This study demonstrates both the significant quantity of soil C that can be found in urban natural areas, as well as the spatial variability across the landscape. Key findings include the large disparity in both total C and total N stocks and densities between upland and wetland ecosystems, such that wetland soils held well over one order of magnitude greater total C and N than uplands, while upland soils had a higher average C:N. As such, of the four types of easily discernible ecosystem characteristics studied to determine their utility in predicting landscape-scale variability in soil C (i.e. topographic position, plant morphology, vegetation community type, and soil type), topographic position (upland vs wetland) was the most robust indicator; it was also the key co-variant driving the significance of other predictors, including vegetation community type and soil type.

Within wetland ecosystems, total C stocks varied widely, range 46–3461 Mg ha<sup>-1</sup>, with baygall, strand swamp, and

basin marsh having the highest average C stocks. Overall, soil C density was higher at woody-dominated sites than herbaceous-dominated, and was greatest in the baygall, strand swamp, and floodplain swamp communities. Much of the spatial variability in wetland soil C pools can be traced to differences in the depth of the peat deposit. All soils were collected to refusal and 32% of wetland points had peat depths >100 cm and 8% were >300 cm. These deepest cores were exclusively in baygall and strand swamp communities, contributing to their consistently high average C storage rates. These data support the need to collect full-depth soil cores in wetlands because limiting collection to only 50 cm would underestimate C stocks by 70% and limiting to 100 cm would result in a 48% underestimation.

Sustainability initiatives and urban planning that strives to reduce C emissions or approach C neutrality should consider the ecosystem services provided by soils, particularly when identifying areas to set aside for green spaces, ecological buffers, and conservation. Based on the findings of this study, urban planners can utilise topographic position as a proxy for the magnitude of soil C storage. Although wetlands can be assumed to have greater C stocks and densities than uplands, probing the soil (with something as simple as a narrow metal rod) to determine the depth to refusal will greatly enhance the accuracy of soil C estimates between different wetlands. Furthermore, soil OM content can be used to estimate C content in the absence of access to an elemental analyser. At our site, a conversion factor of 0.56 could be used to accurately estimate soil C, varying only minimally across topographic position, vegetation community type, and soil depth. However, establishment of a site-specific C:OM conversion factor would improve accuracy for other sites. Soil total N can also be estimated as ~2% of the soil OM pool.

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**Data availability.** The data that support this study will be shared upon reasonable request to the corresponding author.

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