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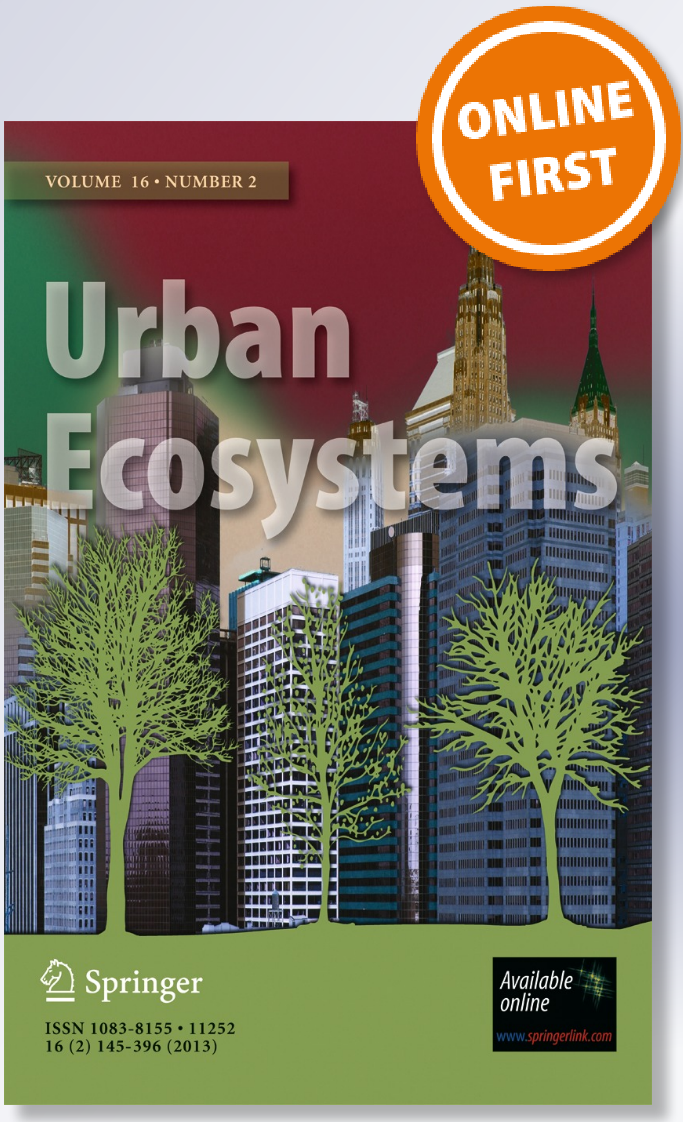

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A comparison of carbon and nitrogen stocks among land uses/covers in coastal Florida

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Abstract Coastal areas are rapidly developing due to population growth and the appeal of coastlines. In order to gain insight into how land use/cover affects carbon (C) storage in a coastal context, we examined soil and vegetation C and soil nitrogen (N) across land uses near Apalachicola, FL. Forested wetlands had the greatest soil C and N storage, while natural pine forests and pine plantations had the least. In paired plots, urban lawns had significantly greater mineral soil N content compared to urban forest remnants. Total ecosystem C (soil + vegetation) was higher in forested wetlands than all other land uses/covers combined due to the high organic content of those wetland soils. Urban forest remnants and lawns had greater total ecosystem C than natural pine forests and pine plantations, which likely reflects the differential influence of prescribed fire and less frequent anthropogenic disturbances between the rural and urban areas, respectively. Projections of land use change in Franklin County, FL combined with these data suggest that increases in C storage are possible with continued urbanization along the Gulf Coast, if forest remnants are left and lawns are incorporated in built-up areas. However, this study does not account for C emissions during land conversion, or any emissions associated with maintaining urban built-up and residential areas. A better understanding of land use/cover

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influences on C pools has applications for planning and development, as well as ecological and environmental protection in the region.

Keywords Soil · Vegetation · Carbon · Nitrogen · Urban · Land use/cover · Lawns

Abbreviations

ANOVA	Analysis of variance
ANPP	Annual net primary productivity
BD	Bulk density
DBH	Diameter at breast height
DOQQ	Digital orthophoto quarter quadrangles
NPP	Net primary productivity
NRCS	National Resources Conservation Service

Introduction

Roughly half of the U.S. population lives in coastal counties (Bourne 2006) and land development occurs to a greater extent in coastal than inland areas. Land use change is an important driver of the C cycle and thus quantification of C storage in urbanizing coastal regions should be a high priority. Additionally, since N regulates C storage to some degree through limitation of primary production, quantification of N storage is also necessary. To date, few studies of the effects of urbanization on C and N storage have been conducted in coastal ecosystems. In particular, the study area exhibits sandy soils, level topography, high water tables (Nagy et al. 2012), generally high net primary productivity (NPP) (Gholz and Fisher 1982), and a prevalence of prescribed fire across rural landscapes. Consequently, the coastal context, combined with the associated features, set the study apart from previous literature.

Soil C changes following urbanization are related to climate, development practices (e.g., site excavation), and use of the site (residential, commercial, etc.). Pouyat et al. (2006, 2007) reported that differences in soil C storage may be related to the pre-urban condition as well. When 'natural' land covers such as forest are converted to urban uses, soil C may decrease in the northeastern U.S., whereas, in warmer and/or drier climates, soil C may increase (Jenerette et al. 2006; Pouyat et al. 2006; Kaye et al. 2008; Lorenz and Lal 2009). As an example, C density in Syracuse, NY was estimated to be 16.2 kg m^{-2} in native cover vs. 7.1 kg m^{-2} in urban cover, while in Atlanta, GA, the estimate was 7.7 kg m^{-2} in native cover vs. 7.8 kg m^{-2} in urban cover (Pouyat et al. 2006). The increases in urban areas may be due to relatively low native soil C storage in warm and/or dry areas such as upland soils in the southern U.S. (Pouyat et al. 2006). Furthermore, natural soil variation can be equally or more influential to C and N cycles than land use/cover (Groffman et al. 2006).

The effects of urbanization on vegetation C depend largely on the pre-urban land cover. For example, deforestation may reduce NPP and decrease the standing stock of vegetation C in the conversion to urban land uses (Houghton and Hackler 1999; Milesi et al. 2003; Tian et al. 2003; Hutyra et al. 2011). Grass in residential lawns and public parks can maintain a substantial pool of C, especially in roots, and can increase inputs to soils (Jo and McPherson 1995; Bandaranayake et al. 2003; Qian et al. 2010). However, compared to C stocks in trees and shrubs, the amount stored in grass may be quite small (Jo and McPherson 1995). Additionally, the composition of species is often altered in urban ecosystems and may include non-native species which could affect both C and N cycling (Lorenz and Lal 2009).

The objectives of this study were to (1) quantify the C and N storage for a representative section of the Gulf Coast of the southeastern United States (Ward et al. 2005) and (2) determine the effect of land use on C and N storage for the same region. The second goal focused on areas where land conversion had already occurred or is likely and these were predominantly the better drained sites. Urban remnant forests were expected to have greater C and N storage than natural pine forests, while pine plantations were expected to have reduced C and N storage compared to natural pine forests due to differences in stand longevity and management practices. These expectations are based on the generally older and larger trees that frequently occurred in urban areas as well as the absence of prescribed fire in those systems. In contrast, natural and plantation pine forests are harvested at younger ages and are often burned. Lawns were expected to have high carbon stocks based on the work of Pouyat et al. (2006) who suggested that forest conversion to urban in warm, humid climates (e.g., southeast United States) may result in higher soil carbon storage. Land use of the study area was classified and used in conjunction with the results from the field study to estimate the total C storage of the region.

Methods

Site description

The study site is a section of the Florida Gulf Coast (Fig. 1) (roughly 29°40′ to 29°55′ N, 84°65′ to 84°35′ W) including the towns of Apalachicola, Eastpoint, and Carrabelle. The climate is humid subtropical and has an average annual rainfall of 1,425 mm and an average annual temperature of 20.3 °C (NCDC 2010). Apalachicola is about 4 m above sea level (NCDC 2010). In general, soils on upland sites are sandy with adequate drainage and range from well drained Quartzipsamments to Alorthods and Alaquods (e.g., the Mandarin, Leon, Rutlege, and Kureb series). However, forested wetland soils are poorly drained and include the Chowan and Brickyard series (Fluvaquents and Endoaquepts respectively). Slash pine (*Pinus elliottii*), sand pine (*Pinus clausa*), live oak (*Quercus virginiana*), water tupelo (*Nyssa aquatica*), and titi (*Cyrilla racemiflora)* are among the prominent overstory species.

The population of Franklin County, Florida rose by 29 % between 1990 and 2011 (http://quickfacts.census.gov/qfd/states/12/12037.html). Land use change projections through the year 2060 estimate that the proportion of Franklin County in urban land uses will increase by 10–25 % (Wear 2011). Although population densities at the county level are low (22/mile^2 or 8/km^2), populations are heavily concentrated along coastlines and, consequently, coastal areas are much more developed than the county as a whole.

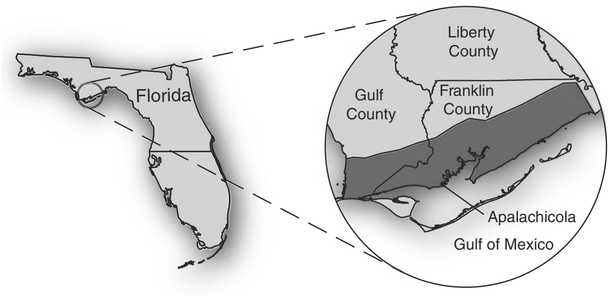

Fig. 1 Location of study site along FL Gulf Coast

Study design

A total of 61 plots were established across the study area within the following land uses/covers: natural pine forest (12), pine plantation (11), urban lawn (14), urban forest remnant (14), and forested wetland (10). These groupings were used to compare land uses across the study area. Plots were circular with a radius of 7.3 m (area=168.3 m^2). Plot selections were based on representation of typical soil and forest vegetation conditions for particular land uses (Fig. 2). These conditions included soil morphology, typical species and age of forest vegetation by land use, and the potential for access. As an example, some land uses were intrinsically associated with particular forest age classes (e.g., trees in urban areas were usually older than those associated with pine plantations) and densities of forest cover. Distribution of soil great groups was similar across land uses with natural pine, urban lawn,

Fig. 2 Example plots of each land use/cover: (**a**) natural pine forest, (**b**) pine plantation, (**c**) urban lawn, (**d**) urban forest, and (**e**) forested wetland

and urban forest categories comprised of approximately 65 % alaquods / alorthods and 23 % psamments / psammaquents respectively. Pine plantations reflected 54 % and 36 % of those respective great groups. Urban lawns were primarily residential yards and public parks, consisting of both pines and hardwoods, within the urban core (Fig. 2). Urban forest plots were minimally disturbed patches of remnant forest within the urban core (without fire or other physical disturbance) and also contained a mix of pines and hardwoods. Forested wetlands tend to occur on poorly drained soils and thus do not likely represent a pre-urban condition for any of the urban plots; however, it is not uncommon for these areas to be converted to plantations. Visual evidence of fire (e.g., charred trunks) in the last 10 years was recorded: natural pine forests and pine plantations showed signs of recent fire, while urban lawns, urban forests, and forested wetlands generally did not.

Among these 61 plots, some plots were selected for a paired comparison of natural pine forest vs. pine plantation (9 pairs) and urban lawn vs. urban forest (11 pairs). Plots within pairs were in close proximity because we aimed to match plot characteristics as closely as possible to reduce variation and better isolate the effects of land use. The similarity of soil profiles of paired plots was verified by a local USDA National Resources Conservation Service (NRCS) soil scientist. In the case of natural pine vs. plantation comparisons, paired plots were also required to have the same dominant overstory species, either sand pine or slash pine. Plots that did not meet requirements for pairing based on these characteristics were excluded from the paired analysis but still used in the overall analysis (61 plots among 5 land uses/covers).

Soils

Soil and vegetation samples were collected between October 2007 and July 2008. The USDA-NRCS provided field assistance in characterizing soils. Three soil cores per plot were taken with a soil auger and subsampled by depths: 0–7.5 cm, 7.5–30 cm, 30–60 cm, and 60–90 cm. At each depth, roots were removed from the sample and the soil was mixed until homogenous and then air-dried. Samples at each depth were analyzed individually in each plot. Concentrations of C and N were determined using the dry combustion method (Sollins et al. 1999) on a LECO 2000 CNS analyzer (LECO Corporation, 3000 Lakeview Ave., St. Joseph, MI). Soil pH was determined using a 1:1 soil:0.01 M $CaCl_2$ suspension (McLeon 1982) with an AS-3000 Dual pH Analyzer (LabFit, P.O. Box 343, Burswood, Western Australia 6100, Australia). In every plot, a separate intact soil core of a known volume (32.5, 140, or 160 cm^3 depending on the corer used) was taken at the same corresponding depth intervals to determine bulk density. Each bulk density sample was dried at 105 °C for a minimum of 72 h (Blake and Hartge 1986) and weighed. Bulk density measurements, in conjunction with C and N concentration data, were used to calculate the C and N content for each soil depth.

To determine the C and N content of the forest floor, or Oi horizon, three samples were collected per plot including all organic matter within a 0.1 m^2 frame down to the upper surface of mineral soil. Samples were dried at 70 °C for a minimum of 72 h and then weighed to measure the total mass of the sample. A subsample was ground in a Thomas-Wiley Intermediate Mill to pass a 20 mesh screen for chemical analyses. Concentrations of C and N were determined using thermal combustion (Perkin-Elmer 2400 series II CHNS/O analyzer; Perkin-Elmer Corp., Norwalk, CT) as outlined in Nelson and Sommers (1996).

Vegetation

Vegetation C was estimated for over-, mid-, and understory. Overstory was categorized as tree/plant heights >4.9 m, midstory was 1.8–4.9 m, and understory was 0–1.8 m. Species-specific dry weight equations, based on the diameter at breast height (dbh) were used to estimate the overstory and midstory standing crop (Taras 1980; Van Lear et al. 1984; Clark et al. 1985; Jenkins et al. 2004). When species-specific equations were not available, general equations (e.g., mixed hardwoods) were used. Equations were often averages from multiple studies reducing the potential for large deviations between actual and predicted biomass (McHale et al. 2009). The applicability of standard equations for trees in urban settings has been debated without resolve (Nowak and Crane 2002; McHale et al. 2009). In this study, the biomass of trees in urban lawns was multiplied by 0.8 to account for the lower biomass in open areas following Nowak and Crane (2002). Tree biomass in urban forests was not corrected. For trees in all land uses, overstory and midstory C content were calculated as 50 % of the biomass of each stratum. For the overstory, tree cores were used to estimate radial growth for all trees ≥12.7 cm dbh. Increment growth for the previous 5 years was measured at the USGS National Wetlands Research Center in Lafayette, Louisiana. Annual aboveground NPP (ANPP) was calculated by subtracting the previous year's biomass from that of the current year; only data for the most recent year's growth are presented.

To estimate understory C, a subsample of plots (at least 1 of every 3 plots) within each land use/cover category was sampled with one- 1 m^2 subplot per plot. The approach for urban lawns was slightly different with three- 0.1 m^2 subplots per plot and all plots in this category were included. Percent cover by species was recorded for every plot. Within the 1 m^2 subplot (or 0.1 m^2 for urban lawns) all living vegetation less than 1.8 m tall was clipped to the ground and dried at 70 °C for at least 72 h or until a constant dry weight was achieved. A subsample was ground for C and N analysis and processed as previously described for the forest floor.

Remote sensing analysis and future projections

Digital orthophoto quarter quadrangles (DOQQs) with 1 m spatial resolution were used to classify dominant land use/cover for the study area (area shown in Fig. 1). April 2004 color infrared DOQQs were obtained from the Land Boundary Information System (2008). Land use/cover classes included open water, natural forest, barren (non-forested, non-wetland areas), urban built-up, urban vegetation (including both lawns and forest remnants), non-forested wetland, forested wetland, and plantation (Fig. 3). A full description of image processing and classification techniques for this analysis is presented in Nagy (2009). An accuracy assessment report calculated an overall accuracy of 81.97 % for the classified image (Nagy 2009) and all classes of interest (natural forest, pine plantation, forested wetland, urban vegetation (forest remnants + lawns), and urban built-up) had user's accuracies of 90 % or higher, except for forested wetland (71.43 %) and natural forest (72.73 %). The area occupied by each land use/cover is presented in Table 1. Plantations and forested wetlands are the most widespread land uses/covers, representing about 32 % and 31 % of the total land area respectively. Urban lands (built-up areas plus vegetated areas (lawns and forests) occupy <5 % of the total land area which is just less than that covered by natural pine forests. The classified image (Fig. 3) was used in conjunction with results from the field analyses to create an estimate of the total C storage for a section of the Florida Gulf Coast.

Statistical analyses

All statistical analyses were performed in JMP version 10.0.0 (SAS Institute Inc. 2012). Relationships were considered significant at $p<0.05$. Shapiro-Wilk tests indicated that distributions of nearly all variables violated normality assumptions, so non-parametric Kruskal Wallis tests were used to determine significant differences of C and N content

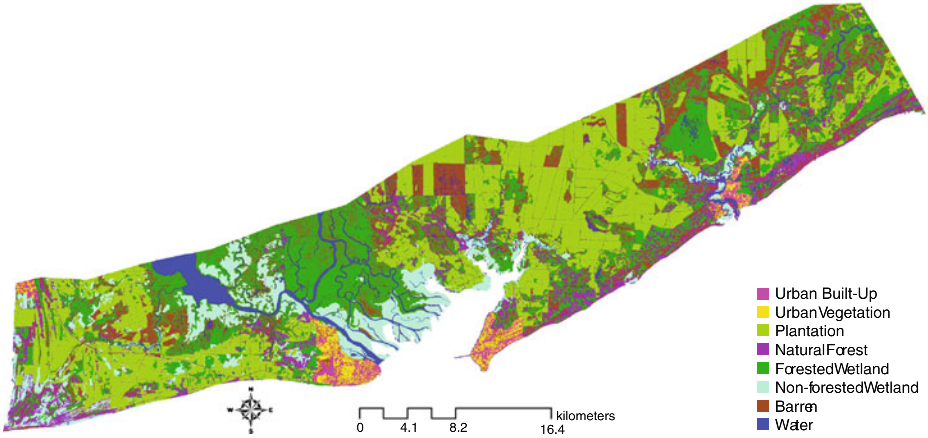

Fig. 3 Land use/cover classification from 2004 digital orthophoto quarter quadrangle (DOQQ) data with 1 m spatial resolution

among land use/cover types. If a significant difference was determined, a non-parametric comparison for all pairs using the Steel-Dwass test was performed. All five categories of land use/cover were included to estimate the total C and N storage across this section of the Florida Panhandle and estimate the effects of land use on C and N storage. Next, comparisons of paired plots (urban lawn vs. urban forest and natural pine forest vs. pine plantation) were conducted with non-parametric Wilcoxon signed rank tests.

Plot characteristics including soil pH, permeability, and water table depth, vegetation species richness (defined as the number of species), mean tree size (dbh), number of trees, number of hardwoods, understory percent cover, and percent cover of saw palmetto (*Serenoa repens*, a dominant understory component) and wax myrtle (*Morella cerifera*, a common N-fixing species) were compared among land uses using Kruskal-Wallis and Steel-Dwass tests. The exception was understory percent cover, which was normally distributed, so a one-way analysis of variance (ANOVA) was used in conjunction with a Tukey's HSD test for this variable. We used non-parametric Spearman's rank correlations to examine

Table 1 Land use/cover area totals from remote sensing analysis

Land Use/Cover	Area (% of Total)	Area (ha)
Natural forest	6.3	6,315
Pine plantation	32.0	31,949
Urban built-up[a]	2.5	2,453
Urban vegetation[b]	1.8	1,802
Forested wetland	30.7	30,730
Other[c]	26.7	26,731
Total	100.0	99,980

[a] Urban built-up consists of buildings and impervious surfaces such as roads and parking lots

[b] In the remote sensing analysis, urban vegetation includes both lawns and forests which differs from the field sampling in which urban lawns were distinguished from urban forests

[c] Other includes barren lands, non-forested wetlands, and open water

relationships among response variables (C or N content, biomass, or productivity) of interest and potential influential variables such as soil properties (pH, permeability, and water table depth), vegetation species richness, and percent cover of wax myrtle.

Results and discussion

Soils

Not surprisingly, mean soil bulk density of forested wetlands was significantly lower than all other land uses/covers for the total mineral soil profile and lower than many of the land uses at individual depths (Table 2). Forested wetlands also had a significantly higher water table than urban lawns, natural forests, or plantations (Table 2). These features, low bulk density soils with a high water table, are characteristic of wetland soils. Mean soil pH in urban lawns was significantly higher than in all other land uses (Table 2). Pine litter in plantations and natural pine forests is acidic and has been linked to losses of soil Ca and Mg and soil acidification (Augusto et al. 2002).

Forest floor C and N

Urban forest remnants and natural forests had significantly greater forest floor C content compared to forested wetlands (Table 3). The forest floor N content of urban forests was significantly greater than forested wetlands or plantations (Table 3). Natural forests also had higher forest floor N content than forested wetlands (Table 3). Forest floor C and N were negatively related to soil pH and positively to soil permeability (Fig. 4a, b). Low soil pH can slow decomposition of organic matter (Neale et al. 1997; Chan and Heenan 1999). We posit that forest floor mass, C, and N content of urban forest remnants may be enhanced due to a combination of relatively high primary productivity, low disturbance (no evidence of recent fire), and older stand age and thus longer time for accumulation. In contrast, areas of periodic flooding, such as forested wetlands, may have high decomposition at the soil surface due to enhanced microbial activity following wet periods (DeBusk and Reddy 1998).

Table 2 Soil characteristics: Mean ± standard error (SE) bulk density (BD) (g cm^{-3}), water table depth (cm), permeability (cm hr^{-1}), and pH

Parameter	Land Use/Cover				
	Natural Forest	Pine Plantation	Urban Lawn	Urban Forest	Forested Wetland
BD: 0–7.5 cm	1.0±0.1 a	1.0±0.0 a	1.2±0.0 a	0.9±0.1 ab	0.5±0.1 b
BD: 7.5–30 cm	1.2±0.0 a	1.2±0.1 a	1.1±0.1 ab	1.1±0.1 ab	0.8±0.1 b
BD: 30–60 cm	1.3±0.0 a	1.2±0.0 a	1.3±0.1 a	1.2±0.1 ab	0.9±0.1 b
BD: 60–90 cm	1.2±0.1 a	1.3±0.1 a	1.2±0.1 a	1.2±0.1 a	0.9±0.1 a
BD: Total mineral soil (0–90 cm)	1.1±0.0 a	1.2±0.0 a	1.2±0.0 a	1.1±0.0 a	0.8±0.1 b
pH: 0–90 cm	3.9±0.2 b	3.7±0.1 b	6.0±0.3 a	4.7±0.3 b	3.9±0.2 b
Water table depth (cm) [a]	56.5±12.1 a	49.9±12.5 a	57.7±7.9 a	50.6±12.5 ab	15.2±5.3 b
Permeability (cm hr^{-1}) [a]	30.7±2.9 a	33.2±2.9 a	27.7±2.0 a	33.2±2.7 a	20.2±3.7 a

Significant differences (p<0.05) among land uses are indicated by different letters

[a] Data from maps by Soil Conservation Service (1994)

Table 3 Mean ± standard error (SE) soil C and N content (kg m^{-2}) by depth, forest floor C and N, and total soil C and N by land use/cover

Element	Pool	Land use/Cover				
		Natural forest	Plantation	Urban lawn [a]	Urban forest	Forested wetland
C	0–7.5 cm	1.0±0.1 c	0.9±0.1 c	1.4±0.1 b	2.1±0.4 bc	4.1±0.5 a
C	7.5–30 cm	1.4±0.2 c	1.3±0.2 c	3.5±0.8 b	4.8±1.3 bc	12.7±2.0 a
C	30–60 cm	1.8±0.3 b	1.7±0.3 b	3.2±0.7 b	3.8±0.9 b	22.4±4.0 a
C	60–90 cm	1.4±0.2 b	3.1±1.1 b	2.6±0.5 b	2.8±0.6 b	22.3±4.6 a
C	Forest floor	1.7±0.1 a	1.8±0.2 ab	–	2.4±0.3 a	1.3±0.3 b
C	Total soil	7.3±0.9 b	8.8±1.6 b	10.7±2.6 b	15.9±4.4 b	63.3±18.2 a
N	0–7.5 cm	0.03±0.00 c	0.03±0.00 c	0.07±0.01 b	0.07±0.01 b	0.19±0.03 a
N	7.5–30 cm	0.04±0.01 c	0.04±0.0 c	0.16±0.04 b	0.14±0.04 bc	0.56±0.10 a
N	30–60 cm	0.06±0.01 b	0.06±0.01 b	0.13±0.03 b	0.11±0.02 b	0.78±0.14 a
N	60–90 cm	0.04±0.00 b	0.09±0.04 b	0.09±0.02 b	0.07±0.01 b	0.69±0.14 a
N	Forest floor	0.03±0.00 ab	0.03±0.00 bc	–	0.05±0.01 a	0.02±0.01 c
N	Total soil	0.21±0.03 b	0.25±0.05 b	0.46±0.11 b	0.44±0.11 b	2.31±0.68 a

Significant differences ($p<0.05$) among land uses are indicated by different letters

[a] Forest floor mass of urban lawn plots is zero

Mineral soil C and N

Mineral soil C concentrations in surface soils (0–7.5 cm) ranged from 11,600 to 182,900 mg kg^{-1} in plantation and forested wetland, respectively, and generally decreased with depth. At each depth (0–7.5, 7.5–30, 30–60, and 60–90 cm), the mean mineral soil C concentration and content were significantly higher in forested wetlands compared to all other land uses/covers (all $p<0.0001$) (Fig. 5a, Table 3).

Compared to either natural pine forests or plantations, urban lawns had significantly higher C content at 0–7.5 cm and 7.5–30 cm (Table 3). Urban forest remnants had higher soil C in surface soils (0–7.5 cm) than natural forests or plantations, but the differences were not significant (p=0.06 and 0.07, respectively). Similarly, elevated C storage in urban forests and residential plots was reported in Pouyat et al. (2006) for warm areas such as the southern U.S. while declines in soil C content following urbanization were found in the northeastern U.S. Regional differences stem from the fact that the northeastern U.S. has naturally high soil C content while the Gulf Coast ecosystems have sandy soils with lower native soil C content, with the exception of forested wetlands (Birdsey 1992). Mineral soil C of urban lawns in this study (10.7 kg m^{-2}) was lower than that reported in Pouyat et al. (2006) (14.4 kg m^{-2} for residential lawns) while soil C storage of urban forests in this study (13.5 kg m^{-2}) was higher (7.7 and 11.6 kg m^{-2} for urban forest soils in Atlanta and Baltimore, respectively). Raciti et al. (2011), also working in Baltimore, estimated soil C densities for residential lawns and forest reference soils at 6.95 and 5.44 kg m^{-2} respectively, and soil C densities in older lawns reached as high as 9–10 kg m^{-2}. It should be noted that in addition to regional differences in soil properties such as texture and C stocks, the composition of these forests is likely different, with more hardwoods in the northeast compared to the southeast U.S.

Low soil C in natural pine forests and plantations compared to other land uses is also consistent with the meta-analysis of Johnson and Curtis (2001) who found reduced C pools in recently burned stands. The soil C stocks reported here (7.0 and 5.6 kg m^{-2} respectively for natural and plantation pine mineral soil) are lower than those reported for a similar total depth (1 m) in 15–16 year old Florida pine plantations (11 kg m^{-2}) by Johnson et al. (2002). However, the sites that Johnson et al. studied had not been burned since site preparation while there was evidence of recent burning (within last 10 years) in pine plantations and natural pine forests in the present study. Johnson (1992) noted that both prescribed burning and forest soil cultivation may result in reduced soil C. The pine plantations in our study had been intensively cultivated during site preparation using a technique called bedding, the use of disc plows to create extended mounds, 30–40 cm high, adjacent to ditches of corresponding depths. It is possible that the combination of cultivation plus periodic burning may have resulted in the lower C values for natural and plantation soils.

Mineral soil N concentrations in surface soils (0–7.5 cm) ranged from 370 to 7,430 mg kg^{-1} in plantations and forested wetlands respectively, and similar to C, generally decreased with depth (Fig. 5b). Mineral soil N content was greatest in forested wetlands and least in plantations

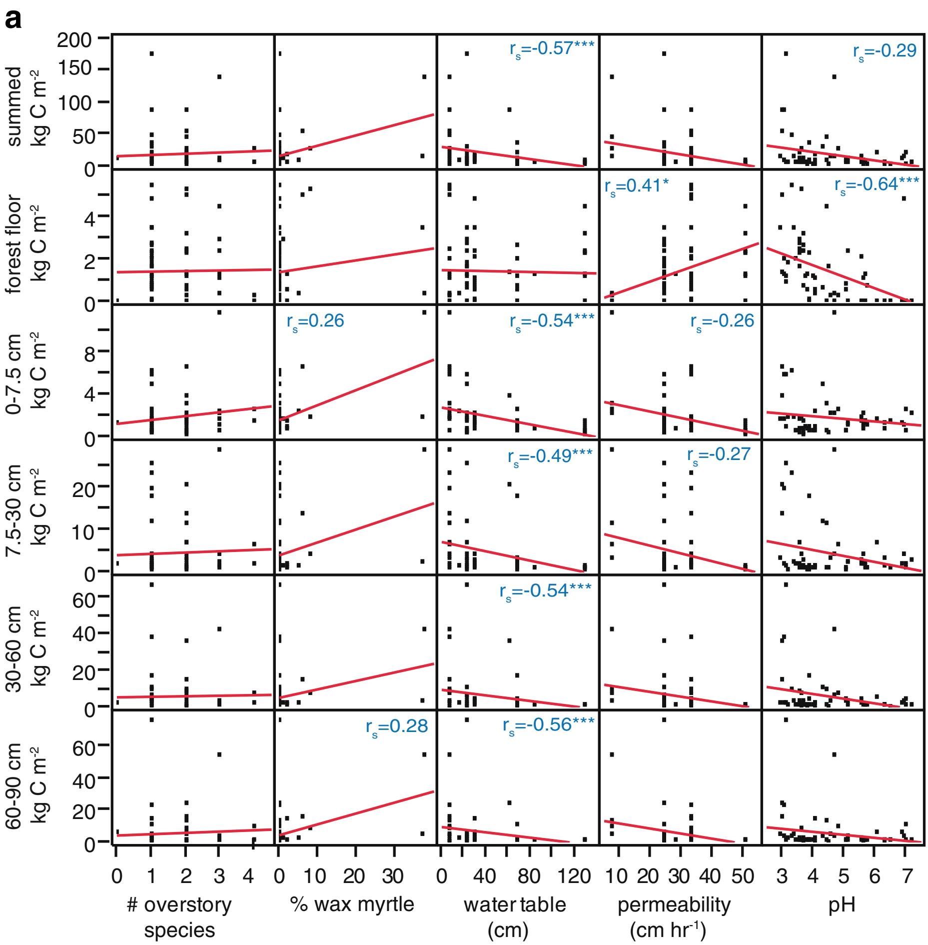

Fig. 4 Scatterplot matrix of (**a**) soil C and (**b**) soil N pools vs. covariates with Spearman correlation coefficients (r_s)

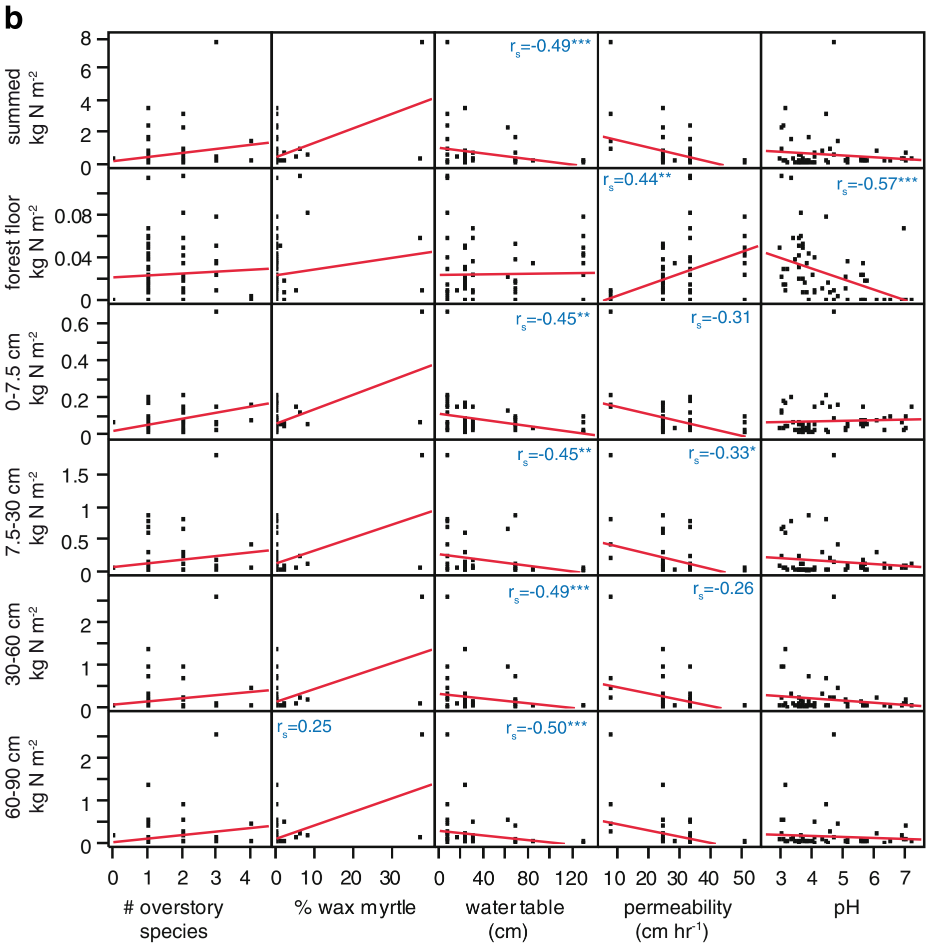

Fig. 4 (continued)

and natural pine forests (Table 3). At each depth, mean N content was significantly higher (at least 5 times greater) in forested wetlands compared to other land uses (Table 3). In addition to the likely more dominant factor of reduced decomposition, higher soil nitrogen in forested wetlands may also be related to the presence of N-fixing plants (or more accurately, plants that form symbiotic relationships with N-fixing bacteria) and cyanobacteria (Mitsch and Gosselink 2007). N-fixation is favored in low oxygen environments such as wetlands because nitrogenase, the enzyme that catalyzes N-fixation, is inactivated in the presence of oxygen (Mitsch and Gosselink 2007). Wetlands did have the highest cover of wax myrtle (Table 5), but correlations with soil N were not significant, or weak in most cases (Fig. 6).

The mean N content at 0–7.5 cm and 7.5–30 cm was higher in urban lawns and urban forests compared to natural forests or plantations (Table 3; all significant at $p<0.05$ except urban forest vs. plantation, $p=0.07$). Soils in urban areas may exhibit increased N storage because of fertilizer application to lawns and/or decreased soil disturbance in forest remnants. Elevated N in urban lawns contributed to a significantly lower mineral soil C:N ratio compared to natural forests, plantations, or urban forests (23.5 vs. 31.8, 31.6, and 30.6

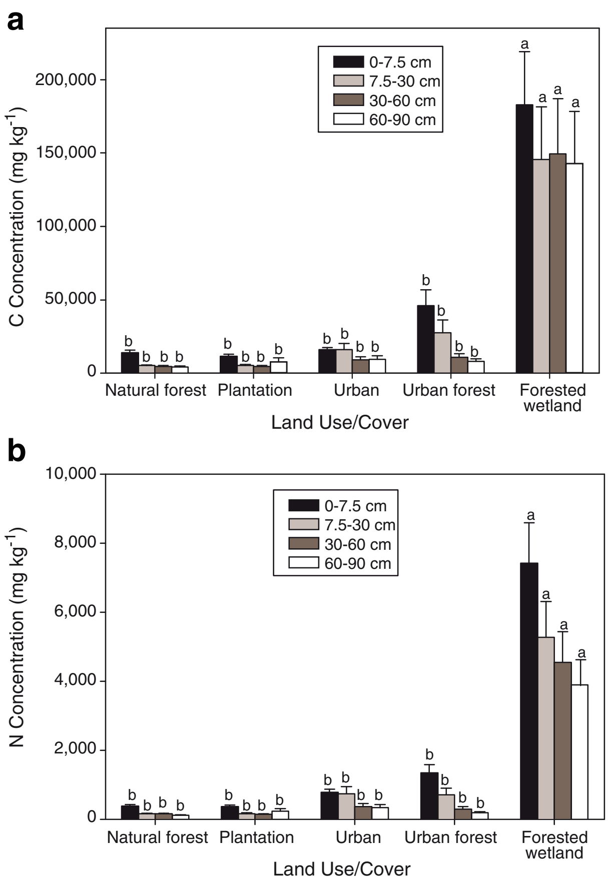

Fig. 5 Mean concentrations (mg kg^{-1}) of (**a**) C and (**b**) N by land use/cover and depth. Error bars represent the standard error (SE)

respectively). Low C:N ratios may be conducive to increased N mineralization and, consequently, beneficial for vegetation productivity in urban lawns.

Total soil C and N: Mineral soil + forest floor

Forested wetland soils had significantly higher total C and N content compared to natural pine forests, pine plantations, urban lawns, or urban forest remnants (Table 3). These results are consistent with other studies that found wetlands to store more C compared to other ecosystems (Schlesinger 1991; Cui et al. 2005). The surface of wetland soils may shift between wet and dry conditions so that decomposition there can be rapid, but declines quickly with depth due to water saturation and oxygen limitation (DeBusk and Reddy 1998). Total soil C and N had a significant, negative correlation with water table depth (Fig. 4a, b). This suggests that the high water table and in the case of N, low permeability (Fig. 4b), of forested wetland histosols may reduce rates of decomposition and thereby lead to increased C and N storage at depth.

N-fixing species such as wax myrtle may influence both C and N pools. For example, in the presence of N-fixing species, productivity and biomass may be increased due to greater N availability. Consequently, soil organic matter may increase with greater inputs of

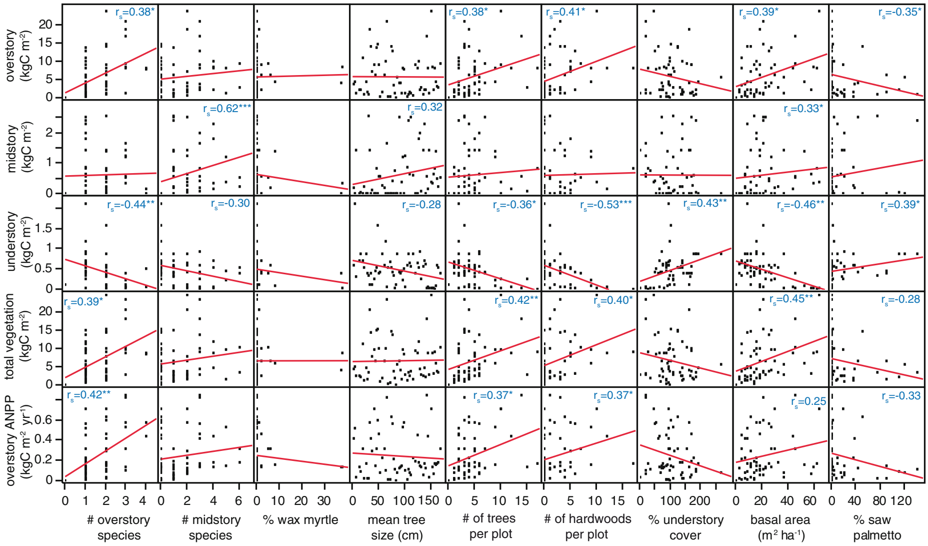

Fig. 6 Scatterplot matrix of vegetation C pools vs. covariates with Spearman correlation coefficients (r_s)

vegetation biomass and reduced decomposition of old soil C (Fisher and Binkley 2000; Johnson and Curtis 2001). Significant correlations of several mineral soil C and N pools with the understory percent cover of wax myrtle (Fig. 4a, b) suggest that the presence of wax myrtle may stimulate C and N storage in these Gulf Coast ecosystems. The percent cover of wax myrtle by land use/cover is presented below in Table 4.

Paired analysis: Natural pine forest vs. pine plantation

Paired plots allowed for a more controlled comparison of natural pine forests and plantations. Mineral soil C content was not significantly different between natural forest and plantations at individual depths throughout the soil profile (p=0.38, 0.70, 0.63, and 0.28 respectively for increasing depths), the forest floor (p=0.76), or the mineral soil + forest floor (p=0.77). Similarly, there were no significant differences observed for soil N content at any individual depth in the mineral soil profile (p=0.49, 0.63, 0.43, and 0.32 respectively for increasing depths), the forest floor (p=0.63), or the total mineral soil + forest floor (p=0.77). Smaller pools of soil C and N were expected in plantations than natural forests in accordance with Chen et al. (2004), Turner et al. (2005), and the meta analysis of Guo and Gifford (2002). Yang et al. (2004) observed that C and N losses due to plantation establishment were mainly in the surface soil. Soil C was relatively high in plantation soils at 60–90 cm which might suggest redistribution of C and organic matter from upper to lower depths due to prescribed burning and/or disking (Fisher and Binkley 2000), but this difference was not significant here. Loss of organic matter due to burning is generally greater in sandy soils such as those found here, but both natural forests and plantations showed evidence of recent fire.

Paired analysis: Urban lawn vs. Urban forest

Variation within urban areas was examined in the urban lawn and urban forest paired plots. No significant differences in C content were observed at depths throughout the mineral soil profile (p=0.18, 0.63, 0.73, and 0.85 respectively for increasing depths) for urban lawn vs. urban forest

Table 4 Vegetation characteristics: Mean ± standard error (SE) overstory species richness (SR), midstory species richness (SR), percent cover of wax myrtle, trees per plot, overstory hardwood trees per plot, mean overstory tree size- diameter at breast height (dbh) (cm), plot basal area (m^2 ha^{-1}), percent cover in understory, and percent cover of *Serenoa repens* (saw palmetto)

Parameter	Land Use/Cover				
	Natural forest	Plantation	Urban lawn	Urban forest	Forested wetland
overstory SR (# of species)	1.3±0.1 ab	1.1±0.1 b	1.4±0.3 ab	2.1±0.2 a	2.2±0.3 a
midstory SR (# of species)	1.7±0.4 a	1.1±0.3 ab	0.4±0.4 b	2.1±0.4 a	3.1±0.6 a
% cover wax myrtle	0.0±0.0 a	3.6±0.4 a	0.1±0.1 a	0.6±0.4 a	5.0±3.7 a
% cover saw palmetto	41.7±12.0 a	21.8±8.1 ab	0.4±0.3 c	16.4±11.2 bc	0.0±0.0 c
% understory cover	121±11 ab	130±14 a	85±4 ab	115±20 ab	68±16 b
# of trees	4.0±0.7 ab	5.4±1.1 a	2.1±0.3 b	4.9±0.9 a	7.7±1.4 a
# of hardwoods	0.9±0.6 bc	0.0±0.0 c	1.1±0.4 bc	2.7±0.7 ab	7.4±1.5 a
dbh (cm)	25.3±2.2 ab	18.6±1.9 b	40.0±4.3 a	31.7±3.0 a	24.6±2.5 ab
basal area (m^2 ha^{-1})	13.8±2.4 bc	16.7±2.0 bc	9.2±1.6 c	22.3±2.7 b	48.0±4.3 a

Significant differences ($p<0.05$) among land uses are indicated by different letters

plots. Because there was no 'forest floor' mass in urban lawn plots, the forest floor C and N storage of urban lawn and urban forest plots was not compared. When the forest floor component (urban forests only) was added to the total of the mineral soil profile (0–90 cm) there was no significant difference between the C content of urban lawn and urban forest plots ($p=0.34$). Other studies have found that fertilizer application and irrigation of turf grass can increase soil C storage to levels approximating grasslands or forests (Golubiewski 2006; Pouyat et al. 2009).

Urban lawns contained significantly greater soil N than urban forests from 7.5 to 30 cm ($p=0.03$), which could be a result of maintenance practices including periodic fertilizer application (Cheng et al. 2008). No significant differences were observed for N content in the other three depths (0–7.5 cm: $p=0.11$; 30–60 cm: $p=0.30$; 60–90 cm: $p=0.73$) or the total soil profile plus the forest floor ($p=0.18$). Urban lawns have the potential to maintain soil N and C pools that approximate the pools found in urban forest remnants despite different maintenance practices and vegetation community structure. Similarly, Raciti et al. (2011) found that residential soils in Baltimore, MD had C and N densities that rivaled or exceeded nearby forest soils.

Summary of multiple approaches

In addition to the clear trend of highest C and N storage in forested wetlands, these analyses showed that C and N stocks were greater in upper mineral soils of urban forests and urban lawns relative to pine plantations and natural pine forests. Furthermore, by controlling soil variation as much as possible, the paired approach showed that there were no significant differences in soil C or N between natural pine forests and pine plantations. The only significant difference between paired urban lawn and urban forest plots was greater soil N below the surface at 7.5–30 cm in urban lawns.

Vegetation

Vegetation structural differences were apparent among land uses/covers. Basal area, a function of both the number of trees and their relative sizes, is used in forest management to infer the stocking level of a stand. Forested wetlands had the highest basal area of all land uses/covers, followed by urban forests (Table 4). Generally, plantations, natural pine forests, and urban lawns had lower basal area. Forested wetlands had significantly greater number of trees per plot and hardwoods per plot compared to urban lawns (Table 4). Urban areas generally had larger trees; both lawns and urban forest remnants had significantly greater mean tree size than pine plantations (Table 4). Understory cover (%) was significantly higher in plantations compared to forested wetlands (Table 4).

Differences were also observed regarding the composition of vegetation among land uses/covers. For example, natural forests had the highest understory cover of saw palmetto (Table 4), significantly more than urban forest, urban lawn, or forested wetland. Wax myrtle cover was greatest in forested wetlands followed by plantations, but there were no significant differences among land uses ($p=0.24$). Plantations had the fewest species in the overstory (significantly lower than forested wetland or urban forest) while urban lawns had the fewest species in the midstory (significantly lower than forested wetland, urban forest, or natural forest) (Table 4).

Overstory C content and productivity

Mean overstory C content was significantly greater in urban forests compared to pine plantations (Table 5). Structural differences among land uses help explain the patterns of overstory biomass and C content. Trees in urban forest remnants were older and larger than trees in pine plantations (mean dbh of 31.7 cm for urban forests compared to 18.6 cm for plantations) and thus the biomass and C storage were higher in the former. Despite the fact that forested wetlands had a higher average number of trees per plot than urban lawns, as well as a greater number of hardwood trees per plot than all other land use/cover types (Table 4), this did not translate into significant differences in biomass or C content. Urban lawns also tended to have large, old trees left onsite. Overstory biomass values were comparable to Gholz and Fisher (1982) for natural and planted slash-pine dominated forests. Overstory C content was significantly, positively related to overstory species richness (Fig. 6); the implications of this relationship are described below with regard to overstory ANPP.

Overstory ANPP was highest in urban forests, but it did not vary significantly among land uses/cover ($p=0.12$) (Table 5). Furthermore, although previous studies have shown that productivity may be enhanced in the presence of N-fixing species, overstory productivity was not

Table 5 Mean ± standard error (SE) overstory, midstory, understory and total vegetation C content and overstory annual net primary productivity (ANPP) by land use/cover

Pool	Land Use/Cover				
	Natural forest	Plantation	Urban lawn	Urban forest	Forested wetland
Overstory C (g m^{-2})	4290±1400 ab	2390±620 b	5680±1380 ab	9260±1680 a	7160±2060 ab
Midstory C (g m^{-2})	910±300 a	910±290 a	30±30 b	740±170 a	630±140 a
Understory C (g m^{-2})	590±60 a	520±60 ab	760±140 a	350±80 ab	180±70 b
Total Vegetation C (g m^{-2})	5790±1270 a	3820±580 a	6460±1420 a	10,350±1740 a	7970±2000 a
Overstory ANPP (g m^{-2} yr^{-1})	260±70 a	110±20 a	210±50 a	350±70 a	240±60 a

Significant differences ($p<0.05$) among land uses are indicated by different letters related to the percent cover of wax myrtle (Fig. 6). Overstory ANPP was significantly, positively related to overstory species richness (Fig. 6) and forested wetlands and urban forests had significantly more overstory species than pine plantations (Table 4). Positive correlations have been reported between species richness and productivity (Waide et al. 1999; Loreau et al. 2001; Catovsky et al. 2002; Hooper et al. 2005; Fargione et al. 2007). However, all land uses/covers here had relatively low species richness compared to other regions and systems, and the relationship is not particularly strong (r_s=0.42), so the ecological significance of this relationship here is uncertain. The productivity of pine plantations and forested wetlands was lower than that found in Gholz and Fisher (1982) and Messina and Conner (1998), for plantations and wetlands respectively. Some plantations in the study area exhibited mortality due to fire and thus may be adversely affected by management practices. The lower productivity of these plantations compared to other plantations in the literature (e.g., 1.1 Mg ha^{-1} yr^{-1} vs. 5 Mg ha^{-1} yr^{-1} in other studies) may also be due to low stocking. Consequently, even if these plantations were at rotation age, the C storage would be less than in urban forests (e.g., plantations would likely have less than 80 Mg ha^{-1} in the standing crop of vegetation while urban forests have 93 Mg ha^{-1}).

Midstory C content

Midstory biomass and C content were significantly lower in urban lawns compared to all other land uses/covers (Table 5). Low values for urban lawn midstory biomass and C content were expected because lawns did not have a developed midstory stratum. Generally these plots are managed to contain a grass understory and a few large trees. In contrast, plantations and natural pine forests had the lowest overstory biomass, and thus plants in the midstory may have reduced competition for resources including light, soil nutrients, and/or water, allowing this stratum to flourish. Additionally, midstory biomass was significantly related to midstory species richness (Fig. 6) and may be a factor of complementary resource use among species in this vegetation stratum; however, as noted above, all land uses/covers were fairly species poor.

Understory C content

Urban lawns and natural forests had significantly higher understory C content than forested wetlands (Table 5). Understory growth in urban lawns may be facilitated by fertilization, irrigation, and greater access to sunlight, as a result of typical manicuring processes that favor an open canopy in yards (Fig. 2). Although the understory percent cover of urban lawns was not the highest (Table 4), the dense coverage of grass in urban lawn understories produces a considerable biomass pool and translates to high C content (Table 5).

Natural pine forests, pine plantations, and some urban forests harbored abundant saw palmetto (Table 4), contributing to the understory biomass, particularly in the former two categories (Table 5, Fig. 6). Similar to urban lawns, the open canopy of plantations (as compared to the mostly closed canopies of urban forests and forested wetlands) allows light to reach the forest floor and promotes understory growth (Fig. 2). Saw palmetto is very flammable (Behm et al. 2004), but it is quick to establish post-fire, which helps explain its presence in plantations and natural pine forests. The understory biomass estimates presented here are higher than those in Gholz and Fisher (1982) for similar slash pine/saw palmetto sites.

Total vegetation C content

Total vegetation C content was numerically higher in urban forests than plantations (Table 5), although no significant differences were found among land use/cover groups

(p=0.06). Reduced vegetation C pools were predicted in urban areas due to initial land clearing. However, the urban forest remnants are large stocks of biomass and C that now exceed those in plantations and natural pine forests. The relatively higher C storage in urban forests of this study probably reflects the longer time since development of older residential areas and parks.

Paired analysis of vegetation: Natural forests and plantations

Paired t-tests showed no significant difference between C content of natural forests and plantations in the overstory (p=0.16), midstory (p=0.93), understory (p=1.00), or total vegetation (p=0.08). Species composition of paired natural forests and pine plantations was similar and these plots had similar mean number of trees and tree sizes. Despite statistically similar overstory C content, overstory ANPP of natural forests was significantly higher (p=0.04) than that of plantations. Differences in ANPP here could be influenced by lower leaf area, and thus lower light interception, and/or low stocking in pine plantations compared to natural pine forests.

Paired analysis of vegetation: Urban lawns and urban forests

Urban lawn and urban forest paired comparisons showed no significant difference in overstory C (p=0.11) content or ANPP (p=0.30). Both urban lawn and urban forest plots tended toward a few large trees per plot including some hardwoods. The midstory of urban forests had significantly higher mean C content than urban lawns (p=0.001). Urban forests had a more diverse vertical structure than their paired urban lawn plots which included a developed midstory stratum in the former. However, urban lawns had significantly higher understory C content than urban forests (p=0.002). Although small in comparison to the magnitude of the total vegetation pool, the C storage of grass is considerable in the understory (Jo and McPherson 1995). Urban lawn vs. urban forest paired plots showed no significant difference in mean total vegetation C content (p=0.06). The absence of fire in urban areas promotes similar vegetation C pools in both lawns and forests despite structural differences.

Summary of multiple approaches

The analysis with all land uses/covers revealed greater overstory C (p=0.01) and total vegetation C (not statistically significant; p=0.06) in urban forests compared to pine plantations. Urban lawns had the lowest midstory C, but highest understory C of the five land uses. The analysis of paired plots confirmed these results with higher productivity in natural pine forests compared to pine plantations, lower midstory C in urban lawns than urban forests, and higher understory C in urban lawns compared to urban forests.

Total ecosystem C

The mean total ecosystem (soils + vegetation) C storage was 13.08, 12.63, 17.11, 26.26, and 71.30 kg C m^{-2} for natural pine forest, pine plantation, urban lawn, urban forest, and forested wetland, respectively (Fig. 7). The importance of forested wetlands for C storage along this coastal region is reiterated by these data and supports the findings of Groffman et al. (2006) indicating that natural soil variation (e.g., differences among soil orders) may be more influential than land use on C and N storage. Plantation establishment has been promoted as a long-term method of sequestering C compared to other land uses such as agricultural systems

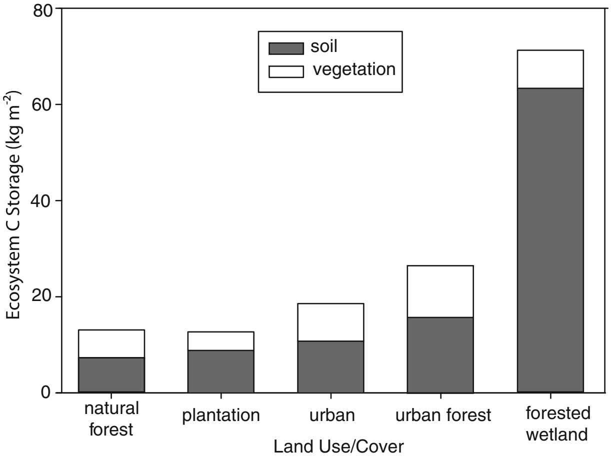

Fig. 7 Mean ecosystem C content by pool (kg m^{-2})

(Jackson et al. 2005). However, in this study, urban vegetated areas had greater total stocks of C than plantations or natural pine forests. Infrequent disturbance regimes in urban areas may allow increased longevity of trees and less organic matter oxidation in surface soils. The results of this study are consistent with the idea of urban homogenization (Pouyat et al. 2006; Pickett et al. 2011), where, as a result of similar features across urban areas in different regions, ecological functions converge on an overall urban mean. As an example, C stocks of areas with low native soil C (e.g., southeast U.S.) increase and C stocks of areas with high native soil C (e.g., northeast U.S.) decrease following urbanization.

Storage estimate and projections of future land use change

Table 6 shows the estimated C storage for this section of the Gulf Coast partitioned by land use/cover. The total C storage of almost 0.03 Pg C (Table 6) is likely underestimated due to fact that the C storage of barren lands and non-forested wetlands is not included. To put this in perspective, all forests of the conterminous U.S. are estimated to store between 41.52 Pg C (U.S. EPA 2007—this includes biomass, deadwood, litter, and soils) and 90 Pg C (Sundquist et al. 2009—this includes soils and biomass). Because forested wetlands in our study region have such high C storage per unit area and occupy such a large area, they contain 80 % of the region's total C (Table 1, Table 6). Pine plantations cover more area than forested wetlands, but store only 15 % of the region's total C.

For Franklin County, Florida, Wear (2011) predicts a 10–25 % increase in urban area from 1997–2060. However, land use change projections aggregated at the county level mask some of the variation at finer scales. For instance, patterns of urban growth here differ from other non-coastal regions as development occurs parallel to the coastline rather than radiating out from an urban core. Although a good portion of Franklin County is public land, including Tate's Hell State Forest and Apalachicola National Forest, privately-owned land along the coast is likely to be developed in coming years. For example, the largest private land owner in Florida, the St. Joe Company, plans to develop ~20,000 ha of the 445,000 ha in the Florida Panhandle (Ziewitz and Wiaz 2004).

More detailed land use change projections are needed to predict future changes in C storage. This would be useful to identify areas with the greatest potential for C loss. For

Table 6 C storage among land use/cover classes as a function of the area occupied by each class

Land Use/Cover	C Storage (Mg C)
Natural forest	826,000
Pine plantation	4,035,000
Urban built-up[a]	206,000
Urban vegetation[b]	391,000
Forested wetland	21,910,000
Other[c]	–
Total	27,369,000

[a] Urban built-up consists of buildings and impervious surfaces such as roads and parking lots. C storage of urban built-up areas estimated from NRCS data of soil organic C which approximates total C as inorganic C in these soils is negligible

[b] In the remote sensing analysis, urban vegetation includes both lawns and forests which differs from the field sampling in which urban lawns were distinguished from urban forests

[c] Other includes barren lands, non-forested wetlands, and open water; C storage was not estimated for these areas

example, if forested wetlands are likely to be encroached upon, either directly by expanding urban growth or, as is more often the case, indirectly by the displacement of plantations, local legislation should encourage development away from these areas. Additionally, on lands slated for urban development, the integration of vegetated areas (e.g., forests and lawns) should be a central theme of development plans on account of their relatively high C storage per unit area (Fig. 7); this could be coupled with denser development in localized areas, allowing for more vegetated area in and around the urban core and thus higher C storage. Strictly speaking, the results of our study suggest that conversion to urban vegetated areas, lawns and forest remnants, could enhance C stocks in this rapidly developing coastal area. However, it must again be noted that this study did not directly measure C stocks in urban built-up areas (e.g., under impervious surfaces) or C emissions during land conversion and development. These values should be included, along with the emissions due to current management practices in urban built-up and residential areas (e.g., fertilization of lawns) when predicting changes in C storage over time.

Conclusions

The results from the land use comparisons generally supported our hypotheses. Forested wetlands had much higher soil C and N content than all other land uses/covers in this coastal region of Florida. By comparison, urban forests and urban lawns ranked second and third, respectively for both soil and ecosystem C storage. Storage of C and N were linked at the landscape scale, as supported by factors such as the positive correlations of the cover of an N-fixing species, wax myrtle, with soil C and N content. Land use, management practices, disturbances, physiographic and climatic conditions, and natural variation in soil properties and vegetation cover influenced C and N storage along the Florida Gulf Coast. The relative effects of each of these factors may vary regionally.

These data combined with land use change projections for the Florida Panhandle suggest that conversion of (non-wetland) forest to vegetated urban land could result in greater C storage due to the absence of fire and other disturbances in urban areas. This conclusion supports the suggestion that conversion to urban land uses in warmer climates may increase C storage and a general pattern of urban homogenization across multiple regions. As management practices, protecting forested wetlands and incorporating green spaces (e.g., forests and lawns) within built-up areas will reduce C losses in the region. However, emissions of C from land conversion and management practices were not accounted for in this study, but would provide a more comprehensive understanding of changes to C and N cycles. With rapidly growing coastal populations, development along coastlines is inevitable. Site assessments coupled with precise land use projections may be used to ascertain probable effects of land conversion, determine where the greatest changes in C storage will occur, and thereby identify critical areas for protection.

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