

Vegetation productivity consequences of human settlement growth in the eastern United States

Tingting Zhao · Daniel G. Brown ·
Hongliang Fang · David M. Theobald ·
Ting Liu · Tao Zhang

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Abstract In this study, we investigated the impact of human settlement growth on vegetation carbon uptake in the eastern United States between 1992/1993 and 2001. Human settlement growth was measured by changes in the density of housing units. Vegetation carbon uptake was estimated with gross primary

production (GPP) based on the light-use efficiency approach applied to satellite imagery. Annual GPP was found to increase by approximately 140 g C m^{-2} on average for the entire study area in 2001 compared to 1992/1993, accompanied by region-wide increases in downward shortwave radiation and minimum daily temperature. Changes in GPP, however, varied significantly by different types of settlement growth. Exurbanized areas, where the rural settlement (less than 0.025 units per acre) converted to exurbs (0.025–0.6 units per acre), were associated with approximately 157 g C m^{-2} increase in GPP due to high vegetation proportions. Suburbanization, the conversion from exurban settlement to suburbs (0.6–4 units per acre), was related with a decline of GPP by 152 g C m^{-2} due to progressive development of built-up land cover. Results help to understand the potential of carbon mitigation in the human-dominated landscapes using vegetation as a natural store of carbon dioxide. This in turn has implications for the low-carbon development planning along the gradient of human settlement densities.

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T. Zhao (✉) · T. Liu
Department of Geography, Florida State University,
323 Bellamy Building, 113 Collegiate Loop, Tallahassee,
FL 32306, USA
e-mail: tzhao@fsu.edu

D. G. Brown
School of Natural Resources & Environment, The
University of Michigan, 3505 Dana Building, 440 Church
St., Ann Arbor, MI 48109, USA

H. Fang
LREIS, Institute of Geographic Sciences and Natural
Resources Research, Chinese Academy of Sciences,
11A Datun Road, Beijing 100101, China

D. M. Theobald
Department of Fish, Wildlife, and Conservation Biology,
Natural Resource Ecology Laboratory, Colorado State
University, Fort Collins, CO 80523, USA

T. Zhang
Department of Biology, University of Florida,
220 Bartram Hall, P.O. Box 118525, Gainesville,
FL 32611, USA

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Introduction

The curbing of greenhouse gases (GHGs) requires lowering the anthropogenic production of carbon

dioxide (CO₂) as well as enhancing the capture and storage of CO₂. Terrestrial ecosystems play an important role in carbon capture and are estimated to absorb 44.4–66.3 petagrams of CO₂ per year globally (Potter et al. 1993; Cramer et al. 1999; Sitch et al. 2003). This carbon regulatory function, however, is influenced by human land-use and management activities (Houghton et al. 1998, 1999; Arora and Boer 2010). In particular, the development of human settlements has generated increasingly complicated impacts on ecosystem CO₂ absorption through not only the varying nature of land-use conversions (e.g., built-up surfaces converted from mature forest vs. from abandoned agriculture) but also differences in development densities.

While carbon impacts from land-cover/land-use changes associated with urban growth have been documented through studies at local (e.g., Zhang et al. 2008), regional (e.g., Milesi et al. 2003), and national (e.g., Imhoff et al. 2004) scales, the consistent and comprehensive assessment of carbon dynamics along the gradient of development densities remains largely incomplete. Research concerning the relationships between settlement densities and vegetation carbon activities is increasingly important for the following reasons: (1) low-density areas, such as exurban development, are often excluded from studies of urban carbon impacts; however, they account for the vast majority of the settled areas in the United States and other countries with similar development patterns (Theobald 2001; Brown et al. 2005). (2) Previous research has forecasted more rapid expansion of suburban and exurban settlement than urban densities in the coming decades (Theobald 2005; Bierwagen et al. 2010). Furthermore, (3) impacts of development densities on vegetation carbon fluxes/storage and driving factors for those impacts are not fully understood. Human settlement has varying influences on carbon dynamics, sometimes enhancing vegetation carbon uptake and boosting the total carbon storage (Churkina et al. 2010). A study in southeastern Michigan found that low-density exurban development was more productive than the abandoned agricultural lands it replaced thanks to a better maintenance of lawns and yards (Zhao et al. 2007).

In this study, we investigated impacts of human settlement growth on vegetation carbon uptake for the eastern United States during the 1992/1993–2001 time period. Our study included all areas east of the Mississippi River. The selection of years was

constrained by the availability of land-cover data, which came from the 1992 and 2001 National Land Cover Database/Dataset (NLCD). These land-cover data and other satellite images were used to estimate vegetation carbon uptake throughout the study area. The time period between October 30, 1992 and October 28, 1993 was selected for the carbon uptake estimation in the early 1990s to (1) minimize the anomalous global dimming effects of the Mount Pinatubo volcanic eruption in 1991; and (2) to avert the excessive missing data (due to cloud covers) on satellite images collected in November and December of 1993.

Human settlement refers to the use of land for residential purposes. Human settlement growth was measured by changes in the density of housing units. Remote sensing data, appealing for settlement mapping over a large spatial extent, were shown to underestimate low-density settlement due to limits of sensor's spatial resolution or mixed land covers/uses (Elvidge et al. 2001; Guindon et al. 2004). To overcome this difficulty, we mapped settlement densities from decennial census housing-unit data gathered for 1990 and 2000, which were the closest match to our study time period. Housing units have advantages over population because they characterize the development of residential structures regardless of whether they are occupied.

Vegetation carbon uptake was measured as gross primary production (GPP) based on the light-use efficiency (LUE) approach applied to satellite imagery (Prince and Goward 1995; Running et al. 2004). GPP is the total amount of carbon entering an ecosystem through photosynthesis during a certain time period, usually a year (Chapin et al. 2002). It indicates the maximum carbon uptake by vegetation from the atmosphere. The mixed nature of land covers in residential and other human settings presents difficulties for the estimation of GPP based on field observations that require steady atmospheric conditions, flat terrain, and homogenous landscape over a large geographic area (Baldocchi et al. 2001). Many of the nationwide and global products of gross and/or net primary production exclude urban regions regardless of their settlement densities (e.g., Zhao et al. 2005). Previous studies encompassing built-up land covers treated them either as the same as non-vegetated surfaces (Imhoff et al. 2000) or as savanna (tree and grassland mixed; Milesi et al. 2003). In this study, GPP

in the built-up areas was estimated based on actual proportions of vegetation (tree and grass) and impervious surface identified from satellite imagery at 30-m resolution. This, compared to previously adopted methods, provides a more concrete approximation of mixed land covers/uses for the built-up type.

Data and methods

Identifying settlement density categories and settlement growth

To measure settlement density in 1990 and 2000, we used housing-unit density (HUD) derived at the scale of U.S. census blocks. Census housing units include houses, apartments, mobile homes, and other living space occupied as separate units. HUD was calculated as the total number of housing units within a block divided by its developable area using a grid at 1-ha resolution. The developable area refers to land excluding public and protected areas, major water bodies, and commercial/industrial/institutional uses (Theobald 2005; Bierwagen et al. 2010). We aggregated these data to 1-km resolution using the majority rule to match the spatial scale used for the estimation of GPP in this study. Four settlement densities were calculated, including urban density settled at 4 or more housing units per acre, suburban at 0.6–4 units per acre, exurban at 0.025–0.6 units per acre, and rural at less than 0.025 units per acre.

The changes in settlement density between 1990 and 2000 were derived by overlaying maps of settlement densities in these two separate years. Settlement growth in this study refers to the categorical changes between settlement densities (Appendix A in Supplementary material). These include urbanization (i.e., urban converted from suburban densities), suburbanization (i.e., suburban converted from exurban densities), and exurbanization (i.e., exurban converted from rural densities). Settlement intensified by two steps forward (such as rural to suburban densities) was also identified and included in the statistical report. Locations with decreasing density (such as suburban to exurban densities) were treated collectively as the “other changes” type in the statistical report for two reasons. First, the decrease in settlement density may not be real but rather a result from census boundary changes during the study period

(Syphard et al. 2009). Second, the sample size of a few decreased types is too small (Appendix A in Supplementary material) to generate statistically significant results when treated separately.

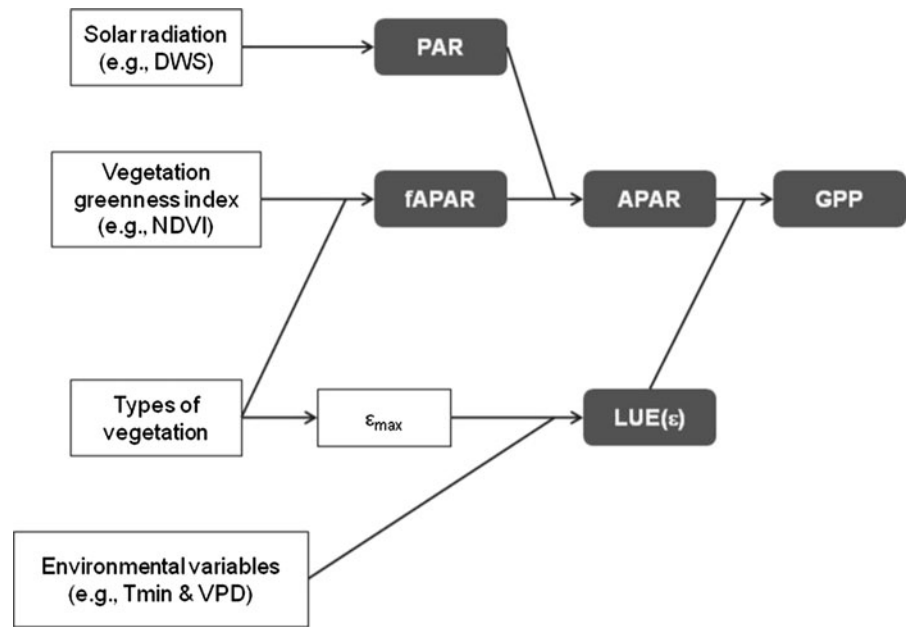
Estimating annual GPP and verification

We used a LUE model to estimate annual GPP. This model calculates productivity as a function of the available light used by plants to convert CO₂ into organic carbon (Monteith 1972; Prince and Goward 1995; Running et al. 2004). According to the LUE method (Fig. 1), the amount of vegetation carbon uptake is determined by the absorbed photosynthetically active radiation (APAR) and LUE (ϵ). APAR is determined by the amount of incident solar radiation (i.e., in wavelengths 400 and 700 nm) and the type of vegetation being exposed to light. ϵ_{\max} , i.e., maximum carbon conversion efficiency, measures vegetation carbon uptake per unit energy (from light) captured under favorable climate and nutrient conditions. ϵ_{\max} for various vegetation types have been derived from field observations and/or ecological process models (Gower et al. 1999). Environmental constraints such as temperature and vapor pressure deficit (VPD) also influence the actual rate of carbon production (Prince and Goward 1995).

The annual GPP was calculated for each land-cover type based on estimates of the LUE parameter (ϵ), vegetation greenness index, and climate variables (Fig. 1). Land-cover types were derived from the NLCD land-cover/use classes for 1992 and 2001, respectively (Vogelmann et al. 2001; Homer et al. 2007). To capture the characteristic LUE among different ecological systems, NLCD categories were grouped into 10 land-cover types, including seven vegetation-dominated classes (agriculture, three forest types, shrubland, grassland, and wetland), a built-up category (with some vegetation), bare land, and water bodies (Table 1). The 30-m regrouped land-cover data were aggregated to 1-km grid, each pixel containing the percentage coverage of individual land-cover types.

The maximum LUE values (ϵ_{\max}) were adopted from previously published research (Yang et al. 2007) except for the built-up and wetland categories (Table 1). The wetland ϵ_{\max} was set as the average ϵ_{\max} of forests, shrubland, and grassland based on the assumption that wetlands are generally a combination of these

Fig. 1 The light-use efficiency (LUE) approach estimates gross primary production (GPP) as the function of absorbed photosynthetically active radiation (APAR) and vegetation carbon conversion efficiency (ϵ). *DWS* downward shortwave radiation, *NDVI* normalized difference vegetation index, *T_{min}* minimum daily temperature, *VPD* vapor pressure deficit



vegetation types. Thus, the variation of plant community and hydrological condition was not taken into account for ϵ_{\max} of wetlands in this study. ϵ_{\max} for the built-up category was estimated as the area-weighted average of ϵ_{\max} for trees (the average of deciduous forest and coniferous forest; 1.29 g C MJ^{-1}), lawns (assigned as the value for grassland; 0.86 g C MJ^{-1}), impervious surface (0), and other non-vegetated land (0). For a built-up pixel at the 30-m resolution, area proportions of trees and impervious surface were extracted respectively from the NLCD percentage canopy cover (Huang et al. 2003) and impervious surface (Yang et al. 2003) datasets. As data on lawn distribution across the entire study area were not available at 30-m resolution at the time of analysis, we had to approximate the proportions of lawns and other non-vegetated land for the remaining area of the built-up pixel. We assumed that half of the remainder of the pixel (i.e., after taking out trees and impervious surface) was occupied by lawns.

The biweekly Advanced Very High Resolution Radiometer (AVHRR) Normalized Difference Vegetation Index (NDVI) was used to estimate the fraction of absorbed photosynthetically active radiation (fAPAR) for each land-cover type. The NDVI data had been processed to minimize cloud cover, sensor degradation, and atmospheric effects (USGS EROS Data Center 2006) before being applied to this study.

We adopted the look-up-table approach developed for the estimation of fAPAR based on the Moderate Resolution Imaging Spectroradiometer (MODIS) NDVI data (Knyazikhin et al. 1999). Before applying the MODIS-based look-up table, AVHRR NDVI was converted into units of MODIS NDVI by multiplying 1.45 to the AVHRR values in the range between 0.12 and 0.62 following Huete et al. (2002). The NDVI time sequence provides information on vegetation greenness during each 14-day time period throughout the continental United States at the 1-km spatial resolution. Twenty-six NDVI images were applied to estimate the annual GPP in 1992/1993 and 2001, respectively, corresponding to the collection of NLCD land-cover/use data. In practice, the 1993 NDVI series were applied to minimize the anomalous effects of the Mount Pinatubo volcanic eruption in 1991. This volcanic eruption was known to have produced a global dimming in 1992 and lowered the vegetation productivity during that particular year (Ramachandran et al. 2000; Tucker et al. 2001). Because high cloud cover existed in the 1993 NDVI data after October 28, the NDVI time series of the last five biweekly time periods in 1993 were replaced with the 1992 NDVI data. Therefore, the complete biweekly time sequence of NDVI used in this study started from October 30, 1992 and ended on October 28, 1993.

Table 1 Land-cover types generated based on the National Land Cover Dataset/Database (NLCD) classification and corresponding documented maximum light-use efficiency (ϵ_{\max}) parameters

	NLCD 1992 ^a	NLCD 2001 ^b	ϵ_{\max} ^c (g C MJ ⁻¹)
Built-up	Low intensity residential (21)	Developed, open space (21)	0.51
	High intensity residential (22)	Developed, low density (22)	
	Commercial, industrial and transportation (23)	Developed, medium density (23)	
		Developed, high density (24)	
Deciduous forest	Deciduous forest (41)	Deciduous forest (41)	1.56
Coniferous forest	Evergreen forest (42)	Evergreen forest (42)	1.02
Mixed forest	Mixed forest (43)	Mixed forest (43)	1.31
Shrubland	Shrubland (51)	Shrub and scrub (52)	0.79
	Orchards, vineyards and other (61)		
Grassland	Herbaceous grassland (71)	Herbaceous grassland (71)	0.86
Agriculture	Pasture and hay (81)	Pasture and hay (81)	1.47
	Row crops (82)	Cultivated crops (82)	
	Small grains (83)		
	Fallow (84)		
	Urban and recreational grasses (85)		
Wetland	Woody wetlands (91)	Woody wetlands (90)	1.11
	Emergent herbaceous wetlands (92)	Emergent herbaceous wetland (95)	
Bare	Bare rock, sand and clay (31)	Barren land (31)	0
	Quarries, strip mines and gravel pits (32)		
	Traditional barren (33)		
Water	Open water (11)	Open water (11)	0
	Perennial ice and snow (12)	Perennial ice and snow (12)	

Numbers in the parentheses are land-cover codes used in the NLCD datasets

^a Vogelmann et al. (2001)

^b Homer et al. (2007)

^c Yang et al. (2007) except for the built-up and wetland categories that were approximated in this study

Climate variables, such as downward shortwave radiation (DWS), surface air temperature, and minimum daily temperature (Tmin), were obtained from the three-hourly North America Land Data Assimilation System (NLDAS) land-surface modeling results (Mitchell et al. 2004). The 0.125° climate data were resampled to 1-km spatial resolution and aggregated temporally to a 14-day time step. DWS multiplied by 0.45 yielded the estimates of PAR (Running et al. 2000). APAR was then estimated by multiplying PAR and the NDVI-based fAPAR. The surface air temperature was used to calculate VPD following Granger (1991). VPD is the difference between the actual and saturated water vapor pressure at a given temperature, with a large discrepancy indicating the decreased amount of moisture in the air. When the air is too dry and/or temperature is too low, photosynthesis

functions only partially or shuts down completely (Prince and Goward 1995). Therefore, VPD and Tmin were used as scalars for ϵ_{\max} (Fig. 1) to determine the photosynthesis rates (ϵ) under unfavorable temperature and moisture conditions following Running et al. (2000) and Heinsch et al. (2003).

At the 1-km resolution, GPP accumulated by a certain land cover during each two-week time period was calculated as the product of APAR and ϵ , multiplied by area proportion of this land cover and by 14 days. Summation of the bi-weekly GPP across all land-cover types over the 26 time periods during a year generated the pixel-wise estimate of annual GPP at the 1-km resolution. Changes in GPP were derived by subtracting the pixel-based GPP values in 1992/1993 from the 2001 estimates. Positive values indicate a greater GPP in the later year, and a negative value a lesser GPP.

The annual GPP estimates were then compared with literature values for different land-cover types. GPP estimates in 2001 were also compared with the MODIS GPP products. Specifically, the Collection 5 MODIS GPP (MOD17A3; Zhao et al. 2005) was acquired for verification purposes. Values of MODIS GPP were extracted for pure pixels of each land-cover type at the 1-km resolution and compared to estimates based on our method.

Examining GPP in association with settlement densities and settlement growth

Pairwise comparisons of means were performed to examine whether the estimates of annual GPP differ among the four settlement densities. Because this study encompasses a wide range of ecological systems, variance of GPP may be attributable to differences in species life traits across ecosystems. To control for such variance, we performed a two-factor analysis of variance on the estimated annual GPP. One factor was the type of settlement densities, and the other was ecoregion. Nine level-II ecoregion units defined by Omernick (1987) were used in this study. These ecoregions were produced based on combined factors of land use, vegetation, soil, climate, and land surface form. The level-II ecoregions throughout the eastern U.S. include two sub-regions of Northern Forests, five sub-regions of Eastern Temperate Forests, a Great Plains sub-region, and a Tropical Wet Forests sub-region (Fig. 2).

Similar statistical tests were applied to investigating changes in GPP between the years 1992/1993 and 2001. First, we ran a pairwise comparison of means to examine whether changes in GPP differ among types of settlement growth. Then, a two-factor analysis of variance on changes in GPP was performed, with one factor being the settlement growth type and the other the ecoregion type. In addition, we performed two-factor analyses of variance on changes in climate, land cover, and NDVI, i.e., variables used to estimate GPP in the LUE model (Fig. 1). These analyses shed some light on which variables contribute to the variance of changes in GPP among different types of settlement growth. The variables included changes in DWS, Tmin, VPD, NDVI, proportion of built-up land cover, proportion of forest, and proportion of agriculture.

Results

Settlement densities and annual GPP

In the eastern United States, less than three percent of the total land was occupied by urban and suburban densities in both census years of analysis (Table 2). Land settled at exurban densities accounted for 32–36 % of the total area. Although area of rural densities decreased between 1990 and 2000, the majority of the entire study area (approximately 60 %) was still occupied by rural settlement in 2000.

The productivity of rural areas, which were characterized by large proportions of woody and herbaceous species (crops mainly), was the highest among all settlement densities in both years (Table 2). GPP in exurban areas, where the combined amount of vegetation cover ranked second, was slightly lower than that for the rural densities. The average annual GPP in urban and suburban areas, where over half of the land was built-up land cover, was estimated to be less than half of the GPP observed in lower settlement densities in both 1992/1993 and 2001. The pairwise comparison of means showed that GPP differed significantly among settlement densities for both years with one exception (Appendix B in Supplementary material). In 2001, GPP in the urban settlement appeared to be lower than that for the suburban settlement by approximately 47 g C m^{-2} ; this difference, however, was not statistically significant.

According to the analysis of variance, GPP varied by settlement densities as well as ecoregions in both years (Table 3). Both the settlement and ecoregion variables had significant effects on GPP ($p < 0.05$). The Partial η^2 statistics, which measure the contribution of each model term, indicated that settlement densities and ecoregions contributed almost equally to the variation of annual GPP. The parameter estimates showed that, after controlling for the variance by ecoregions, the estimate of GPP in 1992/1993 was expected to be lower for the urban, suburban, and exurban densities by approximately 680, 547, and 47 g C m^{-2} than for the rural densities (Table 4). Those differences were approximately 799, 757, and 88 g C m^{-2} in 2001.

Regional changes in GPP

The annual GPP for the entire region was estimated to be 1,078.6 and 1,218.5 g C m^{-2} in 1992/1993 and 2001,

Fig. 2 Omernick (1987) level-II ecoregions in the eastern United States

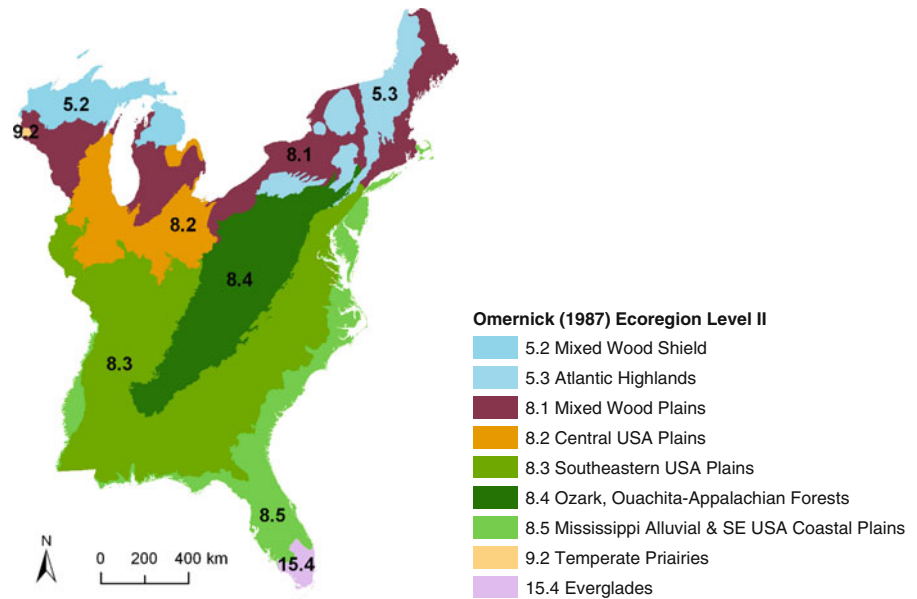


Table 2 Annual GPP and land cover proportions by settlement densities

	Area (km ²)	Annual GPP (g C m ⁻²)		Land cover (% cover per 1-km pixel)							
				Built-up		Forest/shrub		Agri./grass		Other	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
1992/1993											
U	242	390.24	312.02	54.77	35.53	21.12	27.25	5.31	8.95	18.80	11.22
S	38,961	532.45	285.88	51.28	28.15	24.42	21.79	14.69	18.37	9.61	8.67
E	596,765	1,072.67	264.31	5.45	12.52	54.42	29.63	31.29	28.06	8.83	11.48
R	1,196,523	1,099.48	208.18	0.70	3.62	48.51	35.24	40.68	36.38	10.11	16.77
2001											
U	270	436.46	401.80	58.34	38.12	18.63	28.98	3.34	7.82	19.69	29.52
S	42,153	483.40	340.05	65.86	29.75	16.68	19.41	7.13	13.62	10.33	20.52
E	677,398	1,199.62	332.78	12.43	17.18	47.20	28.73	26.50	26.02	13.88	19.06
R	1,139,149	1,257.08	238.20	5.06	6.87	42.84	32.84	37.37	34.79	14.74	22.09

U urban densities, *S* suburban densities, *E* exurban densities, *R* rural densities

The land-cover proportion measures percentage of the corresponding land-cover type within a 1-km resolution pixel

respectively. The region-wide net increase of GPP was approximately 140 g C m⁻² during this period. The total region-wide increase in annual GPP was estimated to be approximately 255 billion kg C between 1992/1993 and 2001. The climate data showed enhanced DWS by 6.54 W m⁻² from 1992/1993 to 2001, combined with higher T_{min} with an average increase of 0.58 °C. The climate variance varied greatly

by ecoregions but not much by settlement growth types; in contrast, changes in the proportion of the built-up land cover varied by a higher amount across the type of settlement growth than by ecoregions (Table 5). This indicates that, in the eastern U.S. between 1992/1993 and 2001, land-cover changes may have a greater impact than climate variance on changes in GPP among different types of settlement growth.

Table 3 Analysis of variance of the estimated annual GPP by the type of settlement densities and ecoregions

	1992/1993 ^a				2001 ^b			
	df	<i>F</i>	Sig.	Partial η^2	df	<i>F</i>	Sig.	Partial η^2
Corrected model	11	55,471.851	0.000	0.250	11	60,401.939	0.000	0.263
Intercept	1	47,974.955	0.000	0.026	1	40,611.661	0.000	0.021
Settlement densities	3	86,931.688	0.000	0.125	3	122,932.686	0.000	0.166
Ecoregion	8	41,868.666	0.000	0.155	8	36,709.843	0.000	0.136
Error	1,831,903				1,858,378			
Total	1,831,915				1,858,390			
Corrected total	1,831,914				1,858,389			

Four types of settlement densities (i.e., urban, suburban, exurban, and rural densities) and nine ecoregions (Fig. 2) were included in the two-factor analysis of variance for each year

^a $R^2 = 0.250$ (adjusted $R^2 = 0.250$)

^b $R^2 = 0.263$ (adjusted $R^2 = 0.263$)

Table 4 Effects of settlement densities and ecoregions (Fig. 2) on the estimated annual GPP in 1992/1993 and 2001

	1992/1993 ^a				2001 ^b					
	<i>B</i>	<i>t</i>	Sig.	95 % Confidence interval		<i>B</i>	<i>t</i>	Sig.	95 % Confidence interval	
				Lower bound	Upper bound				Lower bound	Upper bound
Intercept	1,139.161	382.870	0.000	1,133.330	1,144.993	1,205.076	362.621	0.000	1,198.562	1,211.589
[settl = U]	-680.251	-50.133	0.000	-706.845	-653.656	-799.273	-50.717	0.000	-830.161	-768.385
[settl = S]	-546.759	-500.903	0.000	-548.898	-544.619	-756.656	-586.469	0.000	-759.185	-754.127
[settl = E]	-47.107	-138.163	0.000	-47.776	-46.439	-87.846	-216.536	0.000	-88.641	-87.051
[settl = R]	0 ^c					0 ^c				
[eco = 5.2]	-165.613	-53.954	0.000	-171.629	-159.597	-101.537	-29.461	0.000	-108.292	-94.782
[eco = 5.3]	-26.070	-8.532	0.000	-32.058	-20.081	111.401	32.484	0.000	104.680	118.123
[eco = 8.1]	-84.740	-28.286	0.000	-90.611	-78.868	-9.526	-2.843	0.004	-16.094	-2.958
[eco = 8.2]	-147.749	-49.078	0.000	-153.649	-141.848	-100.595	-29.852	0.000	-107.200	-93.991
[eco = 8.3]	-14.101	-4.728	0.000	-19.946	-8.255	91.476	27.448	0.000	84.944	98.008
[eco = 8.4]	136.513	45.547	0.000	130.638	142.387	242.542	72.344	0.000	235.971	249.113
[eco = 8.5]	-126.205	-41.921	0.000	-132.105	-120.304	4.464	1.325	0.185	-2.140	11.067
[eco = 9.2]	-130.501	-21.360	0.000	-142.475	-118.526	-79.446	-10.825	0.000	-93.831	-65.062
[eco = 15.4]	0 ^c					0 ^c				

U urban densities, *S* suburban densities, *E* exurban densities, *R* rural densities

^a Dependent variable: GPP92/93

^b Dependent variable: GPP01

^c This parameter is set to zero because it is redundant

Settlement growth and changes in GPP

The urban, suburban, and exurban densities all experienced area expansion with a loss of rural areas between 1992/1993 and 2001 (Table 2). While 4.75 %

of the total study area experienced settlement growth, the majority of land remained in a constant settlement density category (Table 6). Exurbanization (4.57 %) occupied more than 25 times the area of suburbanization (0.17 %). The area experiencing urbanization

Table 5 Analysis of variance in climate, NDVI, and land cover changes. These variables were used to estimate annual GPP

	df	Partial η^2						
		Δ DSW	Δ Tmin	Δ VPD	Δ NDVI	Δ Built-up	Δ Forest	Δ Agri.
Corrected model	16	0.373*	0.022*	0.586*	0.094*	0.096*	0.040*	0.069*
Intercept	1	0.003*	0.000*	0.001*	0.001*	0.002*	0.000*	0.000*
Settlement growth	8	0.006*	0.000*	0.009*	0.011*	0.082*	0.011*	0.005*
Ecoregion	8	0.366*	0.022*	0.581*	0.085*	0.021*	0.025*	0.066*
Error	1,831,780							
Total	1,831,797							
Corrected total	1,831,796							

Nine types of settlement growth (i.e., consistently urban, consistently suburban, consistently exurban, consistently rural, urbanized, suburbanized, rural densities converted to suburbs, exurbanized, and other conversions) and nine ecoregions (Fig. 2) were included in the two-factor analyses of variance

* These model terms are significant at the 0.05 level

accounted for a very small portion of land (<0.01 %). Area of suburbs converted from rural densities was also minor (<0.01 %).

The amount of change in GPP varied greatly with changes in settlement density (Table 6). Among the four persistent density types, GPP only decreased in the consistently suburban area (-62 g C m^{-2}), which were characterized by a large increase in the built-up land cover. Among areas of settlement growth, GPP declined by approximately 152 g C m^{-2} in the

suburbanized area, where built-up surface was added at the highest rate. Estimated annual GPP increased by approximately 157 g C m^{-2} in exurbanized areas, which were characterized by only small increases in the built-up land cover. The pairwise comparison of means indicated that the changes in GPP varied significantly across settlement growth types, except for the urbanized areas where a great amount of variance occurred (Appendix C in Supplementary material).

Table 6 Changes in annual GPP and land cover proportions by types of settlement growth

	Area (km ²)	Changes in GPP			Changes in land cover (% cover per 1-km pixel)					
		Mean (g C m ⁻²)		Total ($\times 10^6$ kg C)	Built-up		Forest/shrub		Agri./grass	
		Mean	SD		Mean	SD	Mean	SD	Mean	SD
CU	241	8.97	152.91	2.16	7.43	10.99	-5.61	9.33	-2.18	7.79
CS	38,850	-62.00	192.47	-2,408.62	16.00	17.04	-8.44	12.72	-7.90	12.29
CE	593,399	112.75	188.45	66,903.91	7.87	10.98	-8.32	14.15	-4.61	12.32
CR	1,112,600	160.16	157.21	178,195.88	4.43	5.40	-4.54	15.10	-4.30	11.58
Urbanized	26	37.90	262.00	0.99	12.90	16.88	-4.67	8.02	-4.53	8.06
Suburbanized	3,214	-151.29	314.60	-486.23	27.44	26.63	-14.84	19.84	-10.52	20.79
R2S	62	-234.95	487.85	-14.57	26.30	29.21	-3.24	10.39	-18.22	32.04
Exurbanized	83,799	157.30	179.83	13,181.70	5.39	8.33	-7.67	15.12	-2.94	11.84
Other	180	173.22	191.35	31.18	2.71	5.14	-3.46	13.59	-1.58	8.70

CU consistently urban, CS consistently suburban, CE consistently exurban, CR consistently rural, R2S rural densities converted to suburbs

The total gain (i.e., positive values) or loss (i.e., negative values) of GPP was calculated as the average changes in annual GPP multiplied by total area of each type of settlement growth. The change in land-cover proportion measures the absolute increase or drop of area in percentage within individual 1-km pixels for each land-cover type between 1992/1993 and 2001

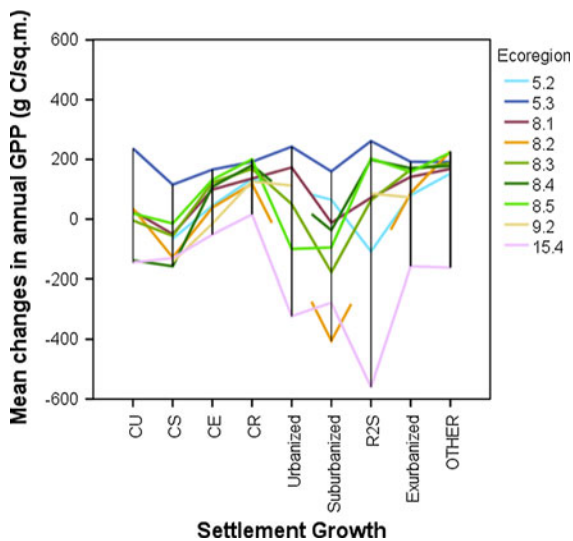


Fig. 3 Changes in GPP by types of settlement growth (*CU* consistently urban, *CS* consistently suburban, *CE* consistently exurban, *CR* consistently rural, *R2S* rural densities converted to suburbs) across ecoregions (Fig. 2)

Changes in GPP were also found to vary by ecoregions (Fig. 3). Such variance was high over areas that had experienced changes in settlement densities, in particular the urbanized areas as well as suburbs converted from rural settlements. The analysis of variance indicated that changes in GPP varied significantly by types of settlement growth as well as ecoregions (Table 7). Types of settlement growth had a greater effect on the total variance of changes in GPP than ecoregions, according to the Partial η^2 statistics. Urbanization, suburbanization, and exurbanization was expected to reduce GPP by approximately 123, 314, and 11 g C m^{-2} , respectively after controlling for the variance in GPP between those two years by ecoregions (Table 8). Meanwhile, built-up surface was expected to increase by approximately 10, 23, and 1 % in urbanized, suburbanized, and exurbanized areas, respectively.

GPP comparisons

The annual GPP estimates of our study are within the range of documented vegetation primary productivity by all land-cover types (Table 9). Our estimates of GPP for deciduous and coniferous forests in 2001 are higher than the MODIS 2001 global averages (Zhao et al. 2005) or tower-based estimates (Heinsch et al.

2006). This may be partly attributed to the different land-cover data sets used in the studies. We used the 30-m NLCD classification to derive 10 land-cover categories for the eastern United States, while the MODIS team used the 1-km MODIS land-cover data for biome type identification across the globe. The MODIS GPP estimates averaged across our NLCD-based classes for pure land-cover pixels at 1-km resolution had relatively large differences for all land-cover types when compared to those averages based on MODIS land-cover classification, indicating that land-cover data may be one important cause of the observed differences in GPP estimates. Other factors such as different climate data used in analysis may also contribute to the observed difference.

The GPP estimates for grassland and agriculture vary significantly in literature, which may result from different site locations and types of species being observed or modeled. For example, the tower-based estimate for grassland ranged between 117 and 1,650 g C m^{-2} varying by species composition, soil type, humidity, and temperature (Heinsch et al. 2006; Yang et al. 2007; Xiao et al. 2010). The grassland GPP estimate in our study is within the documented range and comparable to the temperate grasslands productivity. The productivity values of corn, soybean, and wheat vary widely across and within the three agricultural sub-classes (Lobell et al. 2002; Turner et al. 2005; Yang et al. 2007). Our GPP estimate for agriculture falls at around the middle of the documented range.

GPP in the built-up and wetland categories are not as well-documented as for other land covers. The mixed nature of urban land covers presents challenges for field- or model-based estimation. Wetlands are also a mixed land cover type, often composed of multiple species. In addition, they are heavily influenced by hydrology, which creates temporally dynamic patterns of productivity (Scurlock and Olson 2002). The estimated GPP for the built-up category in our study is higher than the upper bound value of gross carbon uptake documented for several major US cities, where carbon fluxes were considered for urban trees only and overlooked lawns and other vegetation (Nowak and Crane 2002). The wetland GPP estimate is also higher than values from literature (Schwalm et al. 2006), where GPP was documented for three wetland sites in Canada at higher latitudes and colder climate than most US wetlands.

Table 7 Analysis of variance of changes in GPP by settlement growth types and ecoregions

Source of variance	Type III sum of squares	df	Mean square	<i>F</i>	Sig.	Partial η^2
Corrected model	3.987E+09	16	2.492E+08	8,803.195	0.000*	0.071
Intercept	8.835E+04	1	8.835E+04	3.121	0.077	0.000
Settlement growth	2.909E+09	8	3.636E+08	12,844.593	0.000*	0.053
Ecoregion	1.200E+09	8	1.500E+08	5,299.989	0.000*	0.023
Error	5.185E+10	1,831,780	2.831E+04			
Total	9.144E+10	1,831,797				
Corrected total	5.584E+10	1,831,796				

Nine types of settlement growth (i.e., consistently urban, consistently suburban, consistently exurban, consistently rural, urbanized, suburbanized, rural densities converted to suburbs, exurbanized, and other conversions) and nine ecoregions (Fig. 2) were included in the two-factor analysis of variance

* These model terms are significant at the 0.05 level

Table 8 Effects of settlement growth and ecoregions (Fig. 2) on the estimated changes in GPP and proportions of built-up land cover

Parameter	Changes in GPP					Changes in built-up proportion				
	<i>B</i>	<i>t</i>	Sig.	95 % Confidence interval		<i>B</i>	<i>t</i>	Sig.	95 % Confidence interval	
				Lower bound	Upper bound				Lower bound	Upper bound
Intercept	9.700	4.075	0.000	5.034	14.365	4.626	40.256	0.000	4.400	4.851
[SG = CU]	-149.245	-13.766	0.000	-170.494	-127.995	3.676	7.025	0.000	2.651	4.702
[SG = CS]	-220.931	-253.205	0.000	-222.641	-219.221	11.679	277.300	0.000	11.596	11.761
[SG = CE]	-53.776	-194.702	0.000	-54.317	-53.235	3.709	278.206	0.000	3.683	3.735
[SG = CR]	0 ^a					0 ^a				
[SG = Urbanized]	-123.140	-3.732	0.000	-187.816	-58.464	9.996	6.276	0.000	6.874	13.118
[SG = Suburbanized]	-314.554	-105.673	0.000	-320.388	-308.720	23.436	163.112	0.000	23.154	23.717
[SG = R2S]	-321.795	-15.034	0.000	-363.748	-279.842	22.150	21.439	0.000	20.125	24.175
[SG = Exurbanized]	-10.757	-17.776	0.000	-11.943	-9.571	1.188	40.671	0.000	1.131	1.245
[SG = Other]	13.327	1.045	0.296	-11.675	38.328	-1.005	-1.632	0.103	-2.211	0.202
[eco = 5.2]	118.145	48.128	0.000	113.334	122.957	-0.569	-4.804	0.000	-0.802	-0.337
[eco = 5.3]	197.857	80.986	0.000	193.068	202.645	-3.409	-28.911	0.000	-3.640	-3.178
[eco = 8.1]	134.738	56.235	0.000	130.042	139.434	-0.157	-1.360	0.174	-0.384	0.069
[eco = 8.2]	103.523	42.995	0.000	98.804	108.242	2.221	19.112	0.000	1.993	2.449
[eco = 8.3]	161.339	67.646	0.000	156.665	166.014	-0.538	-4.673	0.000	-0.764	-0.312
[eco = 8.4]	162.353	67.736	0.000	157.655	167.050	0.367	3.175	0.001	0.141	0.594
[eco = 8.5]	184.641	76.707	0.000	179.924	189.359	-1.761	-15.152	0.000	-1.988	-1.533
[eco = 9.2]	107.047	21.957	0.000	97.492	116.602	1.462	6.213	0.000	1.001	1.923
[eco = 15.4]	0 ^a					0 ^a				

CU consistently urban, CS consistently suburban, CE consistently exurban, CR consistently rural, R2S rural densities converted to suburbs

^a This parameter is set to zero because it is redundant

Table 9 GPP verification

Land-cover types	Annual GPP (g C m ⁻²)		MODIS 2001 ^a (g C m ⁻²)	MODIS 2001 by NLCD-based land covers (g C m ⁻²)	Tower- and model-based estimates (g C m ⁻²)
	1992/1993	2001			
Built-up	151.26 (72.42)	162.83 (75.40)	n/a	213.06 (436.52)	21–123 ^b
Deciduous forest	1,345.16 (136.46)	1,639.83 (137.41)	1,366	1,423.04 (153.97)	1565 ^c , 1774 ^d , 1358 ^e
Coniferous forest	934.21 (170.36)	1,123.08 (199.11)	818	1,846.52 (611.75)	750 ^c , 1432 ^d , 1104 ^e
Mixed forest	1,033.65 (184.65)	1,205.79 (103.48)	1,125	1,154.44 (198.11)	1277 ^c , 1447 ^d
Shrubland	913.64 (107.36)	803.07 (96.53)	868	1,507.60 (435.40)	304 ^d
Grassland	944.80 (165.71)	791.18 (146.83)	396	1,022.85 (285.29)	272 ^c , 589 ^d , 117–1650 ^f
Agriculture	1,050.60 (144.86)	1,222.12 (194.34)	721	909.34 (235.27)	1500 ^d , 1674 ^e , 758 ^e , 773–1403 ^f , 725–2600 ^g , 253–1800 ^g
Wetland	1,086.39 (294.13)	1,169.30 (409.31)	n/a	1,679.29 (663.86)	310–723 ^h

Numbers in parentheses indicate standard deviation across 1-km pixels. “Annual GPP” refers to estimates based on our method. “MODIS 2001” came from the published data (Zhao et al. 2005). “MODIS 2001 by NLCD-based land covers” represents GPP values extracted from the Collection 5 MODIS GPP over pure land-cover pixels at the 1-km resolution. “Tower- and model-based estimates” came from various literatures as cited

^a Zhao et al. (2005)

^b Nowak and Crane (2002). Estimates are for urban trees only

^c Heinsch et al. (2006)

^d Xiao et al. (2010)

^e Turner et al. (2005). Converted from net primary production (NPP)

^f Yang et al. (2007)

^g Lobell et al. (2002)

^h Schwalm et al. (2006). Observation was conducted in three Canadian wetlands

Discussion

Settlement growth in the eastern United States

Although rural densities still occupied the majority of land in the eastern United States in 2000, they were rapidly replaced by low- and intermediate-density exurban and suburban development during the 1990–2000 time period. This represented a continuing trend of settlement sprawl resulting from population increase, a decline in the average household size nationwide since the 1960s, and less dense settlement patterns. According to the US Census Bureau (1995, 2009), the urban population grew from 69.9 to 79 % of the total US population between 1960 and 2000, while the average number of people living in a housing unit declined from 3.3 to 2.6 persons per unit during the same time period.

Exurbanization, i.e., conversion from rural to exurban densities, was more rapid than suburbanization or urbanization for the study area between 1990 and 2000. This corroborates previous research findings

at the regional and national scales (Theobald 2001; Brown et al. 2005; Clark et al. 2009). The area of exurban settlement was nearly 15 times the area of urbanized settlement observed by census block groups, and contributed to the decrease of cropland by approximately 22 % in areas east of the Mississippi River between 1950 and 2000 (Brown et al. 2005). We also found an approximately 4 % decline in agriculture in the exurbanized land throughout the eastern United States during the 1990–2000 time period.

The aggregation of census data from 1-ha to 1-km spatial resolution may have underestimated proportions of urban densities. This is because census blocks tend to be small in size at places where population density is high. Some tiny urban blocks may not be observed at the 1-km spatial resolution. Spatial scales, i.e., the size of image pixels or the extent of study area, have been well documented to influence the observed composition, proportions, and spatial configuration of landscape components (Wu 2004). However, in this study we did not quantify this scaling effect explicitly.

Changes in GPP and association with settlement growth

Our study shows that GPP increased by approximately 13 % or 255 billion kg C for the eastern United States as a whole between 1992/1993 and 2001. However, neither the region-wide increase in GPP nor GPP increases in low-density development may be attributed to the expansion of forest or agriculture land covers. Instead, DWS and Tmin were both found to increase significantly on average across the entire study area between 1992/1993 and 2001. Such enhancement in light may have favored carbon accumulation of green vegetation since low light intensities limit plant photosynthesis. Increases in Tmin may have enhanced vegetation photosynthesis through the prolonged growing season. In addition, CO₂ enrichment may be another important contributor to the regional increase in carbon uptake throughout the eastern United States. The rising CO₂ concentration in the atmosphere was found to enhance photosynthesis of certain plants, mainly C₃ species, through increasing the partial pressure of CO₂ in the leaf intercellular spaces (Lambers et al. 1998). CO₂ enrichment was shown to enhance vegetation carbon uptake by a greater amount compared to land-cover changes in the 1980s and 1990s (Albani et al. 2006).

Although GPP increased on average across the eastern United States, large spatial variance was observed among different categories of settlement growth. Statistical results showed that GPP decreased by a greater amount where there were greater increases in the proportion of built-up land cover. This implies that the expansion of built-up land cover contributed negatively to changes in GPP among different types of settlement growth. Suburban and suburbanized areas were associated with large amounts of conversion from other land covers to the built-up type; therefore, the carbon uptake by vegetation decreased in these areas. The highest rate of increase in GPP was found in the consistently rural densities, followed by exurbanized areas; the averages in both areas were higher than the regional average increment of GPP. The lower rate of conversion to built-up cover may have contributed to the higher amount of GPP increases in the exurbanized areas. In some cases, conversion of abandoned agriculture to perennial vegetation may also enhance vegetation carbon uptake in low development densities through better land-use management

and/or adopting high-carbon-yield genetics. The human appropriation of vegetation primary production needs to be examined in association with settlement growth for the future research (Erb et al. 2009).

While our study indicated that settlement growth has significant impacts on GPP and possibly through the varying proportions of built-up surface, a more sophisticated design of cause-effect analysis is desired for the future research. This analysis shall focus on disentangling effects of land cover changes, climate variation, and settlement development on changes in vegetation production. Also needed is sensitivity analysis that allows us to evaluate relative importance of land cover and climate variables on GPP. Another important future work is to evaluate uncertainties associated with the estimation of GPP due to errors presented in the input datasets for the LUE model. For example, previous research has documented errors presented in the NLCD land-cover datasets due to difference in the methods used to create each of the datasets (Fry et al. 2009). Although a retrofitted change product exists for NLCD to reduce the error, we used the original NLCD data that permitted separation of different types of forests for the purpose of estimating GPP. The spatial aggregation of NLCD data (from 30-m to 1-km) may have helped reduce errors associated with land-cover datasets (Pontius et al. 2011); however, the impacts of remaining error on GPP were not tested rigorously in the present study.

Our study showed that vegetation carbon uptake rates in the low-density exurban and exurbanized areas are relatively high. Carbon emissions associated with activities such as irrigation and fertilization, which require a large amount of energy and fuel input, may also mount in these areas (Imhoff et al. 2000). Given the higher proportion of vegetation in exurban areas than in urban/suburban densities, a greater amount of carbon uptake may be canceled in part by emissions due to higher maintenance in low-density exurban development compared to urban/suburban settlement. Future research should focus on calculating the carbon balance, which includes both the fossil fuel-related emissions and vegetation carbon sinks over large spatial extents (Zhao et al. 2011).

The quantitative analysis of carbon exchange between vegetation and the atmosphere provides inference on vegetation carbon sinks. The current global accounting of the carbon cycle may underestimate carbon sequestration in the complex mosaic

regions that are neither pure vegetation nor impervious surface. Recent research about global changes in net primary production has indicated continuous productivity increase in most non-urban land covers within the eastern United States during the 2000–2009 time period (Zhao and Running 2010). The trend of primary production in the human-dominated counterparts during the last decade has not been documented, but may be assessed using the same research approach applied to this study. The long-term understanding of carbon fluxes, tied specifically to demographic patterns, contributes to the informed decision making of stakeholders; for example, the development and use of carbon credits accounting and trading programs.

Conclusion

The twenty-first century sees increased integration of carbon management into development strategies for the reduction of atmospheric GHGs in urbanizing regions (DeGrove 2005; Ewing et al. 2008; Porter 2008). Effective low-carbon development planning requires better understanding of the impacts of urban form on carbon fluxes. This study indicates that vegetation carbon uptake is very low in high-density urban and suburban areas due to large proportions (above 50 %) of built-up surface, of which approximately 30 % on average is impervious throughout the eastern United States. Moreover, suburbanization was shown to add built-up proportions at a higher rate than urban or suburban densities. Carbon emission reductions in these high-density developed and developing areas should focus on alternatives such as renewable energy sources, green roofs, and high-carbon-yield fast-growing species (Porter 2008; Dvorak and Volder 2010) to offset the reduced carbon uptake due to built-up expansion.

This study demonstrates a spatially explicit accounting of vegetation carbon uptake through photosynthesis along the urban–rural gradient over a large geographic extent. It is among the first attempts to integrate demographic analysis, ecology, and GIScience for the understanding of human settlement impacts on ecosystem services (Turner et al. 2007; Zhao et al. 2007; Grimm et al. 2008a; Pataki et al. 2009; Robinson et al. 2009; Churkina et al. 2010; Hutyrá et al. 2010). It contributes directly to carbon-cycle science (Dilling 2007; Churkina 2008; Grimm

et al. 2008b) and landscape sustainability (Wu 2010) by both clarifying the effects of these heterogeneous landscapes on the carbon cycle and informing development decisions that have consequences for those effects. The integrated approach of biophysical remote sensing and demographic analysis may be extended further to investigate human carbon impacts that take into account the complex dimension of land-use regulations and policies. A better understanding of vegetation carbon activities along gradients of settlement densities also contributes to knowledge of the carbon balance that takes into account both emissions and sequestration in the human-dominated landscape (Wentz et al. 2002; Pataki et al. 2006, 2009; Zhao et al. 2011).

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