Historical forest baselines reveal potential for continued carbon sequestration

Jeanine M. Rhemtulla[a,1], David J. Mladenoff[b], and Murray K. Clayton[c]

[a]Department of Geography, McGill University, Montreal, QC, Canada H3A 2K6; and Departments of [b]Forest and Wildlife Ecology and [c]Plant Pathology and Statistics, University of Wisconsin-Madison, Madison, WI 53706

Edited by B. L. Turner, II, Arizona State University, Tempe, AZ, and approved February 23, 2009 (received for review October 7, 2008)

One-third of net CO_2 emissions to the atmosphere since 1850 are the result of land-use change, primarily from the clearing of forests for timber and agriculture, but quantifying these changes is complicated by the lack of historical data on both former ecosystem conditions and the extent and spatial configuration of subsequent land use. Using fine-resolution historical survey records, we reconstruct pre-EuroAmerican settlement (1850s) forest carbon in the state of Wisconsin, examine changes in carbon after logging and agricultural conversion, and assess the potential for future sequestration through forest recovery. Results suggest that total aboveground live forest carbon (AGC) fell from 434 TgC before settlement to 120 TgC at the peak of agricultural clearing in the 1930s and has since recovered to approximately 276 TgC. The spatial distribution of AGC, however, has shifted significantly. Former savanna ecosystems in the south now store more AGC because of fire suppression and forest ingrowth, despite the fact that most of the region remains in agriculture, whereas northern forests still store much less carbon than before settlement. Across the state, continued sequestration in existing forests has the potential to contribute an additional 69 TgC. Reforestation of agricultural lands, in particular, the formerly high C-density forests in the north-central region that are now agricultural lands less optimal than those in the south, could contribute 150 TgC. Restoring historical carbon stocks across the landscape will therefore require reassessing overall land-use choices, but a range of options can be ranked and considered under changing needs for ecosystem services.

forest-agriculture trade-offs | old-growth forest | Eastern North America | land-use history | carbon sink

One-third of net CO_2 emissions to the atmosphere since 1850 are the result of land-use change, primarily from the clearing of forests for timber and agriculture (1). Although tropical deforestation is still a major source of CO_2 (2), temperate regions have become a carbon sink, largely because of reforestation of former cutover lands and abandoned farmlands, and woody encroachment resulting from fire suppression (3). This is especially the case in the conterminous United States, where land was first cleared for settlement in the east, and then abandoned as settlers migrated westward (4, 5). Inventory- and field-based studies suggest that land-use history is a more important driver of carbon sequestration in these systems than nutrient deposition, CO_2 fertilization, or climate change (6, 7).

How much potential is there for future sequestration on these lands? Continued forest recovery and reforestation of suboptimal agricultural lands are being promoted as important avenues for future carbon sequestration (8). But the degree to which these ecosystems have already recovered to historical baselines is not known and would provide a critical estimate of future potential sequestration on these lands. The current carbon sink due to land-use change and fire suppression in the U.S. has been estimated at ≈0.33 PgC/year (9), which is approximately equivalent to 15% of annual CO_2 emissions from fossil-fuel burning in the country. Although few quantitative estimates are available, the pace of sequestration is projected to decline over this century as forest recovery tapers off and comes into equilibrium with harvesting practices (6, 9, 10). Birdsey (10) has suggested that carbon storage in U.S. forests will equilibrate by 2040, whereas Hurtt (9) suggests that sequestration will decrease to 0.21 PgC/y by 2050 and 0.13 PgC/y by 2100 (assuming that future land-management practices are similar to those at present). Of course, managing forests to allow the development of old-growth characteristics similar to the original primary forests would increase these levels. Recent research shows that mature and old forests continue to act as carbon sinks long into the future, contrary to previous assumptions (11).

Quantifying changes from historical carbon pools is complicated by the lack of historical data on both former ecosystem conditions and the extent and spatial configuration of subsequent land use. Historical carbon budgets are therefore mostly reconstructed by using potential vegetation maps, coarse-resolution census data, and modeling techniques (1, 12). Here, we draw on 2 remarkable historical surveys, the first conducted before widespread EuroAmerican settlement, and the second at the period of peak agricultural clearing, to reconstruct fine-resolution historical vegetation and land-use data. Using a case study from Wisconsin where primary forests were almost entirely cut by the turn of the 20th century and have since undergone considerable regrowth (13), we use these data to compare current pools of aboveground live forest carbon (AGC) with those before settlement and at the period of peak agricultural conversion. Because Wisconsin is composed of 2 distinct biomes—formerly dense forests in the north and former prairie-savanna in the south—each with differing land-use histories, we also compare trajectories of change in carbon stocks and the potential for future sequestration through both forest recovery and afforestation on current agricultural lands. Although future carbon stocks could certainly be enhanced beyond historical baselines through specialized forest-management practices, our goal here is to estimate an easily attainable carbon benchmark that would not require significant management inputs but would entail land-use change decisions.

Results

Effects of Land Use on AGC. Before EuroAmerican settlement, northern Wisconsin was dominated by coniferous and mixed conifer-hardwood stands, whereas southern Wisconsin was dominated largely by an oak savanna-prairie mosaic (Fig. 1*A*). Logging and agricultural land conversion began in the mid-1800s and peaked in the 1930s–40s (13). Southern Wisconsin was mostly converted to cropland. The northern forests were almost

Author contributions: J.M.R. and D.J.M. designed research; J.M.R. performed research; M.K.C. contributed new analytic tools; J.M.R., D.J.M., and M.K.C. analyzed data; and J.M.R. and D.J.M. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

[1]To whom correspondence should be addressed at: Department of Geography, McGill University, Montreal, QC, Canada H3A 2K6. E-mail: jeanine.rhemtulla@mcgill.ca.

This article contains supporting information online at www.pnas.org/cgi/content/full/0810076106/DCSupplemental.

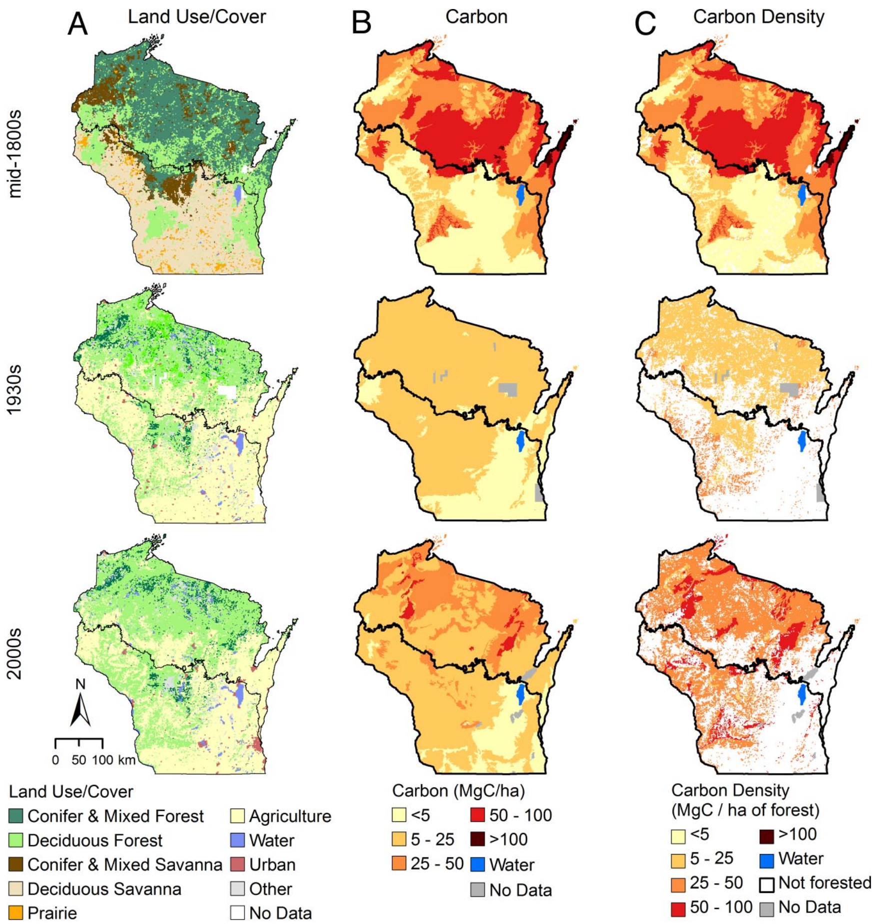

Fig. 1. Dominant land cover/use (*A*), above-ground live forest carbon (MgC per ha of total land area) (*B*), and above-ground live forest carbon density (MgC per ha of forest area) (*C*) in Wisconsin in the mid-1800s (before EuroAmerican settlement), the 1930s (peak agricultural clearing), and the present. Carbon estimates are median values calculated from the Monte Carlo simulation results (to account for uncertainties in the historical data sources).

entirely logged; the more southerly of these forests were subsequently converted to agriculture, whereas those in the far north were left to recover naturally and soon dominated by early successional deciduous species. Little agricultural abandonment has occurred since then; northern forests are still largely dominated by deciduous species, and some forest ingrowth has occurred in remnant stands in the south.

Changes in land use led to a 3.5-fold decline in AGC from the mid-1800s (median = 434 TgC; 95% confidence interval = 364–460 TgC) to the 1930s (median = 120 TgC; CI = 109–137 TgC) (Fig. 2*A*). After forest regrowth in the north and ingrowth in the south over the past century, current AGC has recovered to two-thirds (median = 276 TgC; CI = 275–277 TgC) of its initial value.

However, the distribution of AGC across the state has changed considerably. At the onset of EuroAmerican settlement, AGC was highly spatially variable. Median AGC across northern Wisconsin was 47 MgC/ha (Fig. 2*B*). The highest AGC values occurred in the mixed forests adjacent to Lake Michigan (>100 MgC/ha) and in the northern central region (just north of the north–south boundary) (50–100 MgC/ha) (Fig. 1*B*). Areas characterized by sandy outwash soils, especially low productivity pine barrens, stored the lowest amounts of AGC. Southern Wisconsin, which was dominated by prairie and savanna ecosystems, stored relatively little AGC (median = 12 MgC/ha); the highest values (25–100 MgC/ha) were found in a region of closed deciduous forest in southwestern Wisconsin.

By the 1930s, logging and agricultural conversion led to both a decrease and homogenization of AGC stocks. Logging in the North eliminated the large presettlement AGC stocks; median AGC fell to 11 MgC/ha and the former spatial variability in stocks was lost. Less AGC was lost in the South (median = 6 MgC/ha), where fewer trees occurred in the mid-1800s. Indeed, AGC increased in some areas of the South (Fig. 1*B*), likely because settlement and fire suppression led to forest ingrowth in savanna ecosystems (14).

Over the past 70 years, total AGC in southern Wisconsin has recovered (median = 13 MgC/ha), despite the fact that the south is still largely dominated by cropland (Fig. 2*C*). Although forest regrowth has led to increased carbon storage in northern Wisconsin, AGC values are still approximately half (median = 25 MgC/ha) of those in the mid-1800s and spatial variability has declined. Recovery of AGC has been especially slow in northern central Wisconsin, which was formerly heavily forested and is now predominantly agricultural.

Changes in Carbon Allocation Within Forests. To control for the changes in the total amount of forest, we examined changes in AGC density (AGC per unit of forest or savanna area) (Fig. 1*C*). Because forest and savanna were the dominant land-cover types in the mid-1800s, AGC at that time period was similar whether mapped by total area or forest area (Fig. 1 *B* and *C*). By the 1930s, however, AGC density had declined dramatically in northern Wisconsin, but increased in remnant forests in the south, particularly in the southwest. This trend has continued over the past seventy years. Although AGC density has increased

SUSTAINABILITY SCIENCE

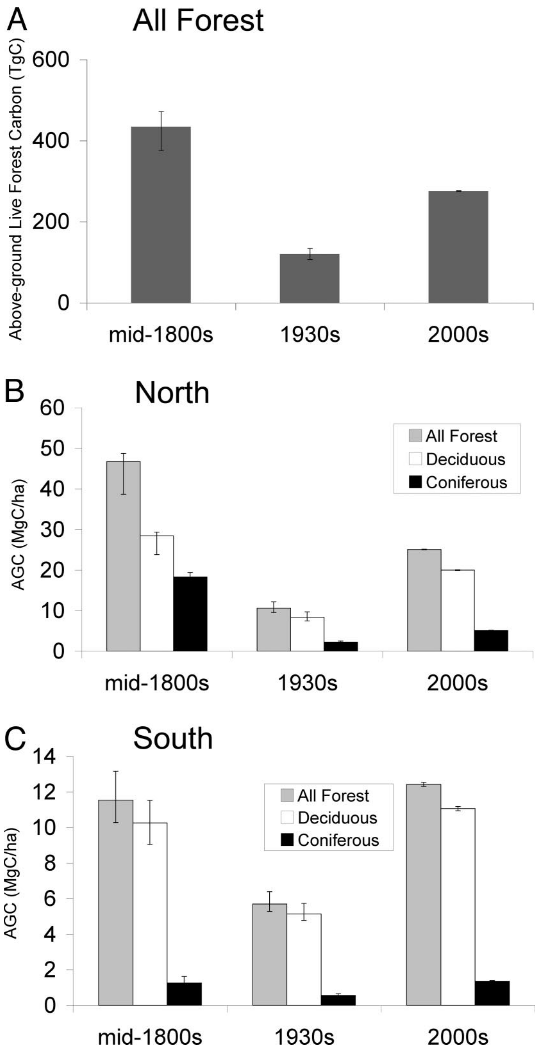

Fig. 2. Total above-ground live forest carbon in Wisconsin (TgC) (*A*) and by forest type (MgC/ha) in northern (*B*) and southern (*C*) Wisconsin from the mid-1800s to the present. Data are medians and 95% confidence intervals.

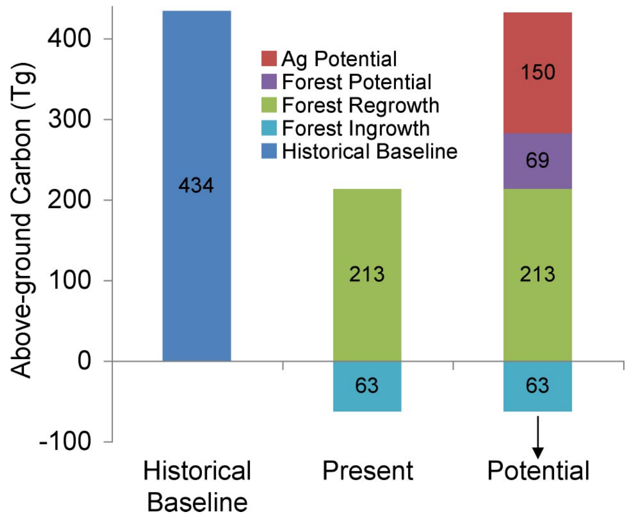

Fig. 3. Potential for carbon sequestration (TgC) in Wisconsin given full forest recovery and reforestation of current agricultural lands. Historical baseline is total above-ground live forest carbon in the mid-1800s, present carbon includes both forest regrowth and ingrowth into areas that historically contained less carbon. Forest potential assumes that all existing forests recover to baseline carbon stocks, whereas agricultural potential assumes reforestation of agricultural lands to historical forest carbon content.

throughout the state, density is still lower in northern forests than it was at the onset of EuroAmerican settlement, but higher in the northwestern pine barrens and southwest because of fire suppression and industrial plantations. Many of the areas of highest AGC density in the mid-1800s (in northern central Wisconsin) are still dominated by (subprime) agricultural land, thus limiting the potential for carbon sequestration.

The relative amount of AGC stored by coniferous and deciduous species has also shifted over the past 150 years. In the mid-1800s, coniferous species stored ≈39% of the total AGC in northern Wisconsin and 11% in southern Wisconsin (Fig. 2). Coniferous species were an important AGC pool across much of northern Wisconsin, whereas deciduous species contained higher amounts of AGC in the region adjacent to Lake Michigan, in northern central Wisconsin, and in the southwest (Fig. S1). By the 1930s, coniferous species contained only 21% of total AGC in northern Wisconsin, mostly in remnant old-growth stands. In southern Wisconsin, however, the proportion of AGC found in coniferous species remained fairly constant (10%). This trend has continued into the present; coniferous AGC is still much reduced in the North (20%) and is largely limited to sandy outwash soils in the far North and in central Wisconsin. There has been greater recovery of deciduous AGC stocks, although they are still lower and less spatially variable than in the mid-1800s.

Potential for Future Sequestration. By using historical conditions as a baseline, the potential for future sequestration can be broken into 2 components: continued recovery in existing forests, and the potential for additional sequestration if current agricultural lands were to be reforested. Forests in Wisconsin historically stored 434 TgC (AGC); forests today store 274 TgC, of which 63 TgC is due to forest ingrowth in areas that historically stored lower amounts of AGC (Fig. 3). Continued forest recovery in existing forests could add 69 TgC storage across the state. Twice that potential exists in agricultural lands, where reforestation and savanna restoration to historical baselines could add a further 150 TgC storage. Most of the potential for additional carbon through continued forest recovery is located in the parts of northern Wisconsin formerly dominated by mixed conifer-hardwoods (red and orange regions in Fig. 4*A*). The agricultural lands with the highest potential sequestration are in central northern Wisconsin, where hardwood-dominated forests formerly stored the greatest amount of AGC in the state (Fig. 4*B*).

Discussion

Presettlement Carbon Estimates. Comparing our estimates of AGC at the onset of EuroAmerican settlement (mid-1800s) to field data from remnant old-growth forest stands suggests that our estimates are reasonable and perhaps conservative. In our analysis, the forests with the greatest AGC in northern Wisconsin ranged from 100–200 MgC/ha. Individual survey sections (2.6 km^2) ranged as high as 700 MgC/ha, with ≈11% of sections storing >200 MgC/ha. Field studies in similar stands have yielded values from 189–330 MgC/ha (15, 16), with one report from an old-growth white pine stand at 681 MgC/ha (Rose in 17). Given that severe wind and fire disturbances were historically rare in these forests (18), we expected that a higher proportion of presettlement stands would have had carbon stocks similar in magnitude to these old-growth stands. Our AGC estimates for most southern oak savannas ranged from 0–50 MgC/ha; although a few field studies of remnant savanna stands have been conducted (e.g., 19), none of these measured carbon, and all of

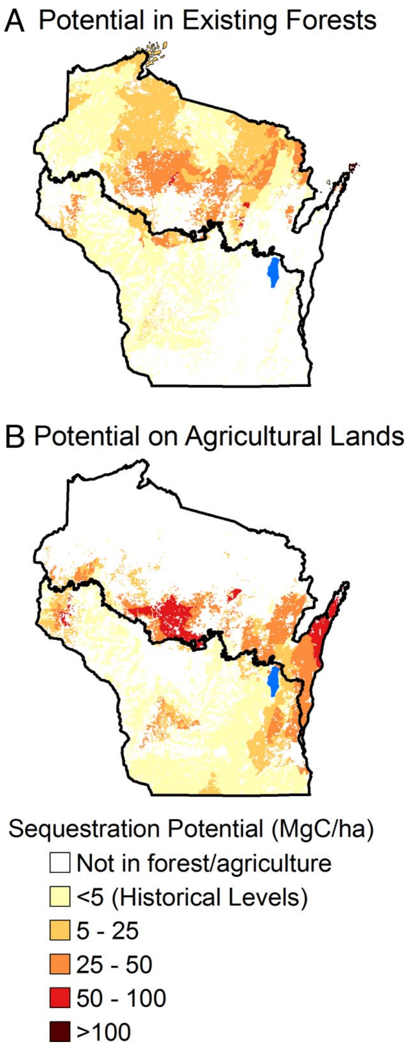

Fig. 4. Carbon sequestration potential (MgC/ha) in existing forests (*A*) and agricultural lands (*B*). Forest potential assumes that all existing forests recover to baseline carbon stocks, whereas agricultural potential assumes reforestation of agricultural lands to historical forest carbon content.

these stands had likely already changed considerably because of the effects of fire suppression (14). That our estimates may be conservative is not surprising given that Public Land Survey methods underestimated both stand density and the number of large trees on the landscape (20). Excluding small trees in our analysis also lowered AGC, although small trees (>10 cm) typically make up only 10% of total carbon in old-growth stands (21). But given early settlers' accounts of the stature and abundance of large trees, especially white pines in the north (17), we expected AGC values to be higher. It is possible that these settlers' accounts were correct but applied only to the very best stands, which may have been noteworthy but not dominant (17).

Studies relying on potential vegetation maps tend to show higher values for presettlement carbon than what we have estimated here, especially in southern Wisconsin. Houghton and Hackler (22) classify southern Wisconsin as broadleaf forest containing 150 MgC/ha in undisturbed vegetation, an order of magnitude higher than our estimate. Their estimate for northern mixed forests (200 MgC/ha) is at the upper end of our estimates for that region. Albani et al. (12) use a somewhat lower presettlement aboveground carbon value in southern Wisconsin (80–100 MgC/ha), but this is still far higher than our estimate. High estimates such as these will tend to overestimate both the total CO_2 emissions to the atmosphere after land-use change, and the potential for future sequestration because of forest regrowth. Our data suggest that average values across the landscape were likely lower than what these models have assumed, although such high values were certainly possible locally.

Constraints and Tradeoffs Limiting Future Sequestration. The potential for future sequestration through continued forest regrowth is highest in the far north, where existing forests are concentrated. After 70–100 years of forest regrowth, AGC has recovered to about 50% of the historical baseline. Assuming that most of this sequestration is due to regrowth rather than growth enhancement from CO_2 fertilization and nitrogen deposition (6), future sequestration will be limited by several factors. First, carbon stocks have rebounded quickly in part because of the shift in species composition away from the historically abundant conifers in favor of hardwoods. Hardwoods are typically denser but smaller and shorter-lived than conifers, so complete recovery of historical biomass may depend on recovery of historical forest composition, which is unlikely (23). Second, many of these forests are actively managed by industrial and private landowners, so total forest carbon will likely be limited by timber harvesting. Over the long term, carbon sequestration could be maximized by allowing these forests to attain old-growth stature. Contrary to earlier assumptions, old growth forests largely do not appear to reach carbon equilibrium as they age, but instead continue to accumulate carbon; the contribution of old-growth forests to global climate regulation has thus been largely underestimated (11).

The highest sequestration potential exists in agricultural lands in northern central Wisconsin, where AGC is only 25–50% of historical baseline values. This region held the highest carbon stocks before EuroAmerican settlement, and thus holds huge potential for future sequestration—if these agricultural lands are reforested. This region is less suited to agriculture than the prime agricultural lands in southern Wisconsin, and may reasonably be reassessed for its best use. As carbon markets and incentives for carbon sequestration grow, societal decisions may shift with respect to afforestation and managing for greater forest C stocks, co-beneficial ecosystem services, on currently subprime agricultural land (24).

The situation in southern Wisconsin is markedly different. Despite the fact that much of the south remains dominated by agricultural uses, total AGC is higher than before settlement because of forest ingrowth primarily in savanna ecosystems after settlement and fire suppression. This additional carbon pool is likely to remain on the landscape into the future, unless management practices are widely implemented to restore the historically open savanna structure in these current forest stands. Although there is little room for future sequestration within these already heavily modified stands, there is some potential for additional sequestration through savanna restoration on current agricultural lands.

Additional Carbon Pools. We have focused here on above-ground live forest carbon, which constitutes only ≈33% of total carbon in temperate forest ecosystems (25) and is typically the quickest pool to recover after disturbance (26). A full accounting of all pools would likely reveal significant additional sequestration potential.

Changes in soil carbon pools, which account for 50–60% of carbon in temperate forest systems (3, 25), are especially critical. Clearing forest for agriculture can result in a 40% decline in soil carbon (27); reforestation of agricultural lands in Wisconsin could thus lead to significant sequestration both above- and below-ground. Moreover, the gains in AGC through forest ingrowth in southern Wisconsin may be balanced by losses below-ground. Although former savanna and prairie ecosystems stored little carbon aboveground, they likely stored in the range of 100 MgC/ha in the soil, 30–35% of which may have been lost

SUSTAINABILITY SCIENCE

on conversion to agriculture (28, 29). This loss in soil C belowground is of a similar magnitude (per ha) to the gain in aboveground carbon from forest ingrowth elsewhere in southern Wisconsin, but given that 4 times more prairie and savanna was converted to agriculture (for a potential loss of ≈120 Tg of soil C) than subject to forest ingrowth (13), there was almost certainly a net loss in total carbon in southern Wisconsin (30).

Dead wood (including coarse woody debris and standing snags) represents another significant carbon pool in old-growth forest. Within old-growth northern hardwood and mixed stands in the region, coarse wood can contain 4.5 to 22.5 MgC/ha (15, 31–33). Standing dead wood can amount to 26% of the live basal area in a stand (31) and contain between 3.9 to 9.9 MgC/ha (32). Given that we estimated most northern forests to contain 50–100 MgC/ha live AGC in the mid-1800s, dead wood pools might add an additional 10–30% of carbon (see also 34). Levels of coarse woody debris and standing dead wood may take several centuries to accumulate and are typically much lower in managed second-growth stands than in old-growth stands (32). Given that much of northern Wisconsin consisted of old seral-stage forests before settlement, the loss of this carbon pool may be significant. Similarly, although forest litter is only a minor component of total aboveground carbon, repeated slash fires accompanying logging at the turn of the century may have led to significant losses of organic matter from both the forest floor and upper soil layers.

Thus, although our analysis suggests that current AGC is approximately two-thirds of that in the mid-1800s, an accounting of all ecosystem pools would likely show that total carbon loss was higher than what we report, especially in former old-growth forest stands in the north and savanna ecosystems in the south. The potential for continued sequestration, therefore, is also likely higher than what we have shown here.

This study shows the value of fine-resolution historical survey data in estimating presettlement carbon stocks and changes because of subsequent land use. Despite 70–100 years of forest regrowth, substantial room remains for future AGC sequestration in these systems, although two-thirds of this potential lies in the reforestation of current agricultural lands. Similar trends might be expected in the northeastern US, although those forests have had longer to recover after agricultural abandonment in the mid-1800s (5), and are likely closer to historical baselines than forests in Wisconsin. Restoring historical carbon stocks across the landscape will therefore require reassessing decisions about overall land-use priorities under changing needs for ecosystem services.

Materials and Methods

The study area was the state of Wisconsin (42°30′to 47°3′N and 86°49′ to 92°54′W), a 145,000-km^2 area in the Upper Great Lakes region of the United States. We used the U.S. Forest Service ecoregional classification to divide the state into two regions: the conifer-hardwoods province in the north and the prairie-savanna province in the south (35). We combined an inventory-based approach to estimate above-ground live forest carbon (AGC) with Monte Carlo simulation to quantify the uncertainties associated with both our historical datasets and model parameters (36). In the following sections, we first describe each of the data sources and associated uncertainties, and then explain how we estimated AGC.

Data Sources. The Public Land Survey (PLS) (mid-1800s) was initiated in 1785 to divide land into civil survey sections (≈1 mile^2) for settlement purposes. Surveyors traversed the land at 1-mile (1.6-km) intervals, recording the species, diameter, and distance to 2–4 ''witness'' trees approximately every half mile (0.8 km) (37). In Wisconsin, the survey proceeded from south to north from 1832–1891 and includes 445,500 trees from approximately 57,000 survey sections. Surveyors did not sample witness trees randomly, resulting in biases in tree sizes and distance measures (used to calculate stand density) (20, 38). Small trees were systematically avoided, whereas larger trees were likely also undersampled. Although the witness trees reflect general stand conditions at a given location (including the effects of disturbance events), the number and size of large trees in uneven-aged old-growth stands in particular are likely under-sampled. To compensate for the size bias, probability distribution functions (PDF) of tree diameters were derived by fitting witness tree data to Weibull (to mimic even-aged stands, e.g., 39) and exponential distributions (for uneven-aged old-growth stands, e.g., 40), thus filling out the ''missing tails'' (20). We fit distributions at the survey section scale with the maximum likelihood function fitdistr{MASS} in R (41), by using all witness trees within 100 m of a given section (mean sample size = 21.6 trees), and assuming that tree size was truncated at a 12.5-cm threshold. We tested the sensitivity of the results to the scale of the analysis and the size threshold and found that the results did not differ significantly (analysis not shown). Stand density (based on point-centered quarter distance method) (42) and species dominance (based on relative basal area) was calculated at the survey-section level. Because surveyors systematically avoided small trees, we assumed that stand density represented only trees >12.5 cm, and thus did not include trees below this threshold in our simulations. The resulting AGC estimates for the mid-1800s thus represent only trees >12.5 cm in diameter.

Wisconsin Land Economic Inventory (WLEI) (1930s). The WLEI was conducted across the state from 1928 to 1938, at the height of the agricultural period. Surveyors traversed the land along the same section lines as the PLS, and mapped general land cover, as well as species composition, stand stocking (a measure of stand density), and diameter class for all forested areas (43). Tables summarizing the total area by land-cover type in each survey section were also produced; we digitized these to map proportional land cover with a spatial resolution of 2.6 km^2. Uncertainties in the WLEI stem from the general classes used to characterize tree sizes and stand density. Surveyors classified forest stands into five size classes and four stocking classes, with little indication of the proportion of trees falling within a given size range, or the likely shape of the distribution. We chose to model shade-intolerant species groups by using a normal PDF, whereas shade-tolerant species were modeled by using an exponential distribution. Parameters describing these distributions were also modeled as PDFs. We modeled mean diameter as a uniform PDF from the minimum to maximum extent of the tree size class. Standard deviation (in the case of normally distributed stands) was variously set so that at least 66%, 80%, and 99% of all trees fell within the given size class. Stand-stocking percent was also modeled as a uniform PDF (percent ranges as in 44), and stocking was transformed to absolute tree density by using species specific equations (44).

WISCLAND Land-Cover Data (1993). WISCLAND is a land-cover data product derived from Landsat TM satellite imagery (30 × 30 m pixel size) acquired between August 1991 and May 1993 (45).

U.S. Forest Service Forest Inventory and Analysis (FIA) (2000s). We used FIA plot data from the most recent (6th cycle) inventory conducted from 2000–2004 (46). The FIA includes 6,478 plots in Wisconsin, and provides expansion factors to extrapolate plot values over larger areas.

AGC Calculations. We estimated AGC by using a Monte Carlo simulation approach whereby the uncertainties in the historical data and the parameters of the equations used to estimate carbon were modeled as PDFs. For the mid-1800s and 1930s datasets, we developed a number of forest condition scenarios ranging from all even-aged stands to all uneven-aged stand (Tables S1–S3). For a given scenario, we simulated tree size distribution and stand density of each forest stand by randomly selecting parameters from the appropriate PDFs. We then randomly chose 100 trees from each forest stand, calculated carbon of each tree by using allometric equations (see below) and then scaled the carbon estimate to represent the total number of trees in that stand. Although it would have been preferable to have simulated all trees in a given stand, this approach was computationally prohibitive for the entire landscape, and tests over smaller areas showed that the mean carbon estimates were similar by using both techniques (differences were ≤1.4%), although the variability declined as sample size increased.

We used regional species-specific allometric equations to calculate volume (47) and oven-dry above-ground biomass (see also ref. 48) of all live trees, including bole, bark, stump, top, and limbs, but not foliage. Merchantable height of each tree was estimated by using Ek (49). We calculated mean site index for each species by U.S. Forest Service ecoregion subsections (35); where species data for a given subsection were missing, we took the average site index across all species for that subsection. For the volume and height equations, we used the standard error estimates provided to estimate uncertainty in biomass values because of error in the allometric equations. We ran the simulations 100 times for each scenario, and calculated the mean and 95% confidence interval of total biomass for each scenario. Biomass was converted to carbon by using a ratio of 0.5 (50). To map the spatial variability in AGC, we combined the results of all scenarios and mapped median AGC by U.S. Forest Service Land Type Association (LTA) (35).

Because the FIA data were statistically representative of the total population, we estimated carbon directly for each tree in the database, and then used the volume and area expansion factors to scale these estimates to the total LTA polygon area and mapped median values as described above. These estimates included two sources of uncertainty: error in the allometric equations and field sampling error (46). We estimated the magnitude of the former by using Monte Carlo simulation and PDFs of the model parameters, and the second by using algorithms published by the USDA Forest Service (46). Because it was not clear how these uncertainties compound into total error, we mapped the larger source of uncertainty, that resulting from sampling error.

ACKNOWLEDGMENTS. We thank M. Hansen for help with the Forest Inventory and Analysis data; J. Hanson, C. Lorimer, and S.T. Gower for assistance in project design; C. Halpin for programming help; W. Cronon, K. Frazier, and the Wisconsin Historical Society for access to archival records; G. Allez, J. Grice, K. Hannon, A. Hill, C. Klaus, I. Mladenoff, and K. Peterson for help with data entry; and W. Cronon, S.T. Gower, V. Radeloff, M. Turner, and an anonymous reviewer for helpful comments on earlier drafts of the paper. The project was funded by the Wisconsin Department of Natural Resources (Pittman-Robertson program), the USDA Forest Service Northern Research Station, and Natural Sciences and Engineering Research Council Canada.

1. Houghton RA (1999) The annual net flux of carbon to the atmosphere from changes in land use 1850–1990. *Tellus* 51B:298–313.
2. Ramankutty N, et al. (2007) Challenges to estimating carbon emissions from tropical deforestation. *Glob Change Biol* 13:51–66.
3. Dixon RK, et al. (1994) Carbon pools and flux of global forest ecosystems. *Science* 263:185–190.
4. Clawson M (1979) Forests in the long sweep of American history. *Science* 204:1168–1174.
5. Foster DR, Motzkin G, Slater B (1998) Land-use history as long-term broad-scale disturbance: Regional forest dynamics in Central New England. *Ecosystems* 1:96–119.
6. Caspersen JP, et al. (2000) Contributions of land-use history to carbon accumulation in U.S. forests. *Science* 290:1148–1151.
7. Barford CC, et al. (2001) Factors controlling long- and short-term sequestration of atmospheric CO_2 in a mid-latitude forest. *Science* 294:1688–1691.
8. Canadell JG, Raupach MR (2008) Managing forests for climate change mitigation. *Science* 320:1456–1457.
9. Hurtt GC, et al. (2002) Projecting the future of the U.S. carbon sink. *Proc Natl Acad Sci USA* 99:1389–1394.
10. Birdsey RA, Plantinga AJ, Heath LS (1993) Past and prospective carbon storage in United States forests. *Forest Ecol Manag* 58:33–40.
11. Luyssaert S, et al. (2008) Old-growth forests as global carbon sinks. *Nature* 455:213–215.
12. Albani M, Medvigy D, Hurtt GC, Moorcroft PR (2006) The contributions of land-use change, CO_2 fertilization, and climate variability to the Eastern US carbon sink. *Glob Change Biol* 12:2370–2390.
13. Rhemtulla JM, Mladenoff DJ, Clayton MK (2007) Regional land-cover conversion in the U.S. upper Midwest: Magnitude of change and limited recovery in Wisconsin (1850–1935-1993). *Landscape Ecol* 22:57–75.
14. Nuzzo VA (1986) Extent and status of midwest oak savanna: Presettlement and 1985. *Nat Area J* 6:6–36.
15. Campbell JL, Gower ST (2000) Detritus production and soil N transformations in old-growth eastern hemlock and sugar maple stands. *Ecosystems* 3:185–192.
16. Mroz GD, Gale MR, Jurgensen MF, Frederick DJ, Clark A, III (1985) Composition, structure, and aboveground biomass of two old-growth northern hardwood stands in Upper Michigan. *Can J Forest Res* 15:78–82.
17. Whitney GG (1994) *From Coastal Wilderness to Fruited Plain: A History of Environmental Change in Temperate North America from 1500 to the Present* (Cambridge Univ Press, New York).
18. Schulte LA, Mladenoff DJ (2005) Severe wind and fire regimes in northern forests: Historical variability at the regional scale. *Ecology* 86:431–445.
19. Bray JR (1960) The composition of savanna vegetation in Wisconsin. *Ecology* 41:721–732.
20. Bourdo EA (1956) A review of the general land office survey and of its use in quantitative studies of former forests. *Ecology* 37:754–768.
21. Schroeder P, et al. (1997) Biomass estimation for temperate broadleaf forests of the United States using inventory data. *Forest Sci* 43:424–434.
22. Houghton RA, Hackler JL (2000) Changes in terrestrial carbon storage in the United States I: The roles of agriculture and forestry. *Global Ecol Biogeogr* 9:125–144.
23. Rhemtulla JM, Mladenoff DJ, Clayton MK (2009) Legacies of historical land use on regional forest composition and structure in Wisconsin, USA (mid-1800s to 1930s to 2000s). *Ecol Appl*, in press.
24. Richards K, Sampson RN, Brown S (2006) *Agricultural & Forestlands: US Carbon Policy Strategies* (Pew Center for Global Climate Change, Arlington, VA).
25. Turner DP, Koerper GJ, Harmon ME, Lee JJ (1995) A carbon budget for forests of the conterminous United States. *Ecol Appl* 5:421–436.
26. Houghton RA, Goodale CL (2004) in *Ecosystems and Land Use Change*, eds DeFries R, Asner G, Houghton RA (American Geophysical Union, Washington, DC), pp 85–98.
27. Guo LB, Gifford RM (2002) Soil carbon stocks and land use change: A meta analysis. *Glob Change Biol* 8:345–360.
28. Tiessen H, Stewart J, Bettany J (1981) Cultivation effects on the amounts and concentration of carbon, nitrogen, and phosphorus in grassland soils. *Agron J* 74:831–835.
29. Davidson E, Ackerman I (1993) Changes in soil carbon inventories following cultivation of previously untilled soils. *Biogeochemistry* 20:161–193.
30. Jackson RB, et al. (2002) Ecosystem carbon loss with woody plant invasion of grasslands. *Nature* 418:623–626.
31. McGee GG, Leopold DJ, Nyland RD (1999) Structural characteristics of old-growth, maturing, and partially cut northern hardwood forests. *Ecol Appl* 9:1316–1329.
32. Goodburn JM, Lorimer CG (1998) Cavity trees and coarse woody debris in old-growth and managed northern hardwood forests in Wisconsin and Michigan. *Can J Forest Res* 28:427–438.
33. Tyrrell LE, Crow TR (1994) Structural characteristics of old-growth hemlock-hardwood forests in relation to age. *Ecology* 75:370–386.
34. Pregitzer KS, Euskirchen ES (2004) Carbon cycling and storage in world forests: Biome patterns related to forest age. *Glob Change Biol* 10:2052–2077.
35. Keys JE, Jr, et al. (1995) in *Ecological Units of the Eastern United States: First Approximation* (USDA Forest Service, Atlanta), p 81.
36. Smith JE, Heath LS (2001) Identifying influences on model uncertainty: An application using a forest carbon budget model. *Environ Manage* 27:253–267.
37. Schulte LA, Mladenoff DJ (2001) The original US Public Land Survey records: Their use and limitations in reconstructing presettlement vegetation. *J Forest* 99:5–10.
38. Manies KL, Mladenoff DJ, Nordheim EV (2001) Assessing large-scale surveyor variability in the historic forest data of the original U.S. Public Land Survey. *Can J Forest Res* 31:1719–1730.
39. Lorimer CG, Krug AG (1983) Diameter distributions in even-aged stands of shade-tolerant and midtolerant tree species. *Am Midl Nat* 190:331–345.
40. Hett JM, Loucks OL (1976) Age structure models of balsam fir and eastern hemlock. *J Ecol* 64:1029–1044.
41. Venables WN, Ripley BD (2002) *Modern Applied Statistics with S* (Springer, New York), 4th Ed.
42. Cottam G, Curtis JT (1956) The use of distance measures in phytosociological sampling. *Ecology* 37:451–460.
43. Bordner JS, Morris WW, Steenis JH, Hilburn ED (1936) *State of Wisconsin Executive Council No.* 3 (State of Wisconsin Executive Council, Division of Land Economic Inventory, Madison, WI).
44. Arner SL, et al. (2001) *National algorithms for determining stocking class, stand size class, and forest type for Forest Inventory and Analysis plots*. Available at http://www.fs.fed.us/fmsc/fvs/documents/gtrs_arner.php. Accessed September 7, 2007.
45. Reese HM, et al. (2002) Statewide land cover derived from multiseasonal Landsat TM data: A retrospective of the WISCLAND project. *Remote Sens Environ* 82:224–237.
46. Perry CH (2003) Wisconsin's forest resources in 2004. *North Central Research Station Resource Bulletin NC-21* (USDA Forest Service, St. Paul).
47. Hahn JT (1984) Tree volume and biomass equations for the lake states. *North Central Research Station Research Paper NC-250* (USDA Forest Service, St. Paul).
48. Smith WB (1985) Factors and equations to estimate forest biomass in the north central region. *North Central Research Station Research Paper NC-268* (USDA Forest Service, St. Paul).
49. Ek AR, Birdsall ET, Spears RJ (1981) *Total and Merchantable Tree Height Equations for Lake States Tree Species* (U. Minnesota, Dept. of Forest Resources, St. Paul).
50. Birdsey R (1992) Carbon storage and accumulation in United States forest ecosystems. *General Technical Report WO-59* (USDA Forest Service, Washington, DC).

Supporting Information

Rhemtulla et al. 10.1073/pnas.0810076106

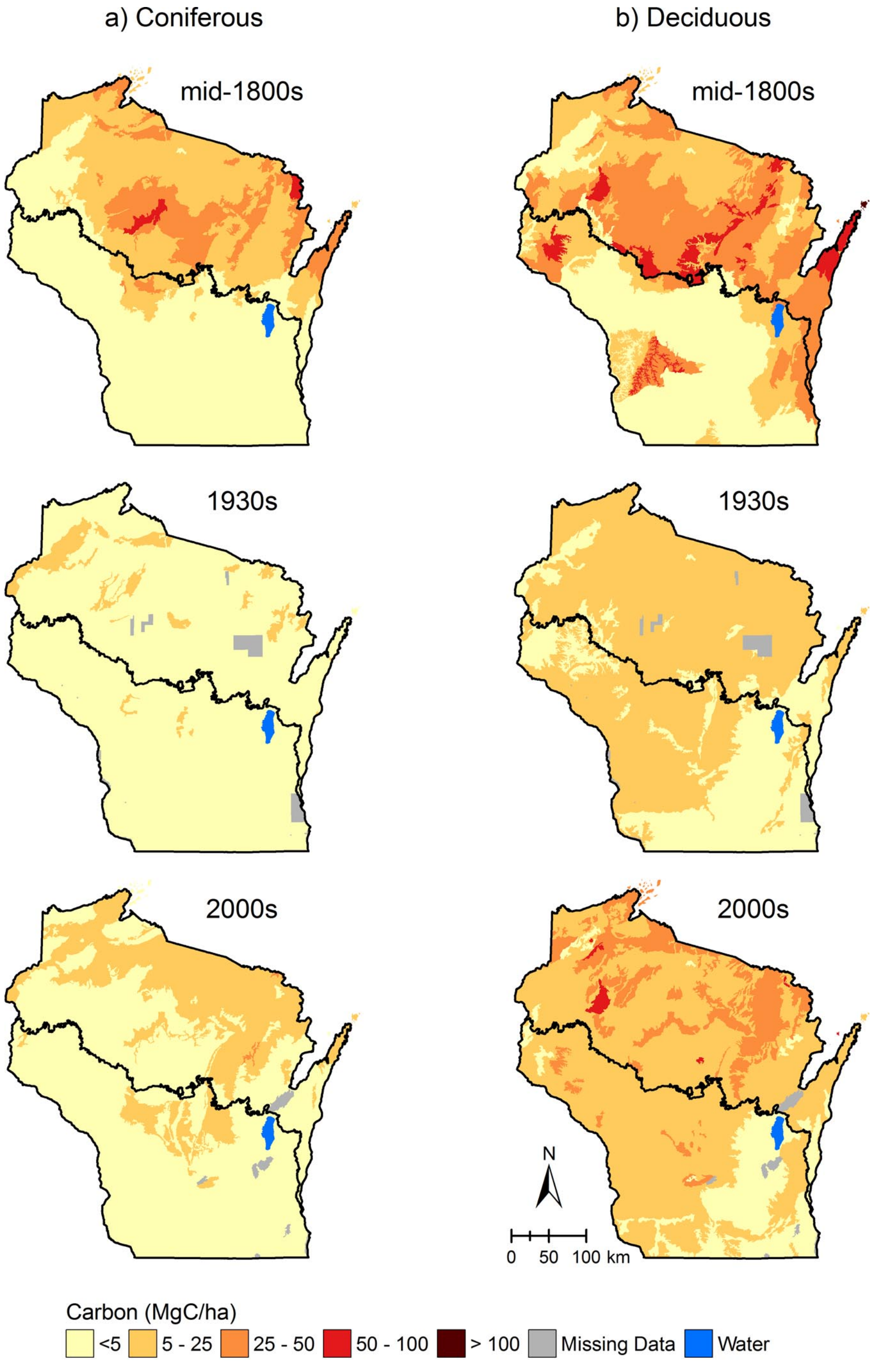

Fig. S1. Above-ground live forest carbon (MgC/ha) by forest type for coniferous (*a*), and deciduous (*b*) forest in the mid-1800s, 1930s, and 2000s. Data are medians calculated from Monte Carlo simulation results.

Table S1. Scenarios used in Monte Carlo simulation runs to estimate uncertainty because of biases in Public Land Survey (mid-1800s) dataset

	Stand Variables	Allometric Equations				
	Shape	Volume	Height	Lower bound, TgC	Median, TgC	Upper bound, TgC
Baseline	weibull/exp*	V	V	434	435	435
Other Scenarios						
Weibull diameter distribution	all weibull	V	V	364	365	365
Exponential diameter distribution	all exponential	V	V	460	460	461
Volume constant (no SE)	weibull/exp*	C	V	419	420	420
Height constant (no SE)	weibull/exp*	V	C	434	434	435

Table shows above-ground live forest carbon estimate for each scenario. Baseline scenario shows the most reasonable values for each model parameter. Lower bound is the 2.5th percentile and upper bound is the 97.5th percentile of all simulation runs within a scenario. V, variable (i.e. coefficients of the allometric equations were modeled as a probability distribution function based on the standard error of the coefficient estimate); C, constant.

*Tree diameter distributions are modeled as a weibull distribution in survey sections dominated by shade-intolerant species (pines, aspen, paper birch, oak, and hickory) and as an exponential distribution elsewhere.

Table S2. Scenarios used in Monte Carlo simulation runs to estimate uncertainty because of biases in Wisconsin Land Economic Inventory (1930s) dataset

	Stand Variables				Allometric Equations				
	Mean DBH	SD, %	Shape	Stocking	Volume	Height	Lower bound, TgC	Median, TgC	Upper bound, TgC
Baseline	V	80	E/U	V	V	V	120	120	120
Other Scenarios									
Midpoint of size class	C	80	E/U	V	V	V	136	136	137
SD ≥ 99%	V	99	E/U	V	V	V	109	109	109
SD ≥ 66%	V	66	E/U	V	V	V	131	131	132
Midpoint of stocking class	V	80	E/U	C	V	V	120	120	120
Volume constant (no SE)	V	80	E/U	V	C	V	117	118	118
Height constant (no SE)	V	80	E/U	V	V	C	120	120	120

Table shows above-ground live forest carbon estimate for each scenario. Baseline scenario shows the most reasonable values for each model parameter. Lower bound is the 2.5th percentile and upper bound is the 97.5th percentile of all simulation runs within a scenario. DBH, diameter at breast height; V, variable (see Table S1 for details); C, constant; E, even-aged (Weibull distribution); U, uneven-aged (exponential distribution).

Table S3. Scenarios used in Monte Carlo simulation runs to estimate uncertainty because of biases in the U.S. Forest Service Forest Inventory and Analysis (2000s) dataset

	Allometric Equations				
	Volume	Height	Lower bound, TgC	Median, TgC	Upper bound, TgC
Baseline	V	V	275	276	277
Other Scenarios					
Volume constant (no SE)	C	V	276	276	276
Height constant (no SE)	V	C	275	276	277

Table shows above-ground live forest carbon estimate for each scenario. Baseline scenario shows the most reasonable values for each model parameter. Lower bound is the 2.5th percentile and upper bound is the 97.5th percentile of all simulation runs within a scenario. V, variable (see Table S1 for details); C, constant.