One-third of net CO₂ 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 above-ground 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.

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. 1A). 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 totally converted to agricultural uses, whereas the southern forests, mostly composed of mixed conifer-hardwood stands, remained more intact. This has resulted in a change in the carbon pool distribution in the state, with southern Wisconsin contributing 60% of the AGC, whereas much of the northern forests contribute an additional 69 TgC. Reforestation of agricultural lands—such as that in the north-central region that are now agricultural lands less optimal than those 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.

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To whom correspondence should be addressed at: Department of Geography, McGill University, Montreal, QC, Canada H3A 2K6; and Departments of Forest and Wildlife Ecology and Plant Pathology and Statistics, University of Wisconsin-Madison, Madison, WI 53706.

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

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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 \(11005^{434}\) TgC; 95% confidence interval \(11005^{364–460}\) TgC) to the 1930s (median \(11005^{120}\) TgC; CI \(11005^{109–137}\) TgC) (Fig. 2A). After forest regrowth in the north and ingrowth in the south over the past century, current AGC has recovered to two-thirds (median \(11005^{276}\) TgC; CI \(11005^{275–277}\) 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. 2B). 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. 1B). 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 pre-settlement 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. 1B), 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. 2C). 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. 1C). 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. 1B 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...
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 $\sim 39\%$ 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 deceduous 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 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.

### 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 km²) ranged as high as 700 MgC/ha, with $\sim 11\%$ 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

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**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.
High estimates such as these will tend to overestimate both the presettlement aboveground carbon value in southern Wisconsin for that region. Albani et al. use a somewhat lower mixed forests (200 MgC/ha) is at the upper end of our estimates magnitude higher than our estimate. Their estimate for northern containing 150 MgC/ha in undisturbed vegetation, an order of estimated here, especially in southern Wisconsin. Houghton and settlers’ accounts were correct but applied only to the very best we expected AGC values to be higher. It is possible that 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 CO₂ 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 CO₂ 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, eco-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.
on conversion to agriculture (28, 29). This loss in soil C below-ground is of a similar magnitude (per ha) to the gain in above-ground 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 subsequent forest growth (131), there is 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, the approach we used to study contemporary 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°30' N and 86°49' to 92°54' W), a 145,000-km² 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 the results of all scenarios and mapped median AGC by U.S. Forest Service Land-Cover Data (1993).

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 stands (Tables S1–S3). For a given scenario, we simulated the tree size distribution and the 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 compounded into total error, we mapped the larger source of uncertainty, that resulting from sampling error.

43. Bordner JD, Morris WW, Steenis HJ, Hilburn ED (1936) State of Wisconsin Executive Council No. 3 (State of Wisconsin Executive Council, Division of Land Economic Inven- tory, Madison, WI).
Supporting Information

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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.

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

<table>
<thead>
<tr>
<th>Stand Variables</th>
<th>Allometric Equations</th>
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<th>Median, TgC</th>
<th>Upper bound, TgC</th>
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<td>Exponential diameter distribution</td>
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<td>C</td>
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</table>

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

<table>
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<tr>
<td>Height constant (no SE)</td>
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</tbody>
</table>

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

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</table>

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.