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Loss of aboveground forest biomass and landscape biomass variability in Missouri, US

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ABSTRACT

Disturbance regimes and forests have changed over time in the eastern United States. We examined effects of historical disturbance (circa 1813 to 1850) compared to current disturbance (circa 2004 to 2008) on aboveground, live tree biomass (for trees with diameters $\geq$13 cm) and landscape variation of biomass in forests of the Ozarks and Plains landscapes in Missouri, USA. We simulated 10,000 one-hectare plots using random diameters generated from parameters of diameter distributions limited to diameters $\geq$13 cm and random densities generated from density estimates. Area-weighted mean biomass density (Mg/ha) for historical forests averaged 116 Mg/ha, ranging from 54 Mg/ha to 357 Mg/ha by small scale ecological subsections within Missouri landscapes. Area-weighted mean biomass density for current forests averaged 82 Mg/ha, ranging from 66 Mg/ha to 144 Mg/ha by ecological subsection for currently forested land. Biomass density of current forest was greater than historical biomass density for only 2 of 23 ecological subsections. Current carbon sequestration of 292 TgC on 7 million ha of forested land is less than half of the estimated historical total carbon sequestration of 693 TgC on 12 million ha. Cumulative tree cutting disturbances over time have produced forests that have less aboveground tree biomass and are uniform in biomass compared to estimates of historical biomass, which varied across Missouri landscapes. With continued relatively low rates of forest disturbance, current biomass per ha will likely increase to historical levels as the most competitive trees become larger in size and mean number of trees per ha decreases due to competition and self-thinning. Restoration of large diameter structure and forested extent of upland woodlands and floodplain forests could fulfill multiple conservation objectives, including carbon sequestration.

1. Introduction

Before Euro-American settlement, perhaps at least half of forests in the central eastern and southeastern United States during the 1800s were oak or pine forest ecosystems (Nowacki and Abrams, 2008; Hanberry et al., 2012a; Thompson et al., 2013). Oak and pine species have functional traits to survive, and possibly facilitate, low severity fire regimes (Beckage et al., 2009) that periodically removed biomass of fire-sensitive species and small diameter oak and pine trees, leaving large, thick-barked oak and pine trees (Nowacki and Abrams, 2008; Hanberry et al., 2012a). Stand structure of open oak and pine forest ecosystems probably was relatively simple, consisting of single canopy layer of large diameter trees and little development of understory layers, which allowed light to reach an herbaceous ground layer (Hanberry et al., 2014).

Nevertheless, a wide range of structural variation was present in forest ecosystems at many spatial scales due to environmental gradients of soil and moisture, which interacted with fire disturbance, to influence tree density and diameter and produce a continuum of forest ecosystems from savannas to open woodlands to closed woodlands to forests (closed woodlands have closed or nearly closed canopies but are open between the ground layer and overstory canopy layer; Guyette et al., 2002; Stambaugh and Guyette, 2008; Hanberry et al., 2012a, 2014). Flat and periodically dry landscapes spread fire that removed small diameter trees, whereas rocky and arid landscapes did not produce enough fine fuels (i.e., herbaceous vegetation and litter) to burn, wetlands of varying types were often too wet to burn, and rough topography disrupted fire spread (Grimm, 1984; Guyette et al.,

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2002; Stambaugh and Guyette, 2008). At the border of prairie grasslands and eastern forests in the United States, fire return intervals and spread were propagated by continuous fine fuels and flat topography of prairies and plateaus, but then fires were disrupted by fire breaks of dissected river hills and major stream networks draining to the Mississippi and Missouri Rivers.

Many open forest ecosystems destabilize without periodic fires to remove fire-sensitive plants (Nowacki and Abrams, 2008; Hanberry et al., 2014). In the eastern United States, even after fire exclusion during the first half of the twentieth century, oak and pine had the advantage of overstory dominance and advance regeneration. Nonetheless, a variety of fire-sensitive tree species established that are more competitive than oaks and pines without fire. Furthermore, previously distinctive forest ecosystem types with spatial variation in structure before Euro-American settlement have become more uniform in structure, as current forests reflect the cumulative effects of frequent tree cutting for various land uses (Birdsey and Lewis, 2003; Masek et al., 2008; Smith et al., 2009).

The effects of historical fire disturbance compared to current land use disturbance on biomass in open forest ecosystems are not well-known and yet important for management of forests and carbon. Forests in Missouri during historical surveys of the 1800s were the product of different disturbance regimes than those that influence current forests. Past forests were largely shaped by a long term fire regime that varied across the landscape in frequency and intensity whereas forests of the past fifty years have been characterized by gradually increasing forest area with periodic partial harvesting concentrated on trees at least 30 cm in diameter. Fire and tree cutting both remove biomass and may temporarily reduce aboveground carbon sequestration, but fire removes biomass based on environmental gradients and ignition patterns, creating forests that reflect underlying environmental variation, whereas tree cutting reflects land use and harvest intensity (Yang et al., 2007). Across Missouri landscapes, or ecological sections of the Ozarks and Plains (Ecomap, 1993; Fig. 1), our objective was to quantify aboveground biomass and biomass variability by smaller scale ecological subsections in pre-settlement forests that were shaped by gradients in fire regimes and compare those past forests to current forests that are disturbed primarily by tree cutting. We additionally examined whether biomass resulting from the historic fire regime produced differences in total aboveground live forest carbon sequestration compared to current forest management and land use.

2. Methods

2.1. Tree surveys

We used the Missouri surveys by the United States General Land Office (GLO) conducted predominantly during 1813 to 1850. The GLO surveys divided public lands into square townships measuring 9.6 km × 9.6 km (6 mi × 6 mi) and subdivided townships into 36–1.6 square km sections (1 square mile). Surveyors selected two to four bearing trees at survey points located at section corners and midpoints between section corners. Surveyors recorded the species, diameter, distance, and bearing of these trees. This produced a sample of current forest conditions, but the sample was biased. We excluded trees with diameters <13 cm measured at 1.3 m above the ground to maintain a consistent minimum diameter threshold, resulting in 290,000 trees in the Ozarks ecological section and 86,000 trees in the combined Till Plains and Osage Plains ecological sections (Ecomap, 1993; Fig. 1).

We estimated historical density for each ecological subsection (Ecomap, 1993; Fig. 1) with the Morisita estimator (Morisita, 1957) for surveys that approximate the point-center quarter method

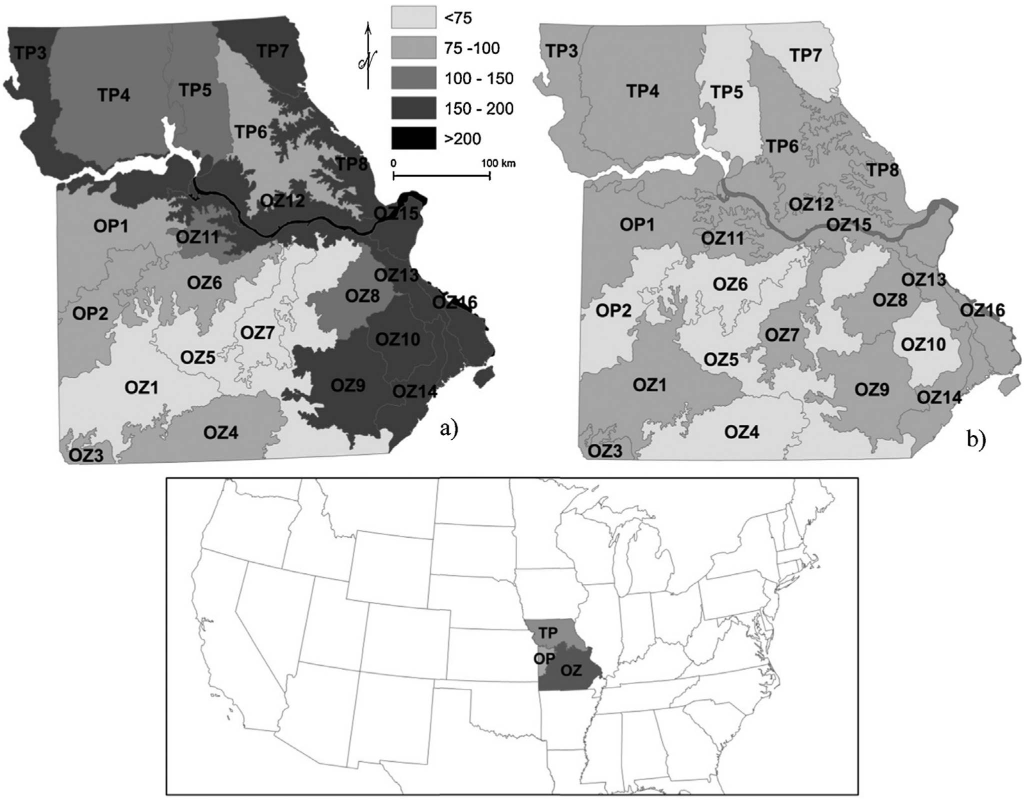

Fig. 1. Historical (upper panel 1a) and current (upper panel 1b) modeled biomass (Mg/ha; trees ≥13 cm diameter) by ecological subsection (outlined and labeled) in the Missouri Ozarks ('OZ' prefix) and Plains ecological sections ('TP', Till Plains; 'OP', Osage Plains). Ecological sections are displayed in lower panel.

(diameters ≥13 cm; Hanberry et al., 2011). Surveyors probably did not select the nearest tree, which will lessen estimates of density. We produced a low and high density value for each subsection using an adjustment for potential spatial patterning (clustered or regular patterns). We used these values to make corrections for surveyor bias based on a rank-based method and bias-based method for non-random tree ratios, and weighted densities basedon count and number of trees per survey point (Hanberry et al., 2012b). Historical forest densities ranged from about 75 to 320 trees per ha by subsection. Surveyors recorded only 2 to 4 trees per survey point and this sample size is too small to use to determine biomass, densities, or diameter for each survey point with any accuracy (Hanberry et al., 2011).

The USDA Forest Service Forest Inventory and Analysis (FIA) conducts complete surveys of long-term forest plots across the nation, maintaining about one plot per 2000–2500 ha (FIA DataMart, www.fia.fs.fed.us/tools-data). Each plot contains four 7.3 m radius subplots, configured as a central subplot surrounded by three outer subplots. Plots typically are remeasured every five years. We used the measurement cycle from 2004 to 2008 in Missouri. We selected live trees with diameters ≥13 cm from plots that had at least two trees and that were located on forestland. FIA defines forest land as an area at least 0.4 hectares in size and about 37 m wide with at least 10% cover by live trees of any size, including recently harvested land that is intended to be forest ("formerly had such tree cover and that will continue to have forest use"). Our sample included 32,715 trees in the Ozarks ecological section and 5620 trees in the combined Till Plains and Osage Plains ecological sections (Fig. 1). The FIA inventories provided current density at each plot (per ha) and supplied biomass estimates for each tree (aboveground stem biomass for trees ≥13 cm, excluding foliage) based on allometric equations (Jenkins et al., 2003). We summed biomass and expanded to a hectare for biomass estimates per plot to Mg/ha.

2.2. Modeled biomass estimation

To determine historical biomass for Missouri forests during the period of the GLO survey (1813 to 1850), we used density estimates and diameter distributions for each ecological subsection and then modeled biomass, similarly to Rhemtulla et al. (2009). For each ecological subsection, we developed parameters for probability distribution functions of tree diameters truncated at 13 cm using lognormal, negative exponential distributions, Weibull, and gamma distributions (Podlaski and Zasada, 2008; SAS Proc Severity, SAS software, version 9.1, Cary, North Carolina), similarly to Rhemtulla et al. (2009). We then simulated 10,000 one-hectare plots using random diameters generated from the parameters of the diameter distributions truncated at 13 cm and random densities generated from density estimates based on observations in the GLO survey (R Runuran; J. Leydold and W. Hörmann, http://statmath.wu.ac.at/unuran, http://cran.rproject.org/web/packages/Runuran/index.html). We used tree diameter and aboveground biomass for trees in the FIA database to develop simple allometric equations of tree biomass as a function of tree diameter (i.e., regression of the log transformation of biomass to the log transformation of diameter) for each ecological subsection. We applied the equations to the trees simulated for each of the 10,000 modeled historical plots to estimate mean biomass and standard deviation per hectare by ecological subsection. To make certain that assumptions and methods we used to develop biomass estimates for the GLO data were compatible with those used in the FIA data, we modeled biomass for the FIA plots using the same method we used for the GLO data.

We then compared observed mean biomass based on FIA plots to the modeled FIA biomass estimates using mean absolute error to determine which of the four fitted diameter distributions (lognormal, negative exponential, Weibull or gamma) produced the smallest absolute differences. We used the diameter distribution with the least absolute differences in biomass per ha for comparisons of historical (GLO data) and current (FIA data) modeled biomass. We used a signed rank test (SAS Proc Univariate) to compare difference in biomass values across the 23 ecological subsections. To visually display variability of one-dimensional data (i.e., modeled biomass estimates), we used a beanplot (R Beanplot; P. Kampstra, http://cran.r-project.org/web/packages/beanplot/index.html), which is a modification of a stripchart with a smoothed histogram, or violin plot. To relate biomass to fire tolerance of trees, we performed a regression between biomass and percent oak composition by subsection.

To provide greater spatial detail for current biomass, we developed spatially continuous estimates of density and biomass and uncertainty based on discrete plot locations using random forests regression trees (Breiman, 2001; Cutler et al., 2007) with the randomForest package (Liaw and Wiener, 2002) in R statistical software (R Development Core Team, 2012) and predictors of ecological subsection and bedrock geology, soil variables, and DEM (digital elevation model)-derived topographic variables (Hanberry et al., 2012a). Because exact coordinates of FIA plots are not released due to landowner privacy concerns, FIA personnel provided a database listing selected environmental variables associated with each plot.

2.3. Total aboveground live tree carbon

Currently, the primary land use/land cover for the Ozarks ecological subsection is 57% forested with 28% in pasture/hay while the Plains ecological sections are 17% forested with 70% in agriculture of crops or pasture/hay (Fry et al., 2011). We do not know the comparable forested extent during 1813 to 1850; however, surveyors were able to record trees in nearly all the systematic survey grid in the Ozarks section and 70% of the Plains sections. Rare, catastrophic fire and wind disturbance, along with small bodies of open water, decreased forested extent and additionally, Native Americans and European American settlers cleared forest. In the Plains sections, annual fires and drought limited tree establishment. To calculate total aboveground live tree carbon for trees >13 cm in diameter, we used forested extents ranging from 60%, or current forested extent, to 100% in the Ozarks section that is 9.3 million ha and 20%, or current forested extent, to 70% in the Plains sections that are 7.5 million ha (Table 2). We used a conversion factor of 0.5 to convert biomass to carbon (the default; e.g. Rhemtulla et al., 2009).

3. Results

The Ozarks and the Plains ecological sections had little difference between modeled current biomass estimates and mean current biomass estimates from the FIA database and the Weibull distribution produced the overall best fitting models. For the 15 ecological subsections within the Ozarks ecological section, the mean absolute difference between modeled biomass of current forests and observed mean biomass estimates from FIA plots was 5.9 Mg/ha for when the gamma distribution was used to model diameter distributions and 6.14 Mg/ha for the Weibull distribution. The other two distributions (lognormal and negative exponential) had mean absolute differences of about 10 Mg/ha. Mean absolute difference between modeled biomass estimates for historical forests and current forests by ecological subsection was 61.6 Mg/ha for the gamma distribution, 62.3 Mg/ha for the lognormal distribution, 65.7 Mg/ha for the Weibull distribution, and 101.7 Mg/ha for the negative exponential distribution. In the

Plains, mean absolute difference between simulated biomass of current forests and mean biomass estimates from FIA plots by ecological subsection ranged from of 2.0 Mg/ha for the gamma distribution to 3.5 Mg/ha for the Weibull distribution. Mean absolute difference between simulated biomass estimates for historical forests and simulated biomass of current forests by ecological subsection ranged from 48.2 Mg/ha for the Weibull distribution, 60.5 Mg/ha for the lognormal distribution, and greater than 165 Mg/ha for the other two distributions.

In the Ozarks section, area-weighted mean biomass density (Mg/ha) for historical forests averaged 111 Mg/ha, ranging from 54 Mg/ha to 357 Mg/ha by ecological subsection (Table 1; Fig. 1). Area-weighted mean biomass density for current forests averaged 83 Mg/ha, ranging from 71 Mg/ha to 144 Mg/ha by ecological subsection. Historical biomass was 135% of current biomass, but ranged from 70% to 290% of current biomass by ecological subsection. In the Plains, area-weighted mean biomass for historical forests averaged 122 Mg/ha, ranging from 84 Mg/ha to 179 Mg/ha by ecological subsection. Area-weighted mean biomass for current forests averaged 81 Mg/ha, ranging from 66 Mg/ha to 89 Mg/ha by ecological subsection. Historical biomass was 150% of current biomass, ranging from 95% to 250% of current biomass by ecological subsection. The estimated historic biomass mean values by subsection were significantly greater than those for current biomass ($P < 0.0001$).

Across the Missouri landscapes, variation in biomass values was smaller in current forests (SD = 16; coefficient of variation = 0.19) compared to historical forests (SD = 74; coefficient of variation = 0.52; Fig. 2). Of the 23 ecological subsections, 20 currently have biomass values between 70 Mg/ha and 100 Mg/ha. In contrast, 16 ecological subsections historically exceeded that range of biomass values. Historical biomass was least where fire-tolerant oak species were the greatest in composition; $R^2 = 0.78$ in GLO surveys compared to $R^2 = 0.23$ in FIA surveys.

Spatially, biomass density appeared to be negatively related to distance from major rivers, reflecting gradients of soil productivity, moisture, and fire protection. Biomass estimates were greatest in subsections along the Mississippi and Missouri Rivers (OZ15 and OZ16) and least in the high, flat Central Plateau subsection (OZ5; Fig. 1). Using the fine scale spatially continuous biomass predictions with the small range of biomass estimates, predicted biomass estimates for current biomass delineated river channels in the Plains (Fig. 3). Predicted biomass estimates more generally reflected ecological subsections in the Ozarks, with an increase in biomass within the shortleaf pine distribution of southeastern Missouri (Fig. 3).

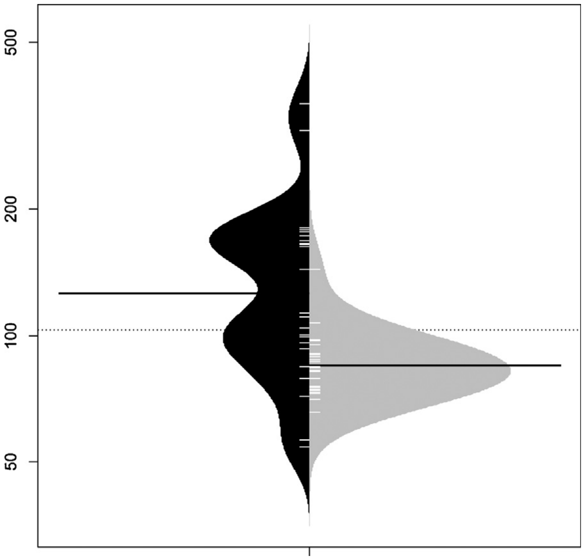

Fig. 2. Variability in historical modeled biomass (in black) and current modeled biomass (in gray; Mg/ha; trees ≥13 cm diameter). Each small line represents biomass by subsection; long lines represent current and historical biomass means and an overall mean. The density trace outlines a smoothed histogram.

Table 1
Historical (circa 1813 to 1850) and current (circa 2004 to 2008) biomass for trees ≥13 cm DBH by ecological subsection in the Ozarks (OZ) and Plains (Till = TP, Osage = OP) landscapes.

	Historical		Current	
Ecological subsection	Mean (Mg/ha)	SD	Mean (Mg/ha)	SD
OZ1	56.3	11.8	84.4	13.0
OZ3	100.2	20.9	89.8	11.3
OZ4	78.8	14.6	73.1	10.0
OZ5	54.1	12.5	70.5	9.4
OZ6	92.9	17.7	74.3	10.7
OZ7	71.4	15.7	75.7	10.4
OZ8	104.3	19.8	90.5	11.9
OZ9	176.5	45.3	82.5	10.2
OZ10	180.4	49.6	75.0	10.6
OZ11	144.0	42.5	97.1	11.0
OZ12	165.7	42.6	97.7	14.5
OZ13	164.3	41.6	95.2	12.6
OZ14	173.4	41.4	82.0	9.8
OZ15	357.2	101.8	143.9	33.9
OZ16	307.5	91.5	107.3	12.7
Ozarks mean	111.5	26.8	82.6	11.6
OP1	99.2	25.5	83.7	12.1
OP2	96.0	19.9	72.8	10.3
TP3	179.0	42.2	87.4	11.7
TP4	113.2	23.4	79.0	11.6
TP5	110.6	22.1	74.0	10.1
TP6	84.3	19.8	88.9	14.2
TP7	162.8	30.8	65.5	11.6
TP8	168.7	48.5	86.6	12.5
Plains mean	122.4	27.9	80.8	11.9

Historical total above ground carbon sequestration in live trees at least 13 cm in diameter, given the Weibull diameter distribution and assuming 90% forested extent, was 465 TgC (1 Tg = 1000,000 Mg) in the Ozarks (Table 2). Current total carbon sequestration, given the Weibull distribution and the current 60% forested extent, was 232 TgC, or 50% of historical carbon sequestration. In the Plains, historical total carbon sequestration, given the Weibull distribution and 50% forested extent historically, was 229 TgC. Current total carbon sequestration, given the Weibull distribution and 20% forested extent, was 61 TgC, or 27% of historical carbon sequestration.

4. Discussion

Historical forests contained greater biomass density (i.e., biomass per hectare) because of overstory trees that generally survived the major disturbance of the time. Pre-settlement fire regimes in Missouri were frequent but not often stand-replacing (LANDFIRE, 2013), and consequently disturbance from surface fires had relatively little effect on growth and survival of dominant trees that contributed the major portion of aboveground biomass and carbon sequestration. Fire disturbance did not prevent historical forests from achieving greater biomass density than current forests in most subsections. Indeed, shortleaf pine historically may have established densely after fire, increasing biomass in southeastern subsections where shortleaf pine occurs in Missouri. Only two relatively flat ecological subsections, the Ozark Plateau (OZ5) and Springfield Plain (OZ1), had lower historical biomass per ha than current forests (54 and 56 Mg/ha compared to 71 and 84 Mg/ha). Lower biomass may be due to more frequent fire disturbance on flat uplands compared to dissected terrain (Stambaugh and

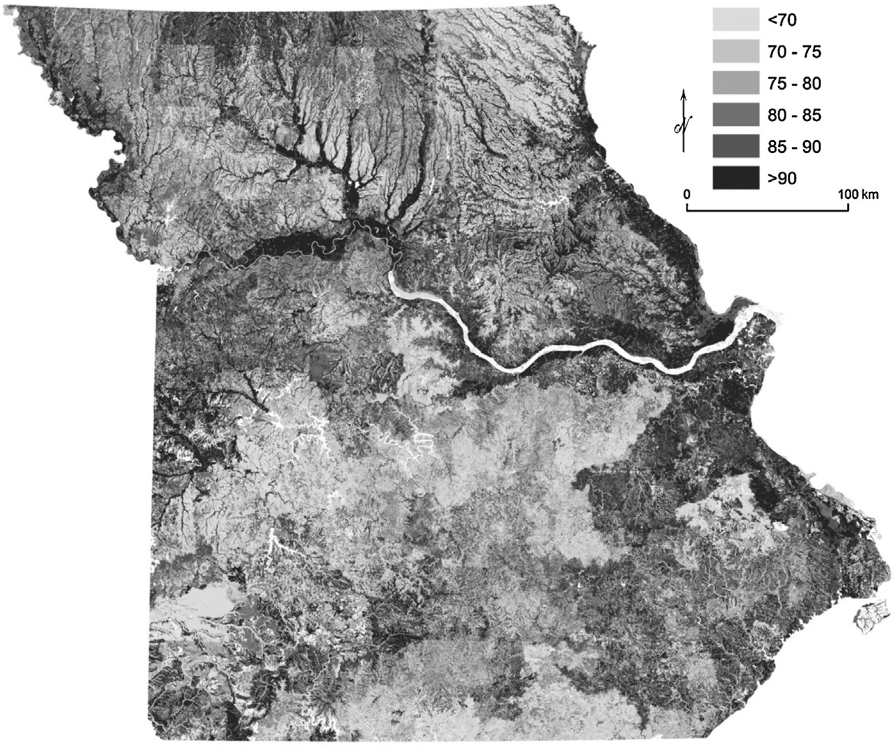

Fig. 3. Spatially continuous estimates of current biomass (Mg/ha; trees ≥13 cm diameter) for Missouri forests, 2008. Greater biomass occurs along major rivers and tributaries.

Guyette, 2008; and indeed, biomass was lowest where fire-tolerant oak species were the greatest in composition) combined with poor site quality due to shallow soils and low precipitation, but grazing or other disturbances also may have reduced woody biomass.

Structural variation occurred historically at many spatial scales due to interaction of wildfire or lack of disturbance with environmental gradients across Missouri landscapes. About half of the ecological subsections had historical biomass <115 Mg/ha, generally away from the Missouri and Mississippi Rivers (the Mississippi River is Missouri's eastern border, while the Missouri River separates the Ozarks from the Till Plains; Fig. 1), particularly the Ozark Plateau (OZ5) and Springfield Plain (OZ1) subsections, which had biomass of only about 55 Mg/ha. About half of the ecological subsections had historical biomass >140 Mg/ha, generallyin river watersheds or on river hills. The Ozarks ecological section had two ecological subsections (OZ15 and OZ16) dominated by floodplain forest where historical biomass was >300 Mg/ha. There appears to be two historical groups of trees in subsections exposed to fire and protected from fire, given the bimodal distribution (Fig. 2) due to the natural break in biomass density between 113 Mg/ha and 144 Mg/ha. Nonetheless, oak percentages excluding flood-tolerant oak species reached up to 70% in a few of the subsections with greater biomass, just slightly less than the minimum oak percentages in subsections with lesser biomass, which suggests an overlap in fire regimes. Any areas that experienced a low severity fire regime similar to that of Missouri or were more protected from fire (e.g., most of the central eastern United States) likely also had greater historical biomass density (Lichstein et al., 2009), resulting from development of large tree diameters over time, than current biomass density. However, biomass removal by fire may have been greater than tree removal by current land uses in some fire-prone landscapes of the eastern United States (e.g., southern Minnesota; Hanberry and He, 2015).

Landscape structural variation, as opposed to internal stand structural variation, resulted from environmental gradients of moisture and soil productivity that directly influenced tree diameter growth and also influenced biomass removal by fire, amplifying spatial variation of biomass. That is, more productive sites with deep alluvial soils and greater soil moisture also protected trees from biomass removal by fire while sites with shallow soils and less moisture were more exposed to fire disturbance. Furthermore, forests in Missouri have become more uniform in biomass among ecological subsections as forests conform to cumulative land use and harvest disturbances across landscapes. Tree cutting periodically removes trees from a given site, typically at least every 100 years (Birdsey and Lewis, 2003; Masek et al., 2008). This creates forests with greater density, smaller tree diameters, and less biomass than historical forests during the early 1800s.

Table 2
Total aboveground carbon for live trees ≥13 cm DBH, varying by forested extent, of the historical (circa 1813 to 1850) and current (circa 2004 to 2008) Ozarks and Plains landscapes.

% Forested	Area (ha)	Total carbon (TgC)	
		Historical	Current
Ozarks			
100	9300,000	516	386
90	8370,000	465	347
80	7440,000	413	309
70	6510,000	361	270
60	5580,000	310	232
57	5301,000	294	220
Plains			
70	5250,000	320	213
60	4500,000	275	182
50	3750,000	229	152
40	3000,000	183	122
30	2250,000	137	91
20	1500,000	92	61
17	1275,000	78	52

Loss of landscape structural variation in forest biomass occurred due to loss of open forest ecosystems and highly productive floodplain forests that varied in biomass across Missouri. Fire exclusion has reduced the role of topography and environmental gradients in influencing fire disturbance, while frequent tree removal has removed protection from disturbance in floodplain subsections, even though site productivity still is apparent (Fig. 3).

Any landscapes that historically contained low severity fire regimes or productive forests along floodplains probably have lost spatial structural variation, or become structurally homogenous. Although the terms heterogeneity and homogeneity are applied widely, including terminology for genetic, taxonomic, or functional diversity or loss of that type of diversity (Olden and Rooney, 2006; Hanberry, 2015), landscape heterogeneity may be defined as a secondary level of variation that arises as a distinct response to multiple types of underlying variation across a landscape, while lack of landscape heteogeneity may be called homogeneity.

The difference between historical and current biomass density per hectare provides an estimate of the minimum quantity of additional biomass (and therefore carbon) that current forests could accumulate in the absence of disturbance. In the absence of disturbance, continued growth of current forest stands will result in fewer but larger trees per hectare. This transition in forest stand development over time is brought about by competition among trees and resultant self-thinning (Oliver and Larson, 1990). Indeed, a combination of large dominant trees and dense, multiple understory layers should increase biomass sequestration per hectare beyond historical ecological levels. Nevertheless, at the current forested extent of 60% in the Ozarks ecological section, biomass sequestration per ha would need to exceed 165 Mg/ha to match total historical carbon sequestration of about 465 TgC in the Ozarks (assuming 90% historical forested extent; see Table 2 for a range of values). At the current forested extent of 20% in the Plains ecological sections, biomass sequestration per hectare would need to exceed 300 Mg/ha to match total historical carbon sequestration of about 229 TgC in the Plains (assuming 50% historical forested extent).

Both upland woodlands and floodplain forests with large diameter trees now are rare, and these forests are important restoration targets for maintaining biodiversity and variation across the landscape, as well as increasing carbon sequestration in woody biomass. Selection of areas with greater historical productivity for woodlands restoration or floodplain forest reforestation should require relatively fewer hectares for the same gain in carbon sequestration. Most of the Plains region is well below its observed potential to accumulate biomass and carbon. The Plains historically had greater mean biomass than the Ozarks (122 Mg/ha compared to 111 Mg/ha) but currently the Ozarks have greater biomass density than the Plains (89 Mg/ha compared to 80 Mg/ha). The Missouri and Mississippi River Alluvial Plain subsections had comparatively great biomass densities historically and the greater potential productivity of alluvial soils will require fewer reforested hectares than upland sites of lower productivity to achieve similar carbon sequestration. However, the relatively high productivity of alluvial soils increases land value, thus restoration of upland forests in some cases may be a more economically efficient use of resources. Restoration often is not possible, but tree retention through variable retention forestry, longer silvicultural rotations, and reduced land clearing will allow trees to reach larger diameters and store greater biomass (Hanberry et al., 2015).

We only examined aboveground biomass. Belowground soil carbon typically ranges from 45% to 85% of total combined aboveground and belowground carbon, decreasing in proportion as forests age (Hanberry et al., 2015). Young forests may have contain about 80% to 90% of the soil carbon that older forests contain (Hanberry et al., 2015). Additionally, we did not include in biomass calculations trees and shrubs <13 cm in diameter that are abundant in current forests but sensitive to fire. Although low severity fire regimes do not remove large trees, surface fires can prevent regeneration of smaller diameter trees that replace canopy trees after mortality, resulting in lower densities rather than maximization of available growing space.

5. Conclusions

Biomass, as measured by density (Mg/ha) and total biomass, was greater in historical forests than in current forests in Missouri. Despite a frequent surface fire regime, historical forests accumulated large dominant trees that survived surface fires and were the major contributors to biomass densities. Current forests already are at least twice as dense as historical forests, and thus, biomass increases will occur through increases in tree size (with attendant reduction in tree density) and/or increases in forested extent.

Forest landscapes contain patterns that reflect environmental gradients. Spatial variation in historical forest biomass resulted from fire disturbance, which maintained open forest ecosystems of savannas and woodlands, and lack of disturbance, which produced closed forests of great biomass along rivers. The amount of disturbance varied spatially along environmental gradients that contribute to productivity. In contrast, current forests are characterized by lower variation in mean biomass among ecological subsections due to changing patterns of land clearing, land abandonment, timber harvesting, fire exclusion, woods grazing, and other land uses during the past century. Restoration of floodplain forests and upland woodlands with large diameter trees will provide landscape variation in biomass, while tree retention and increased forested extent will increase biomass.

Conflict of interest statement

The authors declare that there are no conflicts of interest.

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