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Changes in Forest Composition, Stem Density, and Biomass from the Settlement Era (1800s) to Present in the Upper Midwestern United States

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Abstract:	EuroAmerican land use and its legacies have transformed forest structure and composition across the United States (US). More accurate reconstructions of historical states are critical to understanding the processes governing past, current, and future forest dynamics. Gridded (8x8km) estimates of pre-settlement (1800s) forests from the upper Midwestern US (Minnesota, Wisconsin, and most of Michigan) using 19th Century Public Land Survey (PLS) records provide relative composition, biomass, stem density, and basal area for 26 tree genera. This mapping is more robust than past efforts, using spatially varying correction factors to accommodate sampling design, azimuthal censoring, and biases in tree selection. We compare pre-settlement to modern forests using Forest Inventory and Analysis (FIA) data, with respect to structural changes and the prevalence of lost forests, pre-settlement forests with no current analogue, and novel forests, modern forests with no past analogs. Stem density and basal area are higher in contemporary forests, while biomass is higher in settlement-era forests, but this pattern is spatially structured. Modern biomass is higher than pre-settlement biomass in the northwest (Minnesota and north-eastern Wisconsin), and lower in the east, due to shifts in species composition and, presumably, average stand age. Modern forests are more homogeneous, and ecotonal gradients are more diffuse today than in the past. Novel forest assemblages represent 29% of all FIA cells, while 25% of pre-settlement forests no longer exist in a modern context. Lost forests are centered around the forests of the Tension Zone, particularly in hemlock dominated forests of north-central Wisconsin, and in oak-elm-basswood forests along the forest-prairie boundary in south central Minnesota and eastern Wisconsin. Novel FIA forest assemblages are distributed evenly across the region, but novelty shows a strong relationship to spatial distance from remnant forests in the upper Midwest, with novelty predicted at between 20 to 60km from remnants, depending on historical forest type. The spatial relationships between remnant and novel forests, shifts in ecotone structure and the loss of historic forest types point to significant challenges to land managers if landscape restoration is a priority in the region. The spatial signals of novelty and ecological change also point to potential challenges in using modern spatial distributions of species and communities and their relationship to underlying geophysical and climatic attributes in understanding potential responses to changing climate. The signal of human settlement on modern forests is broad, spatially varying and acts to homogenize modern forests relative to their historic counterparts, with significant implications for future management.
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Additional data availability information:	

Dear Editor:

We are submitting for your consideration our manuscript, "Change in Composition, Density, and Biomass since the Settlement Era (1800s) in the Upper Midwestern United States."

This paper presents new analysis and synthesis of settlement-era forest composition and structure based on Public Land Survey (PLS) data from the Upper Midwestern United States. Our analysis substantially advances from prior PLS-based work by developing new methods for correcting for surveyor bias in a way that accounts for changing survey design throughout the region. This paper is also the first to provide PLS-based estimates of historical forest biomass at this broader regional scale. We aim to show the extent of change in forest composition, describe the spatial patterns of change, and quantify the relationship between ecological novelty and the spatial structure of remnant forests in the region.

We apply the new PLS-based dataset to contrast forest structure and composition prior to Euro-American settlement with modern forest structure from the Forest Inventory and Analysis database. Key findings include:

1) Contemporary forests in the upper Midwest have higher stem density but lower total basal area and biomass than settlement-era forests, likely because of the larger size of individual settlement-era trees and differential changes in landscape level processes between the northern and southern parts of the region.
2) Almost 30% of the modern forested landscape of the upper Midwest is compositionally novel relative to the PLS data, while 25% of forests in the PLS era have no modern analogues.
3) The loss of PLS forests is concentrated in central Wisconsin, near the Tension Zone, and is associated with a weakening of ecotones and an overall homogenization of forest cover across the region.
4) There is strong spatial structure in the presence of novel and remnant forests, with novel forests occurring further from remnant forest than expected by chance.

We anticipate that these PLS-based datasets will become the new standard for settlement-era forest composition and structure, and we are working closely with terrestrial ecosystem modellers to use this as a baseline dataset for a series of historical-to-21st-century experiments and modeling intercomparison protocols. The analysis and data provided here will be of interest to a broad range of researchers including paleoecologists, historical ecologists, ecologists, ecosystem modelers, geoscientists and statisticians. The breadth of our authorship team underscores this point. This paper is partner to a second submission to PLoS One (see below), a paper in revision with the Journal of Geophysical Research and a paper in preparation for resubmission to Quaternary Science Reviews.

Paciorek, C.; Goring, S. J.; Thurman, A.; Cogbill, C.; Williams, J.; Mladenoff, D.; Peters, J.; Zhu, J. & J.S., M. in review. Statistically-estimated tree composition for the northeastern United States at the time of Euro-American settlement. *PLoS One.*

This paper builds on recent analyses including:

Terrail, R.; Arseneault, D.; Fortin, M.-J.; Dupuis, S. & Boucher, Y. 2014. An early forest inventory indicates high accuracy of forest composition data in pre-settlement land survey records. *Journal of Vegetation Science, Wiley Online Library, 25*, 691-702

Thompson, J. R.; Carpenter, D. N.; Cogbill, C. V. & Foster, D. R. 2013. Four centuries of change in northeastern United States forests. *PloS one, Public Library of Science, 8*, e72540

Data notes: In this submission all the code required to run the analysis is provided as Supplement 1. Supplement 1 also includes files necessary to generate several of the figures used in this paper, including files from NaturalEarthData.org. The final submission will be accompanied by a public GitHub repository, and these NaturalEarth files will not be included since we do not have permission to distribute them. In their place will be direct web-links to the files. In addition, this submission contains only a subset of the full PLSS data. This subset should be sufficient to test the code and replicate most of the analysis. We have permission to use the PLS data from Wisconsin, Michigan and Minnesota, but do not have permission to distribute this data. Our final repository will include links to these datasets, along with the code necessary to link the data files together. Lastly, because of the inclusion of a large amount of primary data "Supplement 1" could not be uploaded to the PLoS System. It is available for download here: https://www.dropbox.com/s/577bnxdrgm3sas0/Supplement1_RawCodeandData.zip?dl=0

Thank you for your time and consideration.

Sincerely,

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Witness Tree paper

Simon Goring *et al.*

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Abstract

EuroAmerican land use and its legacies have transformed forest structure and composition across the United States (US). More accurate reconstructions of historical states are critical to understanding the processes governing past, current, and future forest dynamics. Gridded (8x8km) estimates of pre-settlement (1800s) forests from the upper Midwestern US (Minnesota, Wisconsin, and most of Michigan) using 19th Century Public Land Survey (PLS) records provide relative composition, biomass, stem density, and basal area for 26 tree genera. This mapping is more robust than past efforts, using spatially varying correction factors to accommodate sampling design, azimuthal censoring, and biases in tree selection.

We compare pre-settlement to modern forests using Forest Inventory and Analysis (FIA) data, with respect to structural changes and the prevalence of lost forests, pre-settlement forests with no current analogue, and novel forests, modern forests with no past analogs. Stem density and basal area are higher in contemporary forests, while biomass is higher in settlement-era forests, but this pattern is spatially structured. Modern biomass is higher than pre-settlement biomass in the northwest (Minnesota and north-eastern Wisconsin), and lower in the east, due to shifts in species composition and, presumably, average stand age. Modern forests are more homogeneous, and ecotonal gradients are more diffuse today than in the

past. Novel forest assemblages represent 29% of all FIA cells, while 25% of pre-settlement forests no longer exist in a modern context.

Lost forests are centered around the forests of the Tension Zone, particularly in hemlock dominated forests of north-central Wisconsin, and in oak-elm-basswood forests along the forest-prairie boundary in south central Minnesota and eastern Wisconsin. Novel FIA forest assemblages are distributed evenly across the region, but novelty shows a strong relationship to spatial distance from remnant forests in the upper Midwest, with novelty predicted at between 20 to 60km from remnants, depending on historical forest type.

The spatial relationships between remnant and novel forests, shifts in ecotone structure and the loss of historic forest types point to significant challenges to land managers if landscape restoration is a priority in the region. The spatial signals of novelty and ecological change also point to potential challenges in using modern spatial distributions of species and communities and their relationship to underlying geophysical and climatic attributes in understanding potential responses to changing climate. The signal of human settlement on modern forests is broad, spatially varying and acts to homogenize modern forests relative to their historic counterparts, with significant implications for future management.

Key Words: euroamerican settlement, land use change, public land survey, historical ecology, novel ecosystems, biomass, forest inventory and analysis, ecotone, forest ecology

Introduction:

The composition, demography, and structure of forests in eastern North America have changed continuously over the last millennium, driven by human land use [1–5] and

77 climate variability [6–9]. While human effects have been a component of these systems for
78 millenia, the EuroAmerican settlement and industrialization period have increased
79 anthropogenic effects by orders of magnitude [10–12]. Legacies of post-settlement land use
80 in the upper Midwest [13] and elsewhere have been shown to persist at local and regional
81 scales [5,14,15], and nearly all North American forests have been affected by the
82 intensification of land use in the past three centuries. Hence, contemporary ecological
83 processes in North American forests integrate the anthropogenic impacts of the post-
84 EuroAmerican period and natural influences at decadal to centennial scales.

85 At a regional scale many forests in the upper Midwest (*i.e.*, Minnesota, Wisconsin and
86 Michigan) now have decreased species richness and functional diversity relative to forests
87 of the pre-EuroAmerican settlement (hereafter pre-settlement) period [16–18] due to near
88 complete logging. For example, forests in Wisconsin are in a state of regrowth, with an
89 unfilled carbon sequestration potential of 69 TgC [19] as a consequence of these extensive
90 land cover conversions and subsequent partial recovery following abandonment of farm
91 lands in the 1930s.

92 Legacies of land use are unavoidable at regional scales [20]. Under intensive land use
93 change the natural processes of secession, senescense and the replacement of tree species
94 in forests may be masked, or heavily modified by historically recent land use change.
95 Broad-scale land use change can result in changes to forest structure and species pools that
96 may result in non-stationarity within ecosystems that may not be apparent on the
97 relatively narrow time scales at which ecology traditionally operates [21], meaning
98 chronosequences may not be sufficeint to understand shifts in structure and composition.

There is a history of recolonization of forested landscapes following agricultural clearance in the upper Midwest [22], pointing to the importance of understanding ecological trajectories and land use legacies in understanding modern forest dynamics [20]. Cramer et al. [23] point to the literature of succession theory to indicate the likelihood that many old fields will return to a 'natural' state, but point out that recovery is not universal. In particular, intense fragmentation of the landscape can deplete the regional species pool, leading to failures of recruitment that would favor species with longer distance seed dispersersal [24]. In the upper Midwest long seed dispersal would favor species such as poplar (*Populus* sp.), white birch (*Betula papyrifera*) and some maple species (*Acer* sp.), at the expense of large-seeded species such as walnut (*Juglans* sp.), oak (*Quercus* sp.) and others.

While there remains debate over the utility of the concept of novel ecosystems [25,26], the fact remains that there are now forest and vegetation communities on the landscape without past analogues. The long term management of the systems and their associated services requires a broad understanding of the extent to which landscapes have been modified, and the extent to which land use change has potenitally masked underlying processes. It also requires a better understanding of the spatial (and temporal) scales at which novel ecosystems operate. While restoration efforts have generally focused on ecosystems at local scales, there is an increasing need to focus on management and restoration at landscape scales [27]. Thus a better understanding of the landscape-scale processes driving novelty, the spatial structure of novel ecosystems and their ecological correlates, is increasingly important. An understanding of landscape level processes driving ecological novelty can help prioritize intervention strategies at local scales [28],

and give us a better understanding of the role of patches in restoring hybrid or novel landscapes. In particular, how important is the species pool to the development of novel landscapes? Are novel forests further from remnant forests than might otherwise be expected? Is novelty operating at landscape scales in the upper Midwest, and is the spatial distribution of new forests tied to historical patterns vegetation or losses of forest types from the historical landscape?

The upper Midwestern United States represents a unique ecological setting, with multiple major ecotones, including the prairie-forest boundary, historic savanna, and the Tension Zone between southern deciduous forests and northern evergreen forests. The extent to which these ecotones have shifted, and their extent both prior to and following EuroAmerican settlement is of critical importance to biogeochemical and biogeophysical vegetation-atmosphere feedbacks [29], carbon sequestration [19], and regional management and conservation policy [30–33].

Land use change at the local and state-level has affected both the structure and composition of forests in the Midwestern United States [16,17]. Homogenization and shifts in overall forest composition are evident, but the spatial extent and structure of this effect is less well understood. Studies in Wisconsin have shown differential patterns of change in the mixedwood and evergreen dominated north versus the southern driftless and hardwood south. Does this pattern of differential change extend to Minnesota and Michigan? To what extent are land-use effects common across the region, and where are responses ecozone-specific? Has homogenization [16] resulted in novel forest assemblages relative to pre-settlement baselines across the region, and the loss of pre-settlement forest

144 types? Are the spatial distributions of these novel and lost forest types overlapping, or do
145 they have non-overlapping extents? If broad-scale reorganization is the norm following
146 EuroAmerican settlement, then the ecosystems that we have been studying for the past
147 century may indeed be novel relative to the reference conditions of the pre-settlement era.

148 Modern forest structure and composition data [34] play a ubiquitous role in forest
149 management, conservation, carbon accounting, and basic research on forest ecosystems
150 and community dynamics. These recent surveys (the earliest FIA surveys began in the
151 1930s) can be extended with longer-term historical data to understand how forest
152 composition has changed since EuroAmerican settlement. The Public Land Survey was
153 carried out ahead of mass EuroAmerican settlement west and south of Ohio to provide for
154 delineation and sale of the public domain beyond the original East Coast states [35,36].
155 Because surveyors used trees to locate survey points, recording the identity, distance, and
156 directory of two to four trees next to each survey marker, we can make broad-scale
157 inferences about forest composition and structure in the United States prior to large-scale
158 EuroAmerican settlement [37–40]. In general, FIA datasets are systematically organized
159 and widely available to the forest ecology and modeling community, whereas most PLSS
160 data compilations are of local or, at most, state-level extent. This absence of widely
161 available data on settlement-era forest composition and structure limits our ability to
162 understand and model the current and future processes governing forest dynamics at
163 broader, regional scales. For example, distributional models of tree species often rely upon
164 FIA or other contemporary observational data to build species-climate relationships that
165 can be used to predict potential range shifts [41,42].

166 Here we use survey data from the original Public Lands Surveys (PLS) in the upper
167 Midwest to derive estimates of pre-settlement (*ca*. mid-late 1800s) forest composition,
168 basal area, stem density, and biomass. This work builds upon prior digitization and
169 classification of PLSS data for Wisconsin [43,44] and for parts of Minnesota [17,45] and
170 Michigan Michigan (USFS-NCRS http://www.ncrs.fs.fed.us/gla/). Most prior PLS-based
171 reconstructions are for individual states or smaller extents [17,19,45,46] often aggregated
172 at the scale of regional forest zones [16,17], although aggregation may also occur at the
173 section [19] or township scale [47]. Our work develops new approaches to address major
174 challenges to PLSS data, including lack of standardization in tree species names, azimuthal
175 censoring by surveyors, variations in sampling design over time, and differential biases in
176 tree selection among different kinds of survey points within the survey design at any point
177 in time. The correction factors developed here are spatially varying, allowing us to
178 accommodate temporal and spatial variations in surveyor methods.

179 We aggregate point based estimates of stem density, basal area and biomass to an 8 x 8km
180 grid, and classify forest types in the upper Midwest to facilitate comparisons between FIA
181 and PLSS data. We compare the PLSS data to late-20th-century estimates of forest
182 composition, tree stem density, basal area and biomass. We explore how forest
183 homogenization has changed the structure of ecotones along two major ecotones from
184 southern deciduous to northern evergreen forests and to the forest-prairie boundary.
185 Using analog analyses, we identify lost forests that have no close compositional counterpart
186 today and novel forests with no close historical analogs. This work provides insight into the
187 compositional and structural changes between historic and contemporary forests, while

setting the methodological foundation for a new generation of maps and analyses of settlement-era forests in the Eastern US.

Methods:

Public Lands Survey Data: Assembly, and Standardization

The PLSS was designed to facilitate the division and sale of federal lands from Ohio westward and south. The survey created a 1 mile^2 (2.56 km^2) grid (sections) on the landscape. At each section corner, a stake was placed as the official location marker. To mark these survey points, PLSS surveyors recorded tree stem diameters, measured distances and azimuths of the two to four trees 'closest'to the survey point and identified tree taxa using common (and often regionally idiosyncratic) names. PLSS data thus represent measurements by hundreds of surveyors from 1832 until 1907, with changing sets of instructions over time (Stewart, 1979).

The PLSS was undertaken to survey land prior to assigning ownership (Stewart 1935, White 1983), replacing earlier town proprietor surveys (TPS) used for the northeastern states [2,48]. The TPS provided estimates of relative forest composition at the township level, but no structural attributes. The PLSS produced spatially explicit point level data, with information about tree spacing and diameter, that can be used to estimate absolute tree density and biomass. PLSS notes include tree identification at the plot level, disturbance [49] and other features of the pre-settlement landscape. However, uncertainties exist within the PLSS and township level dataset [50].

208 Ecological uncertainty in the PLSS arises from the dispersed spatial sampling design (fixed
209 sampling every 1 mile), precision and accuracy in converting surveyor's use of common
210 names for tree species to scientific nomenclature [51], digitization of the original survey
211 notes, and surveyor bias during sampling [38,50,52,53]. Estimates vary regarding the
212 ecological significance of surveyor bias. Terrail *et al*. [54] show strong fidelity between
213 taxon abundance in early land surveys versus old growth plot surveys. Liu *et al* [38]
214 estimate the ecological significance of some of the underlying sources of bias in the PLSS
215 and show ecologically significant (>10% difference between classes) bias in species and
216 size selection for corner trees. However Liu *et al*. [38] also indicate that the true sampling
217 error cannot be determined, particularly because most of these historic ecosystems are
218 largely lost to us.

219 Kronenfeld and Wang [55], working with historical land cover datasets in western New
220 York indicate that direct estimates of density using plotless estimators may be off by nearly
221 37% due to azimuthal censoring (*i.e.*, the tendency of surveyors to avoid trees close to
222 cardinal directions), while species composition estimates may be adjusted by between -4 to
223 +6%, varying by taxon, although Kronenfeld [56] shows adjustments of less than 1%. These
224 biases can be minimized by appropriate analytical decisions; many efforts over the years
225 have assessed and corrected for the biases and idiosyncrasies in the original surveyor data
226 [17,38,39,53,55,57–60]. And, even given these caveats, PLSS records remain the best
227 source of data about both forest composition and structure in the United States prior to
228 EuroAmerican settlement.

This analysis builds upon and merges previous state-level efforts to digitize and database the point-level PLSS data for Wisconsin, Minnesota and the Upper Peninsula and upper third of the Lower Peninsula of Michigan. These datasets were combined using spatial tools in R [61,62] to form a common dataset for the upper Midwest (Fig 1) using the Albers Great Lakes and St Lawrence projection (see code in Supplement 1, file: *step_one_clean_bind.R*; proj4: *+init:EPSG:3175 – NOTE: Supplement 1 is too large to upload to the PLoS system, it is available here: https://www.dropbox.com/s/577bnxdrgm3sas0/Supplement1_RawCodeandData.zip?dl=0*).

Fig 1. *The domain of the Public Land Survey investigated in this study. The broad domain includes Minnesota, Wisconsin and the upper two thirds of Michigan state. A 8x8km grid is superimposed over the region to aggregate data, resulting in a total of 7940 cells containing data.*

We took several steps to standardize the dataset and minimize the potential effects of surveyor bias upon estimates of forest composition, density, and biomass. All steps are preserved in the supplementary R code (Supplement 1: *step_one_clean_bind.R*). First, we excluded line and meander trees (i.e. trees encountered along survey lines, versus trees located at section or quarter corners) because surveyor selection biases appear to have been more strongly expressed for line trees, meander trees have non-random habitat preferences [38], and the inherent differences in sampling design between line, meander and corner points. We used only the closest two trees at each corner point because the third and fourth furthest trees have stronger biases with respect to species composition and diameter [38]. Corner points were used only if 1) there were at least two trees at a

survey point, 2) the two trees were from different quadrants (defined by the cardinal directions), and 3) there were valid azimuths to the trees (a defined quadrant with an angle between 0 and 90) and valid diameters (numeric, non-zero).

Many species-level identifications used by PLSS surveyors are ambiguous. Statistical models can predict the identity of ambiguous species [51], but these models introduce a second layer of uncertainty into the compositional data, both from the initial surveyors' identification, and from the statistical disambiguation. Given the regional scale of the analysis, and the inherent uncertainty in the survey data itself, we chose to avoid this layer of taxonomic uncertainty, and retained only genus-level identification (Supplement 2, *Standardized Taxonomy*). The ecological implications for the use of genera-level taxonomies are important for this region. While fire tolerance is fairly well conserved within genera, shade tolerance can vary. *Betula* contains shade intolerant *B. paperyfera* and the intermediate *B. alleghaniensis*, while *Pinus* contains the very shade intolerant *P. banksiana*, the intolerant *P. resinosa* and the shade tolerant *P. strobus*. For cases where shade tolerance (or fire tolerance) varies strongly within a genera we examine the data to determine the suitability of the assignment, or extent of confusion within the assigned genera.

In areas of open prairie or other treeless areas, *e.g.* southwestern Minnesota, surveyors recorded distances and bearings to 'Non Tree' objects. When points were to be located in water bodies the point data indicates 'Water'. Points recorded "No Tree" are considered to have been from extremely open vegetation, with an estimated point-level stem density of 0 stems ha^{-1}. We based our estimates on terrestrial coverage, so water cells are excluded

completely. Hence, absence of trees at "No Tree" locations does reduce the gridded estimates of terrestrial stem density, but absence of trees at 'Water' locations does not.

Digitization of the original surveyor notebooks introduces the possibility of transcription errors. The Wisconsin dataset was compiled by the Mladenoff lab group, and has undergone several revisions over the last two decades in an effort to provide accurate data [30,38,43,44,51]. The Minnesota transcription error rate is likely between 1 and 5%, and the treatment of azimuths to trees varies across the dataset [37]. Michigan surveyor observations were transcribed to mylar sheets overlaid on State Quadrangle maps, so that the points were displayed geographically, and then digititized to a point based shapefile (Ed Schools, pers. comm.; Great Lakes Ecological Assessment. USDA Forest Service Northern Research Station. Rhinelander, WI. http://www.ncrs.fs.fed.us/gla/), carrying two potential sources of transcription error. Preliminary assessment of Southern Michigan data indicates a transcription error rate of 3 - 6%. To reduce errors associated with transcription across all datasets, we exclude sites for which multiple large trees have a distance of 1 link (20.12 cm) to plot center, trees with very large diameters (diameter at breast height - dbh > 100 in; 254 cm), plots where the azimuth to the tree is unclear, and plots where the tree is at plot center but has a recorded azimuth. All removed plots are documented in the code used for analysis (Supplement 1: *step_one_clean_bind.R*) and are commented for review.

Data Aggregation

We binned the point data using an 64km^2 grid (Albers Gt. Lakes St Lawrence projection; Supplement 1: *base_calculations.R*) to create a dataset that has sufficient numerical power

for spatial statistical modeling and sufficient resolution for regional scale analysis [63]. This resolution is finer than the 100km^2 gridded scale used in Freidman and Reich [45], but coarser than township grids used in other studies [19,56] to provide a scale comparable to aggregated FIA data at a broader scale. Forest compositional data is based on the number of individuals of each genus or plant functional type (PFT) present at all points within a cell. Stem density, basal area and biomass are averaged across all trees at all points within the cell.

Stem Density

Estimating stem density from PLSS data is based on a plotless density estimator that uses the measured distances from each survey point to the nearest trees at the plot location [64,65]. The Morisita density estimator is then modified to minimize error due to different sampling geometries and several known surveyor biases [17,38,39,53,55,57–60]. The standardized approach for this method is well validated, however surveyors did not use a consistent approach to plot level sampling. Survey sampling instructions changed throughout the implementation of the PLSS in this region and differed between section and quarter section points and between internal and external points within a township [36,38]. Our approach allows for spatial variation in surveyor methods by applying various spatially different correction factors based not only on the empirical sample geometry, but also on known surveyor biases deviating from this design [57]. These estimates are based on empirical examination of the underlying data, and have been validated using simulations on stem mapped stands [57].

We estimate stem density (stems m^{-2}) based on a on a modified form of the Morisita two-tree density estimator, which uses the distance-to-tree measurements for the two closest trees at each point [66]. Our modified form uses explicit and spatially varying correction factors, modeled after the Cottam correction factor [67], that account for variations in sampling designs over time and among surveyors. All code to perform the analysis is included in Supplement 1.

We estimate the basic stem density (stems m^{-2}) using the point-to-tree distances for the closest trees to each point within a defined number of sectors around the point (Reference 64 eqn 31.):

$$\hat{\lambda m}_2 = \frac{k-1}{\pi \times n} \times \sum_{i=1}^{N} \frac{k}{\sum_{j=1}^{k} (r_{ij})^2} \quad (1)$$

where λ is density ; k is the number of sectors within which trees are sampled, N is the number of points over which estimates are aggregated, r is the distance of point-to-tree (as m). This estimate can be modified by a refinement of the Cottam quadrant factors [66,67] which recognizes that different sampling designs, and the order of the distances in different quadrants (or sectors) carry specific weights. This correction, herein called κ, accounts for different sampling designs. When either four quadrants or trees are sampled (point quarter design), or when two trees in opposite semicircles (point halves design) are sampled, the equation is accurate and κ = 1; when the two trees are in the nearest of two quadrants (two nearest quadrants design), κ = 0.857; and when two trees are in quadrants on the same side of the direction of travel (one-sided or interior half design), κ = 2. This parameter, in Cottam's notation [67], is a divisor of the denominator above, or here, the mathematically equivalent multiplier in the numerator of the reciprocal of the squared distances.

We further simplify the density estimate in equation (1) so that it is calculated at each point (N=1) and for two sample trees only (k=2):

$$\lambda_M = \frac{2}{\pi \times \sum_{j=1}^{2} r_j{}^2}$$

Then the point values for any sampling design can be Cottam corrected ($\kappa \times \lambda_M$). For example, the basic Morisita equation for two sectors assumes trees are located in opposite halves, so if the actual design is the nearest tree in the two nearest quadrants, the density from equation 2 will be overestimated and must be correspondingly corrected by multiplying by $\kappa = 0.857$.

Further corrections account for the restriction of trees to less than the full sector (θ), censoring of trees near the cardinal azimuths (ζ), and undersampling of trees smaller than a certain diameter limit (ϕ). These parameters are derived from analyses of measurements of bearing angles and diameters actually observed in surveys of witness trees within a subset of townships across the upper Midwest.

Sector bias (θ). Although the density model for two tree points assumes that the trees are on opposite sides of a sample line (point halves), the actual sample is often more restricted ($< 180^o$) within the sector, or is a less restricted ($> 180^o$) angle beyond the sector (see Supplement 3). This deviation from the equation's assumption of equal distribution of angles across the 180^o sector is quantified using the empirical angle between the bearings of the two trees (pair angle). The pair angle frequencies (Supplement 3) that the observed proportion of trees (p) within any restricted sector divided by the proportion of that angle within the circle (α) are an estimate of the bias imposed by the actual sampling [55]. The

359 factor ($\theta = p/\alpha$) indicates bias associated with differences in geometry of two tree samples.
360 This parameter (θ) varies from 0.71 to 1.27, indicating sampling from effectively 253^o to
361 141^o sectors.

362 Azimuthal censoring (ζ). In addition to sector bias, surveyors did not always sample trees
363 near the cardinal directions [55,58,59]. This azimuthal censoring is commonly found along
364 the line of travel on section lines and sometimes on the perpendicular quarter-section lines.
365 Trees near the cardinal directions were passed over, and a replacement was found within a
366 more restricted angular region. The correction for this bias is calculated following
367 Kronenfeld and Wang [55] in a manner similar to the sector bias. The factor ζ is the ratio of
368 the proportion of trees in the restricted area (p) divided by the proportion of the complete
369 circle (α) that is used. The azimuthal censoring parameter (ζ) ranges from 1.03 to 1.25
370 indicating an equivalent to complete elimination of trees from 10^o to 72^o azimuths adjacent
371 to the cardinal directions.

372 Diameter limit (ϕ). Examination of the diameter distributions from settlement era surveys
373 across the upper Midwest clearly demonstrate witness trees less than 8 inches in diameter
374 were undersampled [38,57,59]. We have confirmed this bias in our own inspection of plots
375 of diameter frequency in the PLSS data, which show a strong mode at 8". This bias can be
376 accommodated by setting a diameter limit, and only calculating the density for trees with
377 diameters above this limit. Total density calculated from all trees is reduced to this
378 reference limit by simply multiplying the total by the percentage of trees above this limit.
379 This effectively eliminates the smaller trees from the total and normalizes the value of trees

above this standard. The parameter (ϕ) represents diameter size bias is simply the percentage of trees ≥ 8" and, in practice, ranges from 0.6 - 0.9.

Because all surveyor bias corrections are simple multipliers of the model density and should be independent, the bias-minimized estimate of the point density of trees ≥ 8" is:

$$\lambda_{\text{Mcorrected}} = \kappa \times \theta \times \zeta \times \phi \times \lambda_{\text{M}} \quad (3)$$

Estimates for each point *i* can be averaged for all *N* points in any region. Correction factors are calculated separately for different regions, years, internal versus external lines, section versus quarter-section points, and surveyor sampling designs (Supplement 4). All code to perform the analyses is included in Supplement 1 and the full rationale for and calculation of these measures is described further in Cogbill et al. [57]. Further, simulation used stem mapped stands from the region presented in Cogbill et al. [57] supports the robustness of this method, as opposed to other methods presented in the literature.

Basal Area and Biomass Estimates

Forest basal area is calculated by multiplying the point-based stem density estimate by the average stem basal area from the reported diameters at breast height for the closest two trees at the point (n=2). Aboveground dry biomass (Mg ha^{-1}) is calculated using the USFS FIA tree volume and dry aboveground biomass equations for the United States [68].

Biomass equations share the basic form:

$$m = \text{Exp}(\beta_0 + \beta_1 * \text{lndbh})$$

where m represents stem biomass for an individual tree in kg. β_0 and β_1 are parameters derived from [68] and described in Table 1. dbh is the stem diameter at breast height (converted to cm) recorded in the survey notes. The biomass estimates are summed across both trees at a survey point and multiplied by the stem density calculated at that point to produce an estimate of aboveground biomass reported in Mg ha^{-1} [68].

Table 1. *Biomass parameters used for the calculation of biomass in the pre-settlement dataset(rounded for clarity).*

Jenkins Species Group	β_0	β_1	PalEON Taxa Included (Supp. 2)
Aspen, Alder, Poplar, Willow	-2.20	2.38	Poplar, Willow, Alder
Soft Maple, Birch	-1.91	2.36	Birch
Mixed Hardwood	-2.48	2.48	Ash, Elm, Maple, Basswood, Ironwood, Walnut, Hackberry, Cherries, Dogwood, Buckeye
Hard Maple, Oak, Hickory, Beech	-2.01	2.43	Oak, Hickory, Beech, Other Hardwood
Cedar and Larch	-2.03	2.26	Tamarack, Cedar
Fir and Hemlock	-2.54	2.43	Fir, Hemlock
Pine	-2.54	2.43	Pine
Spruce	-2.08	2.33	Spruce

Matching PLSS tree genera to the species groups defined by Jenkins *et al*. [68] is straightforward, placing the 22 genera used in this study into 9 allometric groups (Table 1).

However, all maples are assigned to the generic "Hardwood" group since separate allometric relationships exist for soft and hard maple (Table 1). Biomass estimates for "Non tree" survey points are assigned 0 Mg ha^{-1}.

We use the stem density thresholds of Anderson and Anderson [69] to discriminate prairie, savanna, and forest.

FIA Stem Density, Basal Area and Biomass

The United States Forest Service has monitored the nation's forests through the FIA Program since 1929, with an annualized state inventory system implemented in 1998 [70]. On average there is one permanent FIA plot per 2,428 ha of land in the United States classified as forested. Each FIA plot consists of four 7.2m fixed-radius subplots in which measurements are made of all trees >12.7cm dbh [70]. We used data from the most recent full plot inventory (2007-2011). The FIA plot inventory provides a median of 3 FIA plots per cell using the 64km^2 grid.

We calculated mean basal area (m^2 ha^{-1}), stem density (stems ha^{-1}), mean diameter at breast height (cm), and mean biomass (Mg ha^{-1}) for all live trees with dbh greater than 20.32cm (8in). Biomass calculations used the same set of allometric regression equations as for the PLSS data [68].

Gridding and Analysing PLSS and FIA Data

Spatial maps of stem density, basal area and biomass were generated by averaging all PLSS point or FIA plot estimates within a 64km^2 raster cell. Differences in sampling design between PLSS and FIA data combined with spatially structured forest heterogeneity will

affect the partitioning of within-cell versus between-cell variance, but not the expected estimates. Most 64km^2 cells have one or a few intensively sampled FIA plots. Therefore at this scale of aggregation, the low density of FIA plots in heterogeneous forests could result in high within-cell variance and high between-cell variability. For the PLSS plotless (point based) estimates, stem density estimates are sensitive to trees close to the plot center. Point-level estimates with very high stem densities can skew the rasterized values, and it is difficult to distinguish artifacts from locations truly characterized by high densities. To accommodate points with exceptionally high densities we carry all values through the analysis, but exclude the top 2.5 percentile when reporting means and standard deviations in our analysis. PLS-based estimates are highly variable from point to point due to the small sample size, but have low variance among 64 km^2 raster cells due to the uniform sampling pattern of the data. Thus within-cell variance is expected to be high for the PLSS point data, but spatial patterns are expected to be robust at the cell level. The base raster and all rasterized data are available as Supplement 3.

Standard statistical analysis of the gridded data, including correlations, paired t-tests and regression, was carried out in R [61], and is documented in supplementary material that includes a subset of the raw data to allow reproducibility. Analysis and presentation uses elements from the following R packages: `cluster` [71], `ggplot2` [72,73], `gridExtra` [74], `igraph` [75], `mgcv` [76], `plyr` [77], `raster` [78], `reshape2` [79], `rgdal` [62], `rgeos` [80], `sp` [81,82], and `spdep` [83].

We identify analogs and examine differences in composition between and within PLSS and FIA datasets using Bray-Curtis dissimilarity [84] for proportional composition within

raster cells using basal area measurements. For the analog analysis we are interested only in the minimum compositional distance between a focal cell and its nearest compositional (not spatial) neighbor. The distribution of compositional dissimilarities within datasets indicates forest heterogeneity within each time period, while the search for closest analogs between datasets indicates whether contemporary forests lack analogs in pre-settlement forests ('novel forests'), or vice versa ('lost forests'). For the analog analyses, we compute Bray-Curtis distance between each 64km^2 cell in either the FIA or the PLSS periods to all other cells within the other dataset (FIA to FIA, PLSS to PLSS), and between datasets (PLSS to FIA and FIA to PLS), retaining only the minimum. For within era analyses (FIA - FIA and PLSS - PLSS), cells were not allowed to match to themselves. We define vegetation classes for lost and novel forests using k-medoid clustering [71].

The differences in sampling design and scale between the PLSS and FIA datasets, described above, potentially affect between-era assessments of compositional similarity [47]. The effects of differences in scale should be strongest in regions where there are few FIA plots per 64 km^2 cell, or where within-cell heterogeneity is high. For the analog analyses, this effect should increase the compositional differences between the FIA and PLSS datasets. We test for the importance of this effect on our analog analyses via a sensitivity analysis in which we test whether dissimilarities between FIA and PLSS grid cells are affected by the number of PLSS plots per cell. We find a small effect, suggesting that our analyses are mainly sensitive to the compositional and structural processes operating on large spatial scales.

To understand the extent to which novelty operates at landscape scales we relate novelty to the distance to the nearest 'remnant' forest cell. Here we use a threshold of the 25%ile of compositional dissimilarity within the PLSS data, meaning the dissimilarity of any one 'remnant' cell is well within the historical bounds of dissimilarity. We use a general linear model with a quasibinomial family to relate the degree of novelty to the spatial distance to the nearest 'remnant' cell, and examine this relationship for four major forest types within the PLSS data (Oak savanna, Oak/Poplar savanna, Pine/Spruce forest and Maple/Cedar/Hemlock/Birch mixedwood forests). We expect that a weak relationship will indicate that forest recovery following landscape-scale land use change is moderated by a species pool culled from from small remnant patches, individual specimens, or local scale restoration efforts (for example during the 1930s). A significant relationship between distance to remant forest and novelty indicates that small patches have been insufficient to restore natural forest cover within the region, and would indicate that greater efforts are needed to restore landscapes at regional scales.

All datasets and analytic codes presented here are publicly available and open source at (http://github.com/PalEON-Project/WitnessTrees), with the goal of enabling further analyses of ecological patterns across the region and the effects of post-settlement land use on forest composition and structure. Data are also archived at the Long Term Ecological Research Network Data Portal (https://portal.lternet.edu/nis/home.jsp).

Results:

Data Standardization

The original PLSS dataset contains 490,818 corner points (excluding line and meander points), with 166,607 points from Wisconsin, 231,083 points from Minnesota and 93,095 points from Michigan. Standardizing data and accounting for potential outliers, described above, removed approximately 1.5% points from the dataset, yielding a final total of 366,993 points with estimates used in our analysis.

Rasterizing the PLSS dataset to the Albers 64km^2 grid produces 7,939 raster cells with data. Each cell contains between 1 and 94 corner points, with a mean of 61.8 (σ = 15) and a median of 67 corners (Supplement 3). Cells with a low number of points were mainly near water bodies or along political boundaries such as the Canadian/Minnesota border, or southern Minnesota and Wisconsin borders. Only 2.44% of cells have fewer than 10 points per cell.

Species assignments to genera were rarely problematic. Only 18 PLSS trees were assigned to the Unknown Tree category, representing less than 0.01% of all points. These unknown trees largely consisted of corner trees for which taxon could not be interpreted, but for which diameter and azimuth data was recorded. A further 0.011% of trees were assigned to the "Other hardwood" taxon (*e.g.*, hawthorn, "may cherry", and "white thorn").

For maple the class has very high within-genera specificity for a number of assignments. A total of 78478 trees are assigned to "Maple". Of these, surveyors do use common names that can be ascribed to the species level (e.g., *A. saccharum*, n = 56331), but a large number

of the remaining assignments are above the species level (n = 21356). This lack of specificity for a large number of records causes challenges in using the species level data. A similar pattern is found for pine, where many individual trees (125639) can be identified to the level of species (*P. strobus*, n = 41673; *P. banksiana*, n = 28784; *P. resinosa*, n = 28766), but there remains a large class of pine identified only at the genus level, or with unclear assignment (n = 17606).

For ash the data includes both attributions to black or brown ash (n=9312) and white ash (n = 2350), but again, also includes a large class of ash for which no distinction is made within the genera (n = 7423).

These patterns are repeated throughout the data. For spruce this within-genera confusion is even greater, with 50188 assignments to genera-level classes and only 20 to either black or white spruce.

Spatial Patterns of Settlement-Era Forest Composition: Taxa and PFTs

Stem Density, Basal Area and Biomass

The mean stem density for the region (Fig 2a) is 153 stems ha^{-1}. Stem density exclusive of prairie is 172 stems ha^{-1} and is 216 stems ha^{-1} when both prairie and savanna are excluded. The 95th percentile range is 0 - 423 stems ha^{-1}, and within-cell standard deviations between 0 and 441 stems ha^{-1}. Basal area in the domain (Fig 2c) has a 95th percentile range between 0 and 63.5 m^2 ha^{-1}, a mean of 22.2 m^2 ha^{-1}, within-cell standard deviations range from 0 to 76.7 m^2 ha^{-1}. Biomass ranges from 0 to 209 Mg ha^{-1} (Fig 2d), with cell level standard deviations between 0 and 569 Mg ha^{-1}. High within-cell standard deviations

relative to mean values within cells for density, basal area and biomass indicate high levels of heterogeneity within cells, as expected for the PLSS data, given its dispersed sampling design.

Fig 2. *Total stem density (a) in the Upper Midwest, along with forest type classification (b) based on PLSS data and the stem density thresholds defined by Anderson and Anderson [69]; Table 2). Fine lines represent major rivers. To a first order, basal area (c) and biomass (d) show similar patterns to stem density (but see* Fig 3*).*

In the PLSS data, stem density is lowest in the western and southwestern portions of the region, regions defined as prairie and savanna (Fig 2b, Table 2). When the Anderson and Anderson [69] stem density thresholds (<47 stems ha^{-1} for Savanna, Table 2) are used, the extent of area classified as savanna is roughly equivalent to prior reconstructions [22,85,86] (Fig 2b). The highest stem densities occur in north-central Minnesota and in north-eastern Wisconsin (Fig 2a), indicating younger forests and/or regions of lower forest productivity.

Table 2. *Forest classification scheme used in this paper for comparison between pre-settlement forests and the Haxeltine and Prentice [87] potential vegetation classes represented in Ramankutty and Foley [1]. Plant functional types (PFTs) for grasslands (CG, grassland; Non-Tree samples in the PLS), broad leafed deciduous taxa (BDT) and needleleaded evergreen taxa (NET) are used, but leaf area index used in Haxeltine and Prentice [87] is replaced by stem density classes from Anderson and Anderson [69].*

Forest Class	Haxeltine & Prentice Rules	Current Study

Prairie	Dominant PFT CG, LAI > 0.4	Stem dens. < 0.5 stem/ha
Savanna	Dominant PFT CG, LAI > 0.6	1 < Stem dens. < 47 stems ha^{-1}
Temperate Deciduous	Dominant PFT BDT, LAI > 2.5	Stem dens. > 48 stems ha^{-1}, BDT > 70% composition
Temperate Conifer	Dominant PFT (NET + NDT), LAI > 2.5	Stem dens. > 47 stems ha^{-1}, NET + NDT > 70% composition
Mixedwood	Both BDT (LAI > 1.5) & NET (LAI > 2.5) present	Stem dens. > 47 stems ha^{-1}, BDT & NET both < 70% composition

Forest structure during the settlement era can be understood in part by examining the ratio of stem density to biomass, a measure that incorporates both tree size and stocking. Regions in northern Minnesota and northwestern Wisconsin have low biomass and high stem densities (Fig 3, brown). This indicates the presence of young, small-diameter, even-aged stands, possibly due to frequent stand-replacing fire disturbance in the pre-EuroAmerican period or to poor edaphic conditions. Fire-originated vegetation is supported by co-location with fire-prone landscapes in Wisconsin [88]. High-density, low-biomass regions also have shallower soils, colder climate, and resulting lower productivity. High-biomass values relative to stem density (Fig 3, green) are found in Michigan and southern Wisconsin. These regions have higher proportions of deciduous species, with higher tree diameters than in northern Minnesota.

Fig 3. *The major forest types in the pre-settlement Upper Midwest. Five clusters are shown using k-medoid clustering. These clusters represent (b) the ratio between biomass and stem density as an indicator of forest structure. Regions with high stem density to biomass ratios*

(brown) indicate dense stands of smaller trees, while regions with low stem density to biomass ratios (green) indicate larger trees with wider spacings.

Taxon composition within settlement-era forests is spatially structured along dominant gradients from south to north (deciduous dominated to conifer dominated forests) and from east to west (mixed wood forests to open prairie) (Fig 4). Oak is dominant in the south of the region, with an average composition of 21%, however, that proportion drops to 8% when only forested cells (cells with stem density > 48 stems/ha) are considered, due to its prevalence as a monotypic dominant in the savanna and prairie. Pine shows the opposite trend, with average composition of 14% and 17% in unforested and forested cells respectively. Pine distributions represent three dominant taxa, *Pinus strobus*, *Pinus resinosa* and *Pinus banksiana*. These three species have overlapping but ecologically dissimilar distributions, occuring in close proximity in some regions, such as central Wisconsin, and are typically associated with sandy soils with low water availability. Other taxa with high average composition in forested cells include maple (10%), birch (10%), tamarack (9%) and hemlock (8%).

Fig 4. *Forest composition (%) for the 15 most abundant tree taxa. The scale is drawn using a square-root transform to emphasize low abundances. Shading of the bar above individual taxon maps indicates plant functional type assignments (dark gray: needleleafed deciduous; light gray: needleleafed evergreen; white: broadleafed deciduous).*

For a number of taxa, proportions are linked to the total basal area within the cell. For 4 taxa - hemlock, birch, maple and cedar - taxon proportions are positively related to total basal area. For 17 taxa including oak, ironwood, poplar, tamarack and elm, high

589 proportions are strongly associated with lower basal areas (Figures 3 and 5). This suggests
590 that hemlock, birch, maple and cedar occurred in well-stocked forests, with higher average
591 dbh. These taxa are most common in Michigan and in upper Wisconsin. Taxa with negative
592 relationships to total basal area (*e.g.*, spruce and tamarack) are more common in the
593 northwestern part of the domain.

594 Spruce in the PLSS represents two species (*Picea glauca*, *Picea mariana*) with overlapping
595 distributions, but complex site preferences that vary in space. *P. glauca* is generally
596 associated with dry upland to wet-mesic sites, while *P. mariana* is associated with hydric
597 sites, but *P. mariana* also frequently occupies upland sites in northern Minnesota. Both
598 cedar (*Thuja occidentalis*) and fir (*Abies balsamea*) are mono-specific genera in this region.

599 Northern hardwoods, such as yellow birch and sugar maple, and beech, are much less
600 common in the lower peninsula of Michigan, and southern Wisconsin, except along Lake
601 Michigan. Birch has extensive cover in the north, likely reflecting high pre-settlement
602 proportions of yellow birch (*Betula alleghaniensis*) on mesic soils, and paper birch on sandy
603 fire-prone soils and in northern Minnesota (birch proportions reach upwards of 34.1% in
604 northeastern Minnesota). Hardwoods in the southwest, such as oak, elm, ironwood and
605 basswood, are most typically mono-specific groupings, with the exception of oak, which
606 comprises 7 species (see Supplement 2). Hardwoods in the southwest are located primarily
607 along the savanna and southern forest margins, or in the southern temperate deciduous
608 forests. Finally, maple and poplar (aspen) have a broad regional distribution, occupying
609 nearly the entire wooded domain. Poplar comprises four species in the region, while maple
610 comprises five species (Supplement 2). Both hardwood classes, those limited to the

611 southern portions of the region, and those with distributions across the domain,
612 correspond to well-defined vegetation patterns for the region [85].

613 These individual species distributions result in a mosaic of forest classes accross the region
614 (Fig 5). The dominant class is the Hemlock/Cedar/Birch/Maple assemblage in northern
615 Wisconsin, and upper Michigan (Fig 5, yellow). This mixedwood assemblage is interspersed
616 by both Pine dominated landscapes (Fig 5, orange) and, to a lesser degree, the softwood
617 assemblage Tamarack/Pine/Spruce/Poplar (Fig 5, green), which dominates in north-
618 eastern Minnesota. The softwood assemblage is itself interspersed with Pine dominated
619 landscapes, and grades into a mixed-hardwood assemblage of
620 Oak/Poplar/Basswood/Maple (Fig 5, light purple) to the west. Thismixed- softwood forest
621 assemblage grades south into mono-specific Oak savanna (Fig 5, dark blue).

622 **Fig 5**. *The five dominant forest types in the Upper Midwest as defined by k-medoid clustering.*
623 *Forest types (from largest to smallest) include Hemlock/Cedar/Birch/Maple (yellow),*
624 *Oak/Poplar/Basswood/Maple (light purple), Tamarack/Pine/Spruce/Poplar (light green),*
625 *Oak Savanna (dark purple) and Pine (orange). These forest types represent meso-scale*
626 *(64km^2) forest associations, rather than local-scale associations.*

627 The broad distributions of most plant functional types results in patterns within individual
628 PFTs that are dissimilar to the forest cover classes (Fig 5). Thus overlap among PFT
629 distributions (Fig 6) emerges from the changing composition within the plant functional
630 type from deciduous broadleaved species associated with the southern, deciduous
631 dominated region, to broadleafed deciduous species associated with more northern regions
632 in the upper Midwest.

Fig 6. *Proportional distribution of Plant Functional Types (PFTs) in the upper Midwest from PLSS data, for broadleaved deciduous trees (BDT), needleleaved deciduous trees (NDT), and needleleaved evergreen trees (NET). Distributions are shown as proportions relative to total basal area, total biomass, and composition (*Fig 2*). The grassland PFT is mapped onto non-tree cells with the assumption that if trees were available surveyors would have sampled them.*

Structural Changes Between PLSS and FIA Forests

By cell, modern forests (FIA) have higher stem densities (146 stems ha^{-1}, $t_{1,5177} = 51.8$, $p < 0.01$) than PLSS forests, but slightly lower basal areas (-4.5 m^2 ha^{-1}, $t_{1,5177} = -16.4$, $p < 0.01$) and lower biomass (-8.72 Mg ha^{-1}, $t_{1,5177} = -6.55$, $p < 0.01$) (Fig 7). We use only point pairs where both FIA and PLSS data occur since non-forested regions are excluded from the FIA and as such cannot be directly compared with PLS estimates. The similarity in biomass despite lower stem density and total basal area in the PLSS data is surprising. Two likely factors are shifts in allometric scaling associated with changes in species composition, or a higher mean diameter of PLSS trees (Fig 7d). Total biomass was 45,080 Mg higher in the PLSS when summed across all cells coincident between the FIA and PLSS.

Fig 7. *The relationship between (a) average stem density, (b) total basal area and (c) biomass values in the PLSS and FIA datasets. Stem density and total basal area are higher in the FIA than in the PLS, however average cell biomass is higher in the PLSS. A 1:1 line has been added to panels a-c to indicate equality.*

653 The PLSS has a lower overall mean diameter than the FIA (δ_{diam} = -2.9 cm, 95%CI from -
654 17.3 to 8.18cm). FIA diameters are higher than PLSS diameters in the northwestern parts
655 of the domain (on average 6.47 cm higher), overlapping almost exactly with regions where
656 we have shown low biomass-high density stands (Fig 3). At the same time, regions with
657 high biomass and low density stands, in northeastern Wisconsin, and the Upper and Lower
658 Peninsulas of Michigan, had higher average diameters during the PLSS than in the FIA, on
659 average 3.65 cm higher. Thus we are seeing an overal increase in tree size in the sub-boreal
660 region and a decrease in temperate mixedwood forests, where we find tree species with
661 much higher dbh:biomass ratios [68]. This is coupled with declining variance in dbh across
662 the domain (from within cell variance of 37.9 cm the PLSS to 30.7 cm in the FIA). Thus, the
663 mechanism by which low density and basal area produce roughly equivalent biomass
664 estimates between the FIA and PLSS is likely due to the differential impacts of land
665 clearence and subesequent forest management in the south east vs the northwest. The loss
666 of high biomass southern hardwood forests is balanced by higher biomass in the northeast
667 due to fire suppression and regeneration of hardwoods in the northwest. Declining
668 diameters from the PLSS to FIA are most strongly associated with higher abundances of
669 poplar, ironwood and oak, while declining diameters are associated with maple and
670 hemlock, further supporting the assertion that much of the loss in diameter, and,
671 subsequently biomass, is occuring in southeastern mixedwood/hardwood forest, while
672 diameter and biomass increases are occuring in the northwest.

673 Differences between FIA and PLSS data in sampling design are unlikely to be a factor for
674 most measures (see below); these differences are expected to affect how these datasets
675 sample local- to landscape-scale heterogeneity, but should not affect the overall trends

between datasets. Differences in variability introduce noise into the relationship, but given the large number of samples used here, the trends should be robust.

Compositional Changes Between PLSS and FIA Forests: Novel and Lost Forests

Both the PLS- and FIA-era compositional data show similar patterns of within-dataset dissimilarity, with the highest dissimilarities found in central Minnesota and northwestern Wisconsin. High within-PLSS dissimilarities are associated with high proportions of maple, birch and fir while high within-FIA dissimilarities are associated with high proportions of hemlock, cedar and fir. Dissimilarity values in the FIA dataset are less spatially structured than in the PLSS. Moran's I for dissimilarities within the FIA ($I_{FIA} = 0.198$, $p < 0.001$) are lower than the dissimilarities within the PLSS ($I_{PLSS} = 0.496$, $p < 0.001$), suggesting lower spatial autocorrelation in the FIA dataset. Cells with identical pairs represent 5.6% of the PLSS cells and 7.44% of FIA cells. Identical cells in the PLSS are largely located along the southern margin and most (69.5%) are composed entirely of oak. Cells in the FIA with identical neighbors are composed of either pure oak (19.4%), pure poplar (26%) or pure ash (14%).

There is a small but significant positive relationship ($F_{1,5964} = 920$, $p < 0.001$) between the number of FIA plots and within-FIA dissimilarity. The relationship accounts for 13% of total variance and estimates an increase of $\delta_d = 0.0134$ for every FIA plot within a cell. This increase represents only 3.08% of the total range of dissimilarity values for the FIA data. There is a gradient of species richness that is co-linear with the number of FIA plots within a cell, where plot number increases from open forest in the south-west to closed canopy, mixed forest in the Upper Peninsula of Michigan. Hence, differences in within- and

698 between-cell variability between the PLSS and FIA datasets seem to have only a minor
699 effect on these regional-scale dissimilarity analyses.

700 We define no-analog communities as those whose nearest neighbour is beyond the 95%ile
701 for dissimilarities within a particular dataset. In the PLSS dataset, forests that have no
702 modern analogs are defined as "lost forests", while forest types in the FIA with no past
703 analogs are defined as "novel forests". More than 25% of PLSS sites have no analog in the
704 FIA dataset ('lost forests'; PLS-FIA dissimilarity, Fig 8c), while 29% of FIA sites have no
705 analog in the PLSS data ('novel forests'; FIA-PLSS dissimilarity, Fig 8d). Lost forests show
706 strong spatial coherence, centered on the "Tension Zone" [85], the ecotone between
707 deciduous forests and hemlock-dominated mixed forest (Fig 4).

708 **Fig 8**. *Minimum dissimilarity maps. Distributions of minimum (within dataset) dissimilarities*
709 *during the PLSS (a) and FIA (b) show spatially structured patterns of dissimilarity, with*
710 *stronger spatial coherence for the PLS. Lost forests (c) show strong compositional and spatial*
711 *coherence, and have more taxa with percent composition > 10% than within Novel forests*
712 *during the FIA era (d).*

713 Lost forests are drawn from across the domain, and show strong ecological and spatial
714 coherence (Fig 8c). Forest classes generally fall into five classes: Tamarack-Pine-Birch-
715 Spruce-Poplar accounts for 28.8% of all lost forests and 7.97% of the total region. This
716 forest type is largely found in north eastern Minnesota, extending southward to central
717 Minnesota, into Wisconsin and along the Upper Peninsula of Michigan, as well as in
718 scattered locations on the Lower Peninsula of Michigan (Fig 8c). This forest likely
719 represents a mesic to hydric forest assemblage, particularly further eastward. Modern

forests spatially overlapping this lost type are largely composed of poplar ($\overline{x}_{FIA}$ = 12%) and oak ($\overline{x}_{FIA}$ = 12%). Tamarack in these forests has declined significantly, from 23% to only 5% in the FIA, while Poplar has increased from 10% to 22%, resulting in forests that look less mesic and more like early seral forests.

Cedar/juniper-Hemlock-Pine accounts for 19.8% of all lost forests and 5.49% of the total region. This forest type is found largely in northeastern Wisconsin, and the Upper and Lower Peninsulas of Michigan. This lost forest type has been predominantly replaced by maple, poplar, and pine, retaining relatively high levels of cedar ($\overline{x}_{PLS}$ = 19%; $\overline{x}_{FIA}$ = 14%). The loss of hemlock is widespread across the region, but particularly within this forest type, declining to only 3% from a pre-settlement average of 18%.

Elm-Oak-Basswood-Ironwood accounts for 19.6% of all lost forests and 5.42% of the total region. The region is centered largely within savanna and prairie-forest margins, both in south-central Minnesota and in eastern Wisconsin, but, is largely absent from savanna in the Driftless area of southwestern Wisconsin. These forests were historically elm dominated ($\overline{x}_{PLS}$ = 25%), not oak dominated savanna, as elsewhere (particularly in the Driftless). Modern forests replacing these stands are dominated by oak and ash, with strong components of maple, and basswood. Elm has declined strongly in modern forests ($\overline{x}_{FIA}$ = 1%), possibly in part due to Dutch Elm Disease and land use. The increase in ash in these forests is substantial, from $\overline{x}_{PLS}$ = 5% to $\overline{x}_{FIA}$ = 15%.

Hemlock-Birch-Maple-Pine accounts for 19.2% of all lost forests and 5.33% of the total region. This forest type, dominant in north central Wisconsin, was dominated by hemlock ($\underline{x}_{PLS}$ = 26%) and what was likely late seral yellow birch ($\overline{x}_{PLS}$ = 24%), replaced largely by

742 maple (from $\overline{x}_{PLS}$ = 12% to $\overline{x}_{FIA}$ = 27%). Poplar increases from 1% to 13% in the FIA, again
743 indicating a shift to earlier seral forests in the FIA. Hemlock is almost entirely lost from the
744 forests, declining from 26% to 4% in the FIA.

745 Lastly, Beech-Maple-Hemlock accounts for 12.6% of all lost forests and 3.49% of the total
746 region. This forest type is found exclusively on the central, western shore of Lake Michigan
747 and in the Lower Peninsula, in part due to the limited geographic range of Beech in the
748 PLSS dataset (Fig 4). Beech is almost entirely excluded from the modern forests in this
749 region, declining from $\overline{x}_{PLS}$ = 37% to $\overline{x}_{FIA}$ = 4%. Pine in the region increases from 9% to
750 16%, while maple, the dominant taxa in the modern forests, increases from 16 - 25%.

751 On average lost forests contain higher proportions of ironwood (r = 0.203), beech (r = 0.2),
752 birch (r = 0.189) and hemlock (r = 0.188) than the average PLSS forest, and lower
753 proportions of oak (r = -0.28), poplar (r = -0.145), and pine (r = -0.107).

754 The distribution of novel ecosystems (Fig 8d) is spatially diffuse relative to the lost forest of
755 the PLSS and the forest types tend to have fewer co-dominant taxa. FIA novel forest types
756 also have a more uneven distribution in proportion than the PLSS lost forests. Overall,
757 novel forests are associated with higher proportions of maple (r = 0.02), ash (r = 0.03) and
758 basswood (r = -0.04), although basswood is dominant in only one forest type (Poplar-
759 Cedar/juniper-Maple). Novel forests are associated with lower proportions of oak (r = -
760 0.28), and pine (r = -0.11). This analysis suggests that the loss of particular forest types
761 associated with post-settlement land use was concentrated in mesic deciduous forests and
762 the ecotonal transition between southern and northern hardwood forests, while the gains
763 in novelty were more dispersed, resulting from an overall decline in seral age.

By far the largest novel forest type is Maple, which accounts for 37.2% of all novel forests and 2.68% of the total region. As with all novel forest types, this forest type is broadly distributed across the region. This forest type is associated with co-dominant maple ($\overline{x}_{FIA}$ = 23%) and ash ($\overline{x}_{FIA}$ = 22%). Hemlock has declined significantly across this forest type, from $\overline{x}_{PLS}$ = 24% to $\overline{x}_{FIA}$ = 4%.

Poplar-Cedar/juniper-Maple, accounts for 28.8% of all novel forests and 2.08% of the total region. The broad distributiof these novel forests makes assigning a past forest type more difficult than for the PLSS lost forests, the distribution replaces two classes of past forest, one dominated by oak, in southern Wisconsin and Minnesota, the other by mixed hemlock, beech, birch and cedar forests.

Pine-Cedar/juniper-Poplar-Maple forest accounts for 16.3% of all novel forests and 1.17% of the total region. This forest type is again broadly distributed, and is widely distributed across the region, representing a homogenous, early seral forest type, likely associated with more mesic sites. Oak forest accounts for 13.3% of all novel forests and 0.96% of the total region. This grouping again shows a pattern of broad distribution across the region, associated with cedar/juniper percentages near 40%, with smaller components of poplar (14%) and maple (13%).

Spatial Correlates of Novelty

Modern compositional dissimilarity from the PLSS data is related to distance from 'remnant' forest. The dissimilarity quantile of FIA-PLSS distances increases with increasing distance to remnant cells. While it is difficult to quantify exactly what is meant by remnant, given the strong compositional variability within the PLSS dataset, we use the 25%ile

786 quantile of within dataset nearest-neighbor disimilarities for the PLSS as a useful indicator.
787 Results are robust to higher levels of dissimilarity, up to the 90%ile. Using the 25%ile for
788 within PLSS dissimilarity, approximately 67% of FIA cells can be classed as 'remnant'
789 forest. The mean distance to remnant forests for cells with dissimilarities above the 25%ile
790 is 17.7 km, higher than the mean of ~9.6km expected if each 8x8km cell had at least one
791 adjacent 'remnant' cell.

792 **Table 3**. *Spatial distance to FIA-PLS novelty - modeled as a binomial - from remnant forests*
793 *(forests within the first 25th percentile of nearest neighbor distances). The Null model is*
794 *based on the mean minimum and maximum distance to novelty based on bootstrapped*
795 *models (n=100) where quantiles are resampled with replacement.*

Zone	Min (modeled)	Max (modeled)	Min (Null)	Max (Null)
Tamarack	29	43	11	14
Northern Oak	23	33	14	20
Pine	32	56	10	12
Hemlock	0	undef.	11	13
Oak Savanna	17	23	13	18

796 The GLM shows that distance from remnant forests in the FIA is significantly related to the
797 dissimilarity quantile for FIA data ($\chi_{1,4}$=623, $p < 0.001$). The mean distance to novelty
798 varies by PLSS forest type, but is between approximately 20 and 60km for the four forest
799 types examined here (Fig 9), while the null model would predict a distance of 10 - 20km,
800 Table 3). This model appears to show spatial coherence in the structure of forest loss and

801 the gain in novelty. Novel forests are generally further from remnant patches than expected
802 in the null model.

803 **Fig 9**. *The model relating novelty to spatial distance from remnant forest. Here the 25%ile is*
804 *used to indicate remnant forest, and the 95%ile is defined as novelty. We use a binomial*
805 *regression to predict novelty, the red dashed line indicates a response greater than 0.5. The*
806 *curves represent the relationship between spatial distance and compositional dissimilarity for*
807 *each of the five major historic forest types (Fig 5) defined here as Oak Savanna (blue),*
808 *Oak/Poplar/Basswood/Maple (light purple), Tamarack/Pine/Spruce/Poplar (green),*
809 *Hemlock/Cedar/Birch/Maple (yellow) and Pine (orange).*

810 Critically, we see that the Hemlock/Cedar/Birch/Maple forest class (Fig 5 & 10b, yellow),
811 appearing as a flat line, predicts novelty continuously, from distance 0. This is in part due to
812 the very small proporion of Hemlock cells that are considered residual (only 63 of 1780
813 cells in the Hemlock zone are considered remnant) and the very high proportion of novel
814 cells in the zone (923 of 1780 cells, or 52% of all cells).

815 Oak Savanna is the most similar to its null model, with a confidence interval that overlaps
816 slightly with the null expectation (Table 3). Northern softwood forests
817 (Tamarack/Pine/Spruce/Poplar, Fig 5, yellow) reach novelty at between 29 and 43km,
818 northern Oak forests (Oak/Poplar/Basswood/Maple; Fig 5, light purple) reach novelty at
819 23 - 33 km, slightly higher than the 14 - 19km predicted by the null model. Pine forests (Fig
820 5, orange) are three times further than expected by the null, at 32 - 56km (Table 3).

Compositional Changes Between PLSS and FIA Forests: Ecotone Structure

To understand how the ecotonal structure has been transformed by post-settlement land use, we constructed two transects of the FIA and PLSS data (Fig 10a), and fitted GAM models to genus abundances along these transects. Transect One (T1) runs from northern prairie (in northern Minnesota) to southern deciduous savanna in southeastern Wisconsin (left to right in Figures 11c-f), while Transect Two (T2) runs from southern prairie in southwestern Minnesota to northern mixedwood forest in the Upper Peninsula of Michigan (left to right in Figures 11g-j). In general, these transect analyses show: 1) significant differences in ecotonal structure between the present and pre-settlement, and 2) steeper ecotones in the past and more diffuse ecotones today.

Fig 10. *Transects (a) across the region show clear changes in the ecotonal strength. Transect One shows shifts in broad-leafed taxon distributions from the PLSS to FIA (b and c) and in needle-leafed distributions (d and e). Transect Two broadleaf (f and g) and needleleaf (h and i) taxa show shifts that again appear to represent regional scale homogenization. Ecotones in the pre-settlement era were stronger in the past than they are in the present. Fitted curves represent smoothed estimates across the transects using Generalized Additive Models using a beta family.*

For T1, GAM models show significant differences (using AIC) between time periods in curves for all broadleafed taxa (Fig 10b & c) and for al needleleafed taxa (Figures 10d and e). The PLSS curves show a rapid transition in the northwest from oak to poplar dominated open forest that then transitions to a needleleafed forest composed of pine, spruce and tamarack, with high proportions of tamarack grading to pine further to the south east.

Tamarack and poplar proportions decline gradually from the east, being replaced first by pine, then briefly by maple and birch, and then. ultimately by oak as the transect grades into oak savanna. In the FIA dataset oak and poplar in the northwest appears to decline simultaneously, grading into needleleafed forests that are absent from the FIA dataset in the first 100km along the transect. While the PLSS transect shows distinct vegetation types in the central partof the transect, the FIA shows relatively constant proportions of oak, pine, spruce, poplar and maple before pine, oak and elm increase in the southeastern portions of the transect.

The second transect shows a similar pattern, with well defined ecotones in the pre-settlement period(Fig 10f and h), that are largely absent from the FIA data (Fig 10g and i). Oak forest, with a component of elm and poplar in the southwest grades slowly to a rapid transition zone where pine, elm, maple (first), then rapidly birch, hemlock and tamarack, and later, spruce, increase. This region, the Tension Zone, extends from 3×10^5 to 4.5×10^5 meters East, eventually becoming a forest that shows co-dominance between birch, pine, maple, spruce and tamarack, likely reflecting some local variability as a result of topographic and hydrological factors. Missing data at the beginning of the FIA transect reflects a lack of FIA plots in unforested regions in the west

Contemporary forests show broader homogenization and increased heterogeneity (evidenced by the lower within-FIA Moran's I estimates for near-neighbor distances) at a local scale in the region. Homogenization is evident across T1, where Bray-Curtis dissimilarity between adjacent cells declines from the PLSS to the FIA ($\delta_{beta} = -0.22$, $t_{113} = -7.93$, $p<0.001$), mirroring declines in the pine barrens between the 1950s and the present

865 [18]. The PLSS shows strong differentiation in the central region of T2 where maple-pine-
866 oak shifts to pine-poplar-birch forest (Fig 10d). This sharp ecotone is not apparent in the
867 FIA data, which shows gradual and blurred changes in species composition across the
868 ecotone (Fig 10i). β-diversity along T2 is lower in the FIA than in the PLSS (δ_{beta} = -0.19,
869 t_{65}=-7.34, p < 0.01), indicating higher heterogeneity in the PLSS data at the 64 km^2 meso-
870 scale.

871 Across the entire domain, β diversity is lower in the FIA than in the PLSS (δ_{β} = -0.172, $t_{1.3e7}$
872 = 2480, p <0.001), lending support to the hypothesis of overall homogenization. Differences
873 in sampling design between PLSS and FIA data cannot explain this homogenzation, since its
874 effect would have been expected to increase β-diversity along linear transects and at larger
875 spatial scales.

876 ## Discussion

877 Many forests of the PLS, are no longer a part of the modern landscape. Forest types have
878 been lost at the 64 km^2 mesoscale, and new forest types have been gained. The joint
879 controls of broad-scale climatic structuring and local hydrology on forest composition and
880 density can be seen in the pre-settlement forests, particularly along the Minnesota River in
881 south-western Minnesota, where a corridor of savanna was sustained in a region mostly
882 occupied by prairie (Fig 2b), but ecotones in the modern forest composition data are
883 weaker now than in the past (Fig 10), with clear signs of increased homogenization at local
884 and regional scales and decreased spatial structure in vegetation assemblages (Fig 8).

885 The loss of ecotones in the upper Midwestern United States suggests that our ability to
886 predict the abiotic controls on species distributions at the landscape scale may be weaker
887 than in the past, reducing the influence of variables such as climate or edaphic factors, and
888 increasing the relative influence of recent land use history. Work in eastern North America
889 suggests the utility of including spatial structure in species distribution models to improve
890 predictive ability [89]. The spatial random effects may improve models by capturing
891 missing covariates within SDMs [89], but if recent land use history has strongly shaped
892 species distributions, or co-occurence, then the spatial effect is likely to be non-stationary
893 at longer temporal scales. Given the implicit assumption of stationarity in many ecological
894 models [21], the need for longer time-scale observations, or multiple baselines from which
895 to build our distributional models becomes critical if we are to avoid conflating recent land
896 use effects with the long term ecological processes structuring the landscape.

897 Decreased β diversity along regional transects indicates homogenization at meso-scales of
898 100s of km^2, while the overall reduction in Moran's I for dissimilarity in the FIA indicates a
899 regional reduction in heterogeneity on the scale of 1000s of km^2. The selective loss or
900 weakening of major vegetation ecotones, particularly in central Wisconsin, and the
901 development of novel species assemblages across the region. These changes are the result
902 of land use, both agricultural and logging, but affect forests in contrasting ways across the
903 domain. Maple has become one of the most dominant taxa across the region, while in
904 northern Minnesota, forest biomass has increased and species shifts have reflected
905 increases in poplar and pine, while in southern Wisconsin, biomass has declined, and
906 hemlock has been lost almost completely.

907 Anthropogenic shifts in forest composition over decades and centuries seen here and
908 elsewhere [2,48] are embedded within a set of interacting systems that operate on multiple
909 scales of space and time [90]. Combining regional historical baselines, long term ecological
910 studies and high frequency analyses can reveal complex responses to climate change at
911 local and regional scales [91]. Estimates of pre-settlement forest composition and structure
912 are critical to understanding the processes that govern forest dynamics because they
913 represent a snapshot of the landscape prior to major EuroAmerican land-use conversion
914 [38,52]. Pre-settlement vegetation provides an opportunity to test forest-climate
915 relationships prior to land-use conversion and to test dynamic vegetation models in a data
916 assimilation framework [92]. For these reason, the widespread loss of regional forest
917 associations common in the PLSS (Fig 8d), and the rapid rise of novel forest assemblages
918 (Fig 8e) have important implications for our ability to understand ecological responses to
919 changing climate. The loss of historical forest types implies that the modern understanding
920 of forest cover, climate relationships, realized and potential niches and species associations
921 may be strongly biased in this region, even though 29% of the total regional cover is novel
922 relative to forests only two centuries ago.

923 Beyond shifts in composition at a meso-scale, the broader shifts in ecotones can strongly
924 impact models of species responses and co-occurence on the landscape. For example, the
925 heterogeneity, distribution, and control of savanna-forest boundaries [93] is of particular
926 interest to ecologists and modelers given the ecological implications of current woody
927 encroachment on savanna ecosystems [94]. Declines in landscape heterogeneity may also
928 strongly affect ecosystem models, and predictions of future change. Our data show higher
929 levels of vegetation heterogeneity at mesoscales during the pre-settlement era, and greater

930 fine scaled turnover along transects. Lower β diversity shown here and elsewhere [18]
931 indicate increasing homogeneity at a very large spatial scale, and the loss of resolution
932 along major historical ecotones.

933 This study also points to the need for a deeper understanding of some of the landscape-
934 and regional-scale drivers of novelty, given the likely role for climatic and land use change
935 (including land abandonment) to continue to drive ecological novelty [95,96]. In particular
936 the role of regional species pools and remnant patches of forest in driving or mitigating
937 compositional novelty. This work shows that the baseline forest type, and its structure on
938 the landscape moderates the degree to which landscape scale patterns can drive
939 compositional novelty. To some degree relationships between compositional novelty and
940 distance from remnant patches may be dependent on the simplicity or complexity of the
941 species pool and the sensitivity of dissimilarity metrics to β diversity [97]. Our results
942 indicate that diversity alone cannot be the driving factor in determining post-settlement
943 dissimilarity (and novelty), since all forest classes show this pattern of change.

944 Both Pine and the Oak/Poplar/Basswood/Maple forest types are the most fragmented
945 across the region. There is strong evidence that in some locations pine forests have
946 persisted over very long timescales in the region [98], although there is also evidence, in
947 other regions, that these states may shift strongly in response to interactions between
948 landscape level processes such as fire and geophysical features [99]. Thus complex
949 interactions between landscape scale processes, whether they be fire, land use change, or
950 geophysical features, and the species assemblages themselves, point to the difficulty in
951 making simplifying assumptions about species assemblages. Caution in simplifying species

assignments, whether they be plant functional types, species richness, or phylogenetic metrics, is neccessary since this region is dominated by forests that respond very differently to the settlement-era (and pre-settlement) disturbance, but that are composed of different species of the same genera and plant functional type. This caution is clearly warranted since recent ecosystem model benchmarking using pre-settlement vegetation has shown significant mismatch between climate representations of plant functional types across a range of ecosystem models, with no model accurately representing the true climate space of plant functional types in the northeastern upper Midwestern United States [100].

The analysis relating to the distance-to-novelty (Fig 9) points to the possibility that landscape-scale restoriation has high likelihood of success if local-scale restoration focuses on sites where restoration potential is high, as suggested for Hemlock/Cedar/Birch/Maple forests in northern Wisconsin [86]. If some of the novelty is driven by depauparate species pools beyond certain threshold distances from remnant forests then it should also be possible to restore these forest at a regional scale through the translocation of key species [101]. This work is supported by a number of other studies at smaller scales [102–104], for example, the presence of white pine in mesic sites during the PLS era has been attributed to its presence as a seed source on marginal sites at scales of of hundreds of meters [105]. Computer simulations [106] show that seed source distribution can affect community composition over hundreds of years at large spatial scales in a region spatially coincident with this current study. Thus land use change has significantly altered the landscape, both by "resetting" the sucessional clock, but also, because of the extent of change, by impacting

974 the regional species pool and seed source for re-establishing forests that are
975 compositionally similar to pre-settlement forests.

976 Methodological advances of the current work include 1) the systematic standardization of
977 PLSS data to enable mapping at broad spatial extent and high spatial resolution, 2) the use
978 of spatially varying correction factors to accommodate variations among surveyors in
979 sampling design, and 3) parallel analysis of FIA datasets to enable comparisons of forest
980 composition and structure between contemporary and historical time periods. This
981 approach is currently being extended to TPS and PLSS datasets across the north-central
982 and northeastern US, with the goal of providing consistent reconstructions of forest
983 composition and structure for northeastern US forests at the time of EuroAmerican forests.

984 Our results support the consensus that robust estimates of pre-settlement forest
985 composition and structure can be obtained from PLSS data [39,44,46,107,108]. Patterns of
986 density, basal area and biomass are roughly equivalent to previous estimates [16,19]. Our
987 results for stem density are lower than those estimated by Hanberrry *et al*. [17] for eastern
988 Minnesota, but density and basal area are similar to those in the northern Lower Peninsula
989 of Michigan [109] and biomass estimates are in line with estimates of aboveground carbon
990 for Wisconsin [19].

991 These maps of settlement-era forest composition and structure can also provide a useful
992 calibration dataset for pollen-based vegetation reconstructions for time periods prior to
993 the historic record. Many papers have used calibration datasets comprised of modern
994 pollen samples to build transfer functions for inferring past climates and vegetation from
995 fossil pollen records [110–113]. However, modern pollen datasets are potentially

confounded by recent land use, which can alter paleoclimatic reconstructions using pollen data [112]. By linking pollen and vegetation at modern and historical periods we develop capacity to provide compositional datasets at broader spatio-temporal scales, providing more data for model validation and improvement. Ultimately, it should be possible to assimilate these empirical reconstructions of past vegetation with dynamic vegetation models in order to infer forest composition and biomass during past climate changes. Data assimilation, however, requires assessment of observational and model uncertainty in the data sources used for data assimilation. Spatiotemporal models of uncertainty are being developed for the compositional data [63] and biomass data (Feng *et al*. in prep.).

Ultimately the pre-settlement vegetation data present an opportunity to develop and refine statistical and mechanistic models of terrestrial vegetation that can take multiple structural and compositional forest attributes into account. The future development of uncertainty estimates for the data remains an opportunity that can help integrate pre-settlement estimates of composition and structure into a data assimilation framework to build more complete and more accurate reconstructions of past vegetation dynamics, and to help improve predictions of future vegetation under global change scenarios.

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Figure1_Domain

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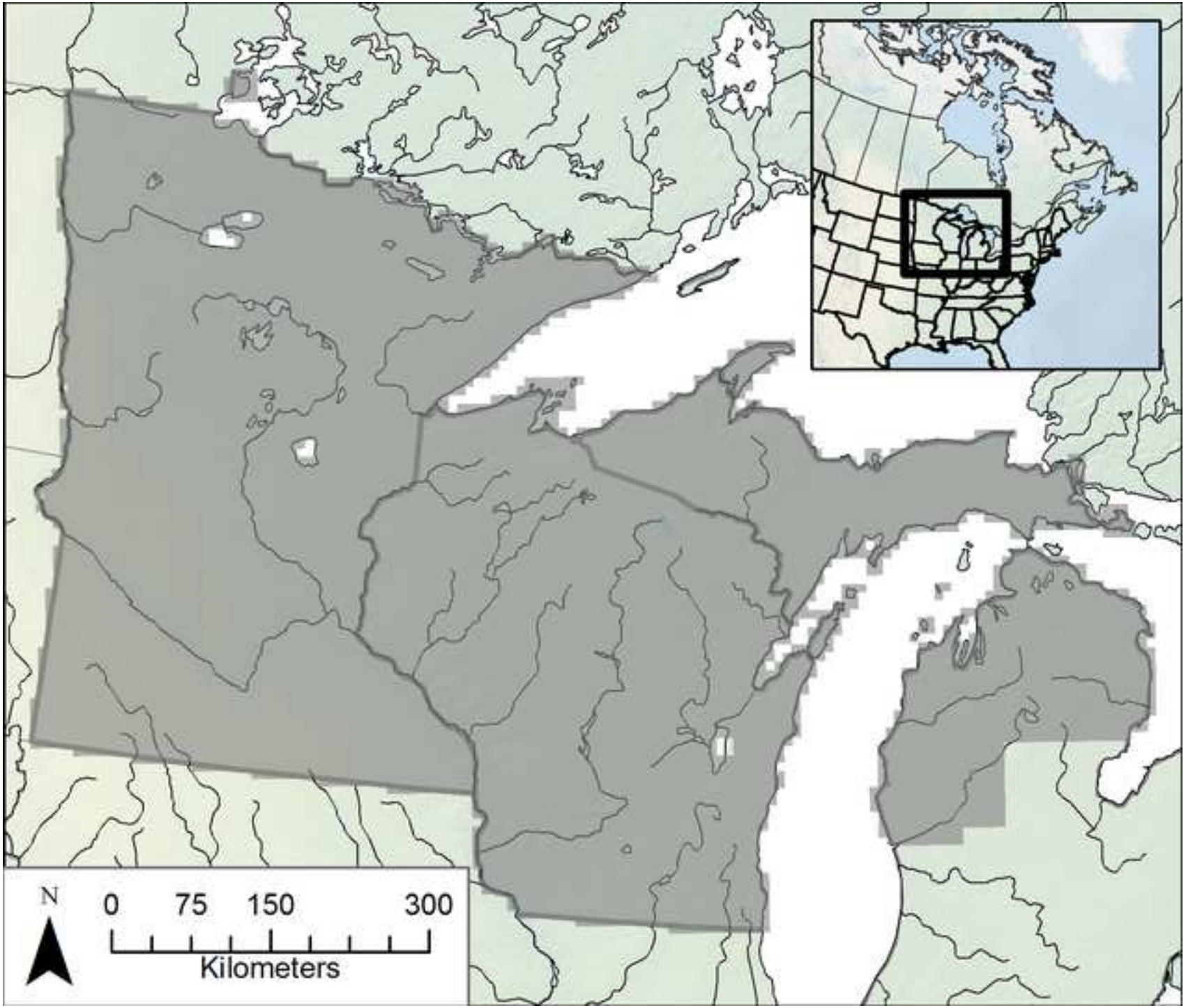

Figure2_DensityBasalAreaBiomass
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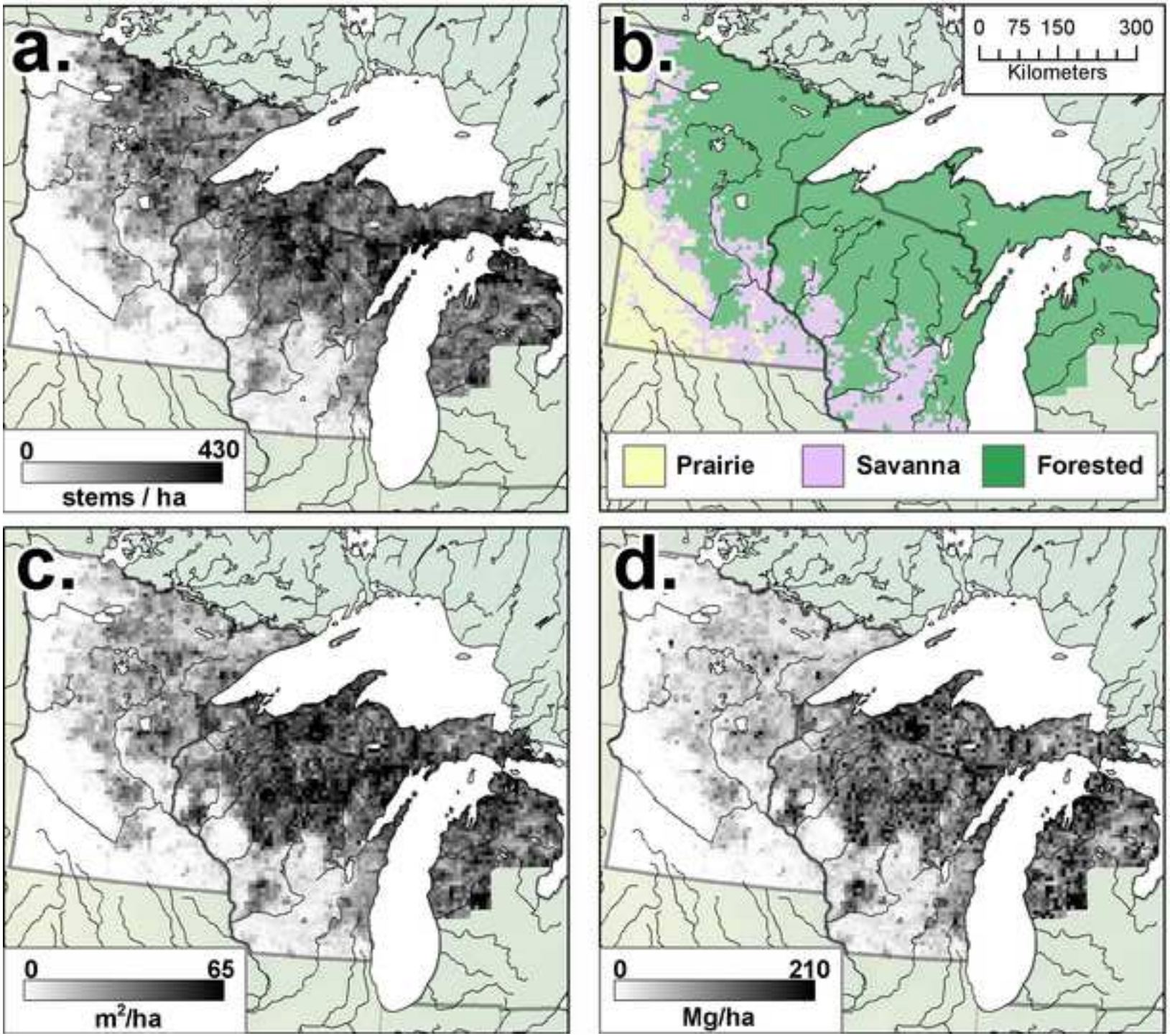

Figure3_DensityBiomassRatio

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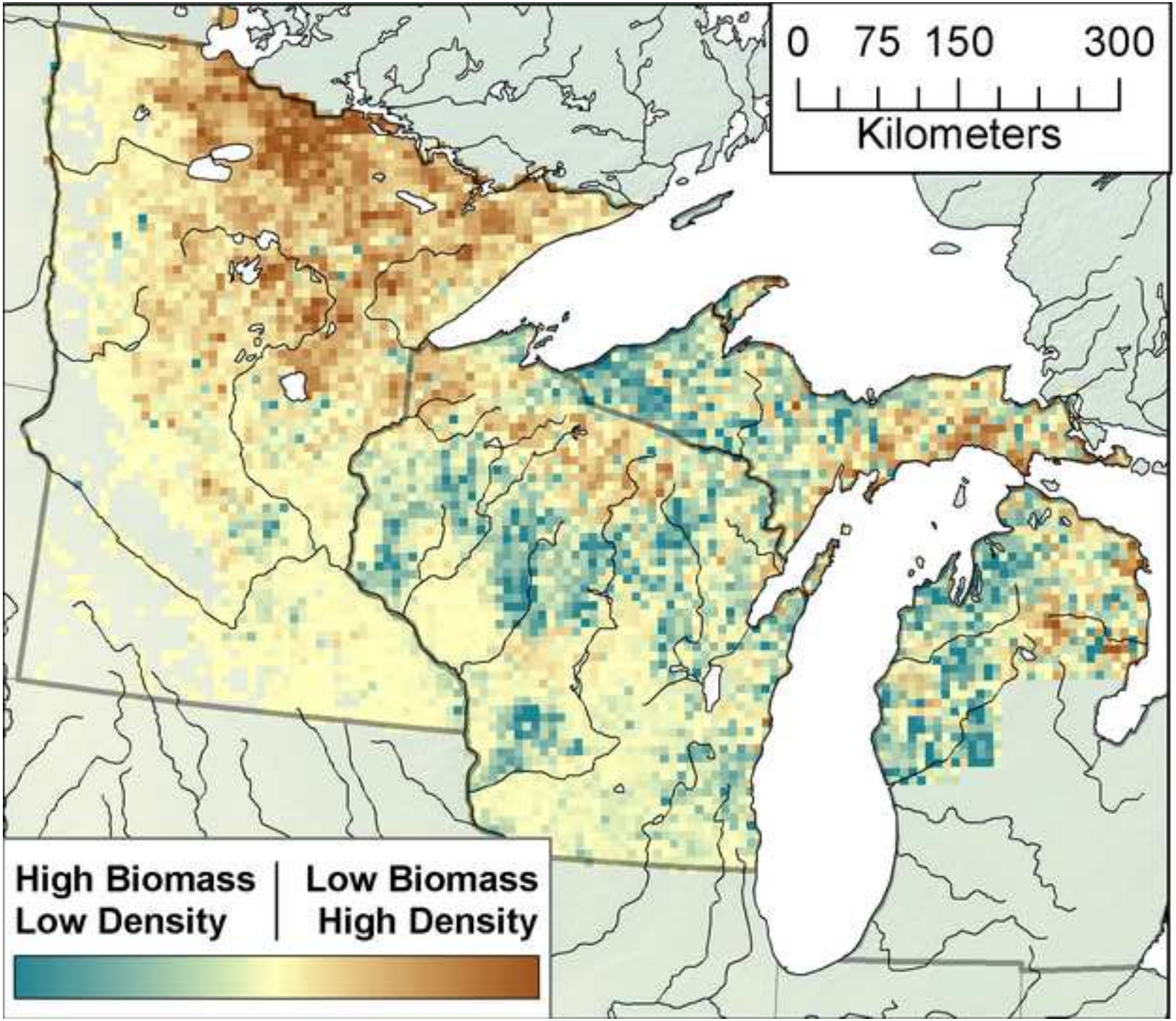

Figure4_compositionPlot
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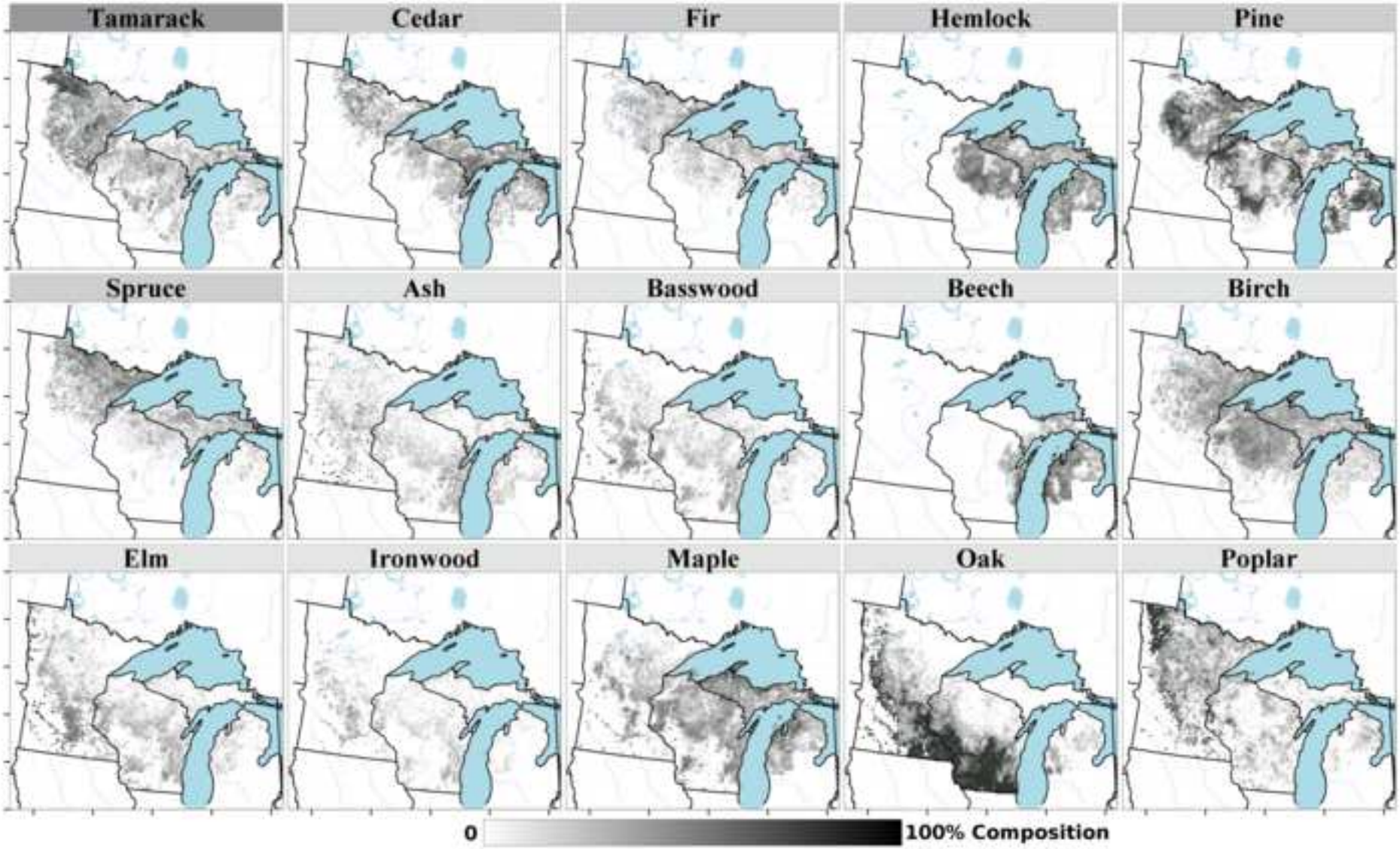

Figure5_ForestClusters

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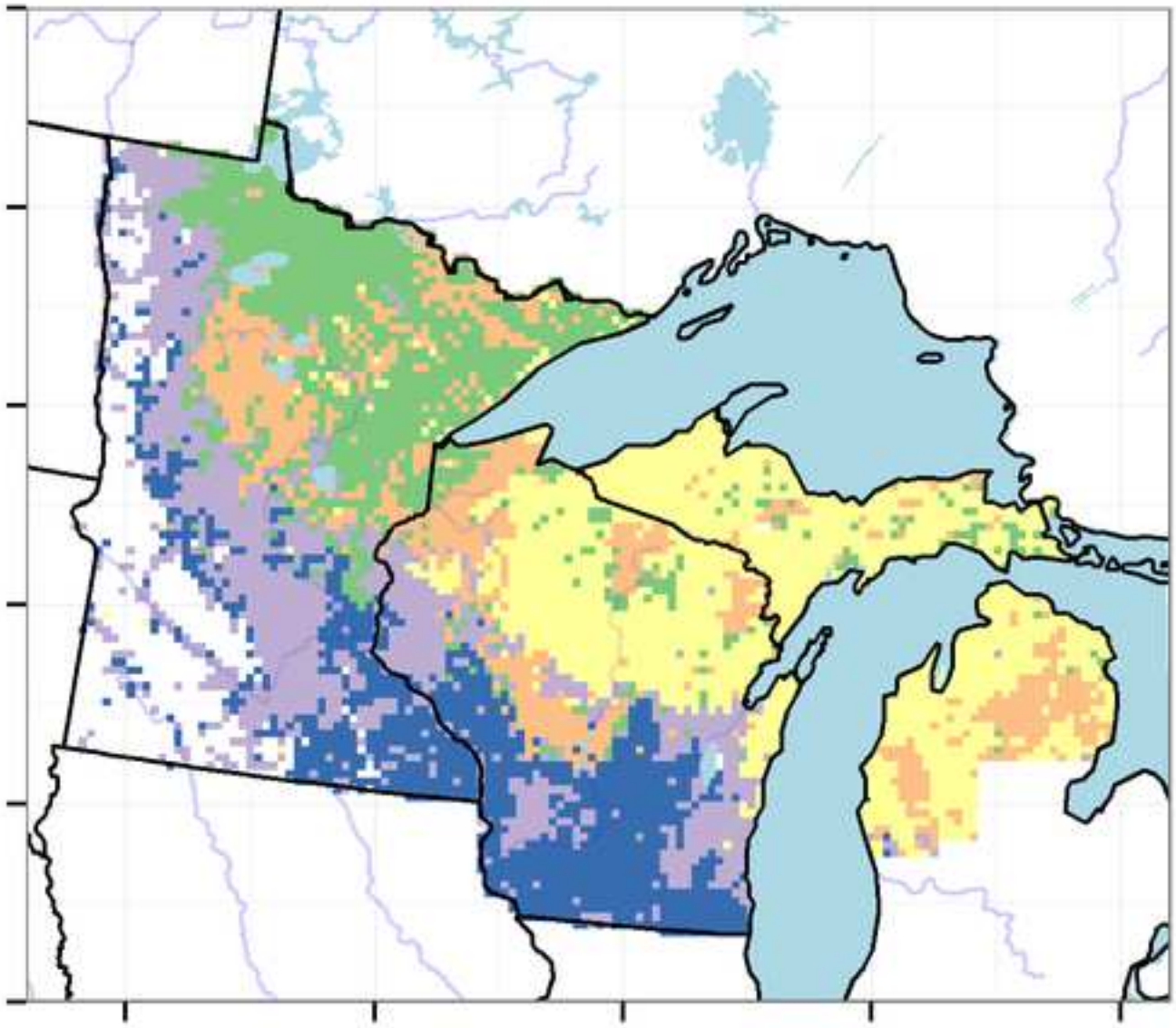

Figure6_PFTRatios
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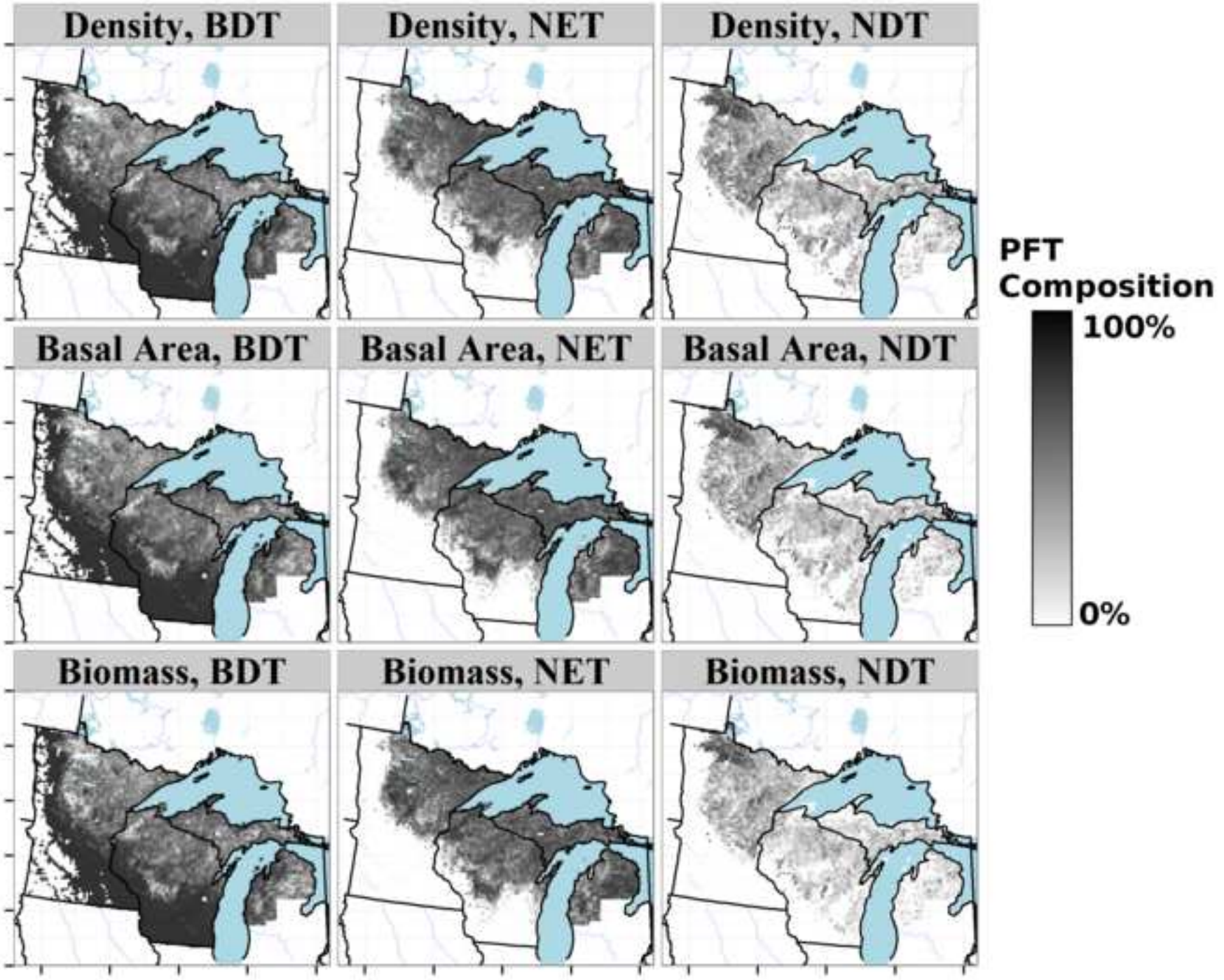

Figure7_FIA_PLSSComparison
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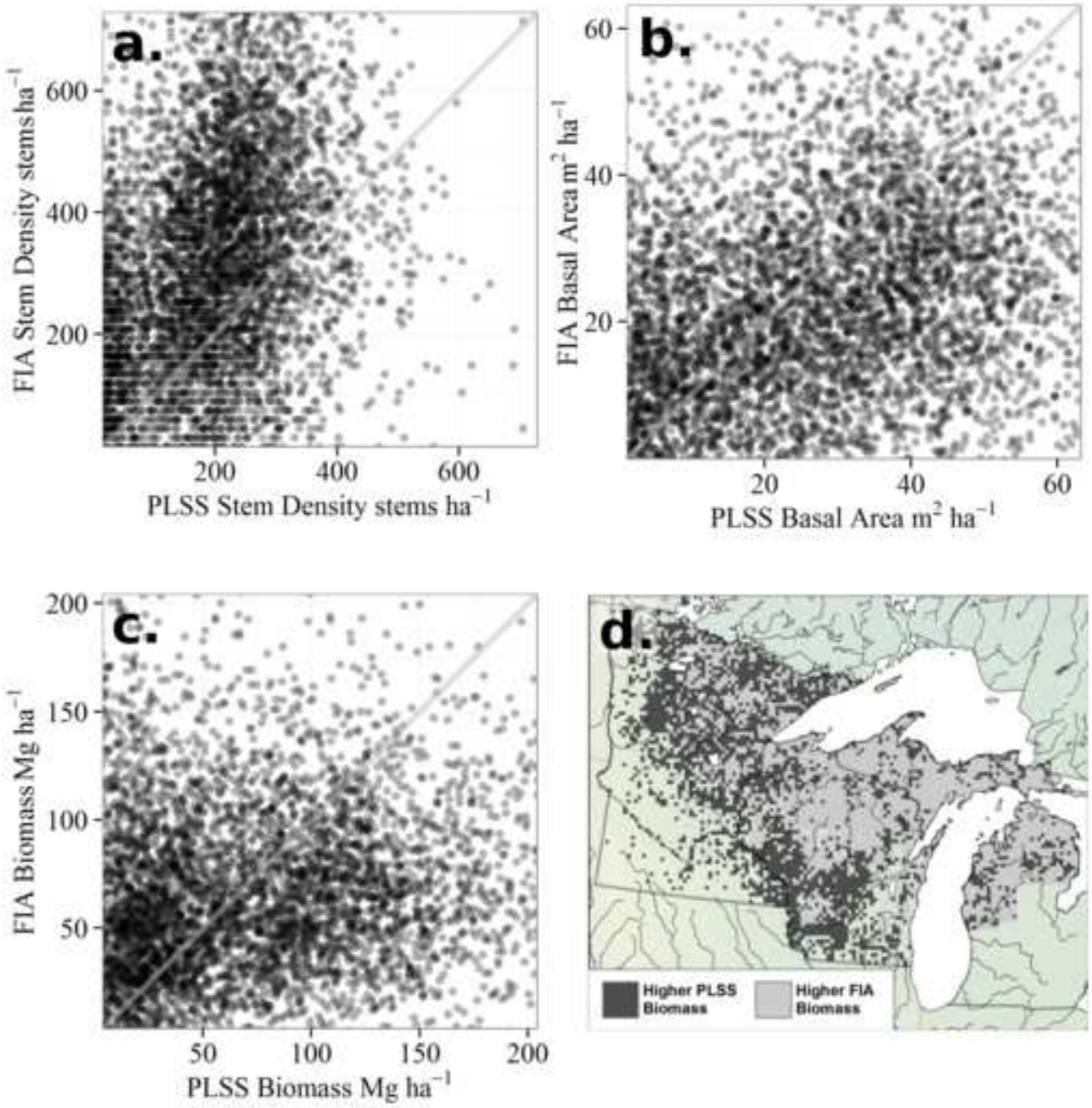

Figure8_NovelLostForests
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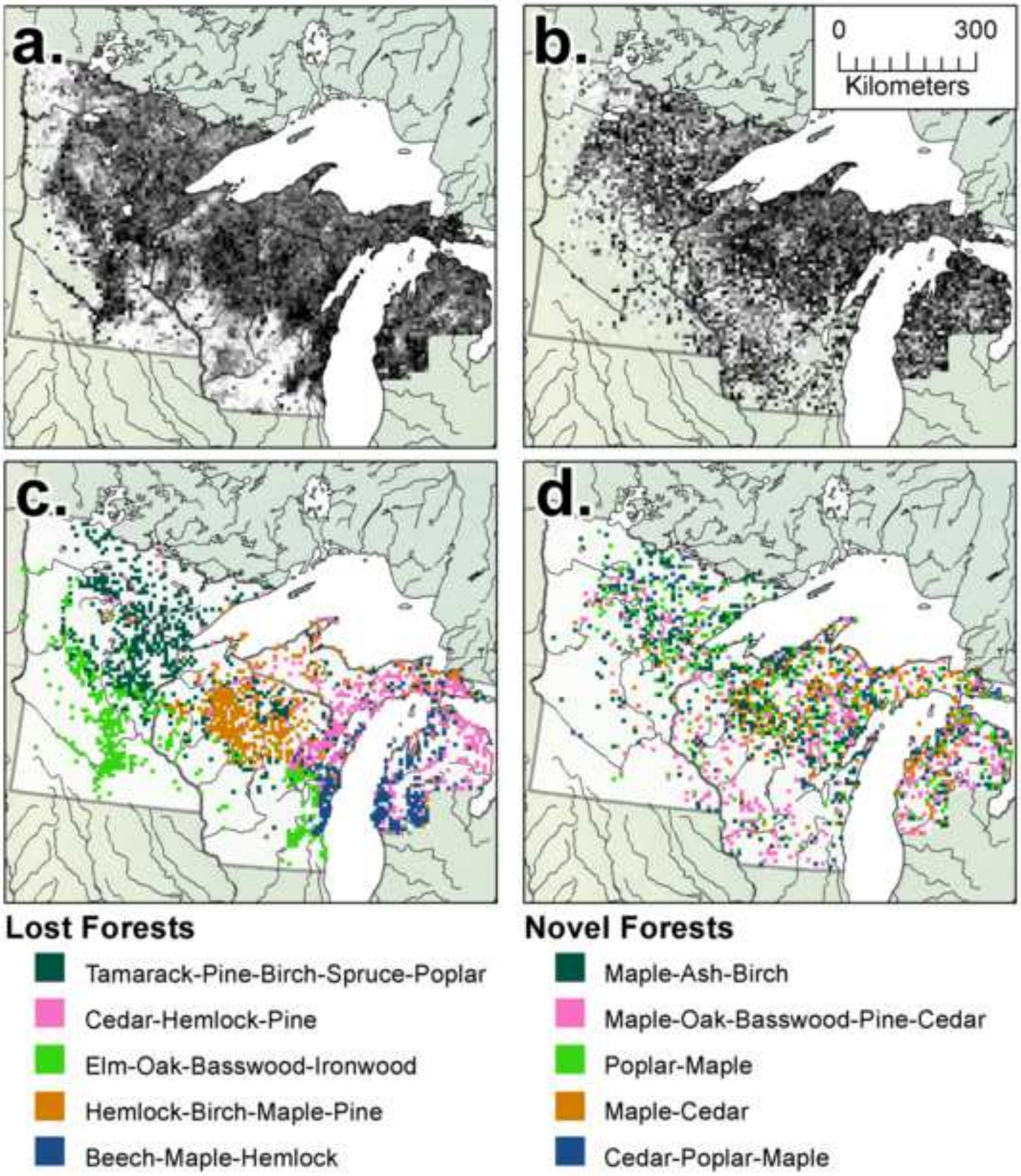

Figure10_TransectPlot

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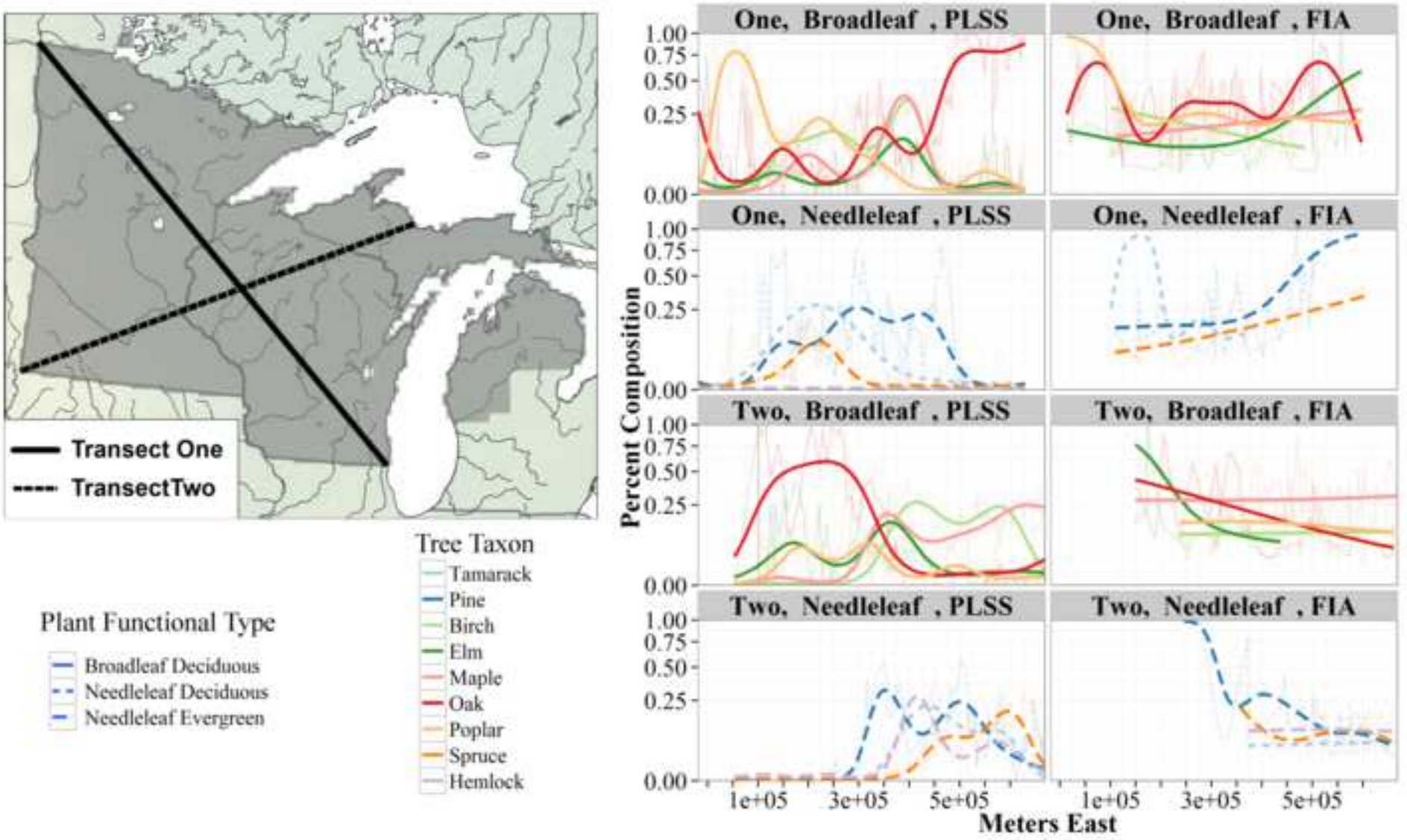

Figure9_DistancePlot
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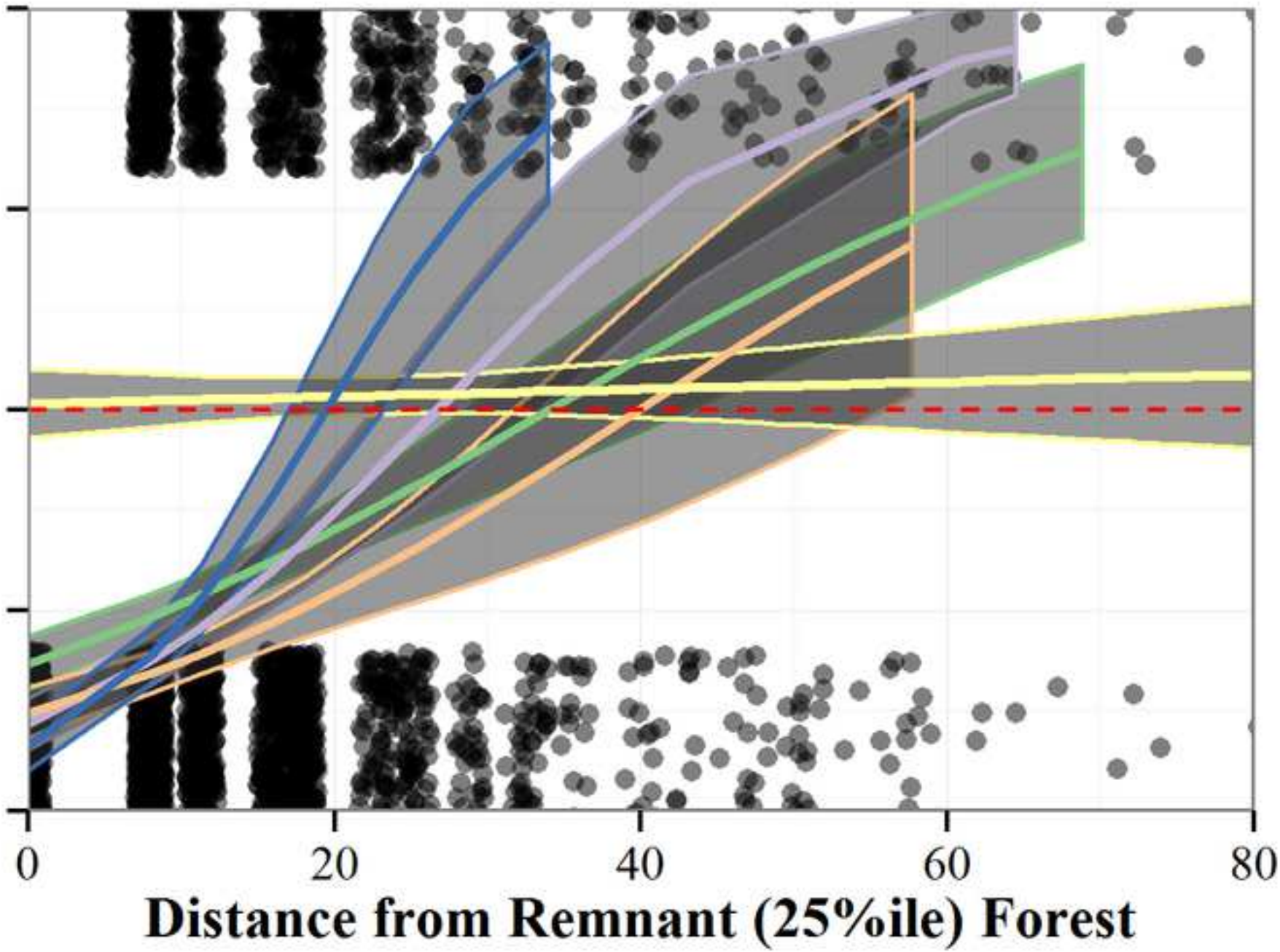

Supporting Information 2 - Taxonomies used

Click here to download Supporting Information - Compressed/ZIP File Archive: Goringetal_supplement2_taxonomies.zip

Supporting Information 3 - Raw output from the Paper

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