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RESEARCH ARTICLE

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Forest structure and biomass in post-agricultural forests: Lessons learned with new spatial tools

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Abstract

Questions: With calls for afforestation to sequester carbon due to climate change, agricultural land will be converted to forests in the near future. Little is known about how the ecosystem services of reforested landscapes with an agricultural land-use history will differ from reference forests. Our objectives were to (i) test the hypothesis that forests with a history of agricultural land use can provide the same carbon storage and biomass ecosystem services as adjacent reference forests, given some recovery time; (ii) explore whether there is a lag in the recovery of forest community composition due to prior agricultural land use; and (iii) demonstrate how remote-sensing methods can improve our understanding of land-use legacies at large spatial scales.

Location: Finger Lakes National Forest, NY, USA.

Methods: Using historic air photos, landscape-scale lidar, and field surveys, we compared differences in biomass storage, forest structure, and vegetation communities between reference forests and post-agricultural forests at different stages of regeneration in the Finger Lakes National Forest, New York, USA. We also used lidar to create a spatial model of biomass across the landscape to analyze the spatial distribution of biomass across our study area.

Results: We found biomass and forest structure in post-agricultural forests generally recovered to levels typical of reference forests within 50 years of abandonment. Conversely, we found the composition of woody and herbaceous communities still varied between reference and post-agricultural forests after 50 years of abandonment.

Conclusions: Collectively our results indicate afforestation efforts can be effective for carbon sequestration at early stages of forest succession. Our spatial model of biomass indicated that biomass levels can be low in forests with extensive edge. Further research is needed to understand how contemporary landscape structure interacts with legacy effects of agriculture to affect biomass and other ecosystem services.

KEYWORDS

afforestation, biomass, ecosystem services, land-use legacy, lidar, post-agricultural forests

1 | INTRODUCTION

There are increasing calls for afforestation efforts to support drawdown of CO_2 levels and help mitigate greenhouse emissions worldwide (Griscom et al., 2017; Hawes, 2018; Nave et al., 2018). In order to produce enough new forests to make an impact, conversion of land to forests will be required (Bastin et al., 2019), including land previously used for agriculture. Abandoned farmlands (i.e., old fields) are important carbon sinks (Kuemmerle et al., 2011), and they provide additional ecosystems services, including water filtration, soil protection, and biodiversity support.

Although the potential benefits of afforestation are clear, it is unclear whether a history of agricultural land use constrains ecosystem services produced by recovering forests (Foster et al., 2003; Perring et al., 2016). For example, tillage associated with row crop agriculture causes substantial disturbance to the soil, leading to a reduction in surface micro-topography and changes in soil heterogeneity (Fraterrigo et al., 2005), reduction of organic matter in the soil (Yesilonis et al., 2016), and change in nutrient availability due to fertilizer use and nitrogen-fixing crops (Foster et al., 2003). These changes in the soil can lead to faster tree growth and reduced wood density, which have opposing effects on carbon sequestration (Alfaro-Sánchez et al., 2019.) In addition to changes in the soil, the seed bed of post-agricultural areas is different, as seeds from forest trees, shrubs, and herbaceous plants are replaced by those of early-successional colonizers (Brudwig et al., 2013). Many forests herbs, in particular, have limited dispersal capacity which can delay community recovery (Bellemare et al., 2002; Flinn & Vellend, 2005; Hermy & Verheyen, 2007). Additionally, non-native plants have been intentionally introduced to agriculture areas (Kuhman et al., 2011; Yesilonis et al., 2016), resulting in substantial changes in the vegetation communities of post-agricultural forests (Holmes & Matlack, 2019). Post-agricultural forests may also have different vegetation communities than reference forests with natural disturbance or silvicultural treatments due to the lack of coppice regeneration in post-agricultural areas (Dyer, 2010).

The northeastern United States have been experiencing afforestation over the past 150 years as former agricultural land was abandoned and allowed to regenerate as forest (Thompson et al., 2013). In the 1930s, governmental programs supported federal purchase of former agricultural land and revegetation through the Civilian Conservation Corps (CCC) program. However, these efforts were not comprehensive (Marks & Gardescu, 1992), resulting in heterogeneous landscapes with a mix of regrown forests, legacy forests (i.e., no known recent history of agriculture), and agricultural artifacts such as fence rows and rock walls. Forests in a previously agricultural setting may coarsely look the same as a forest that was never farmed, but these forest types could provide different levels of carbon storage due to differences in community composition or wood density (Fotis et al., 2018; Alfaro-Sanchez et al., 2019). It is also unclear whether forest structure and community composition diverge in their responses to agricultural land use, because both are related to above-ground biomass (Fotis et al., 2018). For example, it is possible that forest structure and biomass recover quickly in post-agricultural systems because agricultural fields are preferentially located in sites with high productivity, whereas the recovery of community composition may be slower due to invasive species or changes in seed beds (Holmes & Matlack, 2017). Examining the progression of forest recovery will be important for understanding how afforestation efforts will affect ecosystem services, including support for wildlife populations via changes in forest community composition and structure (e.g., Cosentino & Brubaker, 2018; Goldspiel et al., 2019).

New remote-sensing tools available at broad spatial scales can help scientists characterize present-day forest structure and identify evidence of land-use legacies at a fine spatial scale. These include lidar point cloud data, lidar-derived digital elevation models (DEMs), and spatially referenced historic aerial photography. Lidar has been used to understand forest structure for the past two decades, but is increasingly available for broad-scale applications (Brubaker et al., 2014). Additionally, with the use of ultra-high resolution DEMs available from lidar, we can view signatures of historical land use such as rock walls, changes in surface texture, and tillage lines that show a legacy of agriculture (Johnson & Ouimet, 2014, 2016). By using lidar and aerial photography concurrently, we can map historic land use and changes over time, and also create fine-scale spatial models of current forest structure (e.g., tree height, biomass), which can help us understand responses of forest structure to historical land use.

We used remote-sensing data and field sampling to reconstruct historic patterns of land use at the Finger Lakes National Forest (FLNF) in New York, USA. Our objectives were to (i) test the hypothesis that forests with a history of agricultural land use can provide the same carbon storage and biomass ecosystem services as adjacent reference forests, given some recovery time; (ii) explore whether there is a lag in the recovery of forest community composition due to prior agricultural land use; and (iii) demonstrate how remote-sensing methods can improve our understanding of land-use legacies at large spatial scales.

2 | METHODS

2.1 | Study area

FLNF in central New York, USA (42°30′ N, 76°48′ W) is federally owned and managed land that was acquired in the late 1930s and early 1940s as willing landowners sold their farms to the federal government. Currently, the national forest consists of 6,521 ha of multiple-use forest and grassland maintained for cattle grazing. Common forest communities include Appalachian oak–hickory, rich mesophytic, successional northern hardwood, and various species of conifer plantations (Edinger et al., 2014).

2.2 | Field methods

We used Geospatial Modeling Environment (Beyer, 2014) to randomly select 96 locations that were forested on the 2011

National Land Cover Dataset (NLCD) (Jin et al., 2019) and separated by ≥200 m. In summer 2014, we established 200-m^2 circular plots (7.9 m radius) at each location, measured the diameter at breast height (dbh) for trees ≥10 cm dbh, and identified the species of each tree. We estimated percent shrub cover for every woody species <10 cm dbh found in the plot using a cover-class methodology (0%–5%, 6%–25%, 26%–50%, 51%–75%, 76%–95%, 96%–100%) (Daubenmire, 1959). We also established 1-m^2 subplots randomly in each of the four cardinal directions from the centroid of each plot. We estimated herbaceous cover by species in each subplot using the same cover categories used for shrubs. Grasses were included in herbaceous cover estimates but not identified to species. Herbaceous cover was only measured once during summer, so some spring ephemerals were likely missed in the sampling strategy. We found no herbaceous species at two sites.

2.3 | Land-use legacy descriptions

We identified aerial photos, produced by the United States Department of Agriculture, that provided coverage of the study area from both 1938 and 1964 and georeferenced these images using current imagery (2014). For each era, we classified and digitized land cover for FLNF as agriculture, shrub, or forest. Areas were classified as forest if they contained a closed canopy, whereas areas with woody vegetation but no closed canopy were classified as shrubs. Areas classified as shrub were primarily old-field successional areas. Using the land cover maps created from each era, we classified each area forested in 2014 as a reference forest, old post-agricultural forest, or young post-agricultural forest. Reference forests were continuously forested since 1938 and had no evidence of being used for row crop agriculture from the lidar-derived DEM. Because these forests are actively managed, we expect that some timber harvesting occurred in these forests. Old post-agricultural forests were agriculture or shrub in 1938 but forested in 1964, and young post-agricultural forests were not forested in 1964 but forested in 2014. In addition to classifying historical land use at each sampling plot, we determined whether post-agricultural plots were revegetated as a conifer plantation based on field sampling.

As a secondary verification method for historical land-use classifications, we used the lidar-derived 2-m resolution DEM-generated hillshade to examine each plot for signs of previous row crop agriculture. Signs included nearby fencerow features, plow marks, or other textural signatures (e.g. lack of pit and mound topography) that are present in the hillshade (Figure 1). We verified that all reference sites had no record of row crop agriculture using any of our methods (but the site may have been grazed). If a site was forested in 1938 but had clear signs of previous agricultural land use, we changed its classification to old post-agricultural forest (n = 3 sites).

2.4 | Lidar-modeled biomass

Using allometric equations developed by Chojnacky et al. (2014), we calculated the biomass of each tree using the species and DBH, and total biomass was estimated for each plot. We also used raw lidar point clouds to generate models of canopy height and biomass for the entire FLNF. Lidar data were collected as part of a FEMA dataset in 2014, flown and processed by Northrop Grumman, using a Leica ALS 60 and Optec 3,100 airborne lidar sensor during the leaf-off season. This was a relatively low-density dataset with a point spacing of approximately 1.5 m. The final lidar data products were produced within the specifications of the USGS National Geospatial Program LIDAR Base Specifications, Version 1.0. A 2-m resolution DEM was generated by the vendor, with a post-processing root mean square error of 12.5 cm vertically.

Because this was a relatively sparse, leaf-off lidar dataset, we created a 10-m resolution canopy height model to reduce the appearance of gaps (Brubaker et al., 2014) for FLNF using the canopy model tool in FUSION (McGaughey, 2018). We also used the *gridmetrics* tool in FUSION to create quantitative height variables (eg., mean, max, 90th percentile) for the point cloud at a 20-m resolution. *Gridmetrics* creates a series of descriptive statistics for each grid cell (n = 74) as described in the FUSION manual (McGaughey, 2018). We chose a 20-m resolution to increase the number of points found in each cell in order to improve the accuracy of the quantitative metrics.

We used random forest regression to create a model of biomass using the *gridmetric* variables from FUSION. Random forest is a type

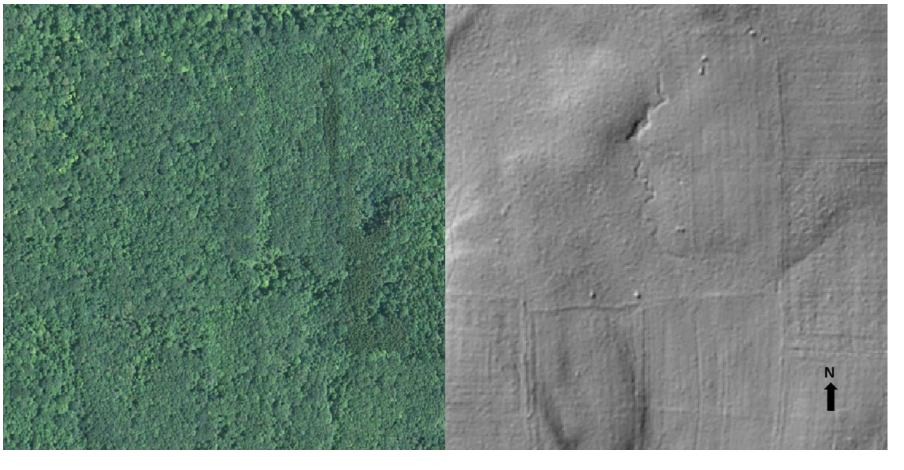

FIGURE 1 Current aerial photograph and lidar-derived hillshade showing the same forested area. Plow lines and other relic agricultural features can be clearly seen in the hillshade in the southern and eastern portion, while the northwest corner does not contain these features. Current aerial photography shows a closed-canopy forest

of classification and regression tree model that uses a randomly selected subset of variables to create a "forest" of regression trees. We chose this method because it has shown to be useful in working with lidar datasets as a result of their large number of variables (Cutler et al., 2007; Hudak et al., 2008; Brubaker et al., 2018). We used the *randomForest* package (Liaw & Weiner, 2002) in R (R Core Team, 2019) to create a model of biomass for FLNF. We initially tested all of the elevation metrics produced by the gridmetrics tool in FUSION, and removed variables with a lower importance value using an iterative method until the amount of variability was maximized with the fewest variables (Díaz-Uriarte & Alvarez de Andrés, 2006). Our final model included three variables: average absolute deviation, 95th percentile height, and percent cover of first returns. Using our best final model, we generated a 20-m resolution biomass map of the FLNF using the lidar-derived grid metrics variables.

2.5 | Statistical methods

For each plot, we calculated basal area and tree density from our field measurements. Each species was classified as native or non-native, and total percent cover, total native percent cover, and total non-native percent cover were calculated by summing the median cover-class values for all species present in a plot. We calculated dominant/co-dominant tree height for each plot using the lidar-generated canopy height model (Brubaker et al., 2014). Trees were considered dominant if their crown received light from multiple sides, and co-dominant if their crowns received full light from above on the area of their crown. We also created a presence/absence matrix of woody and herbaceous species data for each plot. All statistical analyses were conducted in R.

We used ANOVA to compare canopy height, basal area, biomass, percent shrub cover, woody species richness, herbaceous richness, tree density, percent herbaceous cover, and percent non-native shrub cover among reference forests, young post-agricultural forests, and old post-agricultural forests. Assumptions of normality and heteroscedasticity were largely met, and the results of standard ANOVAs were not qualitatively different than permutational ANOVA. For significant ANOVAs we examined all pairwise comparisons using Tukey's Honest Significant Difference approach using a family-wise Type 1 error rate of 0.05.

We used multivariate methods to test for differences in woody and herbaceous community structure among forest types. We generated a Sorensen distance matrix for woody and herbaceous species using the presence/absence data. We then used permutational multivariate ANOVA (PERMANOVA; Anderson, 2001) to test for differences in community composition among forest types for the woody and herbaceous communities. Significant PERMANOVAs were followed up with pairwise comparisons among forest types using the Holm method to control the family-wise Type 1 error rate (Holm, 1979). We used non-metric multidimensional scaling (NMDS; Kruskal, 1964) to visualize differences in community composition among forest types. For the herbaceous community, we had to

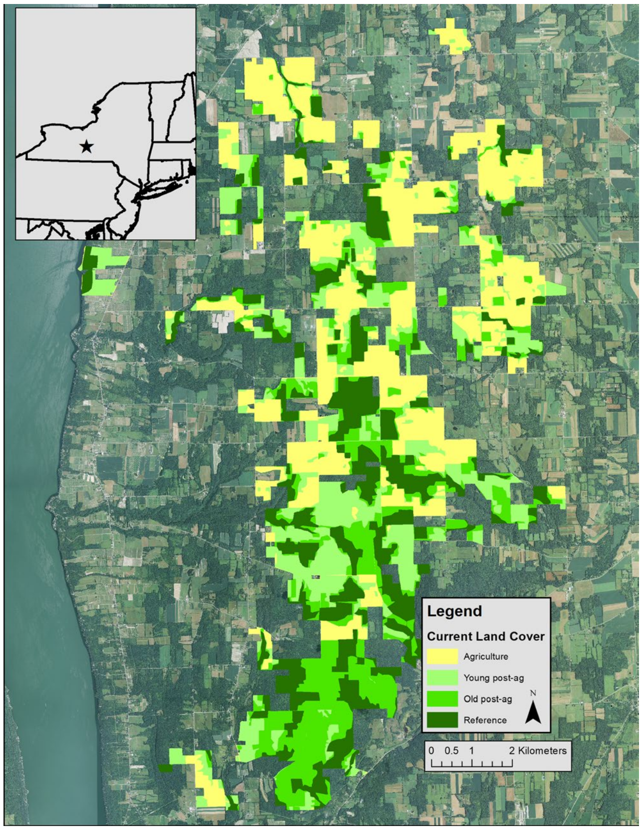

FIGURE 2 Current land cover of Finger Lakes National Forest (FLNF). Reference forests are shown in dark green. Inset shows location of FLNF in New York, USA

remove sites with a single species ($n = 8$) in order to find a convergent solution for the NMDS. We used the *vegan* package (Oksanen & Blanchet, 2019) to conduct the PERMANOVA and NMDS, and the *RVAideMemoire* package to conduct multiple comparison tests (Hervé, 2020).

Finally, we compared the spatial distributions of our modeled biomass values to understand how the spatial patterns of biomass vary across forests with different histories of agricultural land use. We also compared the frequency distributions of biomass values among reference forests, young post-agricultural forests, and old post-agricultural forests.

3 | RESULTS

3.1 | Land-use history and forest structure

Land cover digitized from aerial imagery showed that FLNF consisted of 2,317 ha that are not forested, 1,465 ha of young post-agricultural forest, 1,303 ha of old post-agricultural forest, and 1531 ha of reference forest (Figure 2). A subset of the forest structural attributes we examined varied among reference sites, young post-agricultural sites, and old post-agricultural sites (Table 1, Figure 3). Basal area and canopy height were significantly greater in old than young post-agricultural sites. Woody biomass and canopy height were greater in reference than young sites. Herbaceous cover was greater in young than old post-agricultural sites, but there was no difference between either type of post-agricultural site and reference sites. Non-native shrub cover was significantly greater in young post-agricultural sites than old post-agricultural or reference forests. We found no variation in tree density, woody richness, shrub cover, or herbaceous richness among forest types (Table 1, Figure 3).

3.2 | Vegetation community analysis

Woody community composition varied significantly among forest types (PERMANOVA, $F_{2,93} = 5.28$, $p = 0.001$, $R^2 = 0.10$). Pairwise comparisons revealed significant differences in community composition between each combination of forest types ($p \leq 0.005$). The NMDS ordination (stress = 17.8%) revealed clustering of woody species composition with forest type, with the greatest separation between reference plots and young post-agricultural plots (Figure 4). Early-successional species and non-native species such as *Malus* sp. and *Crataegus* sp. clustered with young post-agricultural sites, whereas late-successional species such as *Ostrya virginiana*, *Tilia americana*, *Acer saccharum*, and *Carya* spp. clustered with the reference sites (Appendix S1). *Quercus* spp. and *Pinus* spp. tended to be most commonly found in old post-agricultural sites. *Acer rubrum* and *Pinus strobus* were common in all forest types. There was considerable overlap in woody community composition, with the vast majority of woody species clustering with at least two forests types (Appendix S1).

Herbaceous plants were detected in all but two plots, and community composition varied significantly among forest types (PERMANOVA, $F_{2,91} = 3.45$, $p = 0.001$, $R^2 = 0.07$). Pairwise comparisons revealed that community composition was significantly different between reference and post-agricultural plots ($p \leq 0.004$), but there was no difference in community composition between young and old post-agricultural plots ($p = 0.12$). The NMDS ordination (stress = 12.3%) corroborated the results of the PERMANOVA, showing the greatest separation between reference and both young and old post-agricultural plots (Figure 5). Species that were present in both the young and old post-agricultural forests, but not the reference forests included *Taraxacum officinale*, *Veronica officinalis*, and *Toxicodendron radicans*. Species present in both old post-agricultural and reference, but not young post-agricultural forests included *Polygonatum biflorum*, *Maianthemum racemosum*, *Maianthemum canadense*, *Caulophyllum thalictroides*, and *Arisaema triphyllum* (Appendix S2).

TABLE 1 Results of ANOVAs comparing forest structure metrics among young post-agricultural, old post-agricultural, and reference forests (group $df = 2$, error $df = 93$). See Figure 3 for group means

Response variable	*F*	*p*
Herbaceous cover	3.2277	0.044
Herbaceous richness	1.0267	0.362
Shrub cover	1.8959	0.156
Non-native shrub cover	6.8091	0.002
Woody richness	0.6389	0.530
Tree density	2.1358	0.124
Tree height	10.717	<0.001
Woody biomass	2.8097	0.065
Basal area	3.9083	0.023

3.3 | Lidar-modeled biomass

The best-performing *randomForest* model explained 52.3% of the variability in biomass using three lidar height variables: average absolute deviation, 95th percentile height, and percent cover of first returns. The biomass model mirrored the forest type map closely, with reference forests tending to have the greatest biomass values. Biomass was lowest in non-forested areas, followed by the young post-agricultural forests, then the old post-agricultural (Figure 6). The frequency distributions of biomass values across forest types for the entire FLNF corroborated the visual patterns. Reference forests had the greatest median biomass (415.3 t/ha), followed by old (370.1 t/ha) and young post-agricultural forests (191.4 t/ha) (Figure 7). Biomass had a bimodal distribution in all forest types. We found the lower peak in biomass (<200 t/ha) corresponded to areas along forest edges, roads, trails, etc.

4 | DISCUSSION

4.1 | Biomass and forest structure

Biomass was lower in young post-agricultural forests than reference forests, but we found no significant difference between the biomass of old post-agricultural forests and reference forests from our field sampling. Our lidar-based model of biomass corroborated these results, showing substantial overlap in the distributions of biomass between old post-agricultural and reference forests. This supports the hypothesis that post-agricultural forests and those created through afforestation efforts can be important for carbon sequestration in the face of climate change. Our results demonstrate that within 50 years of abandonment, post-agricultural forests provide a similar amount of biomass as older forest. However, it should be noted that we only measured above-ground living biomass. Below-ground biomass and coarse woody debris are both known to be an important contributor to forest carbon storage (Nave et al., 2018), but we did not include these in our study. Previous work has suggested a lag in below-ground recovery of carbon (Richter et al., 2000; Kolbe et al., 2016), but more research is needed to understand the magnitude and timing of this recovery.

Multiple patterns emerged from our spatial model of biomass that provide insight into the role of landscape structure in mediating effects of land-use history on biomass. First, we discovered a bimodal distribution of biomass in each forest type. When viewed in GIS, the

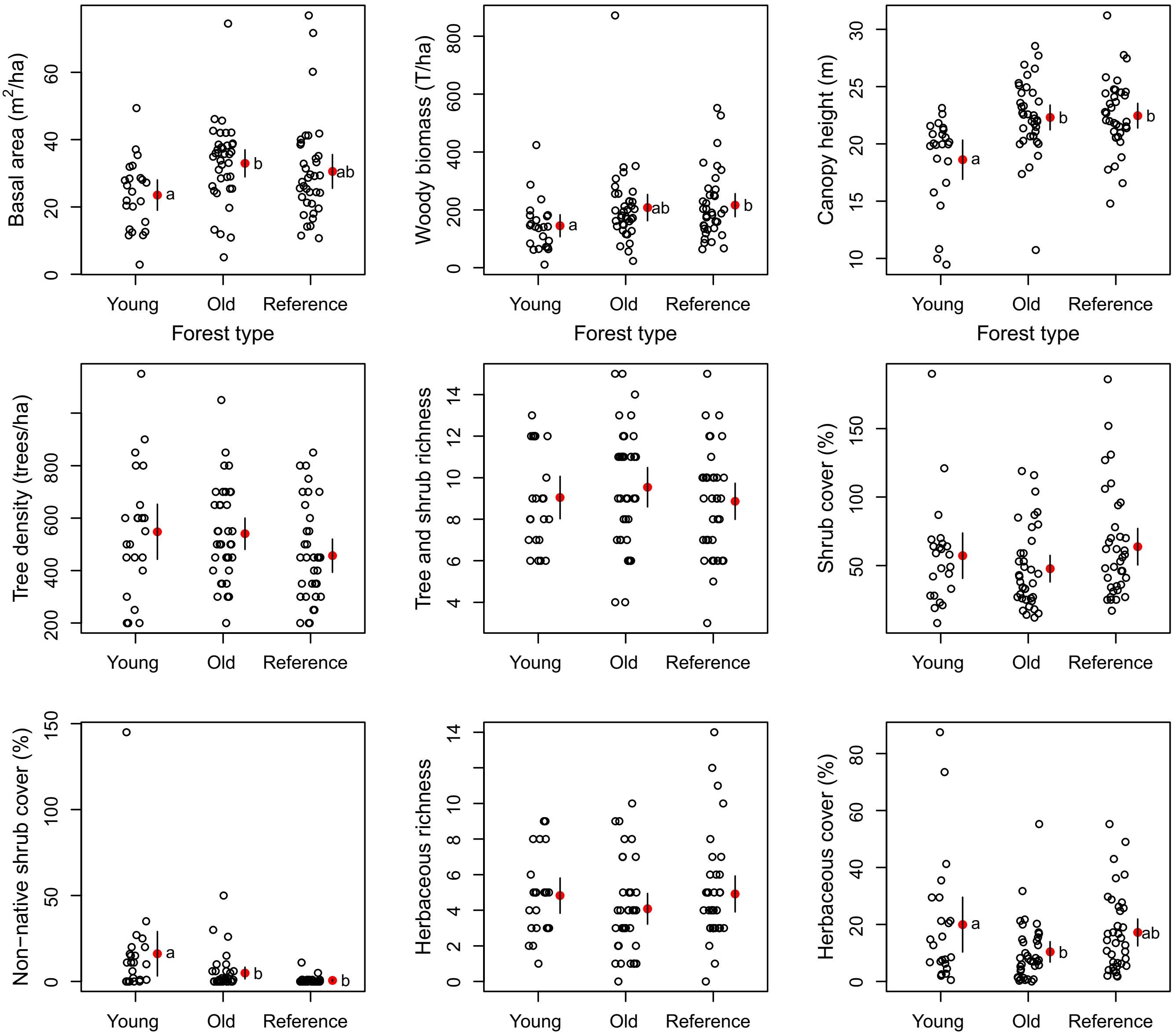

FIGURE 3 Comparison of forest structural metrics among young post-agricultural, old post-agricultural, and reference sites. Open points represent data points, red circles represent means, error bars represent 95% confidence intervals, and letters indicate results of multiple comparison tests at $p < 0.10$

lower peak in biomass values most commonly represented forest edges, and therefore included both forest and non-forest in one cell. Young post-agricultural forests in particular had greater edge habitat than old post-agricultural and reference forests, since they tended to border current agricultural land. This explains the strong peak of low-biomass values in young forests (Figure 7). Second, the range in biomass values was similar among forest types, with high-biomass areas persisting even in young post-agricultural sites. High-biomass areas likely persist in young forests because of the historical presence of hedge rows and other large trees. These landscape elements function as refugia for forest species and can facilitate forest recovery via seed dispersal following agricultural abandonment (Corbit et al., 1999). More generally, the mosaic pattern of historical land use in this system with small farms intermixed with forest stands (Figure 2) likely added resilience to the post-agricultural system by maintaining connectivity of old fields to source populations. Biomass recovery in post-agricultural forests may be more constrained in systems where historical forest loss was rapid and widespread. Despite extensive evidence that historical land use has a greater impact on forest community composition than landscape configuration (e.g., Motzkin et al., 1999; Singleton et al., 2001; Vellend et al., 2006; Brudvig & Damschen, 2011), additional studies are needed to carefully tease apart the independent contributions of historical agriculture and landscape structure on biomass recovery in regenerating forests.

A subset of post-agricultural forests were replanted with native or non-native conifers, a land-use intervention that was common throughout the eastern and northern United States in the 1930s and 1940s (Verschoor & Van Duyne, 2012). These plantations were often reforested in conifers as part of a soil conservation strategy,

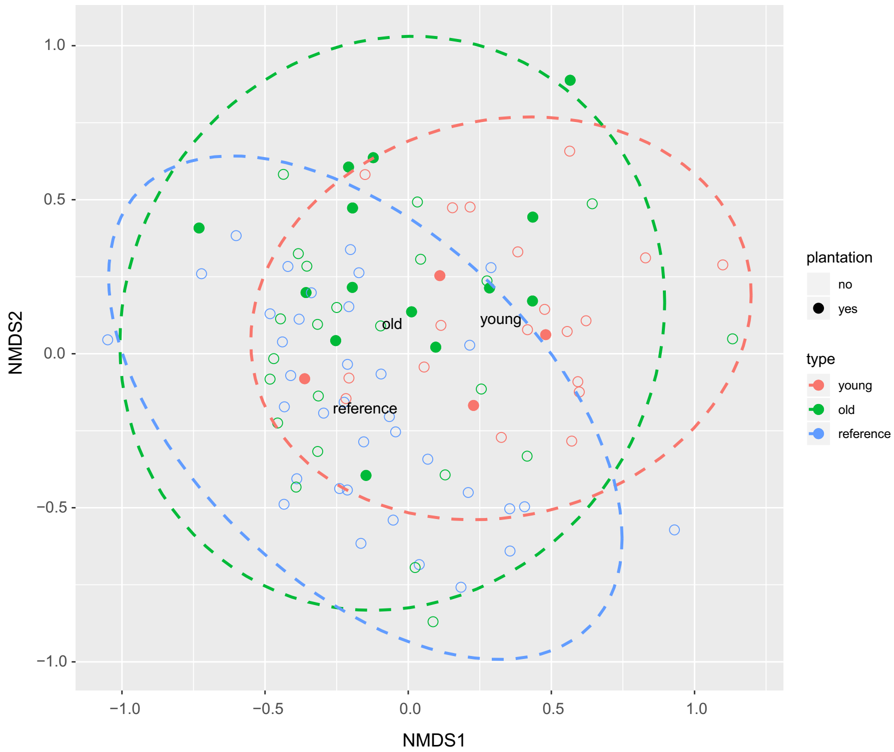

FIGURE 4 Non-metric multidimensional scaling (NMDS) ordination of woody species with covariance ellipses for each forest type. Circles represent sampling plots

and multiple species of conifers were used in different areas, including *Picea abies*, *Pinus sylvestris*, *Pinus resinosa*, and *Pinus banksiana* at FLNF. Most conifer plantations in our study system were in old post-agricultural forests ($n = 14$), so we conducted a post-hoc analysis to compare the mean biomass for plots that were replanted and those that were not ($n = 23$) within old post-agricultural forests. Mean biomass was not significantly different between plantations and non-plantations ($t = 1.50$, $df = 35$, $p = 0.14$). Former plantations often contained a large percentage of hardwoods and other species that have grown in since conifers were planted. In this case, active management with plantations did not appear to increase the speed of biomass recovery among old post-agricultural sites, and plantation strategies have largely been abandoned (Verschoor & Van Duyne, 2012). We were not able to test whether biomass recovery

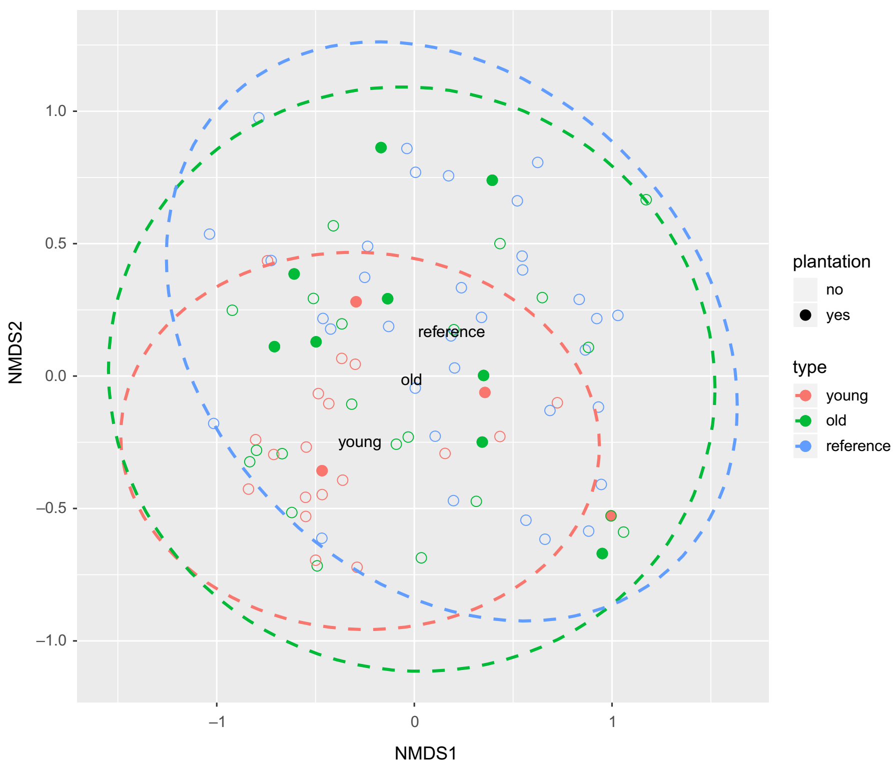

FIGURE 5 Non-metric multidimensional scaling (NMDS) ordination of herbaceous species with covariance ellipses for each forest type. Circles represent sampling plots

was initially accelerated when forests started regenerating because of the low number of plantations in young post-agricultural plots.

Forest structure attributes that we measured (tree height, basal area, tree density, percent shrub cover, and percent herbaceous cover) were similar between reference forests and post-agricultural forests, showing that recovery of structural characteristics can occur without intervention (the majority of old post-agricultural sites were not replanted in conifer plantation). Flinn and Marks (2007) found similarities in stem density and size class distributions between post-agricultural and reference forests, but our study extends those results to include younger post-agricultural forests. Tree height was the only structural attribute that strongly varied between young post-agricultural and older forests.

One reason why post-agricultural forests recovered relatively quickly may be that in our study region, areas that were formerly used for agriculture were at lower elevations, had less steep slope, and more productive soils than those that were left as forest (Flinn et al., 2005). This pattern should hold in other areas being considered for afforestation, as land that is suitable for growing crops could be more productive than regions that were left in forests (Cramer et al., 2008).

4.2 | Forest community data

When we examined the woody plant and herbaceous community data, there was a significant difference between all three forest types in woody and herbaceous plant community composition. This contrasts with our biomass and forest structure data, and suggests that there may be a recovery lag in forest community composition compared to biomass and structural attributes. Flinn and Marks (2007) found similar differences in forest composition between post-agricultural and reference forests, and other studies have shown that changes in vegetation community can persist for decades (Motzkin et al., 1999; Flinn & Vellend, 2005). Because afforestation creates habitat heterogeneity in forest successional states, allowing natural afforestation could result in an increase of beta diversity, and therefore high gamma diversity at a landscape scale. Several bird and mammal species in the northeastern U.S. require early-successional forest habitat or a mosaic of habitat types at different stages of succession (Fuller & DeStefano, 2003; King & Schlossberg, 2014; Bakermans et al., 2015).

Although percent cover of non-native species was greatest in young post-agricultural forests, the future trajectory of these forests is unclear. Young post-agricultural forests probably have less dense canopies, thereby favoring colonization by invasive species which tend to be less shade-tolerant than native forest species (Martin *et al*, 2009). Holmes and Matlack (2019) used a chronosequence approach and similarly found a reduction in invasive species with increased time since disturbance. Young post-agricultural sites may receive greater propagule pressure from non-natives than older forests because of their proximity to roads and agricultural fields (Kuhman et al., 2011), and it is possible that native species outcompete non-native species over time. It is also possible there were fewer non-native species present in the landscape when old post-agricultural forests were abandoned. Many non-native species are more likely to be found in sites with higher pH and cation exchange capacity (Kuhman et al., 2011), which likely include young post-agricultural forests compared to older forests due to the historic patterns of agriculture in this region (Flinn et al., 2005). Further

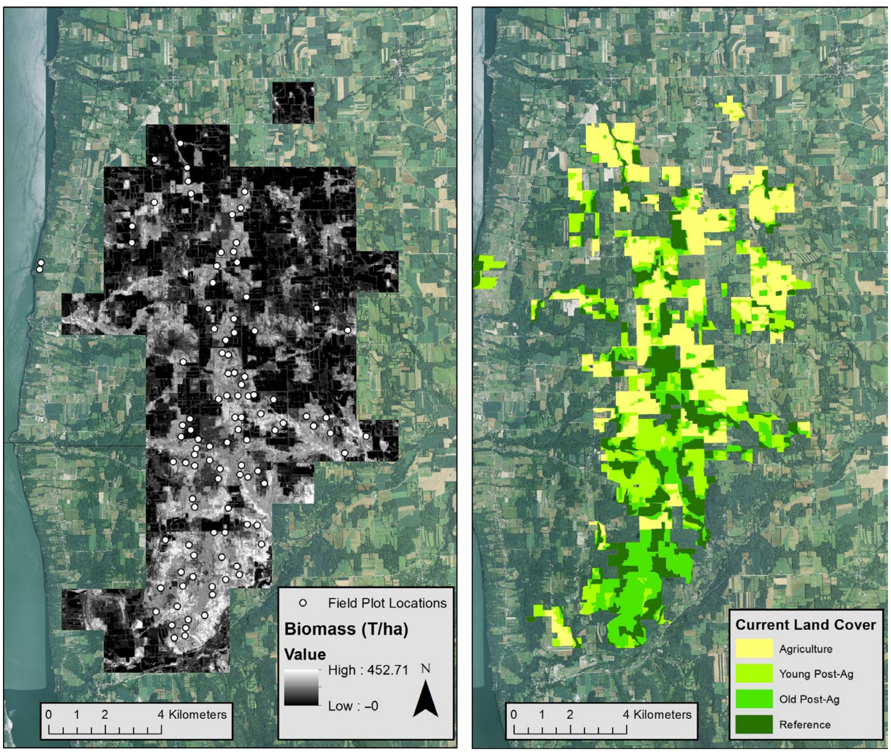

FIGURE 6 Map of modeled biomass (metric tons/hectare). Biomass values were generated with a randomForest model using a lidar point cloud of elevations. Higher values are shown in white and light gray, and lower values are shown in dark gray and black. Land cover is shown for comparison

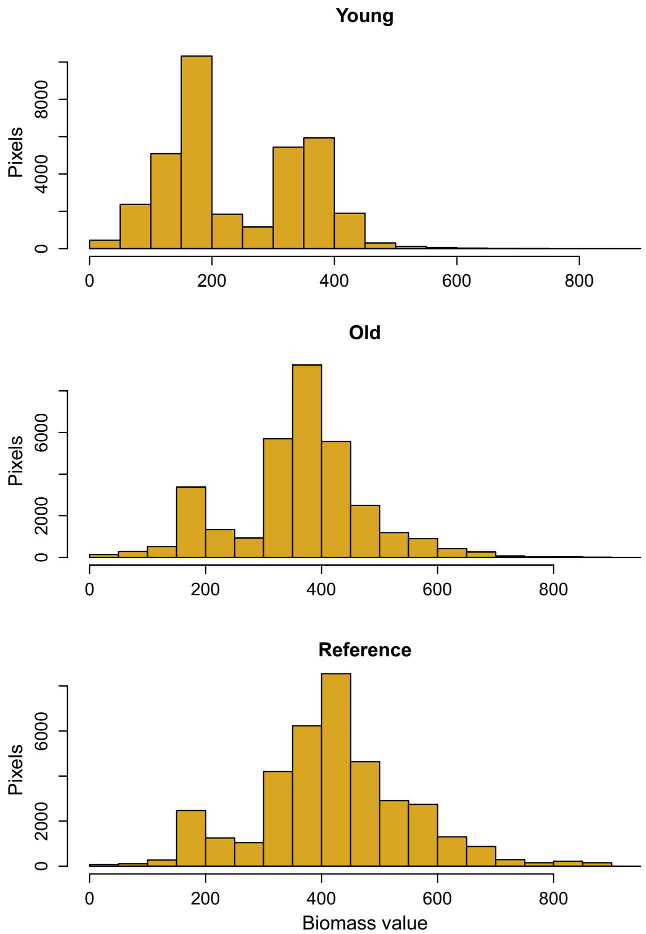

FIGURE 7 Frequency distribution histograms of biomass values in 20-m pixels across the Finger Lakes National Forest for the young post-agricultural, old post-agricultural, and reference forests

studies are needed to understand the mechanisms explaining why non-native cover is greatest in young post-agricultural forests, and whether active management will be needed to restore forest community composition.

5 | CONCLUSIONS

Our results suggest that forest ecosystems in the northeastern U.S. can be resilient to agricultural land use, including a history of intense disturbance (e.g., tillage). Old post-agricultural forests were similar to reference forests in all measures, and post-agricultural forests regain most of their biomass within 50 years. In a time of global change, these results support the calls to reforest large portions of our landscape for the goal of carbon sequestration. They also show that in addition to carbon sequestration, new forests may support a variety of ecosystem services, including wildlife habitat and biodiversity support, water filtration and storage, and nutrient cycling, although some management may be necessary in order to maintain habitat for early-successional species. We also found that remote-sensing methods were useful to increase our understanding of land-use legacy effects in FLNF. The relatively sparse lidar dataset collected over a landscape scale still provided enough data to model biomass and show artifacts of agriculture on the landscape. More research is needed, however, to understand the complicated relationships between current landscape configuration and fragmentation, non-native species, and land-use legacies in order to optimize the ecosystem benefits of afforestation efforts.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Appendix S1. Non-metric multidimensional scaling (NMDS) plot of woody species with species overlain.

Appendix S2. Non-metric multidimensional scaling (NMDS) plot of herbaceous species with species overlain. Species are represented by a code consisting of the first two letters of the genus followed by the first two letters of the species. Corresponding scientific names are listed below.

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