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Regional differences in infilling and land-use conversion characterize woody cover increases across the Eastern United States

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ABSTRACT

Trees and shrubs are expanding into historically open ecosystems across the globe, threatening ecological function and ecosystem services. Across much of the eastern U.S., increasing woody cover has been associated with ecological degradation of forest and savanna ecosystems, and more recently, heightened large wildfire risk. Understanding patterns in woody cover increases will be paramount for assessing potential ecological outcomes and developing region-specific management approaches. Using remotely sensed land-use and vegetation cover data, we quantified changes in woody cover between 2001 and 2021 across land-use types in the eastern U.S. to determine the relative contribution of forest infilling and land-use conversion to woody cover increases. Woody cover increased across a range of land-use types in the eastern U.S. including wetlands, pasturelands, and forests. Infilling of deciduous forests and encroachment in open land-use types such as pasturelands dominated the northeast. In contrast, high levels of land-use conversion from non-woody land-use types to forests along with increasing woody cover in wetlands dominated the southeast. Our findings suggest that increasing woody cover in the eastern U.S. likely reflects both intentional increases of woody cover by silviculture as well as unintentional increases tied to wetland woody encroachment and forest densification. Our findings highlight areas to target ecological impact assessments and management efforts. Further, we demonstrate a growing need to assess the potential impacts of expanding pine plantation area on forest ecology and changing wildfire risk.

1. Introduction

Trees and shrubs are densifying and encroaching historically open ecosystem types across the globe (Archer et al., 2017), driven by factors such as fire suppression, land-use changes, shifting climate, and elevated global CO2. For example, grassland and savanna loss to forests has been documented in both South America (Rosan et al., 2019) and Sub-Saharan Africa (Mitchard and Flintrop, 2013; O'Connor et al., 2014; Stevens et al., 2017; Venter et al., 2018) at an average annual rate of 0.7 % and 0.25 %, respectively (Stevens et al., 2016). In Europe, the abandonment of traditionally grazed grasslands and meadows has led to transitions to shrublands or closed forests across multiple regions (Hansson and Fogelfors, 2000; Zarovali et al., 2007; Kesting et al., 2009). In Asia, shrub encroachment has been documented across numerous regions, including in Eurasian steppes (Liu et al., 2021) and Himalayan alpine meadows (Brandt et al., 2013). In North America, woody cover increases have been documented as ranging from 0.1 % to 2.3 % cover per year, depending on the region (Barger et al., 2011; Ivey et al., 2024). Savannas across Australia are experiencing increasing woody cover in both overstory and understory vegetation (Fensham et al., 2005; García Criado et al., 2020). Even in arctic tundra, rates of woody encroachment are estimated at 0.18 % per year (García Criado et al., 2020). While deforestation of closed systems remains a major threat to species diversity and global above-ground carbon stores (Decaëns et al., 2018; Li et al., 2022), woody densification and expansion pose a substantial threat to open ecosystems, leading to their degradation and, in some instances, driving ecological regime shifts (a hysteretic shift in ecosystem structure, function, and processes) that can lead to the loss of numerous ecosystem services (Scheffer et al., 2001; Nowacki and Abrams, 2008; Collins et al., 2021). Understanding the spatial patterns and dynamics of woody cover change is necessary to understand potential ecological impacts and support preventative management.

In North America, woody cover increases in open ecosystems have

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brought with them a myriad of ecological and economic consequences. For instance, in critical grassland and savanna ecosystems, increasing woody cover has been associated with large-scale ecological regime shifts driving declines in grassland and savanna flora and fauna and the ecosystem services they provide (Nowacki and Abrams, 2008; Ratajczak et al., 2012; Twidwell et al., 2013; Kinnebrew et al., 2020). For instance, the conversion of open lands to closed canopy forests resulting from fire suppression across the eastern U.S. has resulted in rapid ecosystem compositional and structural shifts driving declines in species richness of fire-adapted plants (Nowacki and Abrams, 2008). Over 40 % of grassland obligate bird species are declining in North America (Rosenberg et al., 2019), tied in part to woody encroachment (Sirami et al., 2009; Graves et al., 2010; Andersen and Steidl, 2019). Woody encroachment can alter hydrological processes including increasing runoff (Qiao et al., 2017), which can decrease soil and nutrient retention (Camill et al., 2004). In western United States (U.S.) rangelands, the value of livestock production lost to primarily unintentional woody encroachment between 1990 and 2020 is estimated to be around US$4.84 billion (Morford et al., 2022). Woody cover increases across North America have also been linked to heightened wildfire occurence and severity (Peterson, 2005; Stephens et al., 2012; Keeley and Syphard, 2019; Donovan et al., 2020), most recently in the eastern U.S. (Ivey et al., 2024), where risk to human life and property is extensive due to a high proportion of wildland-urban interface (WUI; Radeloff et al., 2018; Weidig et al., 2024).

Woody cover increased across the eastern U.S. by 37 % between 1990 and 2020 (Parra and Greenberg, 2022; Ivey et al., 2024). However, it is unclear how these increases are distributed across land-use types and thus what the ecological implications of these increases are, nor where management should be targeted. Prior to Euro-American settlement, most forests in the eastern U.S. experienced frequent fire that helped to maintain open forest stand structures and diverse herbaceous understories (Frost, 1998; Nowacki and Abrams, 2008; Guyette et al., 2012; Noss, 2018). Densification of forests and savannas in the east following Euro-American settlement has been tied to fire-suppression in historically fire-frequent forests, in many cases leading to mesophication, an ecological regime shift characterized by a shift from open forests dominated by fire tolerant species to dense forests dominated by shade-tolerant, fire sensitive species (Nowacki and Abrams, 2008; Waters, 2020; Hanberry et al., 2020). This process has been exacerbated by the ever-expanding Wildland Urban Interface (WUI) in the East that is associated with higher levels of woody cover than non-WUI forests due to limited management (Sonti et al., 2022). In addition to forest infilling, woody encroachment into historically herbaceous wetlands has been linked to fire suppression, altered drainage patterns, and land-use legacies in the eastern U.S. (Warren et al., 2007; Knickerbocker et al., 2009; Bart et al., 2016). Planted and managed pines have also been shown to be expanding in the east (Hanberry, 2013). Increases in woody cover may also be tied to purposeful land-use conversion, such as croplands or grazed grasslands being transitioned to commercial pine plantations (Drummond Loveland, 2010; Ramankutty et al., 2010).

Understanding the nature of recent woody cover increases is essential for addressing potential risks to ecosystem services and human activities. We utilize remotely sensed annual woody cover data to assess changes in woody cover between 2001 and 2021 across various land-use types to (1) identify which land-use types have experienced the greatest increases in woody cover and (2) determine the relative contribution of forest infilling and land-use conversion to woody cover increases. Our findings will support targeted regional assessments of the ecological outcomes of increasing woody cover as well as help pinpoint where management may be needed to reduce potential negative outcomes of increasing woody cover.

2. Methods

2.1. Data

We used the Eastern Temperate Forests Level I (L1) ecoregion, as designated by the Environmental Protection Agency (EPA, 2013), to define the eastern U.S. We used Level III (L3) ecoregions to hierarchically spatially subdivide the eastern U.S. to assess smaller-scale trends in vegetation change through time (Figure S1). Ecoregions delineate areas with similar patterns in biotic, abiotic, and anthropogenic ecosystem factors (Omernik and Griffith, 2014). The L1 ecoregions are primarily determined by topographic factors, while L3 ecoregions also integrate soil geology, climate, and potential natural vegetation (Omernik and Griffith, 2014).

We used the National Land Cover Database (NLCD) to characterize land-use types across L1 and L3 ecoregions (EPA, 2013). The NLCD dataset contains 16 different land-use types for the continental U.S. at two-to-three-year intervals between 2001 and 2021. We selected the most abundant land-use categories for our analysis: Deciduous Forest, Evergreen Forest, Mixed Forest, Shrub/Scrub, Grassland/Herbaceous, Pasture/Hay, Emergent Herbaceous Wetlands, Cultivated Crops, Woody Wetlands, and Developed (Figure S2). We merged all the Developed classes (Low Intensity, Medium Intensity, and High Intensity) into one category.

We sourced annual vegetation cover data from 2001 to 2021 from the Rangeland Analysis Platform (Jones et al., 2018; Allred et al., 2021) using Google Earth Engine (Gorelick et al., 2017). The Rangeland Analysis Platform (RAP) provides yearly fractional cover estimates for five functional groups (trees, shrubs, perennial forb and grass cover, annual forb and grass cover, and bare ground) at a 30-m resolution across the conterminous U.S. derived from sub-pixel classification of Landsat imagery. Because the RAP was originally designed for western rangelands where there are often clear distinctions in tree versus shrubs based on height, we combined the tree and shrub functional groups into one 'woody cover' class to avoid misclassification among shrubs and trees, as described in Ivey et al. (2024).

2.2. Objective 1: quantifying the change in woody cover across land-use types

To determine which land-use types are experiencing the greatest increases in woody cover at both the L1 and L3 scales, we quantified the increases in woody cover across three forest land-use types (Deciduous Forest, Mixed Forest, and Evergreen Forest), along with seven other major land-use categories: Shrub/Scrub, Pasture/Hay, Cultivated Crops, Grassland/Herbaceous, Developed, Woody Wetlands, and Emergent Herbaceous Wetlands. Using land-use data from 2021, we quantified the change in woody cover within each land-use type by (1) taking the difference in woody area between 2021 and 2001 and (2) calculating the rate of change in woody cover (Figure S2). Across each land use type, the total area of woody cover was calculated and divided by the area of that land use type and expressed as a percentage. We used Sen's Slope, a non-parametric estimate of the slope of a trend (Pohlert, 2023), to quantify the rate of change. Sen's Slope represents the median of all possible slopes between pairs of points within a dataset and is used to indicate the magnitude of a trend. It ranges from positive to negative infinity (Sen, 1968).

2.3. Objective 2: contrasting the contribution of forest infilling versus land-use conversion

To determine whether forest infilling or land-use conversion contributed most substantially to increasing trends in woody cover across the eastern U.S., we compared the relative increase in woody cover due to forest infilling versus land-use conversion across ecoregions. We defined infilling as increases in woody cover in areas classified as forest (Deciduous Forests, Evergreen Forests, and Mixed Forests) at the start and end of our study period. We classified land-use conversion into two categories: true conversion and early signals of conversion. True conversion was defined as a non-forest land-use type (Cultivated Crops, Emergent Herbaceous Wetlands, Grassland/Herbaceous, Pasture/Hay, Shrub/Scrub, Woody Wetlands) that converted to a forest land-use type over our study period (e.g., Pasture/Hay in 2001 to Evergreen Forest in 2021). Early signals of land-use conversion were non-forest land-use types that experienced an increase in woody cover without experiencing conversion to a forest land-use type. We defined non-forest types into two categories: non-woody (Grassland Herbaceous, Pasture/Hay, Emergent Herbaceous Wetlands) or woody transitional (Shrub Scrub, Woody Wetlands). Areas that experienced early signals of land-use conversion were either (1) areas that fell within the same non-forest or transitional type in 2001 and 2021 but experienced substantial increases in woody vegetation cover that could be reasonably linked to woody encroachment or (2) non-forest types in 2001 that were converted to woody transitional types in 2021 (Figure S2). Because the NLCD Cultivated Crops land-use type can include orchards and vineyards, we did not include this land-use type in our early signals of land-use conversion assessment, as distinguishing between encroachment versus shifts in crops within landscapes was not possible.

2.3.1. Forest infilling

We quantified the rate of change in woody cover area within forests using Sen's Slope (Pohlert, 2023). To further assess patterns of forest infilling, we broke infilling down into forests that remained within the same land-use type between 2001 and 2021 (e.g., Evergreen Forest in 2001 that was still Evergreen Forest in 2021) and areas that changed among forest types between 2001 and 2021 (e.g., Evergreen Forest in 2001 that changed to Mixed Forest in 2021). To determine how much woody cover was changing within forest types that stayed the same, we extracted the area occupied by woody vegetation and the average percent woody cover per pixel across areas that did not change land cover types between 2001 and 2021 and calculated a rate of change using Sen's Slope. We repeated this process for all sites that changed from one forest type to another.

2.3.2. Land-use conversion

We defined land-use conversion as (1) true land-use conversion or (2) early signals of land-use conversion. Areas that experienced true land-use conversion were locations that shifted from a non-forested NLCD land-use type in 2001 to a forested land-use type in 2021 (Deciduous, Evergreen, or Mixed Forest). Early signals of land-use conversion were non-forest land-use types that experienced an increase in woody cover without experiencing conversion to a forest type. This included non-forested areas that stayed non-forested but increased in woody cover and non-forested areas that transitioned to a woody transitional land-use type (Shrub/Scrub and Woody Wetlands). We calculated the area of woody cover (as extracted from the RAP) added within each land-use type that experienced conversion and the rate of increase in woody cover relative to each land-use conversion type using Sen's Slope.

We used Google Earth Engine to extract woody cover across land cover types. We conducted all statistical analysis and visualization in R (R Core Team, 2024) using RStudio (RStudio Team, 2025), the tidyverse suite of packages (Wickham et al., 2019), migest (Abel, 2023), and sf (Pebesma et al., 2024).

3. Results

3.1. Objective 1. quantifying the change in woody cover across land-use types

3.1.1. L1 Ecoregion scale

Across the L1 Eastern Temperate Forests, woody cover significantly increased across all forest types, as well as in Cultivated Crops, Woody Wetlands, and Pasture/Hay fields (Table 1). The greatest rate of increase in woody cover and the greatest overall woody hectares added to the landscape occurred in forest land-use types, which were the dominant land-use type in the eastern U.S. (Table 1). Of the forest types in the east, Mixed Forests experienced the greatest rate of increase (0.8 %/year), followed by Evergreen Forest (0.8 %/year), and Deciduous Forest (0.7 %/year). However, woody cover increases in Deciduous Forests added the greatest total amount of woody hectares in the East over our study period due to their expansive geographic extent (Table 1). Woody Wetlands increased by 0.4 %/year, while Pasture/Hay increased by 0.2 %/year. Cultivated crops showed the smallest significant increase in woody cover, at 0.04 %/year. In contrast, Shrub/Scrub significantly declined in woody cover over our study period (Table 1). There was no significant change in woody cover in Developed areas, Emergent Herbaceous Wetlands, or Grassland/Herbaceous land-use types at the L1 scale (Table 1).

3.1.2. L3 Ecoregion scale

At the L3 scale, woody cover increased in forests across almost every ecoregion (Fig. 1); only the East Central Texas Plains did not experience significant increases in woody cover in any forest type (Fig. 1). This was also the only ecoregion to experience a significant decrease in woody cover in Evergreen Forests (Fig. 1). Significant increases in woody cover in Deciduous Forests were relatively consistent across L3 ecoregions and occurred at lower rates than other forest types (Fig. 1). Increases in woody cover were greatest in both Evergreen Forests and Mixed Forests in northern and north-central ecoregions (Fig. 1).

Patterns in woody cover across L3 ecoregions varied substantially among non-forested land-use types (Fig. 1). Woody cover increased across Pasture/Hay areas at a relatively consistent rate except for in ecoregions in the southwest and in the Southern Coastal Plain (Fig. 1). Trends in woody cover in Grassland/Herbaceous and Emergent Herbaceous Wetlands were largely insignificant; however, there were small clusters of ecoregions in the southwest with significant declines in woody cover and some ecoregions in the northwest with significant increases in woody cover (Fig. 1). Increases in woody cover in Woody Wetlands were concentrated largely along the eastern and central portions of the eastern U.S. (Fig. 1). Significant declines in woody cover in Shrub/Scrub areas were spread across the eastern U.S., with the greatest declines occurring in the southwest (Fig. 1). Developed areas increased in woody cover in multiple ecoregions in the eastern and central portions of the eastern U.S. and declined in multiple ecoregions in the western portion of the eastern U.S. (Fig. 1). Finally, Cultivated Crops experienced the greatest increases in woody cover along the east coast and through portions of the southeast (Figure S3).

3.2. Objective 2: contrasting the contribution of infilling versus land-use conversion

3.2.1. L1 Ecoregion scale

At the L1 scale, forest infilling (land-use types that remained forests and experienced increasing woody cover) added woody cover to the landscape at a higher rate than land-use conversion (0.6 % woody cover per year vs. 0.5 % woody cover per year; Table S1, S2). However, conversion contributed a greater total number of woody hectares to the landscape over our study period (7.3 million ha added from conversion vs. 6.3 million ha added from infilling; Fig. 2). True conversion (non-forested types that became forested types) added 2 % woody cover per year, while early signals conversion (land-use types that remained non-forested but showed increasing woody cover) only contributed an additional 0.3 % woody cover per/year. By comparison, forest infilling added 0.6 % woody cover/year. The highest rates of woody cover increase through conversion occurred through the conversion of Cultivated Crops (3.8 %/year; Table S2) and Pasture/Hay (3.3 %/year; Table S2) to Evergreen Forest. When considered alongside the

Table 1
Changes in woody cover between 2001 and 2021 across 2021 NLCD land-use types.

NLCD Land Cover Type	Total Area (ha) 2021	Woody Cover 2001		Woody Cover 2021		Woody Cover Change			
		Total Area (ha)	Mean Woody Cover (%)	Total Area (ha)	Mean Woody Cover (%)	Change in Woody Area (ha)	% Change in Area	Sen's slope (%/year)	P-value
Cultivated Crops	46,045,336	1065,562	2.3	1507,809	3.3	442,247	42	0.04	< 0.001
Deciduous Forest	53,676,064	39,174,382	73.0	44,995,621	83.8	5821,239	15	0.65	< 0.001
Developed	27,575,936	3686,382	13.4	3835,518	13.9	149,136	4	0.02	0.608
Emergent Herbaceous Wetlands	4442,546	1009,905	22.7	895,195	20.2	-114,710	-11	-0.08	0.065
Evergreen Forest	27,034,662	18,365,968	67.9	22,642,382	83.8	4276,414	23	0.78	< 0.001
Grassland/ Herbaceous	5333,627	2703,092	50.7	1848,795	34.7	-854,297	-32	0.02	0.928
Mixed Forest	18,360,146	12,468,087	67.9	15,195,367	82.8	2727,280	22	0.81	< 0.001
Pasture/Hay	32,375,612	2447,881	7.6	3977,395	12.3	1529,513	62	0.21	< 0.001
Shrub/Scrub	5587,919	3179,073	56.9	2321,122	41.5	-857,951	-27	-1.00	< 0.001
Woody Wetlands	24,759,804	17,210,538	69.5	18,954,508	76.6	1743,970	10	0.42	< 0.001

conversion of Grassland/Herbaceous and Shrub/Scrub to Evergreen Forests, non-forested to Evergreen Forest land-use conversion represented over two-thirds of all woody hectares added through true conversion (2.5 million ha; Table S2, Fig. 2). The conversion of Woody Wetlands to any forested land-use type had the lowest rate of woody cover increase out of all true conversion types (0.7–0.9 %/year).

Early signals of conversion indicated by woody cover increases in non-forested land-use types were found within all early signal land-use types we studied but rates of increases in woody cover varied considerably (Table S3, S4). Woody cover within Pasture/Hay increased by 0.2 %/year, while woody cover within Grassland/Herbaceous increased by 0.6 %/year (Table S3). Emergent Herbaceous Wetlands increased in woody cover by 0.08 %/year (Table S4), but in areas where Emergent Herbaceous Wetlands were converted to Woody Wetlands, woody cover increased at a rate of 1.2 %/year (Table S4). Within Woody Wetlands, woody cover increased by 0.4 %/year (Table S4).

The vast majority of forests that experienced infilling stayed within the same forest type, with only 4 % of the area classified as forests in our study shifting from one forest type to another (Table S1). Of the forest types that stayed the same, the greatest rates of forest infilling occurred within Mixed Forests (0.8 %/year vs. 0.6 %/year Deciduous and 0.5 %/year Evergreen Forest); however, Deciduous Forest added the greatest total number of hectares over our study period due to its substantially larger footprint on the landscape (3.5 million ha added vs. 1.4 million ha Mixed and 1.0 million ha Evergreen; Table S1, Figure S4). Of the forests that shifted among forest types, Mixed Forests that transitioned to Evergreen Forest experienced the fastest rates of forest infilling (0.9 % cover/year), although the geographic area represented by Mixed Forest to Evergreen Forest transition was relatively small (348 k ha; Table S1).

3.2.2. L3 Ecoregion scale

At the L3 scale of the eastern U.S., the contribution of forest infilling versus land-use conversion to increases in woody cover varied spatially (Figs. 3, 4). The vast majority of ecoregions experienced significant increases in woody cover due to both forest infilling and land-use conversion (Fig. 3a, b). Northern ecoregions were characterized by higher rates of woody cover increase and a greater share of woody hectares added due to infilling, while southern ecoregions were characterized by a greater proportion of woody cover increases due to land-use conversion (Fig. 3c). Across most ecoregions, infilling in Deciduous Forests contributed more total hectares than infilling in Evergreen or Mixed Forests (Fig. 4a). However, in a few ecoregions along the Atlantic Coast, Evergreen Forest woody hectares added through infilling exceeded both Deciduous and Mixed Forests (Fig. 4a).

The majority of woody hectares added to the landscape from land-use conversion were tied to early signals of conversion rather than true land-use conversion (Fig. 3d). The rates of woody cover increase per year in areas showing early signals of land-use conversion were lower than the rates in areas experiencing true conversion (Fig. 3d). Areas showing early signals of land-use conversion made up a substantially larger portion of the eastern U.S. land area than areas that were converted from one land-use type to another. Across most ecoregions, the majority of woody hectares added through early signals of land-use conversion occurred in Pasture/Hay fields at rates of up to 0.7 %/year (Fig. 4c). In contrast, while woody cover increases in Grassland/Herbaceous land-use types occurred at rates of up to 1.2 % per year, it only made up a notable portion of the total woody cover added in the Arkansas Valley (Figs. 3, 4c). Woody cover increases in Woody and Emergent Herbaceous Wetlands also made up a substantial portion of increases in woody cover in multiple ecoregions (Figs. 3d, 4c). Shrub/Scrub areas had high rates of woody cover increase across most L3 ecoregions (up to 1.3 %/year) tied to the conversion of Pasture/Hay and Grassland/Herbaceous into Shrub/Scrub and woody cover increases in existing Shrub/Scrub. However, they only made up a large proportion of added woody cover in the East Central Texas Plains (Fig. 4c).

Across many L3 ecoregions, the majority of true conversion originated from Pasture/Hay and Grassland/Herbaceous land use types. Emergent Herbaceous Wetlands and Woody Wetlands contributed a relatively small proportion to the amount of woody cover tied to land-use conversion (Fig. 4b). Regardless of the originating land-use type, land-use conversions to Deciduous Forest and Mixed Forest contributed noticeably to increases in the total woody cover added within ecoregions, mostly in the northern half of the Eastern Temperate Forests (Figure S5). In many southern ecoregions, the conversion of non-woody and woody transitional land-use types (most commonly Grassland/Herbaceous and Shrub/Scrub) to Evergreen Forests made up the greatest portion of added woody cover tied to true conversion (Table S5, FigureS5).

4. Discussion

Woody cover is increasing across a range of land-use types in the eastern U.S. due to a combination of forest infilling and land-use conversion. Forest infilling is occurring at faster rates than land-use conversion, likely driven by a lack of fire combined with shifting climate and increasing CO_2 levels (Wigley et al., 2010; Archer et al., 2017). Infilling was most predominant in the north, where prescribed fire is less common despite relatively frequent fire return intervals within these regions prior to Euro-American settlement (Guyette et al., 2012; Ryan et al., 2013). In contrast, high levels of land-use conversion dominated the south. This was driven both by non-woody land-use types shifting to evergreen forest, likely linked to expanding pine plantations (Drummond Loveland, 2010; Xie et al., 2024), and increasing woody cover within wetlands, likely linked to woody encroachment (Budny and

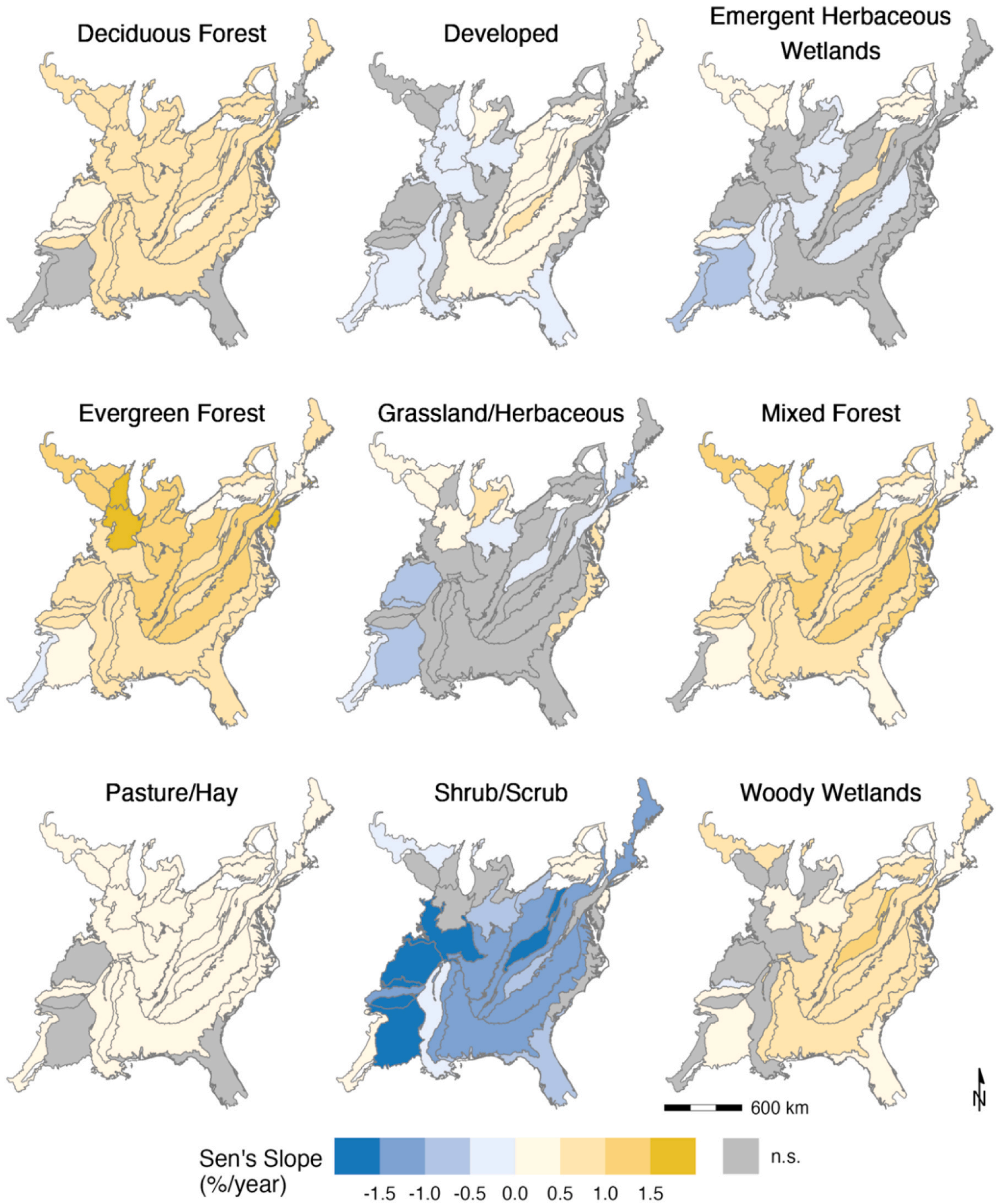

Fig. 1. Changes in woody cover (Sen's Slope of percent/year) from 2001 to 2021 across Level III ecoregions of the eastern United States for each assessed land-use type based on the 2021 NLCD. Significant declines in woody cover are indicated in blue, while significant increases are indicated in yellow, with a darkening color indicating a strengthening slope. The grey color indicates non-significant changes through time.

Benscoter, 2016). Across nearly all ecoregions, there were early signals of woody encroachment in non-forested land-use types like grasslands and pastures. Thus, our findings suggest that while the expansion of silviculture is likely contributing to increasing woody cover, particularly in the southeast, the majority of woody cover added in the eastern U.S. likely results from unintentional increases due to forest infilling and woody encroachment. Forest infilling and conversion of grass-dominated ecosystems to woody-dominated ecosystems have been tied to substantial ecosystem degradation, a loss of fundamental ecosystem services, and increasing wildfire risk (Nowacki and Abrams, 2008; Twidwell et al., 2013; Donovan et al., 2020; Ivey et al., 2024). The findings of our study highlight areas that are likely to be most impacted by woody cover increases and, similarly, where management can be targeted to reduce or halt woody infilling and encroachment.

We found that a large proportion of increasing woody cover in the east is associated with forest land-use types, suggesting the continued densification of eastern forests over the start of the twenty-first century tied in part to fire suppression. While vast swaths of previously open forest were lost due to land-use intensification in the east following Euro-American settlement, densification of the remaining open forests has been linked to a lack of fire and other low-severity disturbances that historically reduced understory trees (Hanberry and Abrams, 2018). Our

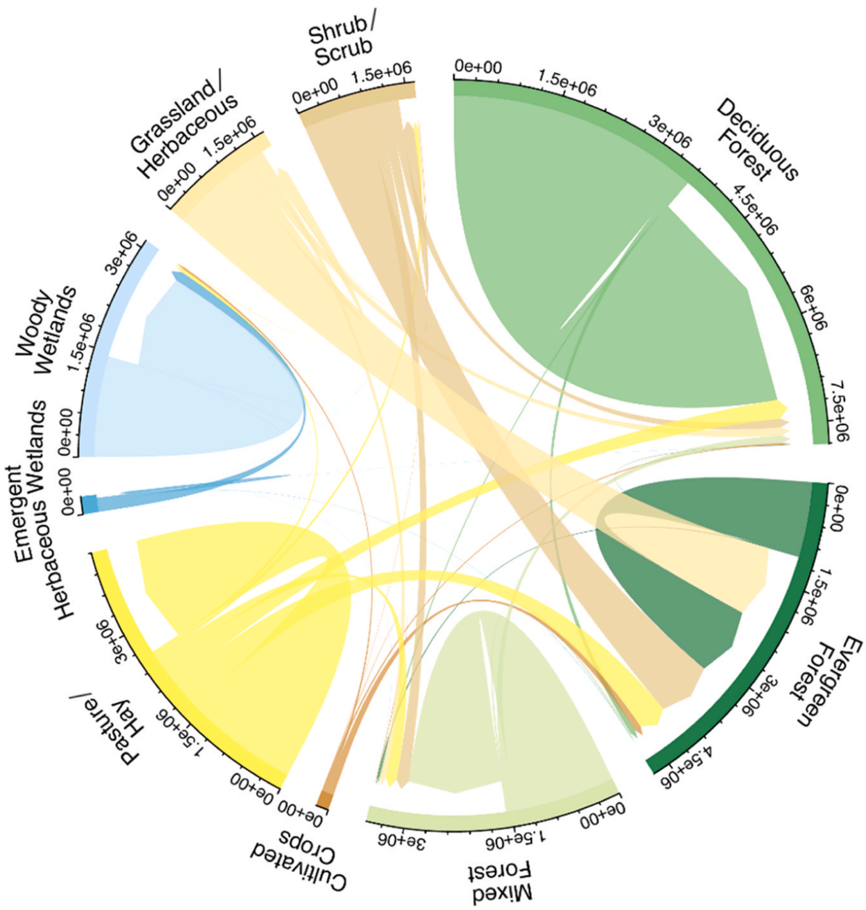

Fig. 2. Chord diagram depicting the proportion of woody cover added to the landscape through infilling, true conversion, and early signals within the L1 Eastern Temperate Forests ecoregion. The external axis is in hectares. The area of each land-use type along the external axis represents hectares of woody cover added from 2001 to 2021 in areas that belong to that land-use type in 2021 or were that land-use type in 2001. Arrows from one type to another indicate a change in land-use type between 2001 and 2021. The relative thickness of the arrow indicates how much woody cover was added in that conversion. When an arrow loops back on itself, it indicates increases in woody cover without a change in land-use type (infilling for forested types and early signals for non-woody and transitional types).

documented increases in woody cover across forests in the east align with documented shifts in forest composition towards shade-tolerant species (Knott et al., 2019) tied to mesophication, an ecological regime shift from fire-tolerant plants to dense shade-tolerant mesophytic species caused by fire suppression that drives numerous alterations in ecosystem function (Nowacki and Abrams, 2008; Hanberry et al., 2020; Hale and Peterson, 2024). Increases in woody cover in forests were more predominant in the northeast, which may be associated with differences in prescribed burn culture across regions. Prescribed fire has been shown to substantially decrease forest density and maintain an open ecosystem structure (Peterson and Reich, 2001; Albrecht and McCarthy, 2006; Addington et al., 2015; Dems et al., 2021). In the southeast, where public acceptance of prescribed fire is high and legislation protects prescribed burners by setting higher thresholds for negligence (Ryan et al., 2013; Wonkka et al., 2015), forest density tends to be lower than in the northeast (Woodall et al., 2006). However, we found that forests in the southeast still experienced increases in woody cover. This may be because frequent prescribed fires in the southeast tend to be clustered in hotspots (Cummins et al., 2023) or because of warming air temperatures and CO2 fertilization, which have been tied to synchronous woody recruitment in numerous regions (Wigley et al., 2010; Cannone and Malfasi, 2024). Regardless, our findings suggest that increasing low-intensity disturbance like prescribed fire within eastern forests should be a priority for reducing the impacts of woody infilling in fire-suppressed, historically open forest ecosystems.

The woody encroachment documented in pasture and hay fields may reflect forest regrowth following agricultural abandonment that has been observed across formerly semi-managed landscapes in the eastern United States (Foster et al., 1998). Without consistent human disturbances such as mowing, grazing, or burning, forests are able to regrow on many pastures and agricultural fields (Matlack, 1997; Foster et al., 1998; Bellemare et al., 2002). Transition of pasture and hay fields to forests over the past century in the eastern U.S. has helped return the abundance of forests in the east closer to the levels found before Euro-American colonization (Jeon et al., 2014; Homer et al., 2020). While some pastures are likely being intentionally converted to forest for commercial or aesthetic purposes, the increase in woody cover within remaining pastures may indicate increasing shrub and sapling cover due to abandonment or ineffective management techniques (Archer et al., 2017). While woody encroachment in pastures could lead to reduced forage quality for livestock (Auken, 2000), it could also represent a transition from a heavily managed habitat primarily dominated by non-native grasses to an early successional forest of native species. Although an old-growth or mature forest cannot be recovered immediately upon abandoned agricultural land, the regrowth of natural forests could provide an offsetting effect to the rapid loss of overall forest cover to urbanization (Jeon et al., 2014).

Increases in woody cover tied to non-forest land-use types being converted to evergreen forests in the southeast likely represents the expansion of pine plantation silviculture. While natural pine forests across the eastern U.S. have decreased in dominance due to fire-suppression, planted and managed pines have been shown to be expanding (Hanberry, 2013; Xie et al., 2024). In the southeast, pine plantations occupy almost a quarter of the landscape (Fagan et al.,

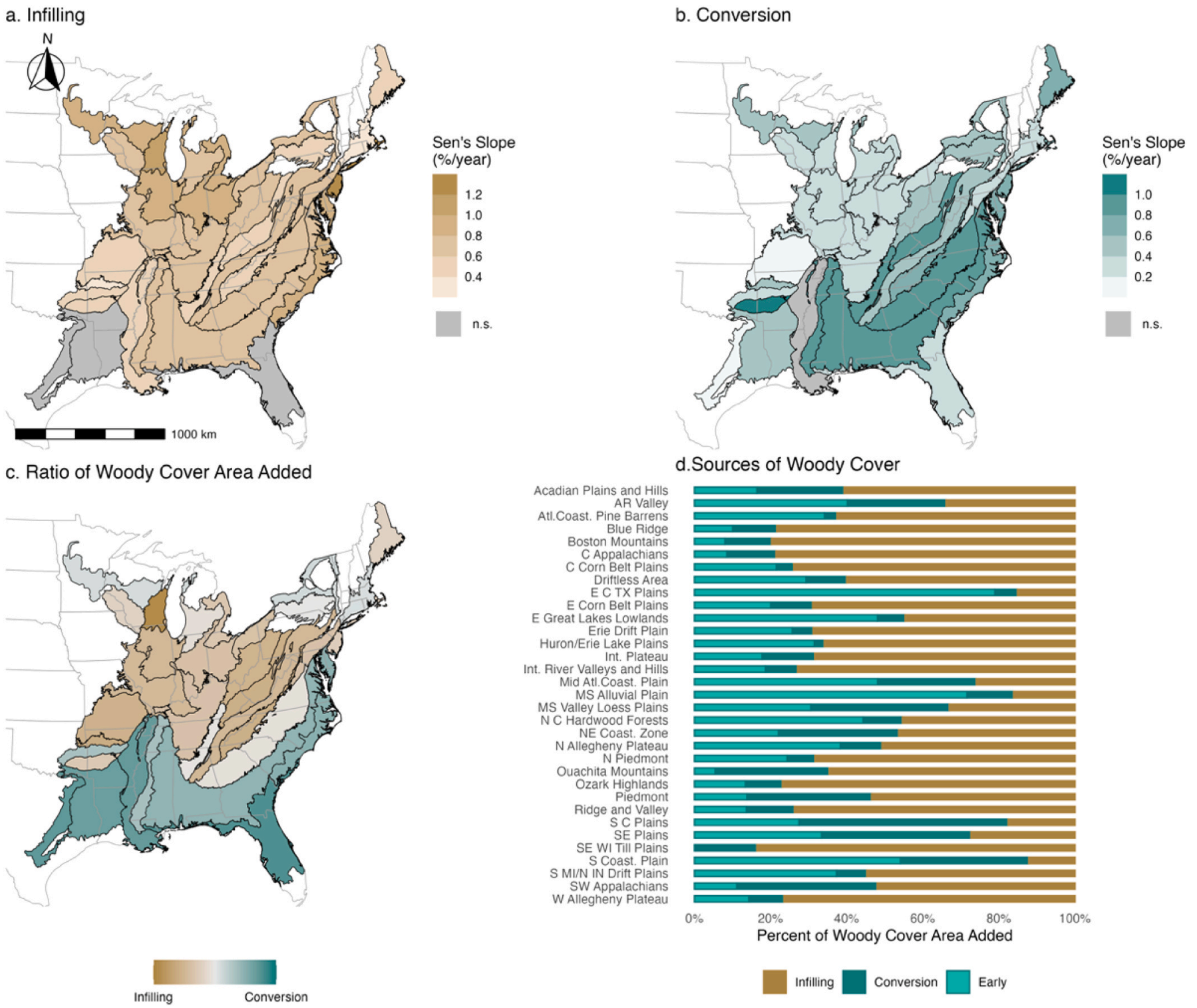

Fig. 3. a & b. Geographic depiction of the rates of woody cover increase (percent cover/year) as measured by Sen's Slope across L3 ecoregions of the eastern United States. Regions with darkening colors represent higher rates of increase in percent of the total landscape occupied by woody cover. Regions with non-significant trends are depicted in gray. a. The percentage of total land cover/year of woody cover added to the landscape through infilling. b. The percent of total land cover/year of woody cover added to the landscape through all land-use conversion (early signals, transitional, true conversion of non-forested land-use types to forested land-use types). c. Geographic representation of the ratio of infilling to land conversion in the total ha of woody cover added to the landscape over the study period (2001–2021). Grey represents areas of equal contributions of infilling and conversion. d. Bar chart depicting the sources of woody cover added to the landscape across regions during the study period.

2018). The ecological outcomes of this transition may vary. Most timber acres are intensively managed with a regime of site preparation, improved stock, short rotation, and clear-cutting, which have been shown to support lower biodiversity than less intensively managed forest (Stephens and Wagner, 2007; Martínez-Jauregui et al., 2016), though these stands may still help support the recovery of open forest ecosystem services in a region that lost substantial amounts of open forest due to land-use intensification (Lugo, 1997; Hanberry and Abrams, 2018; Pawson et al., 2009). The spatial arrangement of pine plantations can also increase positive ecosystem impacts by introducing a diverse mosaic of harvest ages and gap sizes (Thill, 1990; Jones et al., 2010). It is unclear how the structure, composition, and spatial arrangement of pine plantations contribute to increasing wildfire risk in the eastern U.S., which has been linked to higher levels of woody cover (Ivey et al., 2024). Plantations in temperate forests are twice as likely to suffer stand-replacing wildfires than natural production forests (Bousfield et al., 2025). As the region continues to see increasing large wildfires, understanding the role that land-use conversion to pine plantations play in enhancing or mitigating ecological structure and function will be needed.

Woody encroachment in wetlands played a substantial role in increasing woody cover in the coastal southeast, along the Mississippi river, and around the Great Lakes. Woody encroachment and infilling in wetlands are occurring globally (Saintilan and Rogers, 2015; Sun et al., 2024) and can result in significant ecological degradation, including altered hydrological processes (Berg et al., 2009; Budny and Benscoter, 2016), biodiversity loss (Warren et al., 2007), and loss of ecosystem services (Barbosa da Silva et al., 2016). Woody encroachment into wetlands has been associated with shifting climate conditions and altered fire regimes (Clark and Wilson, 2001; Berg et al., 2009; Saintilan and Rogers, 2015). In the southeastern U.S., fire suppression has led to the encroachment of native shrubs and trees like titi (*Cliftonia*

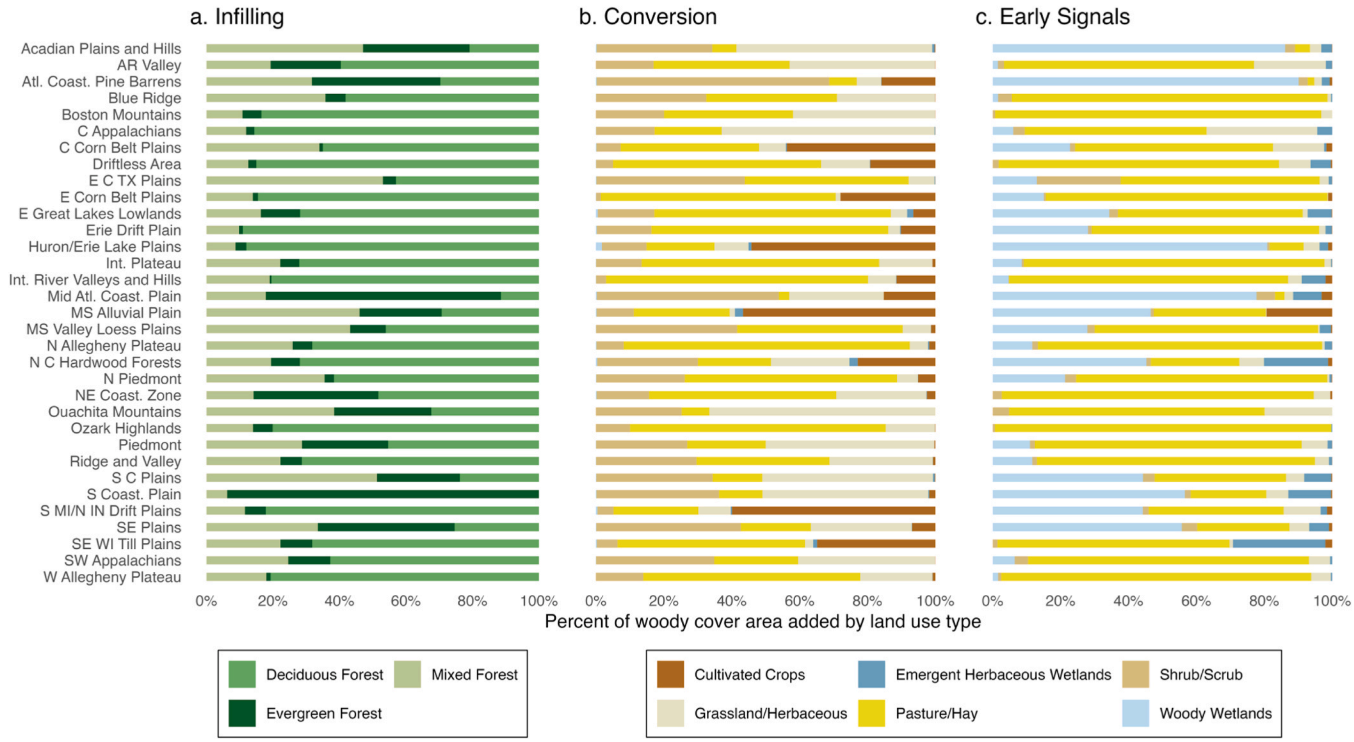

Fig. 4. Stacked bar plot depicting the proportion of woody cover added by each land-use type across ecoregions for (a) infilling, (b) land-use conversion, and (c) early signals of land-use conversion categories.

monophylla) into wetlands, which can form dense thickets that alter water chemistry and decrease herbaceous cover and species richness (Warren et al., 2007; Minogue et al., 2023; Cory et al., 2023). Thus, the observed increases in woody cover could have extensive impacts on wetland function. Restoration of wetlands following woody encroachment may be intensive and require multiple methods to return the system to its original ecological function (Clark and Wilson, 2001; Watson et al., 2016; Ding and Eldridge, 2023). Our results highlight regions where assessments of the ecological impacts of woody encroachment in wetlands could be prioritized, and where management actions could be targeted.

While remotely sensed data like NLCD and the RAP offer the benefit of sampling across vast spatial scales, the limitations of potential misclassifications should be considered when interpreting our results. For example, the prevalence of pine plantations across our study area could be underestimated due to misclassifications by the NLCD. As much as twenty-two percent of juvenile-stage pine plantations have been misidentified as Shrub/Scrub by NLCD and twenty percent misidentified as woody wetlands (Fagan et al., 2018). However, the NLCD Shrub/Scrub land-use type also includes natural forest regeneration, so not all Shrub/Scrub that transition to Evergreen Forest represent plantation pines. Similarly, Emergent Herbaceous Wetlands were the most common land-use type to transition to Woody Wetlands, signifying that encroachment of an existing wetland was more likely than potential NLCD misclassification. It is also possible that a small portion of areas classified in 2001 as Pasture/Hay or Grassland/Herbaceous may represent pre-2001 plantations that were undergoing turnover. In addition, woody cover information obtained from the RAP showed higher levels of year-to-year fluctuations within Emergent Herbaceous Wetlands and Pasture/Hay NLDC classifications, which may represent larger error rates in woody cover classification within these land-use types. That said, increasing trends in woody cover over the 20-year study period still clearly emerged, regardless of inter-year variability.

Increases in woody cover across the eastern U.S. are multifaceted, requiring region-specific understanding of the distribution of woody cover increases across ecosystems. Our findings can be used to identify regions that should be targeted for ecosystem impact assessments tied to increases in woody cover and regions that could be prioritized for management to reduce ecosystem service loss and ecological degradation. For instance, our findings suggest that the reintroduction of prescribed fire combined with other fuel management approaches is likely necessary across multiple ecoregions to halt woody in-filling and help restore deciduous forests that have experience mesophication, though there are numerous legal and logistical barriers that need to be overcome to achieve wide-spread prescribed fire application (Wonkka et al., 2015; Schultz et al., 2019; Kupfer et al., 2020). This will be particularly important under the highly variable conditions predicted under climate change, which may enhance the risk of wildfire within areas with high woody fuel loads (Bedel et al., 2013; Mitchell et al., 2014; Lesinger and Tian, 2022). In contrast, in the southeast, investigations into the role of pine plantations in shaping forest ecology and altering wildfire risk could be prioritized. How woody cover impacts ecosystems will vary based on the social-ecological dynamics of systems within a given region. Regional differences in land use, hydrology, political boundaries, soil qualities, and fire regimes will greatly alter how woody cover shapes ecosystems. Thus, our findings can be used to help identify where it is most crucial to begin these investigations.

Author Contributions

Michaella Ivey, Noah Weidig, and Victoria Donovan contributed to study conceptualization, investigation, and method design. Michaella Ivey and Noah Weidig acquired data and performed formal analysis. Victoria Donovan acquired funding and provided project administration, supervision, software, and resources. Noah Weidig performed visualizations. Alan Ivory performed data validation. All authors contributed to the writing of the original draft and subsequent reviews and editing.

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CRediT authorship contribution statement

Victoria M. Donovan: Writing – review & editing, Writing – original draft, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Alan A. Ivory:** Writing – review & editing, Writing – original draft, Validation. **Noah C. Weidig:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Ivey Michaella Anne-Valkenaar:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

Declaration of Competing Interest

The authors have no relevant financial or non-financial interests to disclose.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.123446.

Data availability

Data is open access and available online. Links to code used for figures provided.

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