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Expanding wildland-urban interface alters forest structure and landscape context in the northern United States

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Abstract

The wildland-urban interface (WUI), where housing intermingles with wildland vegetation, is the fastest-growing land use type in the United States. Given the ecological and social benefits of forest ecosystems, there is a growing need to more fully understand how such development alters the landscape context and structure of these WUI forests. In a space-for-time analysis we utilized land cover data, forest inventory plots, and housing density data over time to examine differences in forest characteristics of the northern US across three WUI change classes: (a) forest that has been in WUI housing density levels since at least 1990 (old-WUI), (b) forest where development crossed the WUI housing density threshold after 1990 (new-WUI), and (c) forest with little to no housing development (non-WUI). Of the 184 million acres of forest in the study area, 34 million acres (19%) were in old-WUI, 12 million acres (7%) were new-WUI, and 136 million acres (74%) were non-WUI. In general, as areas transitioned from non-WUI to newer WUI to older more established WUI, the forest was associated with decreased spatial integrity, increased forest-developed edges, and lower proportions of forest in the surrounding landscape. Forest in the WUI had greater carbon storage, with greater aboveground biomass, relative stand density, and more live trees per hectare than non-WUI forest, suggesting greater capacity to sequester carbon compared to non-WUI forest. At the same time, WUI forest also had significantly reduced structural diversity compared to non-WUI forest, with fewer saplings, seedlings, and dead trees per hectare. Forest that more recently crossed the WUI housing density threshold appeared to be on a trajectory towards that of old-WUI forest. These differences in forest structure across the northern US suggest reduced capacity for forest regeneration in the WUI and the potential for changes in other ecological functions.

1. Introduction

Across the globe, the footprint of development is expanding, often in excess of population growth rates, leading to widespread impacts on forests and other natural ecosystems (Seto *et al* 2011, Bradbury *et al* 2014). Within the United States (US), there has been a sustained expansion of the residential footprint for decades, much of it in low-density exurban areas as homeowners seek rural lifestyles, natural amenities, and/or affordable housing (Brown *et al* 2005, Gosnell and Abrams 2011, Golding and Winkler 2020). When this development occurs within wildland vegetation, it has given rise to a rapidly growing wildland-urban interface (WUI), defined in the US as the zone where housing density greater than 6.17 houses km^{-2} is found within and in close proximity to forest and grasslands (Radeloff *et al* 2018). From 1990 to 2010, the WUI of the conterminous US (CONUS) expanded by 41% in housing units (30.8–43.4 million) and 33% in area (581 000–770 000 km^2). By 2010, such WUI development made up 9.5% of the land area of the CONUS and 33% of all houses (Radeloff *et al* 2018). The WUI has been a useful construct worldwide in identifying where wildfire poses the greatest risk to human communities (e.g. Price and Bradstock

2013, Modugno et al 2016, Miranda et al 2020). Although it has been asserted that the WUI concept is relevant for a broad suite of natural resource management challenges beyond fire (Bar-Massada et al 2014), little is known about how expansion of the WUI affects forest stand structure and landscape context over time, particularly in regions where fire is a less prominent feature of native ecosystems.

With the expansion of development in proximity to forests and grasslands, there is increasing concern about the environmental effects of low-density housing on remaining natural vegetation (Gounaridis et al 2020). Housing growth and associated development can lead to habitat loss and fragmentation (Radeloff et al 2005) that has been linked to decreased biodiversity (Pidgeon et al 2007), altered hydrology and reduced water quality (McGrane 2016), spread of exotic invasive species (Gavier-Pizarro et al 2010), and increased wildfire activity (Balch et al 2017). Despite these concerns, forest cover remains extensive in many areas with housing development. Indeed, most forest is found in proximity to some development, even if low-density (Radeloff et al 2005, Van Berkel et al 2018). When forests and housing are intermingled, forests still provide important ecosystem services to residents from local to regional scales, including maintaining water quality, carbon storage, nutrient cycling, wildlife habitat and biodiversity, and climate regulation, as well as recreation and health benefits (as summarized by Cook et al 2011). Given the extent of forest in close proximity to housing, there is a growing need to more fully understand how development alters the stand structure of remaining forests in these areas and resulting impacts on ecosystem services (Riitters et al 2017, Oswalt et al 2019, Pomara and Lee 2021).

Existing research on changing forest structure in both rural and urbanizing landscapes suggests that forests in the WUI may have a range of stand structure and biomass outcomes, depending on spatial and temporal scales. For example, a local study of urban, developing, and rural forest in the southeast US found changes in forest structure and condition resulting from changes in land use patterns, with housing density alone accounting for the largest portion of the variation (Styers et al 2011). Globally, changing environmental drivers and disturbance regimes are increasing large tree mortality and leading to shorter-statured, younger, lower-biomass forest stands, reducing potential carbon storage (McDowell et al 2020). Similarly, parcelization of forested land in the midwest US was found to increase fragmentation and result in less dense stands with younger and shorter trees (Gustafson and Loehle 2006, Zhu and Liu 2019). However, forest fragmentation associated with urbanization in the northeast US has been associated with increased forest growth and biomass while increasing vulnerability to heat stress (Reinmann and Hutyra 2017; Reinmann et al 2020, Morreale et al 2021). There is also evidence that urban environmental drivers such as climate, biotic invasion, pollution, and disturbance can negatively impact native plant recruitment processes and forest regeneration (Piana et al 2019), leading to divergent successional trajectories in urbanizing forests (Piana et al 2021). Heavy deer browse and invasive understory plants are two of the most widespread threats to forest regeneration in these landscapes (Aronson and Handel 2011), which may lead to substantial differences in tree seedling densities and future WUI forest structure and composition.

As landscapes where people live with, recreate in, and depend on forests, WUI areas have both important ecological and social value and are therefore critical to manage sustainably (Zipperer et al 2023). For this investigation we focus on the northeast and north central US, a region that combines both nationally significant amounts of forest cover and a long history of urban development. Much of the region's forest is spread across numerous small-scale private landowners and supports a diverse timber industry. The region also shares a common land use history of widespread forest clearing throughout the 1800's, starting earliest in the east, followed by widespread forest regrowth as fields were abandoned for agriculture farther west. Urban development of the region also began earliest in the eastern coastal states. The distribution of present-day WUI forest among public and private landowners of the region may provide insight into differences in forest stand structure, as WUI landowners and surrounding communities may have different management objectives and strategies compared to those of more remote wildland forest. For example, non-corporate forest owners in the WUI often rank timber management and harvest lower than other land management objectives, such as investment, aesthetics, and recreation (Zhang et al 2005, Butler et al 2016, 2021). Similarly, management priorities on public forest lands in the WUI are more likely to focus on water quality, wildlife habitat, recreation, and aesthetics, rather than timber harvest (Dwyer and Chavez 2004). WUI communities may also oppose certain management activities (e.g. prescribed fires) and silvicultural treatments such as clear-cutting, thinning and salvage operations, or short-rotation forestry (Kittredge et al 2017), potentially preventing these activities from occurring on public or private lands.

We investigate effects of human development in the WUI on forest extent, landscape context, and stand structure for a 24-state region of the northern US using a combination of remotely sensed land-cover data, forest inventory data, and housing density data that has been processed by Radeloff et al (2017) to allow block-level change analysis back to 1990. To date, it is unclear whether WUI forest characteristics reflect initial disturbance when development first occurred, or whether differences intensify over time with continued presence or intensification of housing development. Using a space-for-time substitution approach we examined three WUI change classes: (a) forest that has been in WUI house density levels since at least 1990 (old-WUI), (b) newer WUI forest established since 1990 (new-WUI), and (c) forest that remained outside of the WUI in 2010 (non-WUI). Our study seeks to answer the questions: (a) what are the range of landscape patterns (e.g. forest fragmentation, proportion of developed landcover) associated with each WUI change class? (b) Are particular forest types and ownerships disproportionately impacted by the WUI? (c) What type of change trajectory is suggested by differences in forest stand structure between the WUI change classes? Does new-WUI forest have structural characteristics that closely resemble old-WUI forest, that are intermediate between older WUI and non-WUI forest, or that are most dissimilar to non-WUI forest? At a time when WUI development is increasingly receiving management attention across the globe, this study provides valuable insight into how forests respond to a profound and widespread source of disturbance.

2. Methods

2.1. Study area

Our study area encompasses 24 states of the northern region of the US, which range from heavily forested in the east to sparse woodlands in the Great Plains states to the west (figure 1). Forests across the northern US are distinguished by strong climatic seasons and vary from conifer and mixed conifer and hardwood types in the north to hardwood-dominated forests characterized by tall tree species towards the south (Smith *et al* 2009). Most present-day forest was established after logging occurred, either after initial harvest or subsequent harvests (Brush 1986, Foster *et al* 1998, Rhemtulla *et al* 2007). Today forests are recognized in state forest action plans (e.g. NYSDEC 2020) for their direct role in state economies through the forest products, outdoor recreation and tourism industries, and for their important role in climate change mitigation, the health of air and water supplies, quality of life for local communities, and wildlife habitat. The region is facing many, potentially compounding, threats to forest health and sustainability. Fragmentation and land use change are major stressors to forest ecosystems, and other threats like non-native species, forest disease and insect pests, and herbivory are themselves heavily influenced by forest fragmentation and urbanization (Brandt *et al* 2014, Handler *et al* 2014, Butler *et al* 2015, Butler-Leopold *et al* 2018, Janowiak 2018). Figure 1 illustrates the distribution of forest land by WUI change class across the study area. Thirty percent of forest in the northeast and 15% of midwest forest was categorized as WUI in 2010 (Zipperer *et al* 2023).

2.2. Data sources

2.2.1. Housing density

Radeloff *et al* (2018) mapped the WUI from 1990 to 2010 based on definitions from the Federal Register (USDA and USDI 2001), combining information on housing units at the census block level from the 1990, 2000, and 2010 Decennial Censuses with wildland vegetation information from the 2011 National Land Cover Database (NLCD) (Homer *et al* 2020). Because census block boundaries change with each Decennial Census, housing units and population from 1990 to 2000 were allocated into 2010 census block geometries (Radeloff *et al* 2018). All WUI areas have $\geqslant$1 house/40 acres (6.17 houses km^{-2}), with housing densities calculated by excluding any public lands in the census block, using Protected Area Database, version 2 (Institute 2012), following Federal Register (USDA and USDI 2001) definitions. As calculated, WUI data (1990–2010) include data on housing proximity to wildland vegetation, as determined by NLCD. Because we use forest structure data from inventory plots, we utilized the housing density threshold alone (6.17 houses km^{-2}) to determine whether a block was in the WUI at each census date.

2.2.2. Landscape pattern

To characterize forest landscape patterns in the WUI we used four metrics: forest area density, proportion of forest-developed edges (Riitters *et al* 2012), landscape mosaic (Riittters *et al* 2009), and spatial integrity index (SII) (Tavernia *et al* 2016, Pugh *et al* 2017). These metrics were chosen both for their robustness for repeated accurate measurements over time (Riemann *et al* 2008), and to characterize general categories of landscape pattern relevant to suspected ecological impacts—patch size distribution, edge and interspersion, connectedness, and land cover context (Riva-Murray *et al* 2010). The first three metrics were analyzed at three neighborhood scales (15 ha, 66 ha, and 590 ha) for each forest plot, using data from the 2011 National Land Cover Database (NLCD) (Homer *et al* 2020). A range of neighborhood sizes was used to measure both finer-scale (and higher spatial frequency) and coarser-scale (and lower spatial frequency) landscape patterns (Ritters *et al* 2002, Seto *et al* 2011). The ‘landscape mosaic’ indicator used here is a metric developed by Riitters *et al* (2009) that characterizes the anthropogenic composition of the neighborhood around a forest plot by translating the percent agriculture, percent developed, and percent

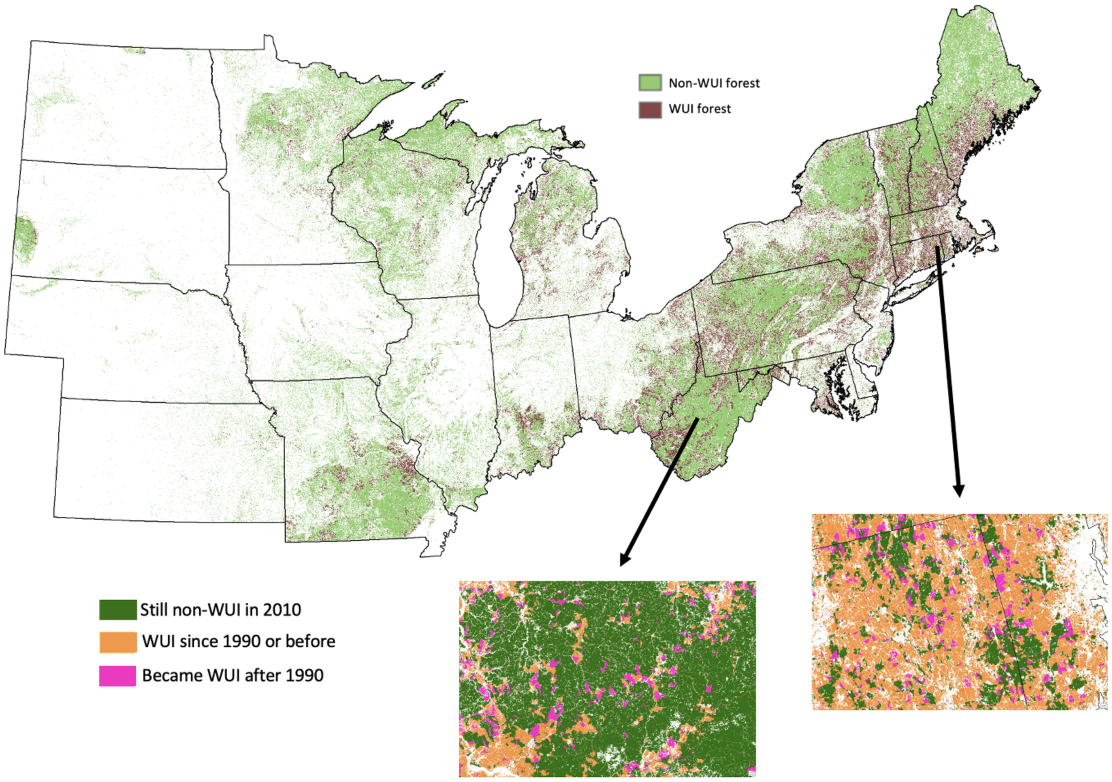

Figure 1. Twenty-four state study region of the northeastern and north central United States showing forest inside and outside the wildland-urban interface (WUI). Inset maps depict WUI change classes.

natural (all other land cover types) of the neighborhood into 19 classes using a tri-polar classification (figure 2). These landscape mosaics can be used to visualize gradients in landscape composition and to characterize landscape differences and transitions over time (Riitters *et al* 2009). Forest SII is a weighted combination of forest area density (weight = 0.25), patch size (0.25), and path distance to nearest forest core patch (0.5), using a method developed by Kapos *et al* (2002) adapted to 30 m resolution land cover data (Tavernia *et al* 2016). The resulting SII values for each pixel range from 0 to 10, with higher values reflecting forest pixels with greater neighborhood forest densities that belong to larger patches and are more proximate to (or within) core forest. The SII metric was calculated at two neighborhood scales (7 ha and 495 ha) using 2006 NLCD, the most recent SII date available.

2.2.3. Forest inventory

National permanent ground plots are distributed approximately every 2428 ha across the 48 conterminous states of the US, at their base sampling intensity. Tree- and site-level attributes are measured continually, with repeat measurements at regular temporal intervals on plots that have at least one forested condition (USDA Forest Service 2021, 2007). For this study, we used '2013' data, which includes USDA Forest Service Forest Inventory and Analysis (FIA) plot data inventoried from 2009 to 2013, to temporally match the 2010 census data. We excluded plot conditions with <5% forest cover. A total of 41 347 inventory plots were analyzed for a variety of characteristics related to forest structure and 37 728 plots were analyzed for tree seedling abundance. Seedling data is collected on four microplots within the FIA plot, resulting in a difference in the number of seedling forest plots available (USDA Forest Service 2021).

Differences in forest structure among WUI change classes was evaluated using: mean aboveground live tree biomass; relative stand density (RSD); live tree, sapling, seedling, and dead tree density (trees per ha); and tree density in 10 cm size classes (diameter at breast height [DBH]). Aboveground biomass includes standing live trees and saplings. Current methods for estimating live tree and sapling biomass in the national FIA database are documented in Burrill *et al* (2018). RSD is calculated using the mean specific gravity of all trees in a stand to predict maximum stand density index (SDI) and subsequently taking current SDI divided by maximum SDI (Woodall *et al* 2006). Summaries of each variable on a per area basis (ratio estimates) were compiled following methods in Bechtold and Patterson (2005).

2.3. Data analysis

Forest inventory plot locations were assigned using their spatial location to one of three WUI change classes using housing density data from 1990 to

2010: (a) old-WUI (forest that has been in WUI since at least 1990); (b) New-WUI (forest that has become WUI since 1990); and (c) Non-WUI (forest that has remained at housing densities below the WUI threshold). 2.5% of forest in the study area switched from WUI to non-WUI housing densities at some point during the study period and these areas were excluded from data summaries and analysis. Landscape pattern metrics were associated with each forest plot using its spatial location and summarized for each WUI change class. To describe general forest and housing conditions in the WUI, we summarized housing density by WUI change class and estimated forest land area by ownership type and forest type by WUI change class.

Generalized least squares (GLSs) regression models were fit using the gls function in the nlme R package (Pinheiro *et al* 2018) to analyze the relationship between WUI change class and each forest structure response variable described above. The use of GLS models allowed for different variance structures by WUI change class, which were incorporated into the models using the varIdent function to meet assumptions of homoscedasticity. Least-square estimated means by WUI change class were compared using Tukey contrasts and differences were considered significant at $\alpha = 0.05$.

3. Results

3.1. Landscape context of forest in the WUI

Of the 184 million acres of forest land in the 24-state study area, 34 million acres (19%) were in old-WUI, 12 million acres (7%) were new-WUI, and 136 million acres (74%) were non-WUI. The study region contains local variation in the proportion of forest in the different WUI classes (figure 1), but this analysis focuses on region-wide patterns. Measures of forest pattern and landscape context around forest plots provide an indication of the extent of several different types of landscape change commonly associated with anthropogenic influence, including forest fragmentation and increasing proximity of developed and agricultural land cover. Summary analysis by WUI change class found consistent patterns of forest landscape context and spatial integrity across all spatial scales examined. Consequently, we present summaries at the 66 ha scale for three of the landscape metrics and at the 7 ha scale for the SII (figure 2).

Across the three change classes, from non-WUI to newer WUI to older more established WUI, we observed a progressively lower proportion of core forest (the highest spatial integrity class) and an increase in forest fragments (the lowest spatial integrity class) (figure 2). Forest landscapes surrounding non-WUI plots had 55% more core forest than landscapes around old-WUI plots and 28% more core forest than landscapes around new-WUI plots. We also observed an increasingly less natural landscape, increasing amount of forest-developed edges, and decreasing forest in the surrounding landscape as we compared non-WUI to new-WUI to old-WUI.

Housing density distributions varied considerably by WUI change class (figure 3). Forest outside of the WUI had housing densities below 6.17 houses km^{-2} by definition, with an average housing density of 1.30 ($\pm$.01 SEM) houses km^{-2}. Forest that had been in the WUI since at least 1990 (old-WUI) had an average housing density of 42.71 ($\pm$1.23) houses km^{-2} and forest that had more recently become WUI (new-WUI) had an average housing density of 12.91 ($\pm$1.02) houses km^{-2}. We found that old-WUI had a more even distribution of housing densities compared to new-WUI, a pattern which may continue to evolve over time as 'newer' WUI areas experience continued development and associated increases in housing density.

3.2. Forest types and ownership in the WUI

Forest in the northern and eastern US is largely held by private landowners with only 27% of forest land in public ownership. WUI forest is even more unlikely to be owned by federal or state government agencies (figure 4; 2% and 3% of forest area, respectively), while 28% of forest owned by local governments was located in the WUI. Most of the WUI forest in the study region was privately owned, with 39% of non-corporate privately owned forest and 18% of corporately owned forest located in the WUI. More recently established WUI (new-WUI) was most prevalent in non-corporate privately owned forest (27%), and least prevalent in local government forest (17%).

Forest types of the northern US that tend to be found at higher elevations, such as maple/beech/birch, aspen/birch, and spruce/fir, have a smaller percentage of their total area in the WUI (24%, 14%, and 7% in WUI, respectively). In contrast, oak-dominated forest types such as oak/pine (40% in WUI) and oak/hickory (31% in WUI) are more impacted by the WUI (figure 5). This pattern may reflect the suitability of different forest ecosystems for commercial harvesting and urban development.

3.3. Forest structure in the WUI

We found statistically significant differences in forest structure by WUI change class (figure 6). Forest in the WUI had significantly greater aboveground biomass ($F = 378.58$; $p < .0001$) and RSD ($F = 81.56$; $p < .0001$) than forest outside the WUI, with older WUI having significantly higher values than newer WUI. Old-WUI and new-WUI forest had 15% and 30% more aboveground biomass than non-WUI forest, respectively. Both old- and new-WUI also had

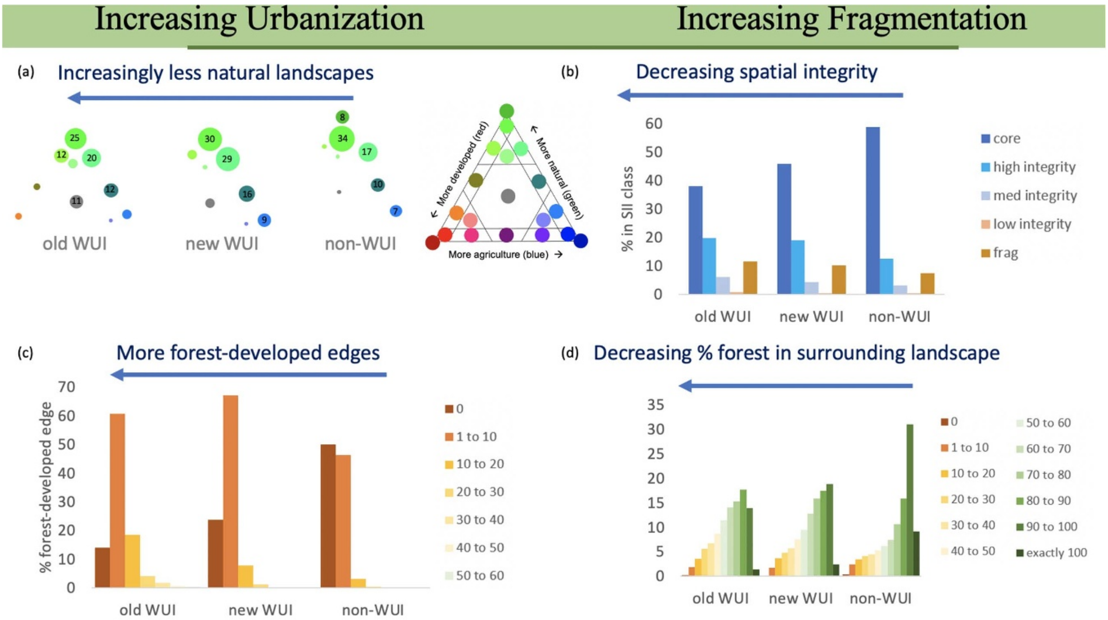

Figure 2. Forest landscape characteristics associated with each WUI change class in the northern US study region. Landscape pattern type (a), forest-developed edges (c), and forest density (d) are summarized at 66 ha neighborhood scale for each forest inventory plot and spatial integrity (b) is summarized at 7 ha neighborhood scale. Labels in the circles in (a) indicate the percent of area in each class; classes with less than 5% are not labeled.

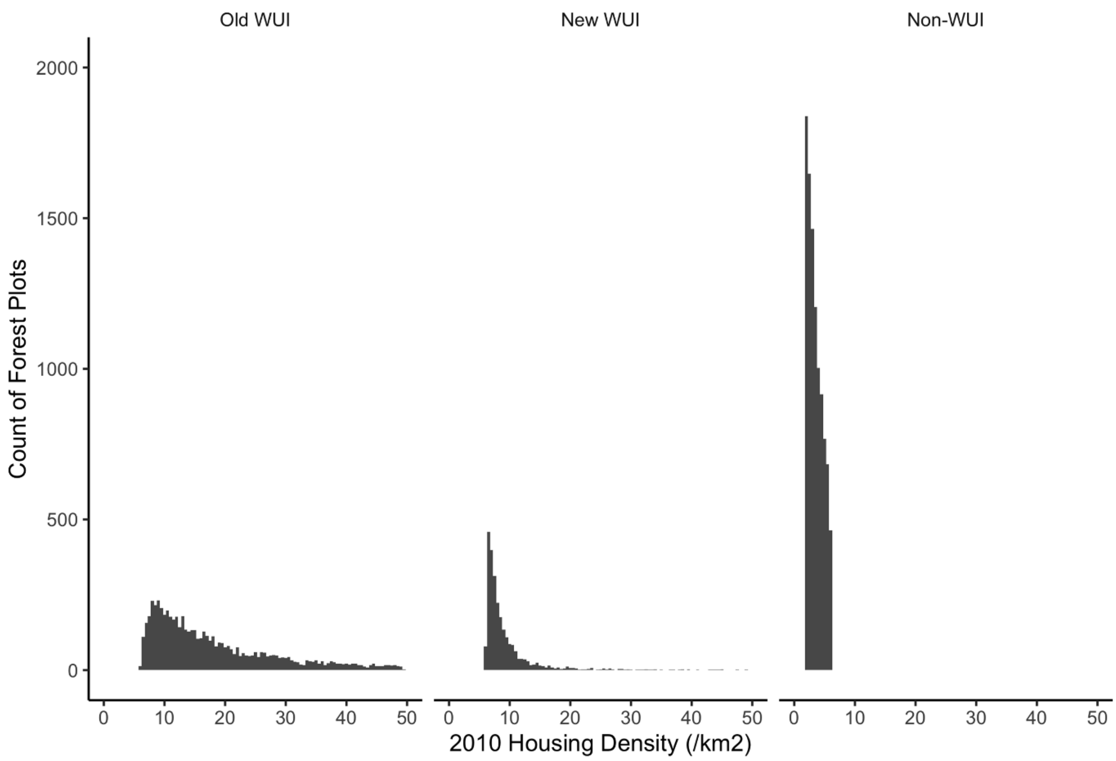

Figure 3. Distribution of 2010 housing density on forest inventory plots by WUI change class in the northern US study region.

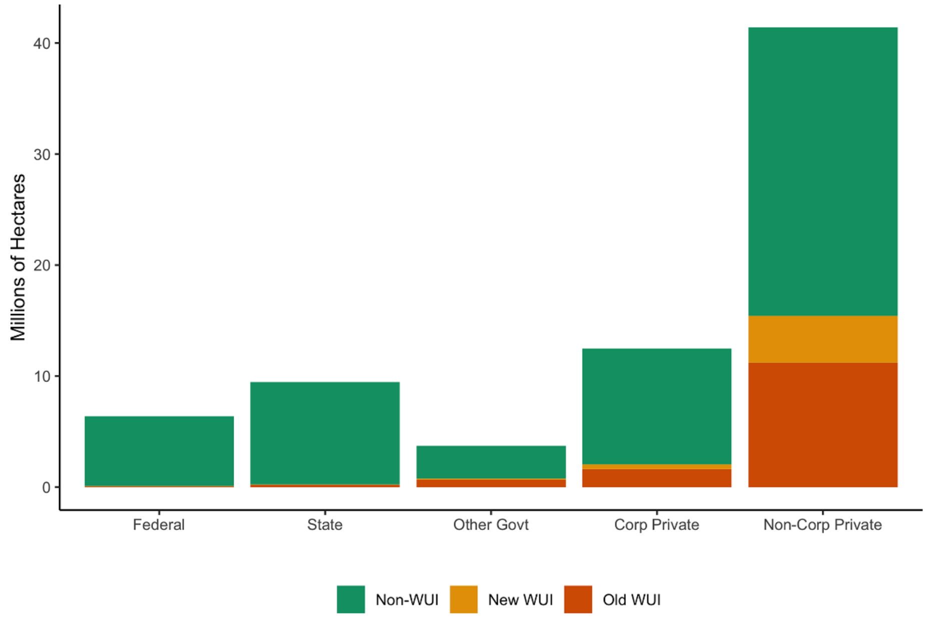

Figure 4. Area of forest in each ownership group by WUI change class in the northern US study region.

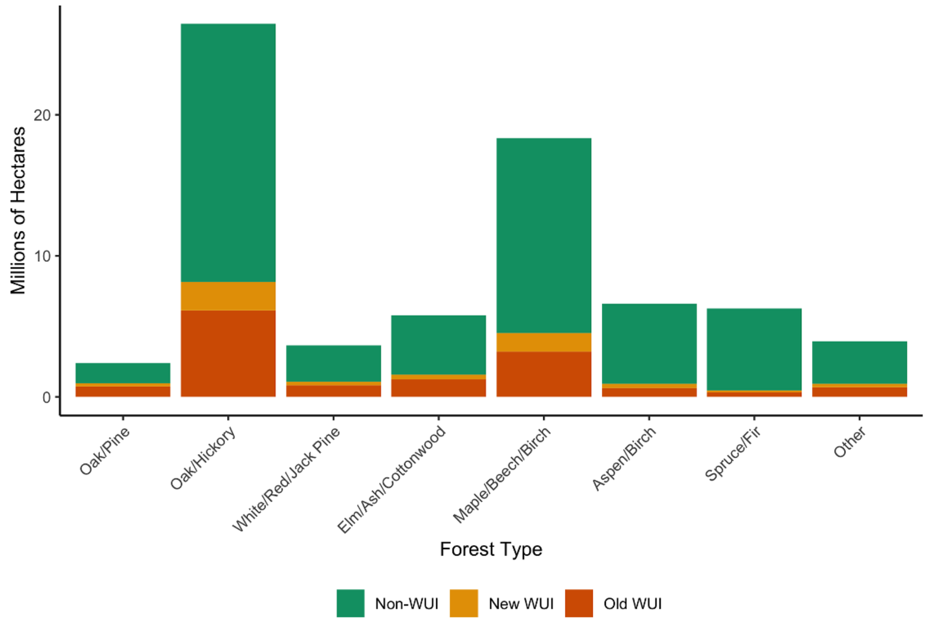

Figure 5. Area of forest type by WUI change class (forest type groups with at least 100 plots in each WUI change class) in the northern US study region.

significantly more trees per hectare (⩾12.7 cm DBH) than forest outside the WUI ($F = 19.83$; $p < .0001$). Conversely, forest outside the WUI had significantly higher densities of seedlings ($F = 261.77$; $p < .0001$), saplings ($F = 296.47$; $p < .0001$), and dead trees ($F = 15.00$; $p < .0001$) than WUI forest. Newer WUI also had significantly higher densities of seedlings and saplings than older WUI. Examining the distributions of tree size classes in more detail, forest outside the WUI has higher densities of small trees per hectare (2.54–22.6 cm DBH) but fewer large trees per hectare (⩾22.86 cm DBH; figure 7). In each size class, newer WUI has a tree density somewhere between older WUI and non-WUI.

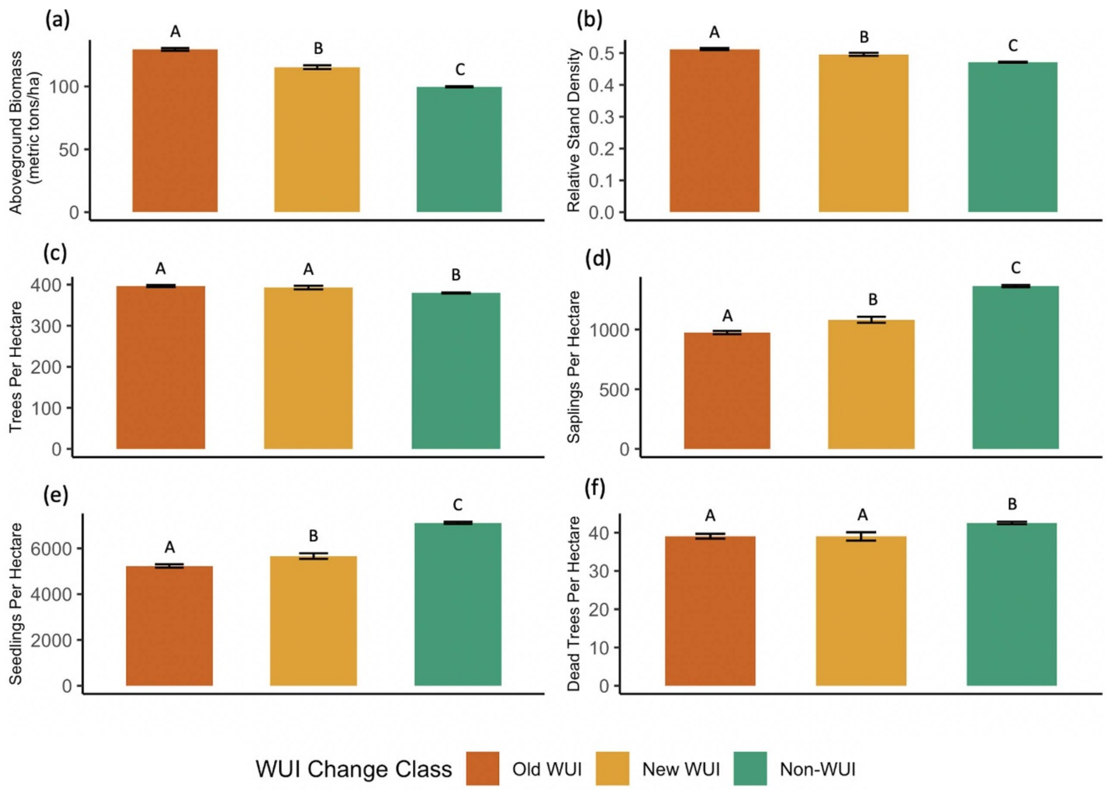

Figure 6. Forest structure characteristics by WUI change class: (a) aboveground biomass, (b) relative stand density, (c) trees per hectare, (d) saplings per hectare, (e) seedlings per hectare, and (f) dead trees per hectare. Values shown are mean ± SEM. Letters show significant differences between WUI change classes ($p < 0.05$).

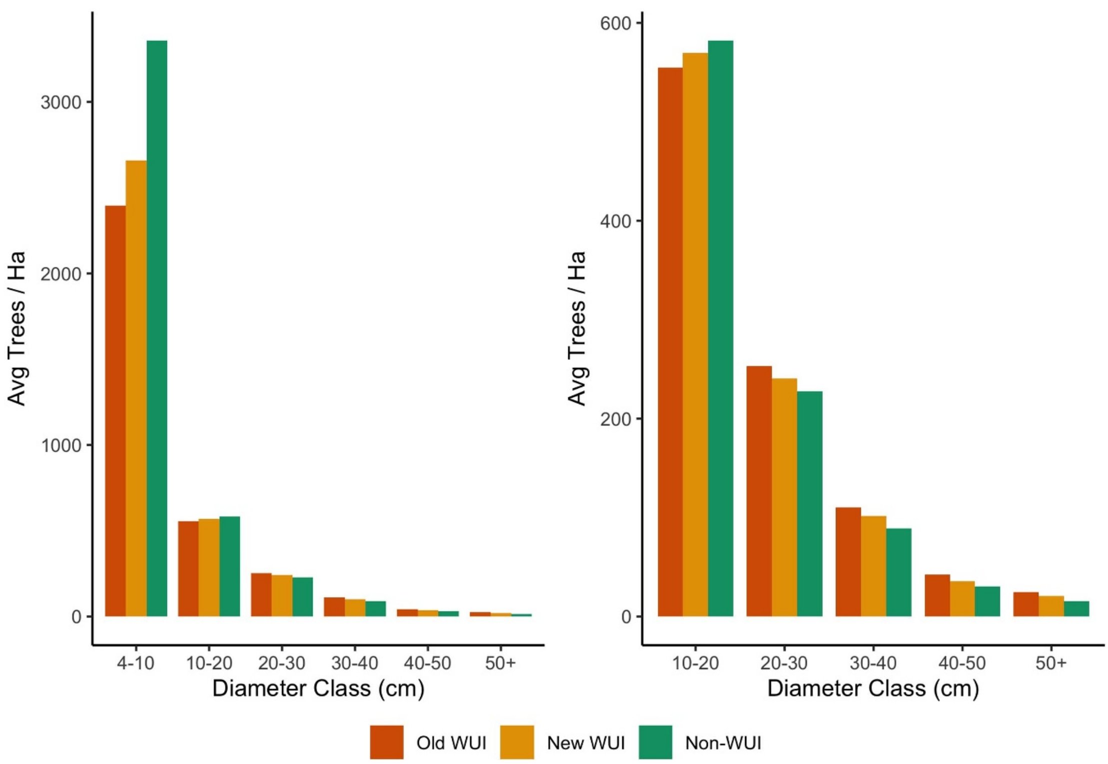

Figure 7. Tree diameter class distribution by WUI change class for all size classes (a) and inset excluding smallest size class (b).

4. Discussion

We found that forest in the WUI had greater carbon storage, with greater aboveground biomass, RSD, and more live trees per hectare, suggesting greater capacity to sequester carbon compared to forest outside the WUI. People prefer forest landscapes with large hardwood trees and may preferentially choose to retain large trees or live near certain forest types (Ryan 2005, Edwards *et al* 2012). In this way, once development occurs, the WUI may actually favor retention of large trees. In contrast to the findings of McDowell *et al* (2020), we did not find smaller, lower biomass stands in WUI forest, suggesting that WUI forest in the northern US differs in structure from global patterns of forest regeneration after disturbance. Our findings in WUI forest are consistent with the enhanced tree growth and biomass found in forest edges of the northeast US, and WUI forests may be similarly vulnerable to heat stress, relative to less fragmented forest outside the WUI, potentially limiting tree growth and biomass accumulation in these forests as global temperatures rise (Reinmann and Hutyra 2017, Reinmann *et al* 2020, Morreale *et al* 2021). Further examination of WUI impacts on forest structure in other regions and ecosystems is needed to determine whether these patterns are universal or are regionally specific due to local ecological, social, and historical context.

Forest ownership can provide insight into management practices, which may have implications for ecosystem structure and function (Spies *et al* 1994). The differences in forest structure found inside and outside the WUI may relate to harvesting intensity, which has been shown to decrease with proximity to urban development (Kittredge *et al* 2017). Our analysis shows that 19% of forest outside the WUI is corporately owned, while only 11% of WUI forest is in corporate ownership. As a result, we might expect higher levels of harvesting in forest outside the WUI, leading to the shift towards less aboveground biomass and smaller tree size classes compared to WUI forest where large trees are not being harvested (Brown *et al* 2018). However, we found no evidence of greater harvesting intensity on forest inventory plots outside vs. inside the WUI (data not shown). Among public ownerships, forest owned by local government is more likely to be impacted by the WUI than federal or state lands. Forest owned by local government makes up a smaller total area, but is more likely to be found in smaller parcels and thus closer to surrounding development. As a result, these lands may be more affected by landscape change than larger state or federal protected areas (Sabor 2010).

We also observed reductions in WUI forest structural diversity compared to non-WUI forest, with fewer saplings, seedlings, and dead trees per hectare. This reduction in structural complexity may lead to diminished ecological function and reduced diversity of wildlife habitat. Standing dead trees and downed woody material facilitate ecosystem processes critical for numerous ecosystem services, including wildlife habitat, nutrient cycling, tree regeneration, and carbon cycling (Woodall *et al* 2009, 2013). The reduction in standing dead tree density in the WUI may reflect homeowner preference for removing dead trees from the landscape (Arnberger *et al* 2017, Ebenberger and Arnberger 2019), which could also result in a reduction in downed woody material. Removal of dead wood from the forest ecosystem could reduce tree regeneration, as well as carbon stocks and wildlife habitat. The lower density of saplings and seedlings in WUI forest may be related to higher deer browse pressure and/or invasive understory plants, both of which are positively related to housing development and associated forest fragmentation. Although a more extreme context, urban forest patches of New York City were similarly found to have more stands with few old, large trees and relatively little recruitment of new canopy trees compared to surrounding rural forests (Pregitzer *et al* 2019).

Light availability may also be driving differences in forest stand dynamics inside and outside the WUI. Forest in the WUI appears to be in a more stable state where the higher density of large trees could lead to a closed canopy with lower light availability and less regeneration. In contrast, forest outside the WUI appears more dynamic, with more standing dead and likely decomposing wood resources to support regeneration in the seedling and sapling size classes, and greater density-dependent mortality due to stem exclusion. However, fewer seedlings and saplings represent diminished regeneration potential and if the large-diameter trees in WUI forest are not being replaced, the future sustainability of these forested landscapes is uncertain.

Analysis of landscape characteristics confirmed that forest in the WUI is more fragmented and less connected to core forest, and contains lower forest densities and more forest-developed edges in the surrounding landscape than non-WUI forest. WUI forest also contains higher percentages of agricultural and developed land cover types in the surrounding landscape. In particular, newer WUI forest had the greatest proportions of agricultural land cover in the surrounding landscape, and this was true at all three neighborhood scales. In some cases, this result may reflect establishment of residential development on agricultural lands (rather than on forest land), turning nearby existing forest into WUI. Over time as more agricultural areas are developed, older WUI forest is no longer in such close proximity to this land cover, but is in proximity to more developed land cover in the surrounding landscape.

In general, more recently established WUI forest has both landscape and structural characteristics intermediate between older WUI forest and non-WUI forest. This pattern supports the idea that forest structure of newer WUI is on a divergent trajectory away from initial non-WUI forest conditions, towards that of more established WUI. We did not see any evidence of an initial disturbance in forest structure followed by recovery towards original conditions over time. On the contrary, not only did older WUI forests tend to show greater differences from non-WUI forest, but the types of forest structural differences we observed, such as reduced seedling and sapling densities, could be an indication of even greater potential differences over time. Future work examining forest and housing density datasets over a longer timescale may reveal whether forest structure continues to diverge with time spent in WUI (possibly related to continued increases in housing density), reaches a steady state, or depends more strongly on other contributing factors.

We found that some forest types in this region were much more likely to be impacted by WUI than others. In particular, the greatest percentage of oak/pine and oak/hickory forest were found in the WUI, likely because these forest types are found in areas and topographies that have been historically most suitable for housing development. In contrast, maple/beech/birch, aspen/birch, and spruce/fir forest are typically not as heavily impacted because they are found at higher elevations where development is more difficult. In a nationwide analysis, Sabor (2010) found the same top five forest type groups to be impacted by WUI as in our analysis, and also found that high elevation forest types are least likely to have housing densities over the WUI threshold. Disproportionate impacts on certain forest types may have implications for carbon storage and other forest ecosystem services at regional scales (Knott *et al* 2022).

Rare and less common forest types that are heavily impacted by WUI are at greater risk for loss of area or integrity, and may impact rare or threatened species that depend on these habitats (Sabor 2010). Analysis of forest health, including tree stress and biodiversity of plants and other taxa might reveal whether certain tree species or forest types are more sensitive to disturbances related to housing development. In addition to continued development, climate change impacts forested landscapes across the region, frequently compounding the stresses on these systems. Trends toward increasing prevalence of forest types associated with dry conditions (e.g. oak/hickory) rather than those associated with moist environments (e.g. maple/beech/birch) may interact with development patterns and pressures in particular forest types and geographies (Swanston *et al* 2018). Climate change is also predicted to lead to greater frequency and intensity of fire and flood events in the eastern US (Swanston *et al* 2018), which will impact both housing and forest structure in WUI landscapes.

The distribution of housing densities found in older vs. more recent WUI supports the idea that the WUI is a varied and dynamic landscape that generally experiences increases in housing density through time (Hammer *et al* 2007). This pattern is further supported by our summary of forest spatial integrity inside and outside the WUI, where older WUI has the least amount of core forest area and highest amount of fragmented forest, followed by newer WUI, followed by non-WUI forest. Although WUI may be a useful construct to delineate particular zones of interaction between housing and forest, housing densities and forest fragmentation within the WUI can have a broad range of values within each WUI class and do increase with time, potentially blurring the relationship between housing density and forest structure that actually exists. Census blocks also contribute spatial uncertainty to our analysis. WUI census blocks average 130 ha and non-WUI census blocks average 353 ha, but both vary greatly in size, affecting the spatial precision with which they describe the housing density around a forest inventory plot.

Forest in the WUI is valuable, but also vulnerable. The combination of smaller forest parcels, diverse landowners, varied legacies of past land use, and interactions among multiple stressors make forest management challenging in the WUI. Homeowners are attracted to landscapes with forest amenities (Gosnell and Abrams 2011), illustrated by the trend that housing growth in and around protected areas has increased at a rate faster than that for the nation as a whole (Radeloff *et al* 2010, Wade and Theobald 2010). However, as development impacts forest structure and regeneration, forest in the WUI may be unable to sustain the characteristics that attracted homeowners in the first place. At the same time, the WUI represents a zone where people live close to wild nature. Residents may be interested in the opportunity to learn more about the values of forests near their homes and in affecting the desired future trajectories for that forest. Particularly in the eastern US where the majority of forest is found on private land, involving residential landowners in the conservation of forest diversity and ecosystem function will ensure provision of critical ecosystem services to increasingly diverse communities for generations to come.

5. Conclusion

Our analysis of forests of the northern US reveals that WUI forests are not only more fragmented and surrounded by a more human-influenced landscape than non-WUI forests, but also appear to be increasingly different in structure over time. In this study, WUI forests were observed to have more live trees in larger size classes, suggesting they have greater carbon sequestration capacity than forest remaining outside the WUI. At the same time, we also found reductions in the structural diversity of WUI forests compared to non-WUI forest, suggesting a reduced capacity for forest regeneration and the potential for changes in other ecological functions. More recently established WUI forest appears to be on a trajectory towards that of older WUI forest. Further study is needed to explore additional forest characteristics and the ecological implications of these differences. Targeted analyses using additional datasets from smaller geographies may reveal differences in downed woody material and/or woody and herbaceous plant diversity and community composition, with further implications for carbon cycling and wildlife habitat. Are WUI forest plant and animal community structures simplified along with forest stand structure? Longitudinal forest inventory data can shed light on tree mortality and regeneration rates and elucidate the trajectories of forest inside and outside the WUI over time, with implications for ecosystem services for surrounding communities and providing management-relevant advice for forest landowners and landscape planners.

Data availability statement

The data that support the findings of this study are openly available at the following URL/DOI: https://apps.fs.usda.gov/fia/datamart/datamart.html.

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