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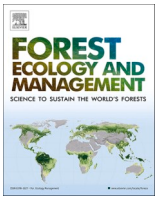

United States forests are increasingly invaded by problematic non-native plants

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ABSTRACT

Non-native invasive plants cause significant ecological impacts to forests while requiring costly management interventions. We used data from Nationwide Forest Inventory plots to assess the extent and recent patterns of invasion by problematic non-native plants across United States forests at multiple scales (county, regional, and national). We estimated the proportion of forests that have been invaded and calculated the mean plot-level richness of invasive plant species during two recent inventory periods (ca. 2010 and 2018). We found that ~99.5 million ha of forest have been invaded by understory non-native plants nationally (37.9 % of the inventoried area) with a greater degree of invasion in the East than in the West. Nationally, the percent of invaded plots and the mean plot invasive richness at the county scale both significantly increased over time while mean plot invasive plant cover decreased. We evaluated potential drivers of invasion using an ensemble learning approach and applying simultaneous autoregressive spatial error models. Recent invasion and change in invasion metrics were associated with anthropogenic fragmentation (a measure of disturbance), change in agricultural land cover (an indirect indicator of propagule pressure), and tree richness and change in tree biomass (measures of forest invasibility). We also found consistent evidence of invasion debt, the temporal lag of invasion outcomes, especially in eastern U.S. forests. These results are important for the long-term monitoring of forest effects associated with invasive plant species and offer a glimpse into ongoing national, regional, and local invasion of United States forests.

1. Introduction

The invasion of natural communities by non-native plant species is an ongoing global phenomenon that, driven by human activities and socioeconomic factors, may be expanding faster than past invasions (Wilson et al., 2007; Gioria et al., 2023). Invasive plants can exert significant negative outcomes on native species, community composition, and ecosystem properties, depending on the interactions between the traits of the non-native plants and the biomes they are invading (Pyšek et al., 2012). They can alter the composition of forest ecosystems via superior competition for resources with native plants, particularly when resources are limited by natural or human-caused disturbances, as well as through allelopathy, ecosystem engineering, plant-soil feedbacks, and effects on pollinators (Mayfield et al., 2021). Additionally, they can degrade the functions of forest ecosystems, including carbon storage and sustainable nutrient and water balances (Miniat et al., 2021). The mean annual economic cost of plant and other non-native species invasions globally was US$26.8 billion between 1970 and 2017, a number that is likely an underestimate and that is exhibiting a consistent tripling per decade (Diagne et al., 2021). The economic costs of invasions include those associated with management, lost agricultural and forest product revenue, reduced recreational opportunities and property values (Pimentel et al., 2005; Aukema et al., 2011). Non-native plant species differ in the degree to which they incur economic and ecological costs,

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however. For example, of the nearly 4000 non-native plant species established in natural ecosystems of the conterminous United States (Simpson and Eyler, 2018), about 750 are defined as invasive (Bradley et al., 2015). Such species are problematic because they currently cause or are likely to cause economic or environmental harm or harm to human health (Ries et al., 2004).

The existence of non-native plant inventory data across broad scales allows for regional or national assessments of invasion processes and patterns as well as evaluations of the drivers of plant invasion. For example, analyses of vegetation data from across Europe found that the frequency of non-native woodland plant species originating from outside of Europe greatly exceeded that of non-natives originating from within the continent (Wagner et al., 2017) and identified regional hotspots of woodland invasion (Wagner et al., 2021). Additionally, an assessment of forest inventory data from a national network of permanent plots across New Zealand determined that canopy disturbance effects on soil properties increased the abundance and richness of non-native plants in natural forests (Jo et al., 2024). Brandt et al. (2023) used broad-scale forest inventory data from across both the United States and New Zealand to investigate the interaction between co-occurring invasive plant species, while several other researchers have used such data to investigate the dynamics of plant invasions regionally in the United States (Huebner et al., 2009; Fan et al., 2013; Riitters et al., 2017; Lázaro-Lobo et al., 2021). Nationwide analyses of invasive plant data revealed that these plants are particularly widespread and common in the eastern United States, where approximately half of the plots were found to contain at least one non-native invasive plant species (Oswalt et al., 2015). Eastern forests also had greater mean invasive plant richness than western forests (Iannone et al., 2015), with greater invasive shrub, vine and tree diversity in the East, greater forb diversity in the West, and high grass diversity in both regions (Iannone et al., 2016a). Eastern forests with higher native tree biomass and evolutionary diversity appeared to have greater biotic resistance to invasion, particularly in the Midwest and Appalachian Mountains (Iannone et al., 2016b), while forests consisting of less closely related native tree species better resisted overall plant invasions in less harsh growing conditions (as estimated by maximum tree height) and in forests where the degree of harshness was more homogenous (Iannone et al., 2018).

While informative, these studies were limited to characterizing the invasion of forests at a specific time. Species invasions are dynamic processes that play out over both time and space, so it is important to assess change in invasion across multiple time periods to better understand the directionality and extent of plant invasions over time nationally and regionally. For example, do regional differences in invasion change mirror regional differences from a single time period? Additionally, understanding the factors associated with invasion processes over space and time – especially disturbance (Hobbs and Huenneke, 1992), propagule pressure (Davis et al., 2016), and habitat invasibility (Richardson and Pyšek, 2006) – could help both help predict the degree of future invasion while also informing measures to counter the establishment and spread of invasive plants in U.S. forests. For disturbance, the first of these invasion factors, fragmentation is a primary driver, particularly when the construction of buildings and roads breaks up forested areas and creates edges (Gavier-Pizarro et al., 2010a) that facilitate the establishment and spread of invasive plants (Hobbs and Huenneke, 1992; Fraver, 1994; Cadenasso and Pickett, 2001). Recent broad-scale research in fact has established that more fragmented U.S. forests were more invaded by non-native plants (Riitters et al., 2017). Similarly, research in Slovenia found that non-native plant species richness, cover, and proportion were higher in fragmented than unfragmented forest (Šipek et al., 2022), while a study in New Zealand revealed strong evidence that forest fragment area and distance to the edge of a fragment positively influenced plot-level non-native plant species richness (Ohlemüller et al., 2006). In the Western Ghats of India, non-native coffee species (*Coffea* spp.) are increasingly common closer to the edges of forest fragments (Joshi et al., 2009). Propagule pressure, meanwhile, is associated with the ability of non-native invasive plants to disperse their seeds long distances into forests (Nuñez-Mir et al., 2019). Developed and agricultural land cover are indirect indicators of invasive plant propagule pressure on neighboring forests (Potter et al., 2024) because the widespread use of non-native plants in residential areas – where gardens and yards often contain fewer native than non-native plants (Smith et al., 2006) – is an important source of invasive species propagules (Davis et al., 2016) and because agricultural areas are vectors for plant invasions via the creation of favorable habitat conditions for the invasion of invasive plants into forests (Gavier-Pizarro et al., 2010b; Boscutti et al., 2022). Indeed, the amount of agricultural and developed land cover in the vicinity of a forest plot increases its likelihood of being invaded, most likely because of non-native plant propagule pressure from those anthropogenic land cover types (Riitters et al., 2017; Waddell et al., 2020). Additionally, an analysis of forest plots within the wildland-urban interface (WUI) in the eastern United States found that invasion of these forests was associated with nearby agricultural, developed, and forested land cover (Potter et al., 2024). Finally, habitat invasibility, the susceptibility of biological communities to colonization and dominance by introduced species (Fridley, 2011), reflects the availability of open niches within a community and thus is influenced by the diversity, biomass and composition of the species in that community (Catford et al., 2012). The effect of invasibility is inversely related to the "biotic resistance hypothesis" (Elton, 1958), which predicts that communities with higher biodiversity are less invasible, in the sense that higher species richness and biomass confer resistance to invasions because of the saturation of available niches (Guo et al., 2015). The directions of the relationships between biodiversity and invadedness are inconsistent, however, and vary with scale (Fridley et al., 2007; Jeschke et al., 2012). At large scales, the same factors that promote greater native plant diversity also enable more diverse non-native floras (Richardson and Pyšek, 2006).

Another reason to track change invasion over time is to better understand and anticipate the spread and dominance implications of "invasion debt" (Crooks, 2005), the time lag between an initial invasion and its full eventual ecological and socioeconomic outcomes (Duncan, 2021; Soto et al., 2025). Such time lags occur throughout the invasion process as described by Blackburn et al. (2011), including during the pre-establishment naturalization stage and the post-establishment spread (increase) stage (van Kleunen et al., 2018; Duncan, 2021; Osunkoya et al., 2021). Much research has focused on the lag associated with the initial establishment phase of plant invasions (e.g., Caley et al., 2008; Aikio et al., 2010; Robeck et al., 2024), which is often challenging to assess because many newly introduced species are difficult to detect and because they don't exhibit characteristics that reveal their potential for invasiveness (Larkin, 2012; Coutts et al., 2018). However, more consistently assembled empirical data, such as invasive plant occurrence information collected by the European Vegetation Archive (Chytrý et al., 2016) or by the Forest Inventory and Analysis (FIA) program in the United States (Burrill et al., 2025), are available to assess invasion lags associated with the spread stage. Invasion lags in this stage can occur when non-native species pools are not fully saturated because of species dispersal limitations (Brown and Peet, 2003; Essl et al., 2012) or when non-native plants have not had the opportunity to invade because of the lack of disturbance in native ecosystems. As a result, established non-native species identified as problematic may not have yet reached their full potential geographic extent and/or may not have established themselves in all the available habitats within their existing distribution. The presence of post-establishment invasion debt can be inferred by the existence of relationships between current invasion metrics and previous drivers of invasion (such as disturbance and propagule pressure) that are stronger than those between current invasion metrics and current drivers of invasion. In other words, post-establishment invasion debt may exist when the current degree of invasion is less than the degree of invasion expected based on the presence of existing invasion drivers. While the relationship between invasion and landscape history

can be complex (González-Moreno et al., 2017), understanding the implications of invasion debt provides a more accurate assessment of the potential spread and dominance of invasive species and is thus important for their effective management (Crooks, 2005). Such evaluations of invasive debt are likely to be more useful when they also take into account the major factors associated with invasion processes (disturbance, propagule pressure, and forest invisibility) while also measuring different aspects of invasion (i.e., invasive plant establishment, invasive plant species dominance, and plant invasion prevalence (Iannone et al., 2015; Iannone et al., 2016b)).

The spatially balanced and relatively intense sample design of the FIA program's Nationwide Forest Inventory (NFI) provides the opportunity to use a macroecological framework (Fei et al., 2016) to assess broad-scale patterns of non-native plant invasion across the United States and to better understand the drivers of plant invasion. Administered by the United States Department of Agriculture Forest Service, the NFI provides the most comprehensive forest database in the United States (Tinkham et al., 2018) and is the main source of information about the status, condition, extent and trends in U.S. forest resources across all ownerships (Smith, 2002). In this study, we compared invasive plant species information collected on 59,425 forest plots from circa 2008–2013 with information collected on 64,134 plots from circa 2014–2020 to test the following hypotheses: (1) forests of the United States are becoming increasingly invaded by non-native plants; (2) regional differences exist in forest plant invasion change in the United States, consistent with regional differences in invasion detected for a single time period; and (3) change in forest plant invasion in the Eastern United States (the region where sufficient data are available) is associated with forest fragmentation (an important disturbance factor in forest plant invasions), propagule pressure (including proportion of nearby developed and agricultural land cover), and forest invasibility (including species and structural diversity) at the county level. Additionally, we leveraged the design of the NFI program and data from 80,912 plots to estimate the recent degree of forest invasion (including the percent of forest invaded by problematic non-native plants) at national, regional, and county scales.

2. Methods

2.1. Forest inventory data

The USDA Forest Service Forest Inventory and Analysis (FIA) program's Nationwide Forest Inventory (NFI) monitors invasive plant species on forest plots across all ownerships throughout most of the United States. The FIA program's definition of invasive plants (here also called "problematic non-native plants") follows that of USA Executive Order 13112, which states that invasive species are those "whose introduction does or is likely to cause economic or environmental harm or harm to human health" (Ries et al., 2004). Invasive plant experts developed the regional lists of the problematic forest plant invaders that field crews inventoried on NFI plots (USDA Forest Service, 2004). (These are listed in Table S2 of Iannone et al. 2015). These lists do not include all non-native plant species and therefore our analyses likely underestimate the total abundance of non-native plants in U.S. forests, though they encompass the non-native species currently understood to be the most problematic. Specifically, we can assess only the spread stage of invasion – and not the earlier stages, including introduction and establishment – because the NFI data are limited to those species that are already established. The NFI maintains a national network of equal-probability sampling plots across all forest ownerships, with each 0.067-hectare plot containing four subplots arranged at the center and vertices of a triangle. To maintain spatial balance and to allow for statistically robust estimates across broad areas (see below), each plot location is selected at random from within a national hexagonal sampling framework and represents an area of 2428 ha (Bechtold and Patterson, 2005). Field crews visit sites that are accessible, safe, and determined via remote sensing to be in forest land use ($\geq$ 10 % tree canopy cover, or evidence of such cover, and $\geq$ 0.4 ha in size and 37 m wide) (Burrill et al., 2025). Plot locations are revisited during discrete evaluation periods that differ by state, with evaluation periods in the East typically spanning 5–7 years and those in the West encompassing 10 years.

We used two NFI datasets for our analyses (Supplementary Figure 1). The first encompassed a recent evaluation period for the 48 states in which invasive plant data are collected (excluding Oregon and Washington) to quantify the national extent of invaded forest. (The California data were limited to National Forests. States in the northern U.S. were sampled for invasive species at a lower intensity than elsewhere (Kurtz, 2023).) These evaluations encompassed 80,912 total plots from the years 2010–2022 for eastern states (a large majority from 2014 to 2020) and 2007–2020 for western states (mostly from 2010 to 2019). We used this dataset to leverage the NFI design to estimate the amount and percent of forestland at different scales (national, regional, and county) that were invaded by problematic non-native plants using the most recently available data. (Alaska was included in the Pacific Coast region while Hawai'i was treated separately because of its differences with continental U.S. forests.) This was possible because the systematic NFI sample design allows for estimates of area across a region within a population of interest (such as the amount of forest with invasive plant species in a county) by summing the amount of forest land represented by all plot conditions for that population (Bechtold and Patterson, 2005; Pugh et al., 2018).

The second dataset encompassed the recent evaluation period along with the evaluation period immediately preceding it for the 44 states that had two complete inventory cycles of invasive species data (excluding the western portions of Texas and Oklahoma). This encompassed 59,425 plots from the earlier evaluation period (mostly 2008–2014 in the East and 2000–2009 in the West) and 64,134 plots from the more recent period (mostly 2015–2021 in the East and 2010–2019 in the West). We used this dataset to assess county-level change in percent of invaded forest plots and plot-level invasive plant richness and cover. We mapped county-level plant invasion metrics for the most recent evaluation period and county-level change in those three metrics between the two evaluation periods using ArcGIS Pro 3.3.1 (ESRI, 2024).

We generated three county-level metrics of plant invasion for our analyses. Two of these – mean plot-level invasive richness and cover – were based on invasion data from each NFI plot on which invasive plant species were inventoried. Invasive richness is an indicator of invasive plant establishment (Iannone et al., 2015), measured as the number of monitored invasive species occurring on the plot. Invasive percent cover is an indicator of invasive species dominance (Iannone et al., 2016b), measured as the total percent cover of all monitored invasive plants on each subplot averaged across the four subplots on a plot. We further determined the percent of plots per county on which at least one invasive species was inventoried, which is a measure of invasion prevalence (Iannone et al., 2015). Counties containing fewer than five NFI plots inventoried for non-native plants during either evaluation period were excluded from analyses. While they vary in area nationally, especially between the eastern and the western parts of the country (means of 1665.1 km^2 and 8095.9 km^2, respectively, for those included in our analyses), we used counties as our sample unit because they represent the smallest consistent administrative division across the United States and thus are often used as the unit of analysis in national forest sustainability reporting, because the average county area is the minimum reporting unit supported by the NFI statistical design, and because we wanted to compare our results to previous county-level analyses (Iannone et al., 2015). Our statistical modeling analyses (see below) were limited to 1281 eastern counties, which ranged in area from 233.9 km^2 to 17,685.9 km^2 with moderate variation (standard deviation = 1195.7 km^2). Only 38 eastern counties exceeded an area of 4000 km^2 and only 41 were smaller than 500 km^2.

2.2. Land cover

To assess the relative influence on forest plant invasion of disturbance (especially forest fragmentation) and propagule pressure (using the amount of developed and agricultural land cover as surrogate indicators), we used data from the National Land Cover Database (NLCD) to (1) determine the percent of forested, agricultural, and developed land cover within U.S. counties and (2) quantify the amount of forest fragmentation (total and anthropogenic) within different neighborhood sizes around forested pixels across each county. Both sets of metrics were calculated using 30 m NLCD land cover data from 2001, 2011, and 2021 (Homer et al., 2020; Wickham et al., 2021). The forest fragmentation metrics were quantified as county-level means of pixel-level measurements within a window around each pixel. At the pixel level, total forest fragmentation is defined as the proportion of a surrounding window that is forested, and anthropogenic forest fragmentation is defined as the proportion of forest pixel edges which are created by developed or agricultural land cover. The measurements were taken for three moving-window sizes of 7.3 ha, 65.6 ha, and 590.5 ha, which enabled us to quantify the importance of relatively fine-scale (small window) and coarse-scale (large window) fragmentation. For our purposes, forest encompassed the NLCD forest land cover classifications (deciduous, evergreen, and mixed) along with woody wetlands. None of the fragmentation indices was correlated with county size at $r > |0.26|$ across the 1281 eastern U.S. counties included in the modelling analyses. The average $|r|$ across the 27 fragmentation metrics was 0.16.

2.3. Statistical analyses

To test our first hypothesis that U.S. forests are becoming increasingly invaded, we conducted a non-parametric Kruskal-Wallis significance test ($\alpha = 0.05$) of county-level differences in invasion metrics (percent of forest invaded and mean plot-level species richness and cover) for the two evaluation periods. This encompassed 1467 counties that had five or more plots inventoried for invasive plants during both evaluation periods. To test our second hypothesis, that regional differences exist in forest plant invasion patterns, we repeated this analysis for each of the three regions (North, South, and Rocky Mountain) for which we had sufficient repeated measurement data (Supplementary Figure 1). (We excluded the Pacific Coast region because no counties had repeated measurements and Hawai'i because it encompassed only three counties.) We additionally tested whether significant differences existed between regions in the degree of change in the invasion metrics, comparing eastern (North and South) with western (Rocky Mountain) counties, and northern with southern counties within the East. Given the lack of normality in the data, we took a conservative approach and applied non-parametric Kruskal-Wallis tests for each of the comparisons using the *NPAR1WAY* procedure in SAS 9.4 (SAS Institute Inc., 2013) in which *p*-values were generated by 10,000 Monte Carlo runs. We used these comparison tests rather than a single linear mixed model because they are easily interpretable, because each test incorporates a different set of counties, and because testing of regional differences was possible for the East but not the West. We then employed the MULTTEST procedure in SAS 9.4 (SAS Institute Inc. 2013) to calculate *q*-values (*p*-values adjusted for the false discovery rate associated with multiple comparisons) for each set of analyses (i.e., county-level differences over time nationally and within the three regions with sufficient data, and county-level change differences between the East and West, and between North and South within the East).

We used a random forests algorithm to test our third hypothesis, that change in forest plant invasion is associated with forest fragmentation, propagule pressure, and forest invasibility. Specifically, we evaluated the relative importance of the potential drivers of the three county-level invasion metrics (mean plot invasive richness, percent of plots invaded, and mean plot invasive species cover), both for the recent evaluation period and for change over time in the metrics (six analyses in total). This set of analyses was limited to the 1281 counties in the East (encompassing the North and South regions) because of the limited number of counties in the West with data from two measurement periods. These analyses evaluated the importance of environment and geography, forest disturbance, propagule pressure, and forest invasibility on county-level plant non-native invasion metrics, encompassing 56 variables (Table 1). Disturbance variables encompassed total forest fragmentation (mean proportion of forest within 7.3, 65.6, and 590.5 hectare moving windows) and forest fragmentation caused by anthropogenic causes (proportion of forest edges with developed or agricultural land cover within 7.3, 65.6, and 590.5 hectare moving windows) within each county for 2001, 2011, and 2021 as well as proportion of forest land cover for those same years. Propagule pressure variables encompassed the proportion of agricultural and developed land cover within each county for the years 2001, 2011 and 2021; and change in these proportions between 2001 and 2021, between 2001 and 2011, and between 2011 and 2021. Forest invasibility variables encompassed live tree biomass and density within the recent NFI evaluation period and change between the two periods, and tree species and structural (diameter class and height class) richness and evenness for the recent period and change between the two periods. We calculated diameter diversity (richness and evenness) after binning trees into 12.7-cm diameter classes for trees with diameters up to 127 cm and into 25.4-cm classes for trees with larger diameters. We calculated height diversity (again, richness and evenness) after binning trees into 3.05-m height classes for trees up to 30.5 m in height and into 6.1-m classes for taller trees. Such structural diversity metrics were important to include in our analyses given the strong relationship between structural diversity and ecosystem function, a relationship that is often stronger than with metrics of species diversity (Crockett et al., 2023; LaRue et al., 2023). We applied a random forests algorithm, using the R package *party*

Table 1
List of 56 county-level metrics used to assess the relationships between environment, forest disturbance, propagule pressure, and forest invasibility on county-level plant non-native invasion metrics, including the expected relationship between each variable and plant invasion.

Variable	Expected relationship
Environment/geography	
Annual precipitation	Negative
Elevation (mean)	Negative
Temperature (monthly mean)	Positive
Region (North or South)	Unknown
Disturbance	
Anthropogenic forest fragmentation	
2001, 2011, 2021; 7.3 ha, 65.6 ha, 590.5 ha neighborhoods	Positive
Total forest fragmentation	
2001, 2011, 2021; 7.3 ha, 65.6 ha, 590.5 ha neighborhoods	Unknown
Percent forested	
2001, 2011, 2021	Negative
Change, 2001−21, 2001–11, 2011–21	Negative
Propagule pressure	
Percent agricultural	
2001, 2011, 2021	Positive
Change, 2001−21, 2001–11, 2011–21	Positive
Percent developed	
2001, 2011, 2021	Positive
Change, 2001−21, 2001–11, 2011–21	Positive
Forest invasibility	
Tree biomass and density (plot means)	
Recent	Negative
Change	Negative
Tree species (plot mean)	
Richness, recent and change	Negative
Evenness, recent and change	Negative
Tree diameter and height class (plot means)	
Richness, recent and change	Negative
Evenness, recent and change	Negative

(Hothorn et al., 2006; Strobl et al., 2007), to grow 5,000 trees to assess the mean decrease in accuracy when each variable was excluded. We next used the R package *flexplot* (Fife, 2022) to assess the out-of-bag performance of the models and to estimate the variance in the invasive species metrics that was explained by the predictor variables (R^2).

We next selected predictor variables for a set of simultaneous autoregressive spatial error (SAR_{err}) models based on the ranked list of variable importance values from the random forests analysis. We standardized the predictor variables [(x-mean[x])/SD(x)] to assess the relative contribution of the variables to each model and to allow for comparisons between models (Schielzeth, 2010). We ran models for each of the six invasion metrics referenced above, limiting our analyses to the 25 most influential variables for each, removing from consideration the less important variable for any pair with ($|r| \geq 0.75$) to avoid collinearity. This eliminated all the fragmentation variables except for one year-neighborhood combination for total fragmentation while also eliminating all the county land cover variables except developed for one year (because forested land cover was highly negatively correlated with total forest fragmentation and because agricultural land cover was highly correlated with anthropogenic forest fragmentation). We inspected variance inflation factors (VIFs) for preliminary linear models (before variable selection; variables listed in Figs. 4 and 5) and found little evidence that collinearity would cause complications in our models (VIF values < 5). We used SAR_{err} models to avoid distorted estimates of statistical significance associated with spatial autocorrelation (Diniz-Filho et al., 2008) because they account for spatial autocorrelation within response variables, predictor variables, and model error terms (Kissling and Carl, 2008). We selected a 1-degree neighborhood distance after inspection of correlograms and AIC scores from preliminary statistical models, and applied a variance-stabilizing spatial link matrix (Tiefelsdorf et al., 1999). We assessed model goodness of fit using pseudo R^2 values (Nagelkerke, 1991) and standardized model residuals (z-scores). We used backward selection to find the most parsimonious models, iteratively removing the variable with the highest p value until all terms had z-score p values < 0.05 (that is, z-scores greater than 1.96 or less than −1.96). We constructed the SAR_{err} models using the *spatialreg* package (Bivand et al., 2021) in RStudio (Posit Team, 2024).

3. Results

3.1. Recent non-native plant invasion

Using the statistical design of the NFI, we estimated that 99.5 million ha of the 262.6 million ha of forest surveyed for invasive plants across the United States were invaded by these species (37.9 %) (Fig. 1). The two eastern regions (South and North) were both more invaded than the western regions (Rocky Mountain and Pacific Coast). In the South, 55.3 million ha of the 104.8 million ha inventoried for invasive plants were invaded, compared to 36.9 million ha of 69.9 million ha in the North (both 52.8 %). In the Rocky Mountain region, 9.9 % of the 64.9 million inventoried hectares were invaded (6.4 million ha), while 1.1 % of the 22.2 million ha inventoried in the Pacific Coast region were invaded (235000 ha). Only 47 % of forest in the Pacific Coast region was inventoried for invasive plants while the entirety of the forest in the other regions (including Hawai'i) was sampled. In Hawai'i, 83.2 % of the approximately 732,000 ha of forest were invaded.

Across the 1819 counties with at least five NFI plots inventoried for invasive plants, 49.2 % of forest area on average was invaded during the most recent inventory period (SD = 34.7) (Fig. 2A). Most eastern counties were highly invaded (>50 % of forest invaded), with the exceptions of parts of New England, the Great Lakes States, the southern Appalachians, the southeastern coastal plain, and western Texas and Oklahoma. Western counties were generally less invaded (<30 %), while those in Hawai'i were highly invaded (>70 %). Eastern and Hawaiian counties had higher mean plot-level invasive plant richness than Rocky Mountain and Pacific Coast counties (Fig. 2B). The mean plot invasive plant richness was 1.21 across U.S. counties (SD = 1.15), 1.53 for counties in the North (SD = 1.44), 1.40 for those in the South (SD = 1.06), 0.14 for the Rocky Mountains (SD = 0.18), 0.03 for the Pacific Coast (SD = 0.04), and 3.16 for Hawai'i (SD = 0.84). Invasive richness was highest in parts of the mid-Atlantic and Midwestern states and along developed corridors in the South. Similar patterns were apparent for invasive plant cover (Fig. 2C). Mean percent plot cover of invasive plants was 7.18 % across counties nationally (SD = 9.53), 8.66 % in the North (SD = 11.87), 8.41 % in the South (SD = 9.19), 0.26 % in the Rocky Mountains (SD = 0.60), 40.67 % for Hawai'i (SD = 7.92), and 0.06 % in the Pacific Coast region (SD = 0.16).

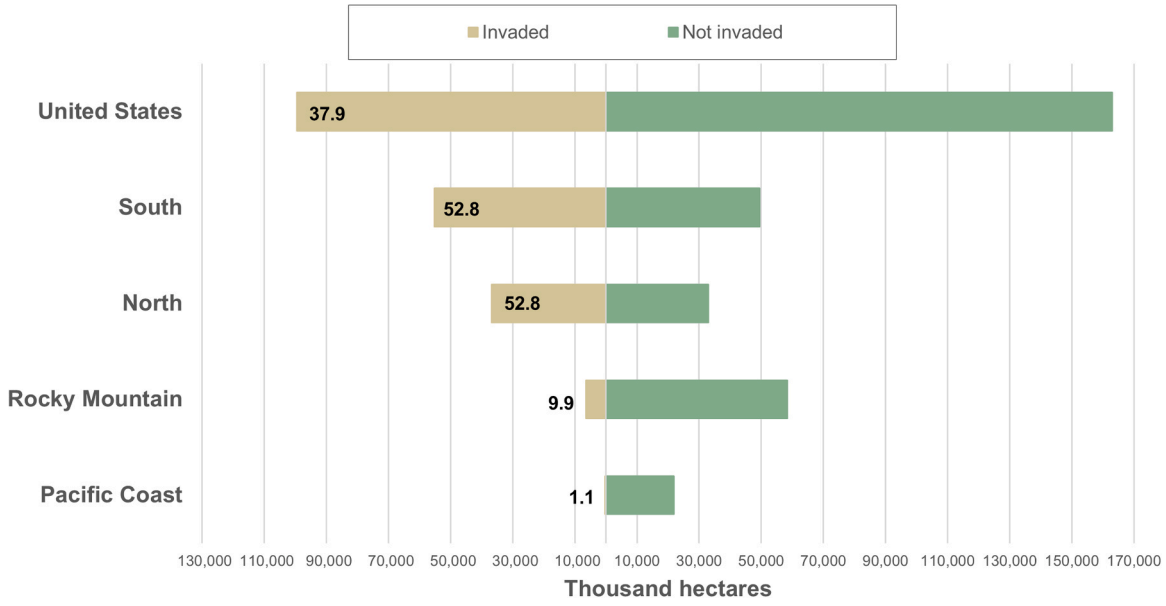

Fig. 1. Area of forest invaded and not invaded for the U.S. and by region. Tan bars to the left indicate invaded forest area; green bars to the right are not invaded. The numbers on the bars are the percent of invaded forest for the region. Across the United States, 91 % of forest land was inventoried for invasive plant species. Within the South, North, and Rocky Mountain regions, 100 % were inventoried, while 47 % was inventoried in the Pacific Coast region. Alaska is included in the Pacific Coast region while Hawai'i is separate, where 83.2 % of the approximately 732,000 ha of forest was invaded.

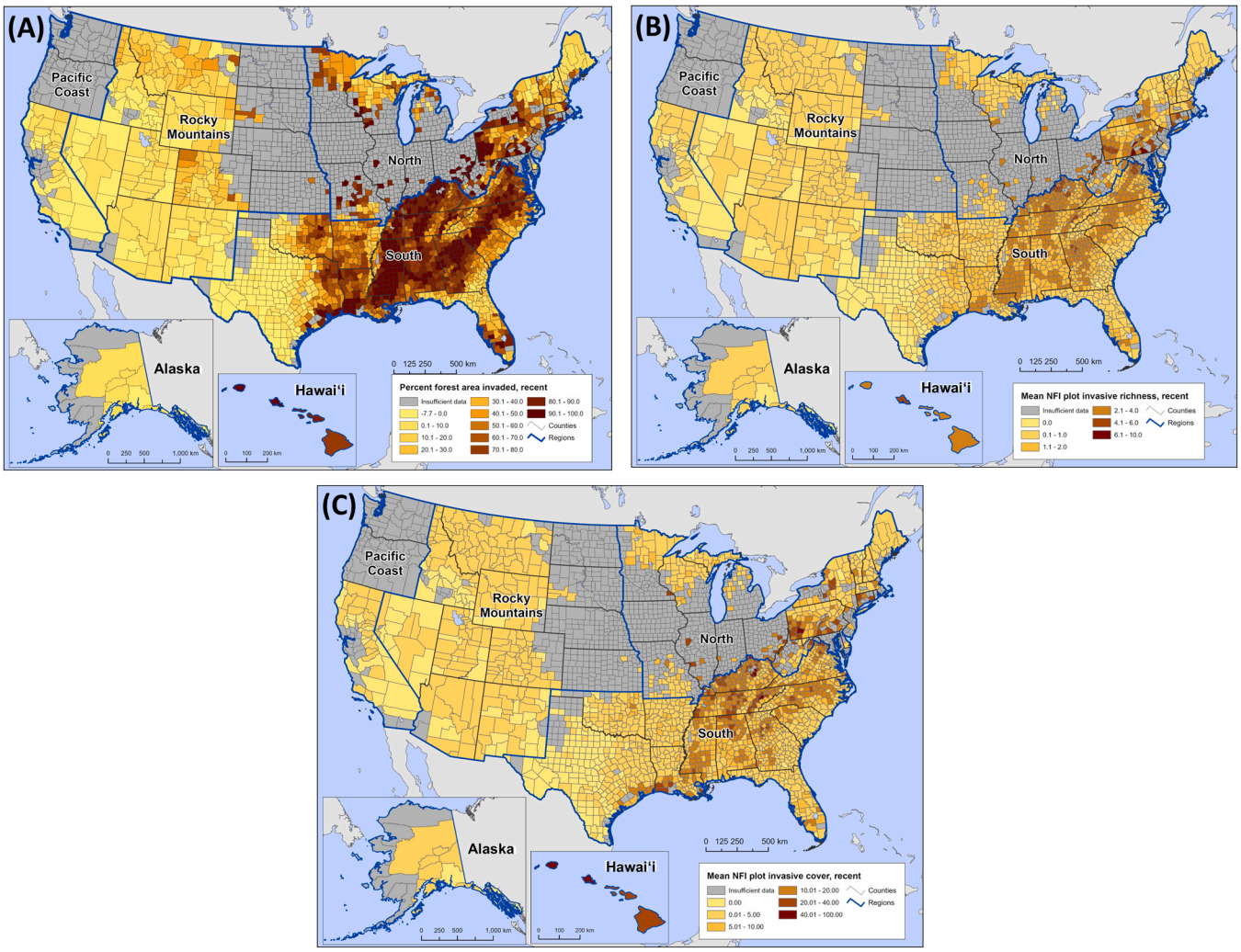

Fig. 2. County-level plant invasion metrics from the most recent Nationwide Forest Inventory (NFI) evaluation period, generally 2014–2020 for eastern states and 2010–2019 for western states: (A) percent of forest invaded, (B) mean plot invasive richness, and (C) mean plot invasive plant cover. Counties were excluded if they encompassed fewer than five plots inventoried for invasive plants. Blue lines delineate regions. Alaska is included in the Pacific Coast region while Hawai'i is separate.

3.2. Change in non-native plant invasion

The assessment of change over time in county-level invasive plant metrics showed a significant increase in mean plot-level invasive richness (1.18 [SD = 0.92] to 1.44 [SD = 1.13]) and mean percent of invaded plots (53.58 % [SD = 30.8] to 57.90 % [SD = 31.1]) across 1467

Table 2
Mean and standard deviations of county-level invasive plant species metrics (percent of plots invaded by invasive plants, mean plot invasive richness, mean plot invasive species cover) for two evaluation periods across the United States and four three U.S. regions, using Forest Inventory and Analysis (FIA) plot data, with q-values (*p*-values from Kruskal-Wallis tests of group differences adjusted for false discovery rate). *q*-values ≤ 0.05 are in bold.

		Percent plots invaded		Invasive spp. richness		Invasive spp. percent cover	
	Counties	mean	SD	mean	SD	mean	SD
United States		***q* < 0.0001**		***q* < 0.0001**		***q* < 0.0001**	
Previous evaluation	1467	53.58	30.84	1.18	0.92	10.4	11.52
Recent evaluation	1467	57.9	31.12	1.44	1.13	8.44	9.67
North		$q = 0.228$		$q = 0.228$		$q = 0.382$	
Previous evaluation	264	49.8	30.59	1.28	1.25	7.2	10.43
Recent evaluation	264	53.61	29.96	1.49	1.44	8.13	11.41
South		***q* < 0.0001**		***q* < 0.0001**		***q* < 0.0001**	
Previous evaluation	1017	62.46	26.16	1.34	0.77	13.1	11.58
Recent evaluation	1017	67.36	25.56	1.67	1.34	10.01	9.3
Rocky Mountains		$q = 0.812$		$q = 0.812$		$q = 0.812$	
Previous evaluation	186	10.35	10.67	0.131	0.15	0.146	0.183
Recent evaluation	186	12.25	13.94	0.157	0.182	0.268	0.548

counties (Table 2). Meanwhile, the mean county plot-level invasive species cover significantly decreased (10.40 % [SD = 11.5] to 8.44 % [SD = 9.67]). No significant differences were detected between measurement periods within the North and Rocky Mountain regions, both with relatively small sample sizes, while the differences in the South were significant and mirrored the national patterns. The extent of change over time in invasive richness and percent of plots invaded was significantly different between counties in the East and the West, while the direction of change in percent invasive cover was also significantly different (negative in the East and slightly positive in the West) (Table 3). When comparing counties within the East, those in the South had a significantly higher increase in invasive richness while invasive cover increased in the North and decreased in the South (a statistically significant difference). We did not detect a significant difference in the percent of invaded plots between counties in the North and South.

A visual inspection of the county-level invasion change metrics reveals that the percent of plots invaded increased across most of the South, with the largest increases in counties in Louisiana, Mississippi, and southern Florida (Fig. 3A; see Appendix A for state names). Scattered counties in the North also experienced an increase in this metric, as did Rocky Mountain counties, mainly in Colorado, Montana, and South Dakota. Patterns of change in county-level mean plot invasive richness were similar with additional increases throughout Kentucky and parts of Virginia and Georgia (Fig. 3B). This increase was most prevalent in counties in Pennsylvania and Minnesota in the North and in Colorado and Montana in the Rocky Mountain region. Some scattered counties in the North experienced relatively high increases in mean invasive plant cover, as did some in Louisiana, Florida and Kentucky in the South (Fig. 3C). Some counties in the Rocky Mountain region had moderate increases in invasive cover. In the South, a swath of Piedmont counties from North Carolina to Alabama had decreases in invasive plant cover, as did several counties in western Kentucky and Tennessee. Counties in the South with decreased plot-level invasive cover had a significantly greater increase in biomass (1402.26 versus 741.03 pounds, Kruskal-Walls test $p < 0.0001$) and a significantly greater decrease in tree density (-17.58 versus −2.66 trees per acre, Kruskal-Walls test $p < 0.0001$) than counties where mean invasive cover remained the same or increased.

3.3. Random forests assessment of variable importance

For the three eastern county-level invasion metrics (mean plot invasive richness, percent of plots invaded, and mean plot invasive species cover) from the most recent evaluation period, the random forests assessment revealed that anthropogenic forest fragmentation metrics were consistently among the most important variables, with the metrics collected earlier and within smaller neighborhoods being more influential. The random forests model for percent of forest invaded explained a substantial amount of variation ($R^2 = 0.540$), with a median difference of 12.7 % between the predicted and out of bag values. The most influential variables were percent agricultural land cover change from 2001 to 2021 (65.4 % accuracy decrease) and from 2011 to 2021 (55.0 % accuracy decrease) followed by tree species richness and evenness (44.9 % and 41.9 % accuracy decrease, respectively) and 2001 anthropogenic fragmentation at 7.3 ha (39.3 % accuracy decrease) (Fig. 4A). The model of invasive richness similarly explained a substantial amount of variation ($R^2 = 0.535$), with a median predicted value of 0.437 species different than the actual (out of bag) value. The most important variable was 7.3 ha anthropogenic forest fragmentation from 2001, with a 0.121 species mean decrease in accuracy when excluded from tree construction (Fig. 4B), followed by the same variables from 2011 and 2021, respectively. Anthropogenic fragmentation metrics at other scales were also influential, as were temperature, tree species evenness and tree species richness, and change in agricultural land cover from 2001 to 2021 and from 2001 to 2011. Finally, the model for percent invasive cover explained slightly less than half of the variation ($R^2 = 0.455$) with a median difference of 3.38 percent cover between the predicted and actual values. The seven most influential variables were anthropogenic fragmentation metrics within different neighborhood sizes and in different years, with fragmentation at smaller scales being the most important (Fig. 4C). Tree species evenness and diversity, along with mean temperature and elevation, were also relatively influential.

The random forest models for change in county-level invasion metrics explained less variability. The model for change in percent invasive species cover explained the most variation ($R^2 = 0.218$ with a median prediction difference of 2.21 % compared to the out of bag value), followed by change in invasive richness ($R^2 = 0.137$, with a median prediction difference of 0.232 species) and change in percent of plots invaded ($R^2 = 0.057$, with a median predicted change of 6.32 %). For invasive cover change, the most influential variables were mean temperature and region, tree species richness, anthropogenic fragmentation, and change in agricultural land cover (Fig. 5C). For invasive richness change, the most important variables were anthropogenic forest fragmentation metrics along with mean temperature and percent agricultural change from 2001 to 2021 (Fig. 5B). For change in percent plot invasion, many of the most influential variables were environmental or geographic (mean temperature, mean elevation, and annual precipitation), in addition to several measures of tree structure and diversity (tree richness, change in mean biomass, tree evenness, change in tree richness, tree height richness, and change in height evenness) and percent of change in forest land cover from 2001 to 2021 (Fig. 5A).

3.4. Simultaneous autoregressive spatial error models

Our SAR_{err} models emphasize the importance of propagule pressure, disturbance, and forest invasibility factors in explaining macroscale

Table 3
Mean and standard deviations of county-level invasive plant species change metrics (percent of plots invaded by invasive plants, mean plot invasives richness, mean plot invasive species cover) between two evaluation periods for eastern and western counties, and for northern and southern counties within the East, using Forest Inventory and Analysis (FIA) plot data, with q-values (*p*-values from Kruskal-Wallis tests of group differences adjusted for false discovery rate). *q*-values ≤ 0.05 are in bold.

		Percent plots invaded change		Invasive spp. richness change		Invasive spp. percent cover Change	
Counties		mean	SD	mean	SD	mean	SD
		$q < 0.0001$		**$q < 0.0001$**		**$q < 0.0001$**	
East	1281	4.67	12.74	0.30	0.48	−2.26	6.24
West	186	1.90	8.92	0.03	0.12	0.12	0.48
		$q = 0.196$		**$q = 0.0002$**		**$q = 0.0002$**	
North	264	3.81	17.50	0.21	0.62	0.93	6.49
South	1017	4.89	11.18	0.33	0.44	−3.09	5.90

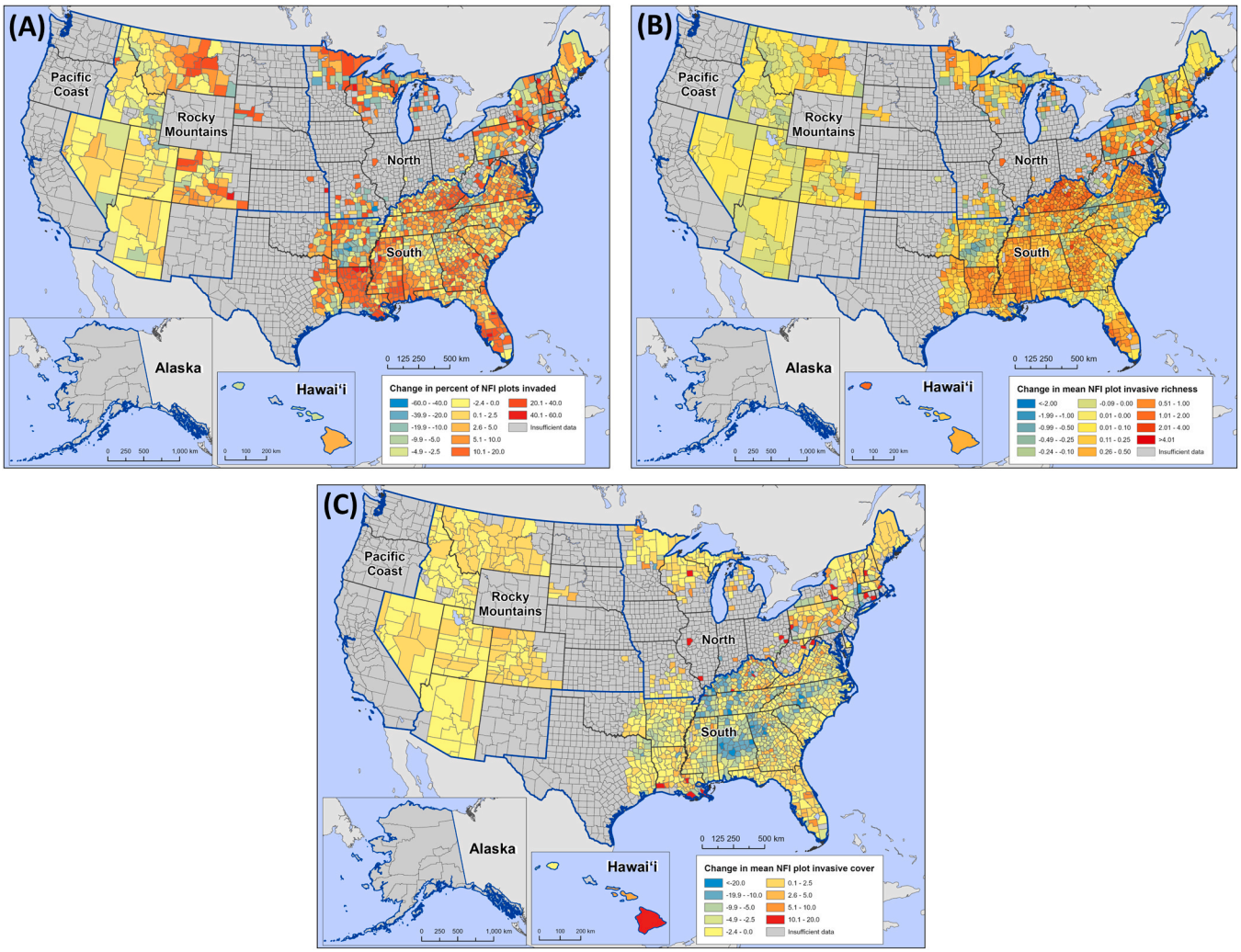

Fig. 3. Change in county-level plant invasion metrics between evaluation periods: (A) percent of Nationwide Forest Inventory (NFI) plots invaded, (B) mean plot invasive richness, and (C) mean plot invasive plant cover. Counties were excluded if they encompassed fewer than five plots inventoried for invasive plants. Blue lines delineate regions. Alaska is included in the Pacific Coast region while Hawai'i is separate.

patterns of recent forest plant invasion metrics in the eastern United States (Table 4a). In particular, one propagule pressure factor (percent change in agricultural land cover) and one disturbance factor (7.3 ha anthropogenic forest fragmentation) were selected variables in the linear regression models for all three recent invasion metrics. As expected, greater forest fragmentation was positively associated with invasion, while, somewhat surprisingly, decreasing agricultural land cover also was positively associated with invasion. Percent developed landcover in 2011 was positively associated with invasive richness. Tree richness, an invasibility metric, was positively associated with percent plots invaded and invasive richness, which is consistent with other analyses (Iannone et al., 2016b), while tree density was negatively associated with invasive richness. Finally, counties with higher mean elevations and lower annual precipitation had a lower percent of plots invaded. The models explained more of the variation in invasive richness (*pseudo* R^2 = 0.648) and percent of plots invaded (*pseudo* R^2 = 0.646) than in invasive species cover (*pseudo* R^2 = 0.536).

SAR_{err} models for change in invasion metrics explained less variation than the models for recent invasion, with those for invasive richness and invasive species cover explaining more (*pseudo* R^2 = 0.253 and *pseudo* R^2 = 0.243, respectively) than for percent plots invaded (*pseudo* R^2 = 0.108). One disturbance variable, 7.3 ha anthropogenic forest fragmentation, was a variable in the final invasive richness and invasive species cover models but had a positive relationship with change in the former and negative with the latter (Table 4b). Invasibility variables were included in the invasive species cover and percent plots invaded models. Tree density, tree diameter class evenness, and tree biomass change were negatively associated with change in invasive species cover. Tree biomass change and tree density were negatively associated with change in percent of plots invaded, while tree richness change and tree height class evenness change were positively associated. The only propagule pressure metric in any of the models was percent change in agricultural land cover from 2001 to 2021, which was negatively associated with invasive richness change. The only environmental variable was mean temperature, negatively associated with change in invasive species cover.

4. Discussion

Non-native plant invasion results in detrimental impacts to forest ecosystems that include changes to ecosystem processes (Yelenik and D'Antonio, 2013; Liebhold et al., 2017) and ecosystem functions (Strickland et al., 2010; Le Maitre et al., 2014) as well as the degradation of native plant and animal biodiversity and habitat (Mack et al., 2000; Pyšek et al., 2012). Non-native invasive plants are widespread across forests of the United States (Oswalt et al., 2015; Iannone et al., 2016a). While recent analyses have assessed the status of non-native plant invasion in U.S. forests (including our analyses here to estimate the recent

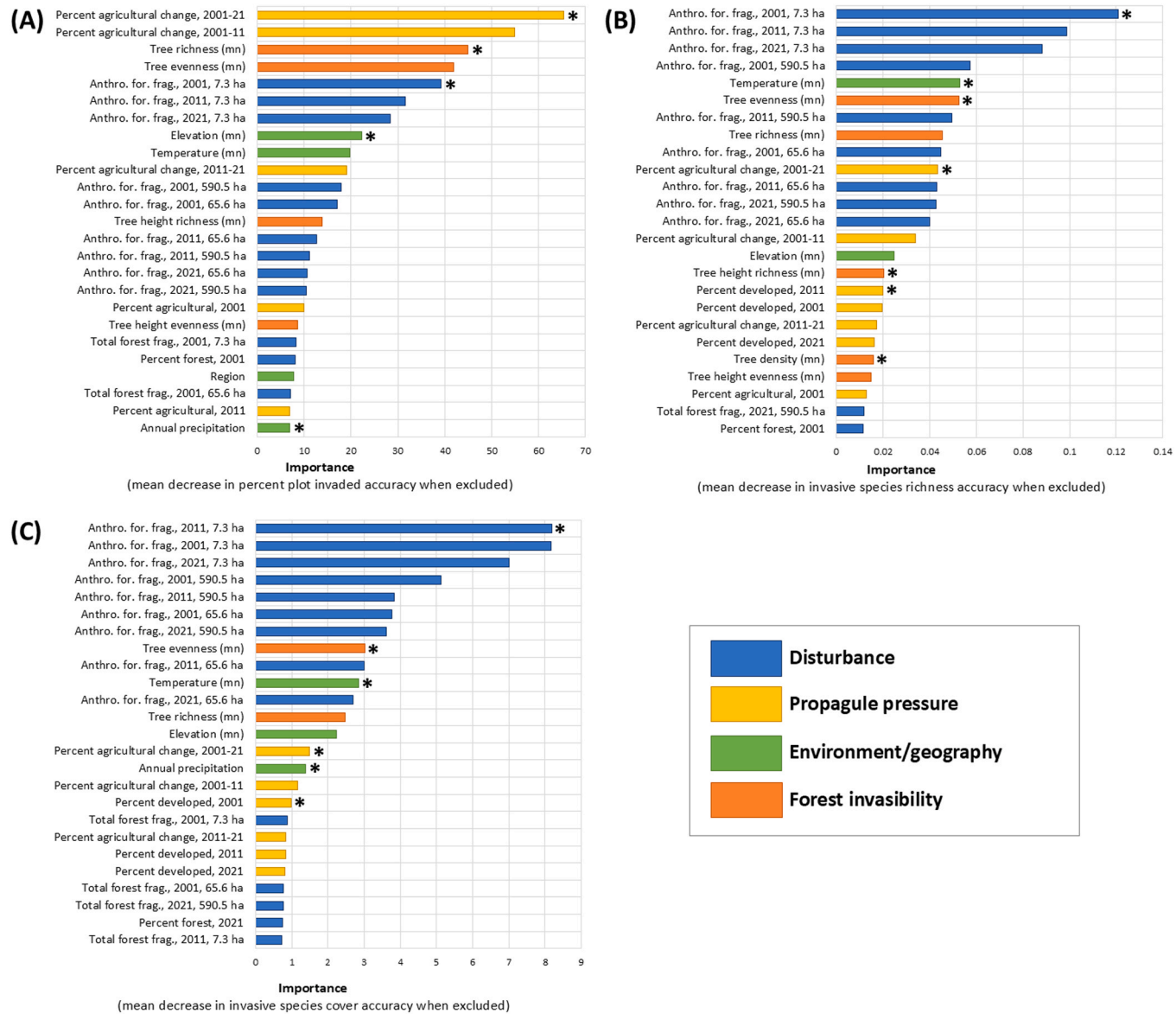

Fig. 4. Mean decrease in the accuracy of random forests predictions for recent county (A) percent plot invasion, (B) mean plot-level invasive richness, and (C) mean plot-level invasive species cover (all from the most recent evaluation period) for the 25 most important variables included in the analyses. The variables are color-coded by type. Variables included in preliminary simultaneous autoregressive spatial error (SARerr) models are marked with *. Values of all importance variables are listed in Supplementary Table 1.

degree of forest invasion at multiple scales), little work has thus far quantified change in broad-scale invasion over time. Our assessment of data circa 2008–2013 from 59,425 NFI plots and circa 2014–2020 from 64,134 NFI plots establishes that U.S. forests are becoming increasingly invaded by non-native plants as measured by several metrics. Significant differences exist among regions, with changes more pronounced in the East than in the West, and – within the East – greater in the South than in the North. Recent invasion and change in invasion metrics are associated with disturbance, particularly anthropogenic fragmentation within small neighborhoods; propagule pressure as measured by agricultural and developed land cover; and forest invasibility, such as tree species and tree structural richness and evenness. We found consistent evidence of invasion debt, including the fact that both recent invasion and invasion change are more strongly related with older than more recent landcover variables such as anthropogenic forest fragmentation.

4.1. *Recent non-native plant invasion results*

The design of the NFI allows for a comprehensive multi-scale assessment of invasion by problematic non-native plants across the United States. This includes areal estimates of invaded forests, although quantifying areal change nationally is not yet possible because many areas of the West (where sampling occurs on a 10-year cycle) have not had a complete second measurement. Leveraging the NFI statistical design, we estimated the proportion of forests that have been invaded by invasive plants and we calculated the mean plot-level richness and cover of invasive plant species at multiple scales (county, regional, and national). We found that almost 38 percent of inventoried forests across the United States was invaded by at least one problematic non-native plant species (Fig. 1). It is particularly sobering that more than half the forestland in the East is invaded. The extent of non-native plant invasion in this half of the United States (more than 55 million ha in the South and nearly 37 million ha in the North) is such that the complete removal of invasive plant species from Eastern forests – and the elimination of the

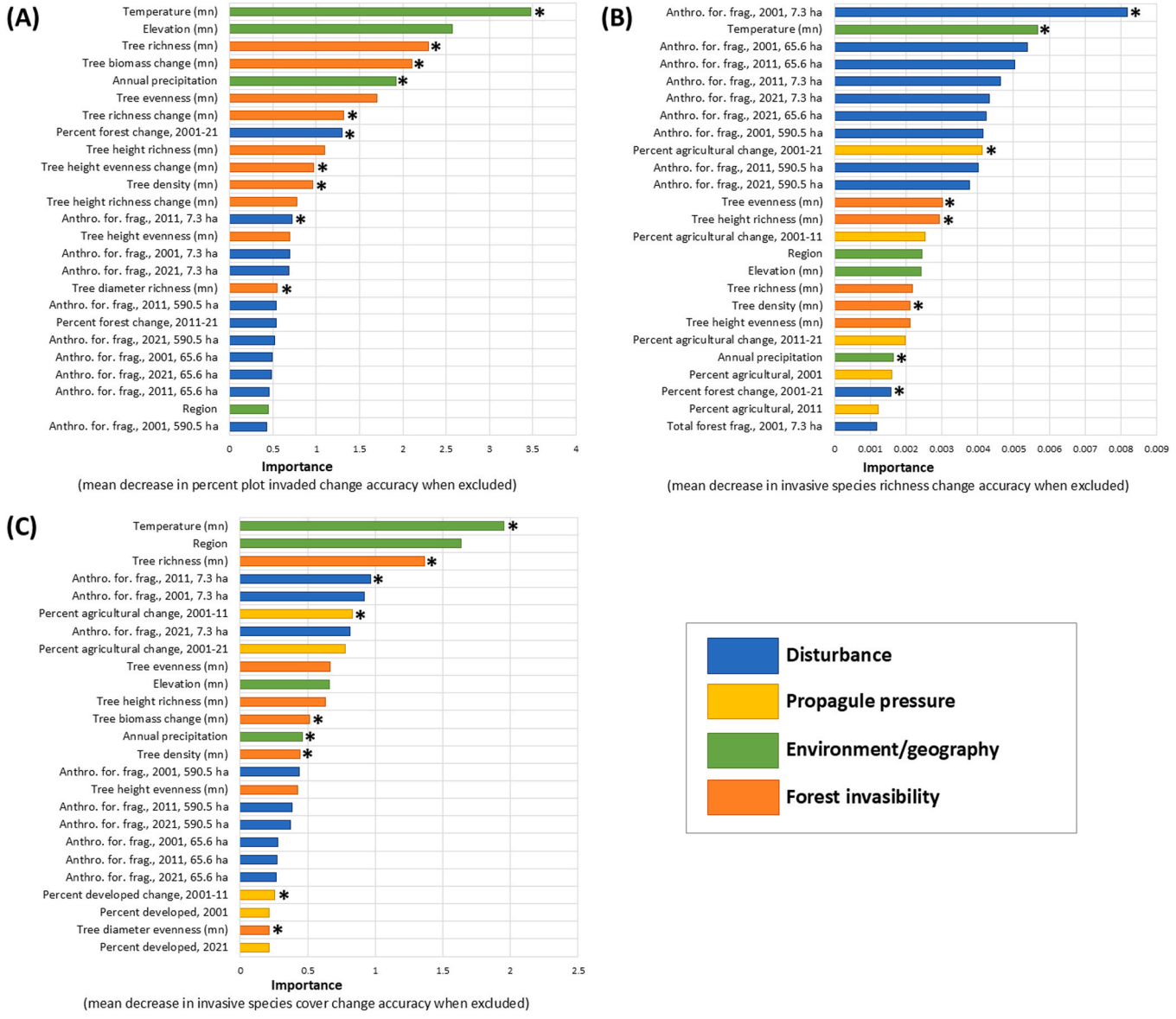

Fig. 5. Mean decrease in the accuracy of random forests predictions for recent county change in (A) percent plot invasion, (B) mean plot-level invasive richness, and (C) mean plot-level invasive species cover (between two evaluation periods) for the 25 most important variables included in the analyses. The variables are color-coded by type. Variables included in preliminary simultaneous autoregressive spatial error (SARerr) models are marked with *. Values of all importance variables are listed in Supplementary Table 2.

impacts they have on ecosystem function and aesthetics – is practically impossible. The spread of non-native invasive plants is largely unchecked in the forests of the South, with some of the most widespread and aggressive species including Japanese honeysuckle (*Lonicera japonica* Thunb.), tree-of-heaven (*Ailanthus altissima* [Mill.] Swingle); Chinese, European and Japanese privet (*Ligustrum* spp.); multiflora rose (*Rosa multiflora* Thunb.); and Japanese stiltgrass (*Microstegium vimineum* [Trin.] A. Camus) (Miller et al., 2015). In the northern United States, the species occurring most commonly during a recent inventory were multiflora rose, garlic mustard (*Alliaria petiolata* [M.Bieb.] Cavara & Grande), non-native bush honeysuckle (*Lonicera* spp.), Japanese stiltgrass, autumn-olive (*Elaeagnus umbellata* Thunb.), Japanese honeysuckle (*Lonicera japonica* Thunb.), Japanese barberry (*Berberis thunbergii* DC), and common buckthorn (*Rhamnus cathartica* L.) (Kurtz, 2023).

At a finer scale, our results show that many Eastern counties are highly invaded, with some exceeding 80 percent of their forests containing invasive plants. This was not the situation in the West. These patterns are consistent with past research (Iannone et al., 2015), as is the higher mean plot-level invasive plant species richness and cover in the East. The forests of this region differ markedly from those of the West in climate, topographic, floristic, and edaphic factors (Cleland et al., 2007; McNab et al., 2007) as well as having distinct ownership patterns (much higher proportion of privately owned forest in the East (Butler et al., 2021) stemming from different settlement legacies (Iannone et al., 2015)). It is additionally possible that a greater proportion of non-native forest plant species in the West have not yet become established to the point that they have been classified as invasive. This could result in an underestimation of the current invasion of western forests relative to those in the East.

We used simultaneous autoregressive spatial error (SAR_{err}) models to assess the degree to which county-level non-native plant invasion metrics in the eastern United States were associated with disturbance, propagule pressure, and forest invasibility factors. Disturbance – in the form of anthropogenic forest fragmentation at a relatively small scale – was positively associated with all three metrics. This is in keeping both with fine-scale findings that forested plots in more disturbed landscapes

Table 4
Relative associations of disturbance (D), propagule pressure (P), environment/geography (E), and forest invasibility (I) variables in final reduced simultaneous autoregressive spatial error (SAR_{err}) models assessing county-level eastern forest invasion metrics for (A) during the recent evaluation period and (B) change across two evaluation periods.

(A) Recent evaluation period

Variable (type)	Estimate	SE	*z*-value	*p*-value
Percent plots invaded (pseudo $R^2 = 0.646$)				
Percent agricultural change, 2001–21 (P)	−0.18	0.02	−7.59	< 0.0001
Tree richness (mn) (I)	0.19	0.03	6.46	< 0.0001
Anthro. for. frag., 2001, 7.3 ha (D)	0.30	0.02	12.17	< 0.0001
Elevation (mn) (E)	−0.20	0.04	−5.16	< 0.0001
Annual precipitation (E)	−0.13	0.04	−3.55	< 0.001
Invasive richness (pseudo $R^2 = 0.648$)				
Anthro. for. frag., 2001, 7.3 ha (D)	0.30	0.03	10.82	< 0.0001
Tree richness (mn) (I)	0.15	0.03	5.19	< 0.0001
Percent agricultural change, 2001–21 (P)	−0.16	0.02	−6.49	< 0.0001
Percent developed, 2011 (P)	0.07	0.02	3.21	< 0.01
Tree density (mn)	−0.05	0.02	−2.16	< 0.05
Invasive species cover (pseudo $R^2 = 0.536$)				
Anthro. for. frag., 2011, 7.3 ha (D)	0.45	0.03	17.20	< 0.0001
Percent agricultural change, 2001–21 (P)	−0.17	0.03	−6.07	< 0.0001

(B) Change across evaluation periods

Variable (type)	Estimate	SE	*z*-value	*p*-value
Percent plots invaded (pseudo $R^2 = 0.108$)				
Tree biomass change (mn) (I)	−0.18	0.03	−5.24	< 0.0001
Tree richness change (mn) (I)	0.11	0.03	3.54	< 0.001
Tree height evenness change (mn) (I)	0.12	0.03	3.83	< 0.001
Tree density (mn) (I)	−0.09	0.03	−2.84	< 0.01
Invasive richness (pseudo $R^2 = 0.253$)				
Anthro. for. frag., 2001, 7.3 ha (D)	0.13	0.03	3.92	< 0.0001
Percent agricultural change, 2001–21 (P)	−0.10	0.03	−2.83	< 0.01
Invasive species cover (pseudo $R^2 = 0.243$)				
Temperature (mn) (E)	−0.12	0.05	−2.56	< 0.05
Anthro. for. frag., 2011, 7.3 ha (D)	−0.17	0.03	−5.01	< 0.0001
Tree biomass change (mn) (I)	−0.07	0.03	−2.36	< 0.05
Tree density (mn) (I)	−0.11	0.03	−3.21	< 0.01
Tree diameter evenness (mn) (I)	−0.10	0.03	−3.13	< 0.01

– in proximity to greater forest fragmentation – were more invaded by non-native plants (Fan et al., 2013; Riitters et al., 2017; Waddell et al., 2020) and with previous analyses of NFI invasion data at the county scale that found a positive association between human-caused forest fragmentation in the eastern United States and both invasive richness and cover (Iannone et al., 2015). The disturbance impacts of anthropogenic forest fragmentation (such as through housing and road construction) are indirect, facilitating the establishment and spread of non-native plants (Hobbs and Huenneke, 1992; Cadenasso and Pickett, 2001) by creating forest edges and breaking up natural areas (Gavier-Pizarro et al., 2010b; Bar-Massada et al., 2014). Inversely, intact forest may either act as a physical barrier to invasive plant propagules or may be associated with smaller regional invasive species pools because they contain less non-native vegetation (Ohlemüller et al., 2006). While we found that anthropogenic fragmentation across a variety of spatial neighborhoods is relevant to non-native plant invasion, it is most strongly related to invasion within smaller neighborhoods (Fig. 4), emphasizing the short distances over which plant invasion processes often unfold.

Meanwhile, we detected negative relationships between the three invasion metrics and 20-year change in agricultural land cover, an indicator of propagule pressure. This result seems counterintuitive, since the likelihood of invasion is highest within landscapes containing more than 10 % agricultural or developed land cover (Riitters et al., 2017). Thus, one might expect that decreasing agricultural land cover over time would equate to less invasion. However, the loss of agricultural land cover is positively correlated with an increase in developed land cover as agricultural areas are converted for housing and commercial purposes (r = -0.413 [$p < 0.001$] between change in agricultural land cover and change in developed land cover from 2001 to 2021). Housing development in particular poses an increased risk of plant invasion given the strong positive relationships between residential development and invasion of forests by non-native plants (Greene and Blossey, 2014; Davis et al., 2016) in part because of the spread of propagules from non-native ornamental plantings in residential landscaping into surrounding areas (Marco et al., 2010; Sipek and Sajna, 2020). Additionally, when abandoned agricultural lands transition to forested land use, those early successional forests may be highly susceptible to invasion by non-native plants that are already present or are nearby. Therefore, the conversion of agricultural land cover to developed land cover increases the exposure of nearby forests to invasive plants, while the conversion of agricultural to forested land cover apparently does not reduce exposure of those forests to invasive plants much, if at all.

Finally, one metric of habitat invasibility – mean plot-level tree richness – was positively associated with both invasive plant richness and percent of plots invaded at the county scale. This is not unexpected, given that many large-scale observational studies have shown positive associations between invasion and native biodiversity (Levine, 2000; Shea and Chesson, 2002; Iannone et al., 2016b), because conditions that are good for native plant biodiversity are also good for invasive plant species (Richardson and Pyšek, 2006).

4.2. Change in non-native plant invasion

To assess the condition and vulnerability of forest ecosystems across broad scales, it is necessary first to understand the direction and extent of plant invasion both nationally and regionally. Across the United States, the county mean percent of invaded forest area increased 4.32 % and mean plot invasive richness increased 0.26 from the first to the second evaluation period, while the mean plot invasive species cover decreased 1.96 % (Table 2). The differences in the metrics between the two evaluation periods were statistically significant in the South, but not in the North or Rocky Mountain regions. The changes in invasion metrics also were significantly different among regions (East vs. West and North vs. South). These results, along with the fact that 58.9 % of counties experienced an increased percent of invaded plots and 73.2 % experienced an increase in invasive richness, demonstrate that non-native plant invasions are intensifying across much of the South and, to a lesser degree, in other parts of the country. The increase in county-level percent of invaded plots and mean county-level plot invasive richness in the South appear to be driven by greater invasion in the states of Louisiana, Mississippi, Florida, and Kentucky, while decreases in county-level mean invasive cover were driven by decreased invasion in parts of Alabama, Georgia, North Carolina, Tennessee, and Kentucky.

Forest invasibility factors were the most important variables in our SAR_{err} models for explaining variation in county-level change in percent of invaded plots. Specifically, change in tree biomass and recent tree density were negatively associated with an increase in the percent of invaded plots, suggesting that greater tree biomass and density may be factors that confer some degree of biotic resistance to invasion by non-native species (Guo et al., 2015). This is consistent with a previous finding that trees – though in a different stratum than most invasive plants in U.S. forests, which tend to be forbs, grasses, vines and shrubs – contribute to invasion resistance in forests (Iannone et al., 2016b), most likely because they constitute the large majority of biomass and primary productivity in forest communities (Muller, 2003). Meanwhile, change in tree richness and change in tree height evenness were both positively

associated with increases in the percent of invaded plots. This is also in keeping with previous work that found strong relationships between biodiversity and invasion at broad scales because of the increased availability of resources and niches that are present in forests with greater biodiversity (Fridley et al., 2007; Iannone et al., 2016b). Meanwhile, one metric each of disturbance and of propagule pressure were the most important predictors of invasive richness change (Table 4). Both of these – small-scale anthropogenic forest fragmentation and percent of agricultural land cover change – were also important in explaining recent measurements of the three invasion metrics. As in those models, fragmentation was positively associated with invasive richness change and agricultural land cover change was negatively associated with it. Landscape-scale forest disturbance and conversion of agricultural land cover to more developed uses, therefore, may enable ongoing plant invasion of forests in the eastern United States. This is consistent with research that found a synergistic effect on invasion by the co-occurrence of agricultural and developed land cover that is associated with greater levels of invasion than when forest land cover is converted to only agricultural or developed land cover (Riitters et al., 2017).

The widespread decrease in non-native plant cover, particularly across the South, was unexpected. One potential explanation is that forests in some counties have changed in a way to make them less susceptible to dominance by understory invasive plants, which may be reflected by our finding that counties in the South with decreased plot-level invasive cover also had a significantly greater increase in biomass and a significantly greater decrease in tree density. Specifically, counties where invasive cover decreased had forests with increasingly more biomass and decreasingly lower tree density (though higher overall tree density than in other counties), suggesting a shift toward more mature forests consisting of larger trees with closed canopies that may be more resistant to invasion by shade-intolerant invasive plants. (This would not likely impact the degree of invasion by an increasing number of shade-tolerant non-native plants (Martin et al., 2009; Fridley et al., 2023). Additionally, shade tolerant invaders such as Japanese stiltgrass could become more dominant in these places in the future.) These counties also had a greater increase in developed land cover and a greater decrease in agricultural land cover, which indicates more urbanization and a potential shift away from active forest management that would likely lead to younger forests on average. This is consistent with findings that forests in the wildland urban interface (WUI) of the northern United States had greater aboveground biomass and stand density, and fewer seedlings and saplings, than non-WUI forests (Sonti et al., 2023). Another possible explanation of these widespread patterns is that increased invasive plant establishment (invasive richness) and prevalence (percent of invaded plots) resulted in a decrease in invasive dominance (invasive cover) as well as potentially native tree species density. It is additionally worth noting that change in invasive cover is not highly correlated with change in the other metrics ($r = 0.150$, $p < 0.0001$, for percent plots invaded, and $r = -0.017$, $p < 0.64$, for invasive richness) in these counties, underscoring that the metrics capture different aspects of invasion which may have varying associations with disturbance, propagule pressure, and forest invasibility factors.

Continuing to follow plant invasions over time will be important to assess the ongoing influence of forest invasibility, disturbance, and propagule pressure. For example, the projected increase of Eastern forestland within the WUI or near developed or agricultural land uses (Costanza et al., 2023) may result in an increase in regional plant invasion rates given the association between plant invasion and both forest fragmentation (via disturbance) and development (via propagule pressure) (Riitters et al., 2017; Potter et al., 2024). Monitoring invasions over time also will be important for attempting to assess the effects of two other factors: the ongoing introduction of additional invasive plants and the effects of changing climate conditions. The ornamental plant trade is likely to continue providing new non-native invasive plant species introduced into and established within U.S. forests (Theoharides and Dukes, 2007). Lists of invasive plant species will correspondingly require ongoing evaluation and expansion to include newly introduced species that have established and spread. Meanwhile, the rapid increases of some resources associated with climate change, such as CO_2, may favor fast-growing non-natives over slower-growing natives; additionally, invasive plant species may be better positioned to take advantage of changes in disturbance regimes and of more frequent extreme climate events to colonize natural ecosystems, particularly where native vegetation has lower resilience (Leishman and Gallagher, 2015; Blumenthal and Kray, 2023). For example, research has showed that non-native plants have greater phenological flexibility that allows them to flower earlier on average, in response to warmer spring conditions, than native plants (Willis et al., 2008; Wolkovich et al., 2013). However, predictions about the invasion risk posed by non-native plants are underlain by uncertainty because of unpredictability regarding how they will respond to changes in climate conditions and to rising CO_2 (Bradley et al., 2010). The consequences of climate change on a specific invasive species in at specific place are likely to depend on the direct effects of the climate on individual plants, the indirect effects that change resource availability and interactions with other species, and human influences that affect the degree to which natural ecosystems are susceptible to invasion (Finch et al., 2021).

4.3. Invasion debt

Evaluating the implications of invasion debt, the lag between an initial invasion and its full eventual ecological and socioeconomic outcomes (Rouget et al., 2016; Duncan, 2021), allows for a fuller understanding of the processes and ecological and economic effects of non-native invasions (Crooks, 2005). For example, recent work found evidence that forests in the WUI of the eastern United States have experienced invasion debt following housing development, including significantly greater non-native plant invasion of forested plots that had been in the WUI longer (Potter et al., 2024). The results underscored the need to monitor and manage forests that have recently entered the WUI before the invasion debt associated with changing land uses comes due. Similarly, an analysis in New Zealand found that non-native plant richness was more highly correlated with 1945 than 2000 suburban population density (Sullivan et al., 2004) while a study in southwestern Spain found that non-native plant richness was more highly correlated with land-cover variables from 1956 than from 2007 (González-Moreno et al., 2017).

In the current analyses, we found indications that plant invasion debt is playing out in forests across the eastern United States, both when considering invasion during a recent evaluation period as well as change over time. Most importantly, we detected an increase over time in the county-level percent of plots invaded and plot-level invasive richness. This change was statistically significant in the South, though the lack of statistical significance of similar results in other parts of the country was likely affected by smaller sample sizes. Secondly, we found that measures of recent plant invasion were more highly associated with earlier levels of anthropogenic forest fragmentation (2001) than more recent levels (2011 and 2021). This was the case across all three invasion metrics (Fig. 4), with these variables being the most important in the random forest assessments of invasive plant richness and percent cover. These results underscore the lasting implications of fragmentation on the invasion of forests by non-native plants, given the trend since ca. 2011 of lower rates of fragmentation of U.S. forests and of forest conversion to other forest types (Riitters et al., 2023). Additionally, for two metrics – percent of plots invaded and invasive richness – agricultural land cover was an increasingly more influential variable farther back in time (2001 was more important than 2011, and 2011 more important than 2021). For invasive richness and invasive species cover, the percent of 2001 developed land cover was more important than for 2011, which in turn was more important than 2021. All these results emphasize the degree to which the historical legacy of past land uses affects current

plant invasions (Vilà and Ibáñez, 2011).

The pattern of older land use variables being more influential than recent ones was apparent for two metrics of invasion change. For invasive richness change, the percent of agricultural land cover in 2001 was more important than for 2011 or 2021, though these metrics were not among the most influential overall. For change in invasive species cover, the percent change of both agricultural and developed landcover from 2001–2011 was more influential than for 2011–2021. Earlier agricultural land cover change was additionally among the most important variables overall. Clearly, invasion lag is manifested not only in the static measurement of forest plant invasion but also in invasion change.

These results are particularly useful given that current invasion debt, along with past levels of invasion, can together indicate future forest plant invasion trends (Vilà and Ibáñez, 2011; González-Moreno et al., 2014). It may be possible, for example, to use invasion lag information to make projections about future change in forest plant invasion across relatively large areas. This could be done while incorporating information about the extent of climate change and about the traits of individual plant species, as these factors are likely to influence how invasion debt unfolds. At the same time, it is important to underscore the limitations of focusing on non-native species currently defined as problematic, as we have done in this study, because this likely underestimates the future impacts (and current invasion debt) associated with species in the early stages of invasion (Blackburn et al., 2011) that have not yet been found to cause environmental harm or harm to human health. We are unaware of any relatively fine-scale resolution data collected consistently across broad geographic regions on all non-native plants, including those in the transport, introduction, and establishment stages of invasion; this information might allow for a more comprehensive assessment of invasion debt. Such data would be particularly useful given that the best chance for controlling potentially invasive non-native plants exists when they are low in abundance during their initial establishment (Osunkoya et al., 2021), though paradoxically they are often cryptic and offer few clues about their potential for invasiveness during this stage (Larkin, 2012; Coutts et al., 2018).

5. Conclusions

Invasive non-native plants are widespread throughout forests of the United States, especially in the eastern half of the country, with nearly 100 million ha of U.S. forests invaded. U.S. forests are becoming increasingly invaded as indicated by measures of invasive plant establishment and plant invasion prevalence but less so by a measure of plant invasion dominance. Measures of disturbance (especially anthropogenic forest fragmentation), propagule pressure (especially change in agricultural land cover), and habitat invasibility (including tree richness and change in tree biomass) are important variables for explaining both recent levels of forest invasion and recent change in invasion. U.S. forests are experiencing invasion debt, as demonstrated by metrics of invasion that are more closely associated with earlier measures of disturbance than more recent ones.

The results of this study can help guide the long-term monitoring and management of forest effects associated with invasive plant species while offering a glimpse into ongoing national, regional, and local patterns in the invasion of United States forests. For example, the results underscore the importance of the roles that disturbance, especially human-caused forest fragmentation, and propagule pressure, primarily via horticultural plantings of non-native species, play in the invasion of U.S. forests. Thus, they indicate that management actions relating to these drivers could affect the establishment and spread of invasive plants in U.S. forests, particularly in the East. Future work across broad scales will be needed to quantify the potential impacts on forest ecosystem services that are associated with increasing invasive plant species establishment, prevalence, and dominance. Broad-scale monitoring of non-native plant species, such as is provided by the NFI program (USDA Forest Service, 2022), will continue to be central to these efforts, as will tools that enable managers, scientists, and policymakers to identify and prioritize both the non-native plant species that are likely to be most invasive and the locations where they are most likely be problematic. One starting point could be a spatially explicit invasive species management tool that utilizes information from such sources as the NFI and the National Non-native Plant Database (Guo et al., 2009). Another would be to combine plot-level NFI invasives information with a stochastic modeling system that incorporates exogenous variables such as climate and human population growth and income while accounting for forest growth, aging, regeneration and forest type transitions over time (Coulston et al., 2023).

CRediT authorship contribution statement

Kevin M. Potter: Writing – review & editing, Writing – original draft, Visualization, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Basil V. Iannone:** Writing – review & editing, Writing – original draft, Methodology, Conceptualization. **Kurt H. Riitters:** Writing – review & editing, Writing – original draft, Methodology, Data curation, Conceptualization. **Qinfeng Guo:** Writing – review & editing, Writing – original draft, Conceptualization. **Karun Pandit:** Writing – review & editing, Writing – original draft, Conceptualization. **Christopher M. Oswalt:** Writing – review & editing, Writing – original draft, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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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.2025.123281.

Data Availability

Data will be made available on request.

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