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RESEARCH ARTICLE

Forest plant invasions in the eastern United States: evidence of invasion debt in the wildland-urban interface

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Abstract
Context Non-native invasive plants are a growing threat to forests. Meanwhile, the amount of forest within the wildland-urban interface (WUI) is increasing, with housing-associated disturbances enabling the spread of non-native plants.
Objectives We tested whether (1) WUI or non-WUI forests are more invaded, (2) WUI intermix forests (houses mingling with forest) are more invaded than interface forests (housing abutting forest), (3) invasion in WUI forests is delayed (invasion debt) following housing development, and (4) WUI forest invasion is associated with land cover context (a proxy for disturbance and propagule pressure).
Methods We conducted statistical comparisons of plant invasion metrics using WUI status information intersected with ~45,000 forest inventory plots (collected ca. 2015). We evaluated potential drivers of invasion using an ensemble learning approach and adopted a mixed-effects modeling framework to assess relationships between drivers and invasion.
Results Our analyses revealed that the degree of invasion in WUI forest plots was significantly higher. We found evidence for invasion debt, including greater invasion of plots in the WUI longer. WUI interface forests were more invaded than intermix forests. Agricultural and developed land cover at medium to large scales (~66 – 5,300 hectares) were most highly associated with WUI forest invasion.
Conclusions These findings elucidate dynamic plant invasion patterns and processes occurring within the WUI. They underscore the importance of monitoring and managing forests that have recently entered the WUI, with an emphasis on sources of exotic plant propagules at relatively large scales, before the housing invasion debt comes due.

Keywords Invasive species · Invasion debt · Ecosystem management · Forest inventory and analysis (FIA) · Disturbance · Propagule pressure

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Introduction

Non-native plants are a persistent threat to the forests of the United States (Iannone et al. 2015, 2016a), particularly in the eastern part of the country where approximately half of all forest plots contain at least

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one non-native plant (Oswalt et al. 2015) and where the spread of such plants is largely unchecked (Miller et al. 2015). The impacts of non-native plants on forests include changes in nutrient dynamics (Strickland et al. 2010; Yelenik and D'Antonio 2013), impacts on ecosystem function (Williams et al. 2011; Le Maitre et al. 2014), degradation of diversity and habitat (McKinney and La Sorte 2007; Williams et al. 2011), and landscape metamorphosis (Fei et al. 2014). In the eastern United States, the likelihood of invasion is highest in fragmented forests within landscapes containing more than 10% agricultural or developed land cover (Riitters et al. 2018). Forests in urban and suburban landscapes have been found to contain a greater diversity of non-native plant species than in those in landscapes dominated by agriculture and less disturbed forest (Duguay et al. 2007), while the presence and diversity of introduced plants in relatively undisturbed forest were associated with proximity to residential areas (Vieira et al. 2014).

The wildland-urban interface (WUI), the area where housing and wildland vegetation intermingle or abut each other (Radeloff et al. 2005; Martinuzzi et al. 2015b), is the fastest-growing land use type in the United States (Radeloff et al. 2018; Sonti et al. 2023). The WUI encompassed 9.5% of the land area of the continental United States in 2010 after expanding by 33% over the previous two decades, from 581,000 to 770 000 km^2, with greater rates of WUI growth in the eastern U.S. than the western part of the country (Radeloff et al. 2018). WUI forests in the northern U.S. have significantly reduced structural diversity than non-WUI forests; additionally, forests that have been in the WUI longer have decreased spatial integrity evidenced by more forest-developed edges and lower proportions of forest in their surrounding areas (Sonti et al. 2023). While much WUI-related research in the United States has focused on the heightened wildfire risk within the WUI (Hawbaker et al. 2013; Radeloff et al. 2018), there is an ongoing need to quantify how human settlements interact with neighboring ecosystems through such biotic processes as non-native species introduction, wildlife habitat loss, and landcover conversion (Bar-Massada et al. 2014). For example, a county-scale analysis of forests across six New England states found that invasive plant richness was positively associated with the WUI area, along with housing density and income (Gavier-Pizarro et al. 2010a). Meanwhile, research in South Africa determined that natural areas in the wildland-urban interface are especially vulnerable to invasion by non-native plants because of edge effects associated with fragmentation, including by roads, and because of their proximity to sources of introduced plants in suburban gardens (Alston and Richardson 2006). In southeastern Australia, exotic species have spread into the interface between urban areas and native eucalyptus forests via long-distance seed dispersal and the dumping of garden refuse in the forest (Gill and Williams 1996), while non-native plant invasion in New Zealand native coastal forests was associated with the proximity and density of housing (Sullivan et al. 2005). Assessments at broader scales and at finer resolutions could further fill gaps in our understanding about the patterns and processes of forest invasion by non-native plants in WUI forests.

Housing development within the WUI has numerous effects on natural ecosystems, including habitat modification and fragmentation that are followed by diffusion processes, through which the direct and indirect effects of anthropogenic activities spread into neighboring ecosystems at different scales (Bar-Massada et al. 2014). In the context of non-native plant species, these effects play out (1) through human-driven disturbances to native ecosystems that promote their invasion and (2) by the establishment and spread of non-native species into those ecosystems (propagule pressure) (Gonzalez-Moreno et al. 2017; Vieira et al. 2014). The disturbance component of this process revolves primarily around the indirect impacts of forest fragmentation, as housing construction and related development in the WUI fragments natural areas and creates forest edges (Gavier-Pizarro et al. 2010a), facilitating the establishment and spread of non-native plants (Hobbs and Huenneke 1992; Fraver 1994; Cadenasso and Pickett 2001). The diversity and abundance of non-native plants tend to be greater at the edge of forest fragments than in the interior, with a sharp decline in invasion away from the edge (Vila and Ibanez 2011), while woody invasive plant diversity in New England was higher in landscapes with more edge forest relative to core forest (Allen et al. 2013). Relatedly, invasive plant diversity in forests decrease with distance from roads and other transportation corridors (Ward et al. 2020) which are a key component in housing development and fragment the forest. Suburban forests additionally have greater proportions of edge habitats resulting from human

activities than rural forests (Ariori et al. 2017). The propagule pressure component of WUI plant invasion, meanwhile, occurs through the spread of propagules from ornamental plantings in residential landscaping into surrounding areas (Marco et al. 2010; Cubino et al. 2015; Sipek and Sajna 2020). Non-native species typically dominate the flora of residential landscapes (Cook et al. 2012) resulting in positive relationships between residential development and invasion of forests by non-native plants (Greene and Blossey 2014; Davis et al. 2016). At the same time, housing in rural settings may also contribute to the invasion of forests via the establishment and spread of propagules from non-native ornamental landscape plants (Gavier-Pizarro et al. 2010b) as well as by the construction and maintenance of roads in formerly road-free areas (Riitters et al. 2018). Understanding the relative importance of disturbance, primarily via forest fragmentation, and propagule pressure, primarily via horticultural plantings of non-native species, on the invasion of forests could help to guide the most efficient and effective measures to counter the establishment and spread of invasive plants in suburban and rural landscapes. The prevalence of forest fragmentation and non-native propagule pressure within both suburban and rural landscapes further suggests an expectation of greater forest invasion in intermix WUI areas – that is, where structures are scattered within the forest – than in interface WUI areas, where settled areas abut forest. However, previous work at the county scale in New England found a stronger relationship between invasive plant richness and WUI interface area than intermix area (Gavier-Pizarro et al. 2010a). A clearer understanding of the relative susceptibility of intermix and interface WUI forests could aid in the prioritization of areas on which to focus efforts to stem the establishment and spread of invasive plants.

While evidence demonstrates that natural communities are more invaded if they are surrounded by a human-dominated landscape than by a natural one, the historical legacy of that landscape is also important (Vila and Ibanez 2011). That is because a time lag usually exists between disturbances and the full realization of their consequences (Lindenmayer et al. 2008), a phenomenon called an "invasion debt" when it involves the eventual ecological and socioeconomic impacts associated with non-native species (Rouget et al. 2016; Duncan 2021). This can play out as a delayed rather than an immediate increase in invasion levels following a change in landscape composition. While this relationship between landscape history and invasion can be highly complex (Gonzalez-Moreno et al. 2017), understanding invasion debt is important for the effective management of non-native species because this provides a more accurate assessment of invader spread and dominance (Crooks 2005). An assessment of WUI forests in the northeastern United States demonstrated that forest structure of newer WUI areas was on a divergent trajectory away from non-WUI forest conditions and toward more established WUI areas (Sonti et al. 2023). Similar analyses of non-native plants in the WUI can quantify the relative extent of invasion debt in areas where development intermixes with and abuts forestland while offering insights into how that debt may be realized over time.

In this study, we used invasive plant species information from ~45,000 forest inventory plots (collected circa 2015 by the United States Department of Agriculture Forest Service) across the eastern United States; WUI spatial data from 1990, 2000, and 2010; and land cover data from 2001, 2006, 2011, and 2016 to test four hypotheses: (1) forests that are in the WUI are more invaded by non-native plants than those that are not; (2) WUI intermix forests (where houses mingle with forest) are more invaded than interface forests (where housing development abuts forest); (3) WUI forests experience a delay in invasion following housing development (i.e., an invasion debt); and (4) the invasion of WUI forest plots is associated with disturbance (measured as the fragmentation of forest in the neighborhoods around plots) and propagule pressure (measured as the proportion of developed and agricultural land cover around the plots).

Methods

Forest inventory data

The USDA Forest Service administers the national Forest Inventory and Analysis (FIA) program, which encompasses a sampling intensity of approximately one plot per 2,428 ha across all forest ownerships (Bechtold and Patterson 2005). The FIA program identifies FIA plot locations using a spatially balanced sampling framework using a national lattice

of 2,468-ha hexagons. A randomly selected location within each hexagon is visited by a field crew when the location is determined by remotely sensed data to be in forest land use and the location is both accessible and not hazardous. The inventory crews collect a wide variety of data on a plot after confirming it is forested, which is defined as having ≥ 10% tree canopy cover (or evidence of such cover) and being ≥ 0.4 ha in size and 37 m wide. Plots contain four subplots arranged at the center and vertices of a triangle that together cover 0.067 hectares (Burrill et al. 2021).

On all plots in the South and about 20% of the plots in the North, field crews record the identity and cover of non-native invasive plant species. These are defined, in accordance with USA Executive Order 13,112, as those that cause economic or environmental harm or harm to human health, or that are likely to do so (Ries et al. 2004). Local experts determine the regional lists of invasive plant species that are inventoried (USDA Forest Service 2004). In the eastern United States, 44 taxa are on the monitoring list for the northern region (USDA Forest Service 2023) and 72 are on the list for the southern region, of which 23 are inventoried only in Florida (USDA Forest Service 2022). Twenty-four taxa are included on both regional lists. The difference in sampling intensity between the regions does not affect statistical analyses across broad scales (Iannone et al. 2016b).

We estimated two invasion measures for each FIA plot. Invasive species richness, the count of monitored invasive species occurring on the plot, is a measure of invasive plant establishment (Iannone et al. 2015). Invasive percent cover, the summed percent cover of all monitoring invasive plants for each subplot averaged across the four subplots on a plot, is a measure of invasive species dominance (Iannone et al. 2015).

Our analyses were based on data collected from 44,956 FIA plots in the 37 eastern United States (excluding the western portions of Texas and Oklahoma) between 2010 and 2018 (Fig. 1). This evaluation period was selected to center on the years following the 2010 U.S. Census to allow for analyses of WUI data generated using information from that census. The median year of collection varied between 2013 and 2016, depending on the state, with the median for 28 of the 37 states being 2014 or 2015. The plots were intersected with USDA Forest Service ecoregion sections, defined based on similarity in geology, climate, soils, and potential natural communities (Cleland et al. 2007), to allow for the spatial summarization of the plot-level invasion metrics and for inclusion of ecoregions in random forest models and mixed-effects models.

Wildland-urban interface data

The wildland urban interface (WUI) encompasses areas where houses and wildland vegetation intermix and intermingle, as defined by the U.S. government (U.S. Department of Agriculture and U.S. Department of Interior 2001). Interface WUI exists where settled areas abut wildlands and intermix WUI exists where structures are scattered throughout a wildland area. Interface WUI areas have less than 50% wildland vegetation and are within 2.4 km of a densely vegetated area (having at least 75% wildland vegetation) of at least 5 km^2. Intermix WUI areas have a housing density of at least 6.17 houses per km^2 and have at least 50% wildland vegetation (Radeloff et al. 2018).

Radeloff et al. (2018) identified and mapped WUI areas nationally by incorporating housing data from the U.S. Census and wildland vegetation information from the National Land Cover Database (NLCD). Housing and population data were gathered at the census block level for 1990, 2000, and 2010, but the 1990 and 2000 data had to be allocated into the 2010 census block geometries because the boundaries change between decennial censuses. Housing densities were calculated for the census blocks after excluding public lands. The percent of wildland vegetation cover within each 2010 census block was estimated using the 1992, 2001, and 2011 NLCD land cover products; the forest and grass/shrub land cover classes were considered wildland vegetation, but wetlands, open water, barren, urban, and ice/snow classes were not.

Each of the 44,956 FIA actual plot locations was intersected with the WUI spatial data from 1990, 2000, and 2010 (Radeloff et al. 2017) to determine whether they were within the WUI at each time step and, if they were, whether they were in the intermix or interface. We recognize that the WUI spatial data are subject to the scale aspect of the modifiable areal unit problem (MAUP), through which the aggregation of finer resolution data to different, coarser units can result in alternative combinations that yield

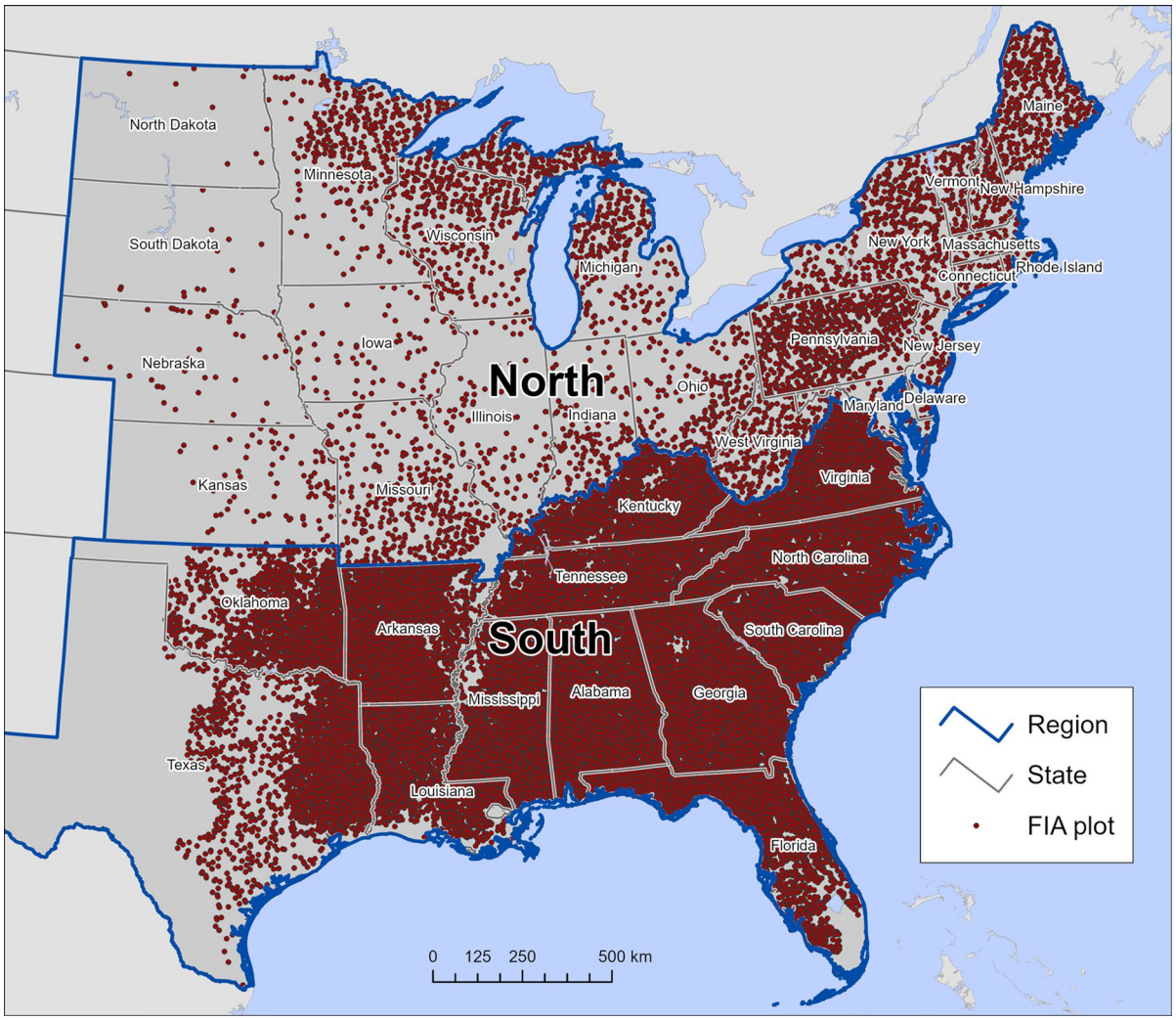

Fig. 1 Forest Inventory and Analysis (FIA) plots (approximate locations) inventoried for invasive plants across the eastern United States

dissimilar values and inferences (Dark and Bram 2007; Jelinski and Wu 1996). This is because census blocks vary in size and shape, which can lead to inconsistent representations of housing density, the basis for WUI classification. Using a point-based WUI classification approach would reduce the effects of the MAUP. Newer 30 m resolution WUI raster data (Carlson et al. 2022) have been developed based on building locations, but this dataset is limited to a single period in time (circa 2015) while we needed to assess plant invasions in WUI forest plots over time. In our assessment of the relationships between invasion metrics and land cover variables (see "Statistical analyses" below), we applied a mixed-effects modelling approach with ecoregion as a random effect to reduce the influence of both the scale and zoning aspects of the MAUP (Hamil et al. 2016). The zoning aspect of the MAUP is the situation through which differently delineated units of the same size can result in different conclusions (Jelinski and Wu 1996; Dark and Bram 2007).

Landscape context

Previous work established that the amount of developed and agricultural land cover around forested

plots in the eastern U.S. is strongly associated with the likelihood that those plots are invaded by non-native plants, potentially the result of invasive species propagule pressure from developed and agricultural areas (Riitters et al. 2018). Additionally, forested plots that exist in a more disturbed landscape – that is, surrounded by greater forest fragmentation – were more invaded by non-native plants (Riitters et al. 2018; Waddell et al. 2020). To assess the relative importance of propagule pressure (developed and agricultural land cover) and disturbance (forest fragmentation), we intersected the actual FIA plot locations with 30 m NLCD land cover data from 2001, 2006, 2011, and 2016 (Homer et al. 2020; Wickham et al. 2021). Specifically, we measured the percent of agricultural, developed, and forested land cover within five square neighborhoods surrounding each plot (4.41 ha, 15.21 ha, 65.61 ha, 590.49 ha, and 5314.41 ha). Roads were classified as developed land cover.

Statistical analyses

We tested our first hypothesis (that WUI forests are more invaded by non-native plants than non-WUI forests) by assessing whether significant differences existed in the two invasive species metrics. This comparison was between the 10,546 plots in the WUI in 2010 and the 34,086 plots that were neither in the WUI nor in a densely populated non-WUI area. To test our second hypothesis (that intermix forests are more invaded than interface forests), we assessed whether significant differences existed in the invasion metrics between plots in the intermix and interface for plots that were in the WUI in 2010 ($n = 10{,}546$; 9,538 intermix, 1,008 interface). To test our third hypothesis (that WUI forests experience a delay in invasion following housing development), we assessed whether significant differences in the invasion metrics existed between plots that were in the WUI in 1990 versus those that entered the WUI in either 2000 or 2010 (sensu Sonti et al. 2023), again for the 10,546 plots in the WUI. For each of these comparisons, we applied non-parametric Kruskal-Wallis tests 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 conducted further Kruskal-Wallis comparisons of tree species richness between the plots in these three groupings (WUI vs. non-WUI, WUI intermix vs. interface, and older vs. newer WUI) to assess whether differences exist between these groups in niche availability, habitat heterogeneity, and edge effects that could influence the prevalence of forest plant invasion. (Understory native plants are not inventoried on all plots.)

Next, we tested our fourth hypothesis, that the invasion of WUI forest plots is associated with disturbance (fragmentation of forest in the neighborhoods around plots) and propagule pressure (the proportion of developed and agricultural land cover around the plots), in two ways. First, we assessed the relationships between the two invasion metrics and change over time (2001 to 2016, 2006 to 2016, and 2011 to 2016) in the percent of agricultural, developed, and forested landcover around each plot within a 590.49 ha neighborhood, using Spearman correlation coefficients because of the non-normality of the data. This analysis encompassed the 10,546 WUI plots in 2010. (This also addresses our third hypothesis).

Second, we implemented a two-step modeling process that (1) evaluated potential drivers of the two invasion metrics using an ensemble learning approach that applied a random forests algorithm and (2) adopted a mixed-effects modeling framework to assess the relationships between the invasion metrics and the land cover variables identified in the ensemble learning step as being most important. We applied the ensemble learning approach to evaluate the relative importance of an extensive number of land cover and environmental variables in explaining variation in plot-level invasion metrics, and thus identify appropriate predictor variables for our mixed-effects modeling framework. For this random forest analyses of variable importance, we used the R package *party* (Hothorn et al. 2006; Strobl et al. 2007) to grow 5,000 trees to ensure the stability of variable importance measures (that is, the mean decrease in accuracy when each variable is excluded) and the package *flexplot* (Fife 2022) to assess out-of-bag performance of the models and estimate the amount of variance in the invasive species metrics explained by the predictor variables (R^2). We evaluated the importance of variables associated with WUI status (whether the plot was in the interface or intermix in 2010 and whether the plot entered the WUI more recently [i.e., in 2000 or 2010]); environmental characteristics (ecoregion, elevation, slope, and an ordinal measure of relative site productivity [low, medium, and high] for tree

growth (Burrill et al. 2021); the proportion of agricultural, developed, and forested land cover around each plot in the five neighborhood sizes and during the four NLCD measurement years; and change over time in agricultural, developed, and forested land cover within the 590.49 ha neighborhood between 2001 and 2006, 2006 and 2011, and 2011 and 2016. We then used the ranked list of variable importance values to select predictor variables for our mixed-effects modeling framework, focusing on (1) the most influential neighborhood/year combination for each of the three land cover types (agricultural, developed, and forested) to assess the relative importance of the land cover types (two models, one each for invasive species richness and cover) and (2) the most influential variable for each land cover type for each neighborhood size, to assess the relative importance of neighborhood sizes (six models, three each for invasive species richness and cover). For the second set of models, we identified the most influential measurement year within each neighborhood, because neighborhood measurements across time were highly correlated with each other (for example, 2001 agricultural land cover within the 590.49 ha neighborhood, which was correlated at $r \geq 0.99$ with the other three measurement years). Land cover variables at different neighborhood sizes were not generally highly correlated. These analyses encompassed 10,504 FIA plots, after eliminating those from ecoregion sections containing fewer than five plots in the WUI (76 total ecoregions; Supplementary Fig. 1).

We constructed a mixed-effects modeling framework because it accounted for potential spatial heterogeneity in relationships between invasion metrics and predictor variables (Hamil et al. 2016), and because it controlled for regional differences in the density of sampling for invasive plants and avoided potential statistical complications that can occur when using very large datasets (Iannone et al. 2016b). Specifically, having a large number of observations can result in the identification of weak but statistically significant relationships that may not be important ecologically (Spanos 2014; Woodall and Westfall 2010). Our modeling approach is described in detail by Iannone et al. (2016b). Briefly, we assembled a statistical model for each invasion metric containing the variables noted above as both fixed effects and random effects within ecoregions, each having independent intercept and slope estimates. This accommodates the potential spatial heterogeneity in associations between the invasion metrics and the environmental and land cover variables, based on the assumption of independence among ecoregions given the environmental differences among them and the relative homogeneity of the environmental attributes within them (Cleland et al. 2007). All predictor variables were standardized to better allow comparison among their associations with the invasion response variables (Schielzeth 2010). Because invasive species richness is a count variable, we performed Poisson regression using a log-link function for this response variable. We fit the mixed-effects models using the *lme4* package in R (Bates et al. 2015) and conducted bootstrap analyses with the *boot* package (Canty and Ripley 2022).

Results

Geographic patterns of invasion

Mean FIA plot-level invasive plant species richness (circa 2015) was highest in a handful of ecoregion sections in the northern states, particularly in the Central and Mid-Atlantic regions (Fig. 2A). Specifically, it was highest in the Northern Appalachian Piedmont stretching from north-central Virginia to southern New York (mean of 4.04 invasive species per plot), in the Interior Low Plateau-Bluegrass of northern Kentucky and southeastern Indiana (3.46 invasive species), and Central Till Plains-Beech-Maple in central Indiana and western Ohio (3.43 invasives species). Ecoregions in the northern part of the Great Lakes states, in northern New England, in the southern Great Plains, and along the Southern Atlantic Coast had relatively low mean plot species richness. Mean plot-level invasive cover was also high in the Mid-Atlantic and Central regions (21.39% in the Northern Appalachian Piedmont and 20.10 in the Interior Low Plateau-Bluegrass region) but was highest in eastern Tennessee (28.12% in the Central Ridge and Valley region) (Fig. 2B). It was low in the same areas as invasive species richness.

WUI group comparisons

Of the 44,956 plots in our study, 7,241 (16.5%) were in the WUI in 1990, increasing to 9,339 (20.8%) in 2000 and 10,546 (23.5%) in 2010. Plots in the WUI

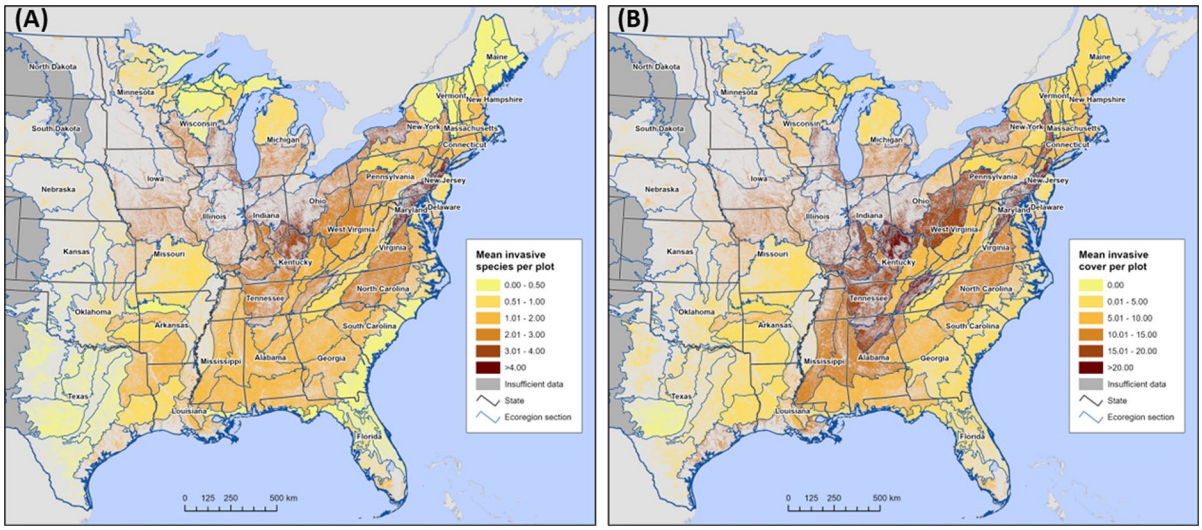

Fig. 2 Mean plot-level invasive species richness (**A**) and invasive species cover (**B**) from Forest Inventory and Analysis (FIA) plots circa 2015, by ecoregion section

in 2010 had significantly higher invasive plant species richness and invasive species cover than non-WUI plots in "natural" areas (that is, areas without high housing densities). On average, plots in the WUI contained 1.79 invasive plant species and 10.77% invasive species cover, compared to 1.12 species and 6.11% cover on the non-WUI "natural" plots. WUI plots had significantly higher tree species richness than non-WUI plots (6.57 species per plot compared to 5.92; Table 1.)

Among the 10,546 plots in the WUI circa 2015, those in the WUI interface (where settled areas abut wildlands) were significantly more invaded than those in the WUI intermix (where structures are scattered in a wildland area). Interface plots encompassed 2.27 invasive plant species and 15.40% invasive cover on average, compared to 1.74 species and 10.29% cover for intermix plots (Table 1). At the same time, intermix plots encompassed significantly higher tree species diversity (mean of 6.69 species per plot) than interface plots (5.41 species). Additionally, FIA plots that were in the WUI longer (since at least 1990) were significantly more invaded than those that had entered the WUI more recently (in 2000 or 2010). Older-WUI plots had 1.90 invasive species on average compared to 1.57 for newer-WUI plots, while the

Table 1 Mean and standard errors of Forest Inventory and Analysis (FIA) plot-level measures of invasion by 2010 wildland urban interface status, 2010 WUI type (intermix or interface), and the length of WUI status (old: since 1990; new: since 2000 or 2010), with *p*-values from Kruskal–Wallis tests of group differences

	Plots	Invasive spp.		Invasive spp.		Tree spp.	
		Richness		Percent cover		Richness	
		Mean	SE	Mean	SE	Mean	SE
2010 WUI status		***p* < 0.0001**		***p* < 0.0001**		***p* < 0.0001**	
WUI	10,546	1.79	1.68	10.77	18.75	6.57	3.49
Non-WUI (natural)	34,086	1.12	1.36	6.11	13.79	5.92	3.48
2010 WUI type		***p* < 0.0001**		***p* < 0.0001**		***p* < 0.0001**	
Intermix	9,538	1.74	1.66	10.29	18.13	6.69	3.50
Interface	1,008	2.27	1.79	15.4	23.37	5.41	3.11
Length of WUI status		***p* < 0.0001**		***p* < 0.0001**		$p = 0.393$	
Older (since 1990)	6,811	1.9	1.74	11.7	19.64	6.58	3.44
Newer (since 2000 or 2010)	3,735	1.57	1.54	9.09	16.89	6.55	3.58

p-values ≤ 0.05 are in bold

invasive species cover was 11.70 on older-WUI plots and 9.09 on newer-WUI plots. At the same time, we detected no significant difference in tree richness by length of WUI status, which may be attributable at least in part to differences in life histories between native trees and more rapidly establishing and growing understory invasive plants.

Invasion metrics and land cover

Relationships between both invasion metrics and 2016 land cover were strongest at 590.49 ha for percent forested ($r = -0.268$ for invasive species richness and $r = -0.269$ for invasive cover) and percent developed ($r = 0.257$ and $r = 0.238$), while the relationships with percent agricultural were strongest at 65.61 ha for invasive species richness ($r = 0.340$) and at 590.49 ha for percent invasive species cover ($r = 0.334$) (Supplementary Tables 1 and 2). Percent forested land cover was negatively correlated with the percent of both agricultural and developed land cover ($r = -0.725$ and $r = -0.429$, respectively, for 2016). Percent agricultural and percent developed land cover were positively but less strongly correlated ($r = 0.280$ for 2016). The two invasion metrics, meanwhile, were highly but not perfectly correlated ($r = 0.913$).

Our assessment of the relationship between invasion and change over time in land cover showed that higher levels of invasion on the 10,546 WUI plots were significantly associated with decreases in agricultural land cover in 590.49 ha neighborhoods around the plots (Table 2). This relationship was stronger for changes farther back in time, that is, more strongly for decreases in agricultural land cover between 2001 and 2006 and between 2006 and 2011 ($r = -0.141$ and $r = -0.160$, respectively, for invasive species richness and $r = -0.177$ and $r = -0.182$ for invasive species cover) than between 2001 and 2016 ($r = -0.087$ for invasive species richness and $r = -0.100$ for invasive species cover). Meanwhile, the invasion metrics were positively and significantly associated with increases in developed land cover, except between 2011 and 2016, when they were not significantly correlated. The strength of these relationships was relatively weak (between $r = 0.048$ and $r = 0.074$) but was significant for the years 2001–2006 and 2006–2011. Finally, we did not detect significant relationships between invasion and change in forested land cover, except for a weak negative relationship between invasive richness and forest cover change for 2006–2011 and a weak positive relationship between invasive cover and forest cover change for 2011–2016. Change in agricultural land in the 590.49 ha neighborhoods was negatively correlated with change in both developed and forested land cover ($r = -0.227$ and $r = -0.089$ for 2001–2016), while developed land cover change was also negatively associated with forested land cover change ($r = -0.192$ for 2001–2016). On average, the 590.49 ha neighborhoods around the circa 2015 WUI plots experienced a 1.13% decrease in agricultural land cover, a 0.84% decrease in forested land cover, and a 0.98% increase in developed land cover between 2001 and 2016.

Table 2 Spearman correlations between Forest Inventory and Analysis (FIA) plot-level measures of invasion with change over time in the percent of agricultural, developed, and forested land cover in 590.49 ha neighborhoods around each of 10,546 plots in the wildland urban interface circa 2015

	Agriculture	Developed	Forested
Invasive species richness			
2001–2016	**– 0.201**	**0.072**	0.004
2001–2006	**– 0.141**	**0.048**	– 0.004
2006–2011	**– 0.160**	**0.074**	**– 0.020**
2011–2016	**– 0.087**	0.018	0.015
Invasive species cover			
2001–2016	**– 0.237**	**0.066**	0.012
2001–2006	**– 0.177**	**0.050**	– 0.005
2006–2011	**– 0.182**	**0.055**	– 0.009
2011–2016	**– 0.100**	0.015	**0.030**

p-values ≤ 0.05 are in bold

Random forests assessment of variable importance

The random forests classification of invasive species richness explained a modest amount of variation ($R^2 = 0.219$) with a median predicted value of 0.985 species different than the actual (out-of-bag) value. Ecoregion was by far the most important variable, with a 0.251 species mean decrease in accuracy when excluded from tree construction (Fig. 3, Supplementary Table 3). Two other environmental variables were the next most influential, elevation (0.065 species accuracy decrease) and slope (0.035 species accuracy decrease). Aspect and productivity were moderately important variables but were less so than a set of agricultural and developed land

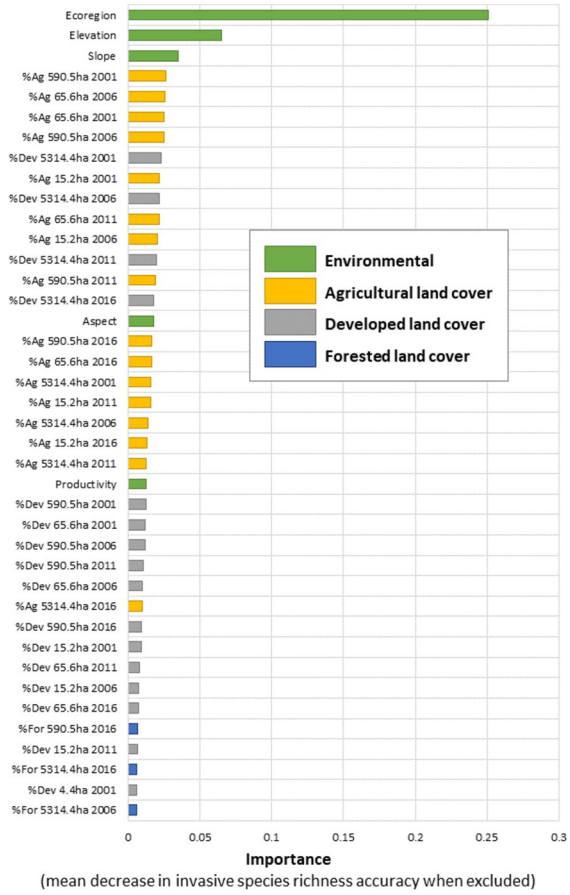

Fig. 3 Mean decrease in the accuracy of plot-level invasive species richness predictions for the 40 most important variables included in the random forests analysis. The variables are color-coded by type. Values of all importance variables are listed in Supplementary Table 3

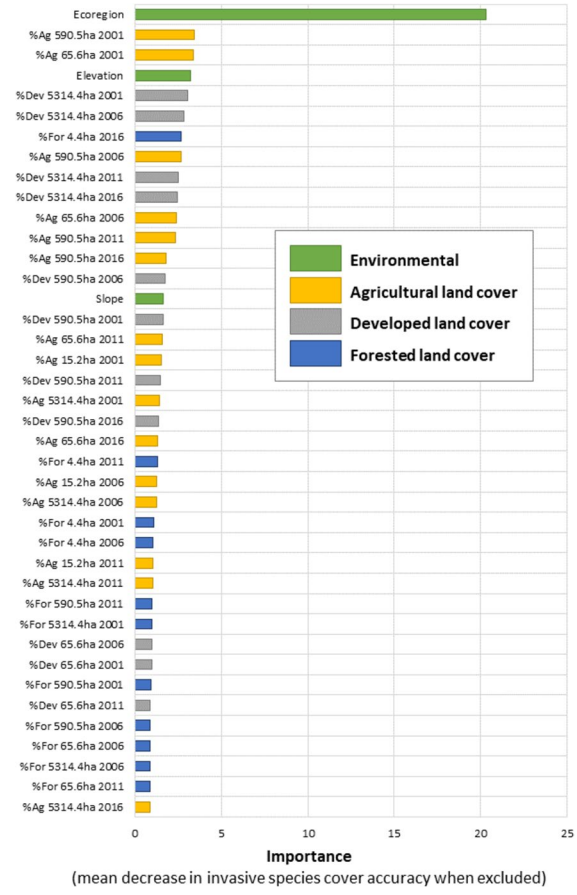

Fig. 4 Mean decrease in the accuracy of plot-level invasive species cover predictions for the 40 most important variables included in the random forests analysis. The variables are color-coded by type. Values of the importance variables are listed in Supplementary Table 4

cover variables. Of these, the percent of agricultural land cover in moderately sized neighborhoods was the most influential (for example, 0.026 species accuracy decrease for 2001% agriculture in the 590.49 ha neighborhood) followed by developed land cover in the largest neighborhood (5314.41 ha). For the most part, agricultural land cover was more important than developed land cover. Also, earlier agricultural and developed land cover variables were more important than recent measurements. Forested land cover was generally less influential; the most important of these were percent forest in the 590.49 ha neighborhood and in the 5314.41 ha neighborhood, both for 2016. Across all land cover types, smaller neighborhoods (4.41 ha and 15.21 ha) generally were less important than medium and large ones. WUI attributes and changes in land cover were among the least important variables.

The random forests model predicted less variation in invasive species cover ($R^2 = 0.123$) with the difference between the predicted and actual values being 7.95% cover. As with species richness, ecoregion was the most important variable (20.29% cover mean decrease in accuracy when excluded from tree construction), though other environmental predictors (elevation, slope, and aspect) were not as influential as some land cover variables (Fig. 4, Supplementary Table 4). Specifically, 2001 agricultural cover in the 590.49 ha and 65.61 ha neighborhoods were the second and third most important variables (3.41% and

3.38% cover accuracy decreases, respectively), followed by elevation and developed landcover in the 5314.41 ha neighborhood for 2001 and 2006. Forest landcover variables were generally more important for predicting invasive species cover than for invasive species richness, particularly 2016 forest cover within the smallest neighborhood, 4.41 ha (2.67% cover accuracy decrease). In general, developed cover within larger neighborhoods was more influential than in smaller neighborhoods, while medium-sized neighborhoods were the most important for agricultural land cover. Again, more recent agricultural and developed land cover variables were less important than earlier ones, and WUI attributes and landcover change were among the least important variables.

Mixed effects models

For our first mixed-effects modeling framework, we selected the most influential variable for each land cover type (agricultural, developed, and forested) for both invasive species response variables (species richness and cover). Both models included the percent agriculture in the 590.49 ha neighborhood for 2001 and the percent developed in the 5314.41 ha neighborhood in 2001 (Table 3). The most important forested land cover metrics were different, though: for invasive richness, this was percent forested in the 590.49 ha neighborhood for 2016, while for invasive cover it was percent forested in the 4.41 ha neighborhood for 2016. The 95% confidence intervals (CI) for the bootstrapped distributions of section-level slope estimates (conditional plus fixed slope estimates) indicate whether the landscape metrics are significantly associated with the invasion metrics (that is, if they do not overlap 0) and the directions of these associations. The agricultural and developed land cover variables were positively and strongly associated with both invasion metrics (Fig. 5), while the forested variables were, respectively, negatively and weakly associated with invasive species richness and positively and weakly associated with invasive species cover. The extent to which association magnitudes varied among ecological sections (as determined by the 95% CI ranges) was greater for the agricultural and forested land cover metrics than for developed land cover in the invasion richness model, while it was greatest for developed land cover and lowest for forested land cover in the invasive cover model (Fig. 5, Supplementary Table 5).

In our second mixed-effects modeling framework, we separately chose the most influential variable for each neighborhood for each of the land cover types (Table 3). As noted above, the most important agricultural variables were those at medium scales measured earlier, while the most important developed land cover variables were at large and medium scales and measured earlier. The importance of forested land cover variables differed between the two invasion metrics. All the agricultural land cover metrics were positively associated with invasion, except at the smallest scale (Supplementary Fig. 2). Agricultural land cover in the 15.21 ha neighborhood was particularly strongly associated with both invasive richness and cover. Developed land cover associations were less consistent between the invasion measures (Supplementary Fig. 3): For invasive richness, developed cover in the 15.21 ha neighborhood was not different than 0, while it was negatively associated with invasion in the 590.49 ha neighborhood. For invasive cover, developed land cover at the smallest scale was negatively associated with invasion while the rest of the metrics were positively associated. For both invasion measures, developed cover at the 5314.41 ha and 65.61 ha neighborhoods was most strongly positively associated with invasion. Forest land cover was negatively associated with both invasion measures at all but the smallest scale (Supplementary Fig. 4).

Discussion

Non-native plants are a persistent and growing threat to U.S. forests, eroding forest productivity, hindering forest use, and degrading diversity and habitat. They generate extensive financial costs relating to resource damages and losses (Fernandez et al. 2023). The degree of invasion by non-native plants in wildland-urban interface (WUI) forests has not been comprehensively quantified across broad regions. Our assessment of data from ~45,000 forest inventory plots across the eastern United States establishes that forests within the WUI were more invaded by non-native plants than those outside it. Somewhat unexpectedly, interface forests (those where housing abuts the forest) were more invaded than intermix forests (those where houses mingle with the forest). Several results

Table 3 Results from each of eight mixed-effects models, two encompassing the most influential neighborhood/year combination for each of the three land cover types (agricultural, developed, and forested), one each for invasive species richness and invasive species cover, and six incorporating the most important year of measurement for each neighborhood within each land cover type, three each for invasive species richness and invasive species cover

Model	Variables					R^2	AIC
Invasive species richness							
All	%Ag 590.5 ha 2001	%Dev 5314.4 ha 2001	%For 590.5 ha 2016			0.482	35228.0
Agricultural	%Ag 590.5 ha 2001	%Ag 65.6 ha 2006	%Ag 15.2 ha 2001	%Ag 5314.4 ha 2001	%Ag 4.4 ha 2001	0.562	35583.6
Developed	%Dev 5314.4 ha 2001	%Dev 590.5 ha 2001	%Dev 65.6 ha 2001	%Dev 15.2 ha 2001	%Dev 4.4 ha 2001	0.328	35750.8
Forested	%For 590.5 ha 2016	%For 5314.4 ha 2016	%For 65.6 ha 2011	%For 15.2 ha 2001	%For 4.4 ha 2016	0.426	35236.4
Invasive species cover							
All	%Ag 590.5 ha 2001	%Dev 5314.4 ha 2001	%For 4.4 ha 2016			0.156	90006.1
Agricultural	%Ag 590.5 ha 2001	%Ag 65.6 ha 2001	%Ag 15.2 ha 2001	%Ag 5314.4 ha 2001	%Ag 4.4 ha 2016	0.142	90251.2
Developed	%Dev 5314.4 ha 2001	%Dev 590.5 ha 2006	%Dev 65.6 ha 2006	%Dev 15.2 ha 2006	%Dev 4.4 ha 2016	0.154	90320.9
Forested	%For 4.4 ha 2016	%For 5314.4 ha 2001	%For 590.5 ha 2001	%For 65.6 ha 2006	%For 15.2 ha 2006	0.156	90085.5

The variables are listed in order of importance derived from the random forests analysis

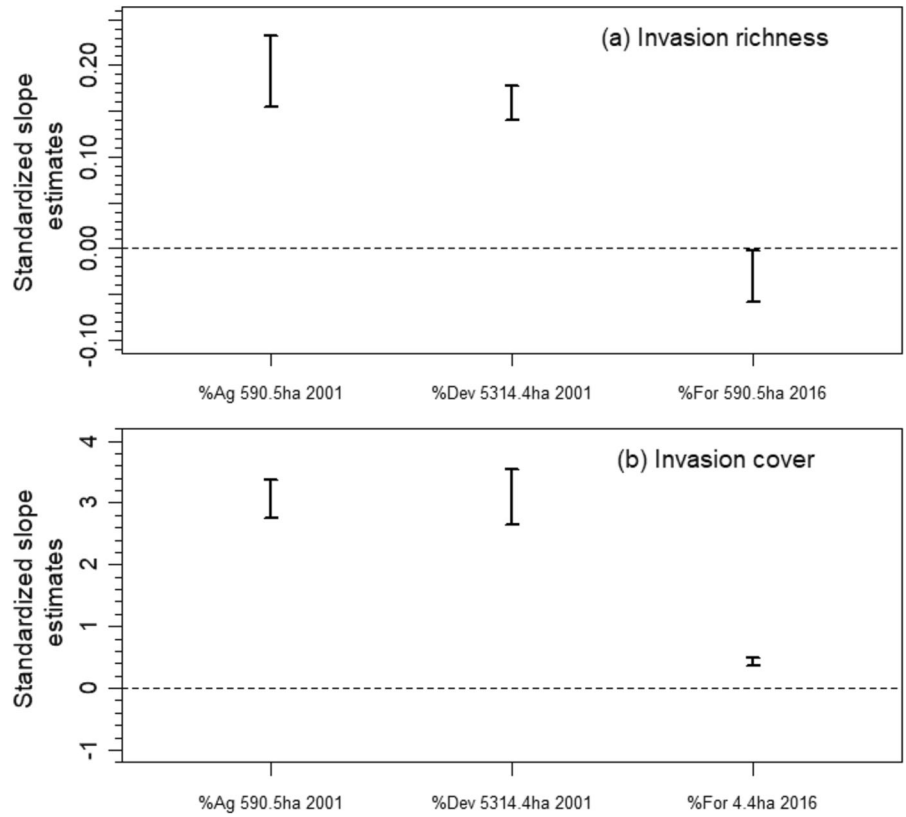

Fig. 5 Bootstrapped 95% confidence intervals for section-level slope estimates (i.e. conditional plus fixed slope estimates) of land cover metrics for the 76 ecological sections in models for (**a**) invasion richness and (**b**) invasion cover across the eastern United States. Increased interval size suggests greater spatial variability in slope estimates across the 76 ecological sections

clearly point to the existence of invasion debt in these WUI forests, as an apparent lag exists in the degree of invasion following forest entry into the WUI. Finally, the invasion of WUI forests is associated with both propagule pressure (the proportion of developed and agricultural land cover around forest plots) and disturbance (the proportion of forest cover in the neighborhoods around plots), though sometimes in unexpected ways within different neighborhood sizes.

The degree of WUI forest invasion

Our study confirms that WUI forests are more invaded by non-native plants than those that are not in the WUI. Specifically, WUI plots averaged 0.67 more invasive species than plots not in the WUI (a 59.8% increase) and had nearly 5% more invasive species cover (a 76.3% increase). These differences are not unexpected, given that WUI forests are on a continuum between more intact natural forests and urban areas and are a mosaic of remnant, managed, and abandoned forest patches (Huebner et al. 2012). Previous research has found that invasive species generally benefit from urbanization, obtaining higher abundances and greater diversity in more urbanized habitats (Cadotte et al. 2017). Studies in several locations have found this to be the case specifically with non-native plant species (Jang et al. 2020; Wania et al. 2006; Yang et al. 2023). In at least one case, forests in the urban-rural interface had higher frequencies and abundances of understory non-native plants than settings that were either primarily urban or forested (Loewenstein and Loewenstein 2005). A factor potentially contributing to the prevalence of invasive plants in urban and suburban settings is greater environmental variability in these areas, since landscapes with more spatial heterogeneity in abiotic conditions can sustain more species, both native and non-native (Davies et al. 2005). We found significantly higher tree species richness on WUI than on non-WUI forest plots in the eastern U.S. (Data were not available to assess species richness across all plant species.) Thus, the environmental conditions that benefit native species richness in these forests also appear to favor non-native species richness without allowing the exclusion of the non-native understory plants by the native

trees, a pattern detected in other forests (Belote et al. 2008; Gilbert and Lechowicz 2005). This suggests the possibility that the greater degree of invasion in these forests may be linked to higher habitat heterogeneity, which is often associated with higher plant biodiversity because of niche differentiation among species (Levine and HilleRisLambers 2009; Lundholm 2009).

It is important to note that relationships between invasiveness and population density and/or urbanization vary by species. In northeast Connecticut, for example, some species (including *Ailanthus altissima* (Mill.) Swingle, *Acer platanoides* L., and *Ligustrum* spp.) were most common in urban areas while others (such as *Frangula alnus* Mill. and *Lonicera* shrub species) were most frequent in suburban forests (Ariori et al. 2017). In South Carolina, a relationship appeared to exist between urbanization and the invasion of *Ligustrum sinense* Lour., but all floodplain forests were considered at risk from invasion by the shrub regardless of proximity to urban areas (Greene and Blossey 2014). In southern Wisconsin, *Rhamnus cathartica* L. and *Lonicera* spp. were strongly associated with rural housing and fragmentation (Gavier-Pizarro et al. 2010b). Meanwhile, the widespread introduction of the alien grass *Cortaderia selloana* (Schult. & Schult.f.) Asch. & Graebn. in southern France has resulted in its naturalization in anthropogenic habitats, but it has thus far not spread extensively into natural habitats (Charpentier et al. 2020).

Invasion of WUI Intermix vs. interface

We expected that intermix forests (where houses mingle with forest) would be more invaded than interface forests (where housing development abuts forest) because the disturbance associated with development within these forests (including the removal of trees and the installation of infrastructure such as roads and water lines) might increase their vulnerability to invasion, while the occupied homes in these forests are likely sources of non-native invasive plant species (Huebner et al. 2012). Instead, we found that interface forest plots on average contained about 0.5 more invasive plant species than intermix plots (a 30.5% increase) and had 5.1% more invasive species cover (a 49.7% increase). This is the case even though intermix forests have significantly higher tree species richness, indicating that WUI interface forests have more invasive species on average despite potentially encompassing less niche availability than intermix forests.

Two factors may be responsible for the unexpectedly higher invasion in interface than intermix forests. First, the WUI forest interface's greater proximity to high-density urbanization and its plentiful sources of non-native plant propagules may outweigh its lesser spatial interaction with areas of higher housing density in determining forest invasion. In the Chicago metropolitan region, for example, the occurrence of several non-native plant species in more than 2000 wetlands was associated with proximity to the city, reflecting either an area's degree of urbanization or the outward dispersal of plants from an earlier establishment within the urban center (Skultety and Matthews 2017). Similarly, Alston and Richardson (2006) found in a forest near Cape Town, South Africa, that non-native plant richness increased with increasing levels of human disturbance and proximity to putative source populations. Meanwhile, in the WUI intermix, the lower density of housing may be a more important factor in forest plant invasion than the more complex intermingling of housing-related disturbances and forestland. In other words, the higher exposure to invasive plant propagules in WUI interface forests appears to have a stronger effect on the prevalence of non-native plant invasion than the increased invasion opportunities that exist in WUI intermix forests or than the greater niche availability that seems to be present in intermix forests, as indicated by higher tree species richness. A second possible explanation, as Gavier-Pizarro et al. (2010a) noted when they found a surprisingly weak relationship between intermix WUI and invasive plant richness in New England, is that intermix WUI areas generally have been developed more recently than interface areas, with interface forests the culmination of a progression of increased development around remnant forest patches. An invasion lag may cause a delay between the initial development of these areas and the eventual invasion-related consequences of that development. Future work could assess the degree to which the difference is attributable to greater edge effects, such as light availability and more frequent disturbance, in interface forests.

Invasion debt in the WUI

Multiple results of our analyses confirmed that WUI forests in the eastern United States have experienced a delay in invasion following housing development (i.e., an invasion debt). First, plots that were in the WUI since 1990 had an average of 2.6% more invasive plant cover (a 21.1% increase) and 0.33 more invasive plant species (a 28.7% increase) than those that became WUI in 2000 or 2010. This is consistent with recent findings that, over time, WUI forests in the northern United States experienced decreased spatial integrity, increased forest-developed edges, and lower proportions of forest in the surrounding landscapes (Sonti et al. 2023) – all factors that would increase their susceptibility to invasion.

Second, earlier agricultural and developed land cover neighborhood variables were more important than more recent ones in explaining both invasive richness and cover. For agricultural land cover, the five most influential metrics for invasive richness and the four most influential metrics for invasive species cover were measured in 2001 and 2006. Similarly, the developed land cover variables from 2001 to 2006 were more influential than those from 2011 to 2016 for all neighborhoods. Third, measures of invasion generally were more strongly correlated with earlier than more recent changes in land cover. For example, a significant positive relationship existed between invasion and increases in development from 2001 to 2006 and from 2006 to 2011, but not 2011–2016. These findings underscore the importance of the historical legacies of previous land uses (Vila and Ibanez 2011).

Invasion debt associated with non-native plants is a widespread phenomenon, including in southwestern Spain (Gonzalez-Moreno et al. 2017), where non-native richness was more closely associated with land-cover variables in 1956 than 2007, and in New Zealand, where exotic plant richness was more strongly correlated with suburban population density in 1945 than 2000 (Sullivan et al. 2004). The delay in the realization of invasions may be the result, at least in part, of growing human populations and the fragmentation of natural communities over time, which together increase the landscape complexity of urban areas (Ellis et al. 2006) and their susceptibility to invasion by non-native plants.

Because the information we take from past invasions offers the best glimpse of how future invasions could develop (Gonzalez-Moreno et al. 2014), the existence of current invasion debt may indicate how future invasions will unfold (Vila and Ibanez 2011). Current and evolving land use conditions thus can give us a picture of potential future forest invasions. Because we expect the prevalence of invasive non-native plants to increase as a result of future housing growth and land use change, these can be considered central factors in efforts to monitor and manage plant invasions (2010a). For example, projections indicate that land-use changes before 2051 will increase the novelty of ecosystems across broad areas, especially in the eastern United States (Martinuzzi et al. 2015a). Such areas are at heightened risk of non-native plant invasion.

Disturbance and invasion in the WUI

Finally, we found that the invasion of WUI forests was associated with agricultural, developed, and forested land cover around each forested plot. Overall, agricultural land cover variables in medium neighborhood sizes (590.49 ha and 65.61 ha) were the most important in explaining both invasive species richness and cover, while the largest neighborhood size (5314.41 ha) was the most important for developed land cover. The greater importance of agricultural than developed land cover is consistent with other work that examined the probability of forest invasions across the eastern United States beyond the WUI, and may relate to the fact that FIA forestland plots are not typically located in heavily urbanized areas (Riitters et al. 2018). Agricultural land cover metrics were positively associated with invasion, except at the smallest neighborhood size (4.41 ha), while developed land cover was more consistently positively related to invasive species cover than invasive species richness, except at the smallest neighborhood size. Forested land cover was less important than agricultural and developed land cover in explaining the invasion metrics.

Agricultural and developed land cover metrics serve as indicators of invasive species propagule pressure. Agricultural land cover is a vector for plant invasions as rural housing introduces non-native plants via landscaping and by creating habitat conditions favorable for their invasion into nearby natural

landscapes (Boscutti et al. 2022; Gavier-Pizarro et al. 2010b).

Meanwhile, increasing urbanization can be a major driver of plant invasions across heterogeneous landscapes (Boscutti et al. 2022). Gardens and yards in developed areas often contain more non-native than native plant species (Smith et al. 2006), with propagule pressure arising from the widespread use of exotic plants in residential yards representing an important driver of invasion (Davis et al. 2016). At the same time, urban habitats can have significant environmental differences from rural habitats, including more open canopies, forest edges, and impervious surfaces, and more coarsely textured and alkaline soils (Ariori et al. 2017), factors that potentially increase their invasion vulnerability. Not surprisingly, non-native plant richness has been found to be positively correlated with housing density (Sullivan et al. 2004; Gavier-Pizarro et al. 2010a, b).

Previous work provided evidence of synergistic effects between agricultural and developed land cover, suggesting that different pools of invasive plants may originate from each and that the potential exposure of forested areas increases in proximity to both land cover types (Riitters et al. 2018). Newer WUI forests in the northern U.S. were close to higher proportions of agricultural land cover at a variety of scales, seemingly reflecting the establishment of residential development on former agricultural lands; as more agricultural areas are developed over time, older WUI forests become surrounded by more developed land cover (Sonti et al. 2023). This dynamic perhaps explains our finding that greater WUI forest invasion was correlated with the loss of agricultural land cover but with the increase of developed land cover over time. It may also account for the counterintuitive negative association between WUI forest plot invasion and agricultural land cover and the positive association between invasion and forest cover, both at the smallest neighborhood size.

The amount of forested land cover around plots, meanwhile, provides a proxy for forest disturbance, with lower amounts of forest cover indicating forest fragmentation. The natural-rural-urban continuum exists as a gradient of remnant, managed, and abandoned forest patches (Huebner et al. 2012), with higher invasion in small and isolated fragments than in connected patches (Vila and Ibanez 2011). Previous analyses of FIA invasion data indicated that human-caused forest fragmentation was positively associated with both invasive species richness and cover in the eastern United States (Iannone et al. 2015). We found that the percent of forest cover around a WUI forest plot was consistently negatively associated with both invasive richness and cover at all scales, except the smallest (4.41 ha). The finding at the smallest scale was not unexpected because forest tends to be locally dominant where it occurs regardless of the degree of invasion by non-native plants. Also, FIA protocols require that plots be located in forest patches at least 0.4 ha in size and 37 m wide (Burrill et al. 2021), potentially eliminating from consideration more highly invaded forest locations surrounded by less forest cover in their immediate neighborhoods. The switch in the relationship between forest cover and invasion at next largest size (15.21 ha) may reflect the increasing likelihood of encountering agricultural land cover and developed land cover (including roads) at larger scales and therefore the invasive species associated with them. Untangling the relative importance of land cover types within different spatial neighborhoods is complicated by the land use history of forests, which is not reflected in the WUI data (e.g., WUI areas may have previously been in an agricultural land use) and by the gradients that exist within neighborhoods between natural and developed land cover, between natural and agricultural land cover, and between agricultural and developed land cover (Riitters et al. 2009).

Our results demonstrate that spatial scale matters when assessing the impacts of propagule pressure and disturbance on the invasion of WUI forests by non-native plant species. Assessments of invasion patterns across multiple scales are rare but can generate important insights into the invasion process since both the dispersal of invasive plant species and the ecological effects of these invasions are scale-dependent (Pauchard and Shea 2006). Consistent with a previous assessment of FIA plot-level invasion probability (Riitters et al. 2018), the best scales of measurement for the agricultural and developed land cover variables indicate the likely successful long-distance dispersion of invasive plant propagules within relatively large neighborhoods. Other work similarly has found that the number of houses in a 1 km buffer around a plot was the variable most strongly associated with the abundance of non-native invasive

plants (Gavier-Pizarro et al. 2010b). These results underscore the long-distance seed dispersal ability of successful invasive exotic plant species into forests (Nunez-Mir et al. 2019). Roads also play an important role in this dispersal process in forests, with the odds of invasion and diversity of invasive plants increasing with proximity to roads (Riitters et al. 2018; Ward et al. 2020) across a pervasive road network in the eastern United States (Riitters and Wickham 2003). In finding that ecoregion designation was consistently the most influential variable explaining forest invasion metrics in the random forests assessments, our results align with previous work showing that spatial autocorrelative processes contributing to macroscale invasion patterns likely occur at distances smaller than the areas of these regions (Iannone et al. 2015, 2016b). These results also affirm the reasonableness of our assumption of independence among these regions; that is, plots within an ecoregion section are more similar to one another for such environmental characteristics as geology, climate, soils, potential natural vegetation, and potential natural communities (Cleland et al. 2007) than they are to plots in other ecoregions.

Management implications and future directions

The WUI is a focal area for human-environmental conflicts, including habitat fragmentation, biodiversity decline, the destruction of homes and other buildings by wildfire, and the introduction of exotic species (Radeloff et al. 2005). New scientific, management, and policy tools are needed to better understand the WUI as a unique social-ecological zone and to mitigate the negative consequences of its continued growth (Bar-Massada et al. 2014). The results of our study demonstrate that the combination of WUI maps with plot-level forest inventory data and remotely sensed land cover data can inform the management and monitoring of invasive forest plant species.

Forest management in the WUI is challenging because of its combination of diverse landowners, smaller forest parcels, varied land use legacies, and interactions among multiple stressors (Huang et al. 2013; Sonti et al. 2023). Effective management of WUI forests will require engagement with individual landowners while mitigating denser interface development near areas of high forest conservation value, such as national forests (Mockrin et al. 2022). Possible approaches to mitigate invasive plant impacts in the WUI include spatially explicit land use planning and management that discourages housing development inside or adjacent to forests of high conservation value (Gavier-Pizarro et al. 2010b; Huebner et al. 2012) and efforts to influence the decision-making of homeowners to encourage more native and environmentally friendly private landscapes (Gavier-Pizarro et al. 2010b; Cubino et al. 2015). At the same time, it is important to acknowledge that non-native invasive plants provide ecosystem and cultural services such as shade, carbon and pollutant sequestration, wildlife shelter and food, and aesthetic value (Huebner et al. 2012; Potgieter et al. 2017).The cultural value of these plants may create complications for preventing new invasions in nearby forests.

The results of our study additionally suggest the importance of monitoring and managing forests that have recently entered the WUI, with an emphasis on sources of exotic plant propagules at a medium scale, before the invasion debt associated with land use comes due. It is important, however, to recognize the limitations of land-use policies given the magnitude of predicted land-use changes in the United States and the powerful demographic factors driving them (Radeloff et al. 2012).

At the same time, future efforts can assess how projected land-use change in the United States will impact the invasion of forests within the WUI by non-native plants. This will be challenging, because predictions about the future invasion of WUI forests will have to incorporate our existing knowledge about the relationships between invasion and land use with projections about where and to what extent land use changes will occur. Furthermore, accounting for invasion debt – the eventual ecological and socioeconomic impacts associated with non-native species (Rouget et al. 2016; Duncan 2021) – will be necessary. This will be easier with the development of grid-based WUI data such as those of Carlson et al. (2022) across multiple time steps and as newer FIA plot-level invasive species data become available to assess multiple time steps to quantify forest WUI invasion trends. Additionally, it would be useful to better understand the mechanisms driving invasion of WUI forests by individual invasive species, particularly the degree to which environmental heterogeneity enables WUI invasion, the factors

behind the importance of medium-to-large-scale agricultural and developed land cover in WUI forest invasion, and the relative importance of housing proximity versus the recentness of its development in explaining the greater invasion of interface than intermix forests. Finally, while FIA data have enabled analyses of plant invasion within WUI forests, the invasion of other ecosystems within the WUI, such as wetlands and prairies, deserve additional attention, particularly since these systems may be more susceptible to invasive because of greater light availability. Comparisons of the degree of invasion among ecosystem types would be possible by calculating the proportion of the total species richness and biomass in each community attributable to exotic species (Guo et al. 2015).

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Author contributions Conceptualization- all authors, led by KMP; Data Curation- KMP, KHR; Formal analysis- KMP; Methodology- KMP, KHR, BVI, QG; Project administration- KMP; Visualization- KMP; Writing – original draft- all authors, led by KMP; Writing – review & editing- all authors, led by KMP.

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Data availability The data that support the findings of this study are openly available in the USDA Forest Service Research Data Archive at https://doi.org/10.2737/RDS-2024-0033. FIA data are additionally available at https://www.fia.fs.usda.gov/library/database-documentation/index.php.

Declarations

Competing interests The authors declare no competing interests.

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