Biol Invasions (2020) 22:3051–3066
https://doi.org/10.1007/s10530-020-02308-3

ORIGINAL PAPER

Effects of terrestrial transport corridors and associated landscape context on invasion by forest plants

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Received: 8 August 2019 / Accepted: 29 June 2020 / Published online: 8 July 2020

Abstract The construction, use, and maintenance of terrestrial transport corridors [roads and railroads (TTCs)] facilitate the spread of invasive plants, but the distances at which plants typically spread away from TTCs, and how that process is mediated by landscape context, is not well understood. We compiled data on the number of invasive plant species per $\sim$ 672 m^2 plot (= invasive richness) from 44,000 + forest inventory plots in the eastern USA. Using a generalized linear model framework, we investigated how invasive richness is influenced by distance from the nearest TTC, surrounding land use type, and ecological province. Invasive richness in forests decreased as distance from the nearest TTC increased. Directly adjacent to TTCs, there were an estimated 1.4 $\pm$ 0.01 SE invasive plant species per plot compared to 0.8 $\pm$ 0.01 and 0.2 $\pm$ 0.01 species at 1 and 3 km, respectively, away from the nearest TTC. Invasive richness was highest on plots associated with a combination of agriculture/development (2.1 $\pm$ 0.03 species per plot) and in the Midwest Broadleaf Forest province (2.1 $\pm$ 0.06). Our macroscale analysis also demonstrated that rates of decay in invasive richness away from TTCs were mediated by the types of land use and ecological provinces within which plots were located. The influences of TTCs and associated activities (e.g., construction, travel) on invasive plant richness were widespread across forests of the eastern USA, but the relative importance of TTCs for facilitating spread appears to be highly context dependent.

Keywords Ecological province · Forest · Invasive plants · Land use · Macroscale · Road ecology

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s10530-020-02308-3) contains supplementary material, which is available to authorized users.

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Introduction

Forests provide a multitude of ecosystem services, sequestering carbon (Bonan 2008), improving water quality (Fiquepron et al. 2013), and regulating local and regional climates (Bonan 2008). Invasive plants pose significant threats to forest ecosystem functioning (Martin et al. 2009; Pejchar and Mooney 2009; Fei et al. 2014) by driving changes in native plant community composition (Hejda et al. 2009), nutrient cycling (Ehrenfeld 2003; Vilà et al. 2011), hydrology (Ehrenfeld 2010), and fire regimes (Brooks et al. 2004). Investigating how different landscape features (e.g., roads and railroads) and landscape contexts (e.g., land use types) mediate the spread of invasive plants could help elucidate underlying drivers of invasions and indicate areas currently most at risk from invasive plant impacts.

Roads and railroads (henceforth terrestrial transport corridors; TTCs) are extremely common landscape features that cause a multitude of ecological impacts (Forman and Alexander 1998; Forman and Deblinger 2000; Trombulak and Frissell 2000) and serve as conduits for the spread of invasive plants (Tyser and Worley 1992; Parendes and Jones 2000; Gelbard and Belnap 2003; Christen and Matlack 2006, 2009; Flory and Clay 2006; Dimitrakopoulos et al. 2017; Skultety and Matthews 2017). The construction of TTCs results in habitat fragmentation that increases edge habitat (Ibisch et al. 2016), a location in which invasive plants often invade before spreading into adjacent forests (Saunders et al. 1991; Yates et al. 2004; Fei et al. 2008). Habitats directly adjacent to TTCs are also associated with high frequencies of disturbance from maintenance (e.g., mowing and thinning) and mineral deposition (e.g., salt application), both of which can increase the likelihood of invasion (Johnston and Johnston 2004; Mortensen et al. 2009; Barbosa et al. 2010). Indeed, grading can spread invasive propagules along the sides of rural TTCs (Rauschert et al. 2017). Long-distance dispersal of invasive plants can occur by travel via TTCs (Schmidt 1989; Watkins et al. 2003), for example, through seeds hitchhiking on vehicles (Rew et al. 2018).

In addition to TTCs, landscape context is an important driver of plant invasion dynamics (Vilà and Pujadas 2001; Lundgren et al. 2004; Pauchard and Alaback 2004). Areas with higher human activity are often associated with greater abundances of invasive plants (Catford et al. 2011; Riitters et al. 2018) and both contemporary and historical land use type can influence patterns of invasion (Csecserits et al. 2016; Holmes and Matlack 2019). For example, in the southern Appalachians, landscapes with a history of agricultural use had higher non-native plant abundance (Kuhman et al. 2011) whereas increased forest cover was associated with decreased abundance of non-native plants (Kuhman et al. 2010). Agriculture and development can disturb adjacent forests, impacting biodiversity and soil quality (Compton and Boone 2000; Stoate et al. 2001; Dupouey et al. 2002), which in turn might also influence invasibility. Regional level factors (e.g., climatic variables) have also been linked to landscape-scale patterns of plant invasions (Pino et al. 2005; Bradley et al. 2010; Iannone et al. 2015). Indeed, the incidence (presence/absence) of invasive plants on plots across the eastern USA varied among different ecoregions (Riitters et al. 2018), which are determined in part by unique climatic regimes and other biotic and abiotic factors.

Several studies have focused on the roles of TTCs in invasions at smaller spatial scales (e.g., within counties or national parks and/or within 100 m of TTCs) and/or considered a limited number of plant species. It is less understood, however, if TTCs interact with landscape context to influence the spread of invasive plants at local (i.e., surrounding land use) and/or regional (i.e., ecological province) scales. There is also a dearth of studies investigating how local and regional level processes simultaneously influence invasion under a macroscale context. Here, we intended to quantify the effects of TTCs on plant invasions across forests of the eastern USA. Moreover, we investigated how land use type and ecological province, representing local and regional scale processes, respectively, interact with TTCs to mediate plant invasions.

Materials and methods

Study region

The eastern United States is the most populated and TTC-dense portion of the USA (Heilman et al. 2002), highly invaded by non-native plants (Iannone et al. 2015; Oswalt et al. 2015), and, as a result, a potentially informative area for quantifying effects of TTCs on invasion. Thirty-seven states were examined in this study, which included the eastern parts of Texas, Oklahoma, Kansas, Nebraska, South Dakota, and North Dakota and all states eastward (Fig. 1a). Our study area encompassed 15 ecological provinces, including several mixed deciduous (e.g., beech-birch-maple forest) and coniferous forests in the upper Midwest and southeast, oak-hickory forests of the

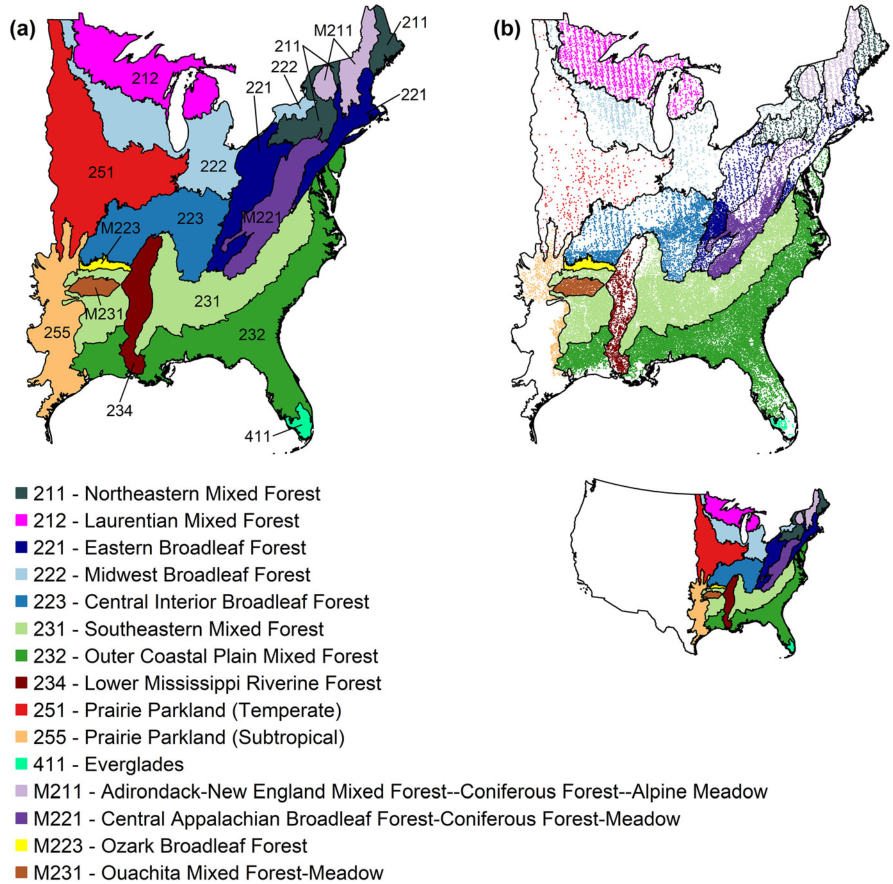

Fig. 1 Maps displaying **a** ecological provinces and **b** plot locations, indicated by circles that merge together and appear as solid colors in areas with high densities of plots, across the eastern United States

Midwest, and subtropical moist hardwood forests at the most southern latitudes. Climatic regimes ranged from the humid temperate to the humid tropical domains, spanning areas with long and severe winters and a short growing season to typically frost-free areas with > 1200 mm of rainfall per annum. Elevations ranged from 0 to 2000 m.

Invasive plant data

The USDA Forest Service Forest Inventory and Analysis (FIA) program (www.fia.fs.fed.us) divides the USA into hexagons ~ 2400 ha in size each with at least one permanent plot placed at random on forested land (Bechtold and Patterson 2005). Plots within a hexagon are assigned to one of five panels that are typically sampled on a rotating basis every ~ 5–7 years in the eastern USA. Since 2001, the forest inventory program has surveyed invasive plant occurrence across the eastern USA within each FIA plot (Oswalt et al. 2015). The FIA defines an invasive plant as an exotic plant species of any form likely to cause environmental or economic harm (Ries et al. 2004). We acquired data describing the occurrence of each invasive plant in the FIA database (see Oswalt et al. 2015 and citations therein) across 44,404 FIA plots in the eastern USA (Fig. 1b). Each FIA plot consists of four circular subplots (7.3 m in radius, ~ 168 m^2) on which invasive plants were surveyed. Thus, for simplicity, we refer to the number of invasive plant species across the four sampled subplots (= species per 168 m^2 × 4, or species per 672 m^2) as "invasive richness" or "invasive species per plot". Each plot was only represented once in the data. Plot data came from the most recent sampling period in the database on the date of extraction (6 July

2012) and plots could have been sampled anytime between 2001 and 2011, providing a snapshot of invasive richness.

TTC and landscape context data

Data for TTCs, which included roads and railways of any size, were obtained from the US Census Bureau's Topologically Integrated Geographic Encoding and Referencing (TIGER) line database (USCB 2016). We included all TTCs in our analysis, but note that different types (e.g., paved vs. unpaved) can be associated with disparate influences on invasion (Joly et al. 2011). Railways might also have unique effects, but are known to facilitate invasion (Hansen and Clevenger 2005) and thus were also included. The Euclidean distances to the nearest TTC from the center of each FIA plot were measured using ArcGIS (ESRI 2016).

We use the phrase "landscape context" to refer to the land use types and ecological provinces within which plots were located. Land use types and ecological provinces covered vastly different spatial scales and thus we refer to their influences as local and regional scale effects, respectively. We evaluated local-level effects on plant invasion using land use classifications from the 2006 National Land Cover Database (NLCD), which has a spatial resolution of 0.09 ha (Fry et al. 2011; USGS 2014; Riitters et al. 2018). We measured land use types surrounding each plot within 590×590 ha square (3481 km^2) neighborhoods and classified each square following the exact approach of Riitters et al. (2018): $< 10\%$ agriculture and $< 10\%$ development (= "natural land"), $> 10\%$ agriculture (= "agriculture"), $> 10\%$ development (= "development"), $> 10\%$ agriculture and $> 10\%$ development ("agriculture/development"). Note that in the 2006 NLCD database, development was comprised of four subclasses (Open Space, Low Intensity, Medium Intensity, and High Intensity) and agriculture was comprised of two subclasses (Pasture/Hay, Cultivated Crops). We included all subclasses within land use types in our analysis but did not distinguish among subclass variations with each land use type.

To describe regional scale landscape context, we grouped each FIA plot into one of 15 ecological provinces (Fig. 1). Each province comprised an area of 12,889 to 789,232 km^2 with distinct physical and biological components having similar productive capabilities, responses to disturbances, and potentials for resource management (Bailey 1995; McNab et al. 2007). Inclusion of ecological provinces in our analyses can also help account for potential latent variables that may vary by region (e.g., disturbance history or sampling intensity).

Statistical analysis

We quantified the effects of distance (km) from the nearest TTC, land use, and ecological province on number of invasive plant species per plot through a three-step process, building a series of generalized linear models (Table 1). For all models, we used a negative binomial (vs. Poisson) regression framework to model counts of invasive plants and account for overdispersion; a log link function was used in each model. For the first step, we fit three models evaluating the effect of each variable individually on invasive richness. For the second step, we fit two models evaluating the effects of interactions between distance from TTC and either land use or ecological province on invasive richness. For the third step, we fit a full model evaluating the effects of distance from TTC, land use, ecological province, and interactions between distance from TTC and each landscape context predictor (i.e., distance from TTC $\times$ land use, distance from TTC $\times$ ecological province) on invasive richness. We reduced this full model using backwards selection by removing interaction terms first, and if applicable, main effects for variables with $P > 0.05$ (statistical significance throughout was defined using $\alpha = 0.05$). We included all main effects for variables when they also appeared as part of an interaction term. Fitting interactions in steps two and three resulted in a unique slope, which we also refer to as decay rate(s), relating invasive richness to distance from the nearest TTC for each level of land use type or ecological province.

We conducted pairwise comparisons of mean invasive richness (models evaluating landscape context variables only) and decay rates in richness (models evaluating interactions of TTCs with landscape context variables) between levels of our landscape context variables using Tukey's HSD (honestly significant difference) tests. We conducted these comparisons via the emmeans package in R (Lenth 2020), using the emtrends function to compare decay

Table 1 Summary of models developed to estimate invasive plant richness as a function of distance (km) from the nearest terrestrial transport corridor ("DIST"), land use type ("LU"), and/or ecological province ("EP")

No.	Predictors	FM[a]	MeanPW[b]	SlopePW[b]
1	*DIST*	F2		
2	*LU*	T2	TS1.2	
3	*EP*	T3	TS1.3	
4	$DIST + LU + DIST \times LU$	F3a; T4		F3b; TS1.4
5	$DIST + EP + DIST \times EP$	F4a; T5		F4b; TS1.5
6	$DIST + LU + EP + DIST \times LU + DIST \times EP$	F5; T6		F6; TS1.6a,b

Each model was a negative binomial regression fit using a log link function

[a]FM: Summary statistics for full models are reported in the indicated figure (F) or table (T)

[b]MeanPW or SlopePW: Pairwise comparisons of means (Models 2–3) or slopes (Models 4–6), respectively, between each level of a categorical predictor were conducted using Tukey's HSD tests and are provided in the indicated figure (F) or table (T). Numbers preceded by an "S" are in supplementary material (e.g., Table S1.2 is the second table of Online Resource 1)

rates. In comparing decay rates in our full model, rates within each land use type were averaged across ecological provinces, and vice versa. In some instances in the results, we report findings from Tukey's HSD tests as an absolute, minimum value (e.g., all $|Z| > x$). In such instances, we have provided the smallest Z-value estimated when comparing the mean richness or decay rate for a specified level (e.g., "agriculture/development") to all other levels (e.g., "natural land", "agriculture", and "development") on a pairwise basis, rather than reporting all comparisons. However, all pairwise comparisons between means and slopes for each model, including Z-values, are provided in Online Resource 1. Table 1 provides a key of where each model and the associated pairwise comparisons are presented in the main text and/or supplemental materials. All analyses were completed using R (R Core Team 2020), and estimates of invasive richness are provided as average number of invasive plant species per plot ± SE. Data supporting the results are available from the Purdue University Research Repository (PURR; https://doi.org/10.4231/fv6t-nq34).

Results

Invasive plant richness ($\ln(x)$-transformed) on forested plots decreased nonlinearly as distance (km) from TTC increased (Fig. 2; slope = -0.62 ± 0.02, $Z = -35.20$, $P < 0.0001$). According to our model of invasive richness as a function of distance from TTC

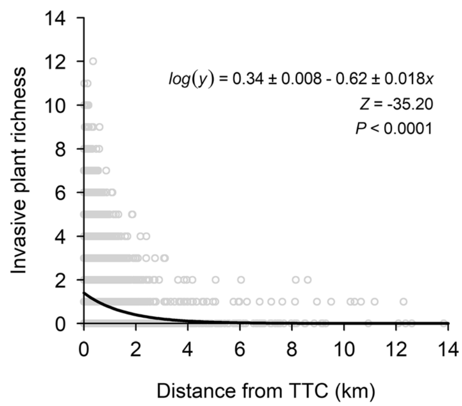

Fig. 2 Invasive plant richness as a function of distance (km) from terrestrial transport corridor (TTC) (Model 1 in Table 1; each point indicates a plot). Invasive plant data are from USDA Forest Service Forest Inventory and Analysis plots across the eastern USA. Model summary statistics in panel pertain to the slope coefficient for distance

(i.e., without adjusting for local or regional scale influences), there were 1.4 ± 0.01 species per plot directly adjacent to TTCs compared to 0.8 ± 0.01 and 0.2 ± 0.01 species at 1 and 3 km away, respectively, from the nearest TTC.

The local level landscape surrounding each plot significantly influenced invasive richness (Table 2; $\chi^2_3 = 4629.74$, $P < 0.0001$). Areas associated with human activities typically had higher invasive richness: forested plots associated with agriculture/development had 2.1 ± 0.03 invasive species per plot, more than any other land use type (Tukey's HSD: all $|Z| > 13.22$, $P < 0.0001$). Plots associated with

Table 2 Summary statistics from a negative binomial regression with a log link function predicting invasive richness as a function of land use (χ^2_3 = 4629.74, $P < 0.0001$; Model 2 in Table 1)

Covariate	Coefficient	SE	Z	P	HSD[a]
Intercept: Natural land	− 0.29	0.01	− 32.70	< 0.0001	a
Agriculture	0.65	0.01	54.13	< 0.0001	b
Development	0.69	0.02	31.58	< 0.0001	b
Agriculture/Development	1.03	0.02	54.46	< 0.0001	c

For example, the mean number of invasive plant species per forest plot associated with agriculture was ~ 1.4 (= $e^{-0.29+0.65}$)

[a]Results from a Tukey's HSD test. Different letters indicate statistically different groupings. Complete summary statistics are provided in Table S1.2 of Online resource 1

development had 1.5 ± 0.03 invasive species per plot and plots associated with agriculture had 1.4 ± 0.01 species per plot, which were statistically equivalent (Tukey's HSD: $Z = -1.98$, $P = 0.20$). There were 0.7 ± 0.01 invasive species per plot associated with natural land, significantly lower than all other land use types (Tukey's HSD: all $|Z| > 31.57$, $P < 0.0001$). For pairwise comparisons between all land use types, see Table S1.2 in Online Resource 1.

Invasive richness also varied significantly across ecological provinces (Table 3; χ^2_{14} = 5843.42, $P < 0.0001$). Provinces with the highest invasive richness were the Midwest Broadleaf Forest province (Province 222), which had 2.1 ± 0.06 invasive species per plot, and the Eastern Broadleaf Forest province (Province 221), which had 1.9 ± 0.04 invasive species per plot. These estimates were statistically equivalent (Tukey's HSD: $Z = -2.95$, $P = 0.17$) but significantly higher than all other provinces (Tukey's HSD: all $|Z| > 5.46$, $P < 0.0001$) when each was compared to all other provinces on a pairwise basis. The Adirondack-New England Mixed Forest—

Table 3 Summary statistics from a negative binomial regression with a log link function predicting invasive richness as a function of ecological province (χ^2_{14} = 5843.42, $P < 0.0001$; Model 3 in Table 1)

Covariate	Coefficient	SE	Z	P	HSD[a]
Intercept: Northeastern Mixed Forest (211)	− 0.21	0.04	− 4.60	< 0.0001	de
Laurentian Mixed Forest (212)	− 0.71	0.06	− 12.15	< 0.0001	b
Eastern Broadleaf Forest (221)	0.84	0.05	17.14	< .0001	i
Midwest Broadleaf Forest (222)	0.94	0.05	17.60	< 0.0001	i
Central Interior Broadleaf Forest (223)	0.69	0.05	14.43	< 0.0001	h
Southeastern Mixed Forest (231)	0.63	0.05	13.78	< 0.0001	gh
Outer Coastal Plain Mixed Forest (232)	0.02	0.05	0.48	0.63	e
Lower Mississippi Riverine Forest (234)	0.01	0.06	0.13	0.90	e
Prairie Parkland-Temperate (251)	0.50	0.07	7.34	< 0.0001	g
Prairie Parkland-Subtropical (255)	− 0.23	0.06	− 3.48	0.0005	c
Everglades (411)	− 0.38	0.13	− 2.99	0.0028	bcde
Adirondack-New England Mixed Forest (M211)	− 1.31	0.10	− 13.53	< 0.0001	a
Central Appalachian Broadleaf Forest (M221)	0.26	0.05	5.19	< 0.0001	f
Ozark Broadleaf Forest (M223)	− 0.68	0.08	− 8.20	< 0.0001	b
Ouachita Mixed Forest-Meadow (M231)	− 0.19	0.06	− 3.13	0.0018	cd

For example, the mean number of invasive plant species per plot in province 212 was ~ 0.4 (= $e^{-0.21-0.71}$)

[a]Results from a Tukey's HSD test. Different letters indicate statistically different groupings. Complete summary statistics are provided in Table S1.3 of Online resource 1

Coniferous Forest—Alpine Meadow province (Province M211) had the lowest invasive richness (0.2 ± 0.03) compared with all other provinces (Tukey's HSD: all $|Z| > 5.64$, $P < 0.0001$). For pairwise comparisons between all ecological provinces, see Table S1.3 in Online Resource 1.

The second step of our analysis provided insight into how landscape context mediated the effects of TTCs on invasive richness. We found that land use influenced the rate at which invasive richness decayed with distance from TTC (Table 4, Fig. 3a; distance from TTC × land use: $\chi^2_3 = 39.73$, $P < 0.0001$). Despite that plots associated with agriculture/development had higher mean invasive richness than all other land use types (Table 2), invasive richness decayed at similar rates to plots associated with agriculture and agriculture/development (Fig. 3b; Tukey's HSD: $Z = -1.00$, $P = 0.75$). Forested plots associated with development were associated with the most rapid decay in invasive richness compared to all other land use types (Tukey's HSD: all $|Z| > 3.99$, $P < 0.0005$). For example, at 10 m away from the nearest TTC, plots associated with natural land had an estimated 0.9 species compared to 1.7 species on plots associated with development. At 500 m away, plots associated with natural land had an estimated 0.7 species whereas plots associated with development had 1.0 species. For pairwise comparisons between decay rates to plots associated with different land use types, see Fig. 3b and Table S1.4 in Online Resource 1.

There was also significant variation in decay rates of invasive richness among the 15 ecological provinces (Table 5, Fig. 4a; distance from TTC × ecological province: $\chi^2_{14} = 394.60$, $P < 0.0001$). The Adirondack-New England Mixed Forest-Coniferous Forest-Alpine Meadow (M211) had the fastest rates of decay whereas the Lower Mississippi Riverine Forest (234) had the slowest (Fig. 4b). Decay rates for these provinces, while significantly different from one another (Tukey's HSD: $Z = 5.68$, $P < 0.0001$), were statistically equivalent to some other provinces; that is, these provinces represented the fastest and slowest decay rates we estimated, but other provinces had statistically similar high or low estimates when conducting pairwise comparisons (Fig. 4b). For example, plots in provinces M211 and 234 were estimated to have 0.5 and 0.9 species, respectively, 10 m away from the nearest TTC compared with 0.2 and 0.8 species, respectively, 500 m away from the nearest TTC. For pairwise comparisons between decay rates within ecological provinces, see Fig. 4b and Table S1.5 in Online Resource 1.

The third step of our analysis—fitting a single, full model with interactions between each landscape context variable and distance from the nearest TTC—demonstrated that the effect of TTCs on plant invasions was influenced by local scale effects from

Table 4 Summary statistics from a negative binomial regression with a log link function predicting invasive richness as a function of distance (km) from nearest TTC, land use, and distance from TTC × land use (Model 4 from Table 1)

Covariate	Estimate	SE	Z	P
Intercept (Natural land)	− 0.15	0.01	− 12.09	< 0.0001
DIST ($\chi^2_1 = 378.65$, $P < 0.0001$)				
Distance from nearest TTC	− 0.36	0.02	− 17.30	< 0.0001
LU ($\chi^2_3 = 2106.74$, $P < 0.0001$)				
Agriculture	0.65	0.02	38.26	< 0.0001
Development	0.71	0.03	22.97	< 0.0001
Agriculture/Development	0.95	0.03	33.61	< 0.0001
DIST × *LU* ($\chi^2_3 = 39.73$, $P < 0.0001$)				
Distance × Agriculture	− 0.14	0.04	− 3.75	0.0002
Distance × Development	− 0.75	0.14	− 5.29	< 0.0001
Distance × Agriculture/Development	− 0.02	0.12	− 0.14	0.89

For example, invasive richness at one km away from the nearest TTC in forest plots associated with agricultural land was ~ 1.0 ($= e^{-0.15\,+\,0.65\,+\,(-0.36\,-\,0.14)\,\times 1\ \mathrm{km}}$). Fit model is displayed graphically in Fig. 3a and pairwise comparisons of slopes within each level of land use type are provided in Fig. 3b

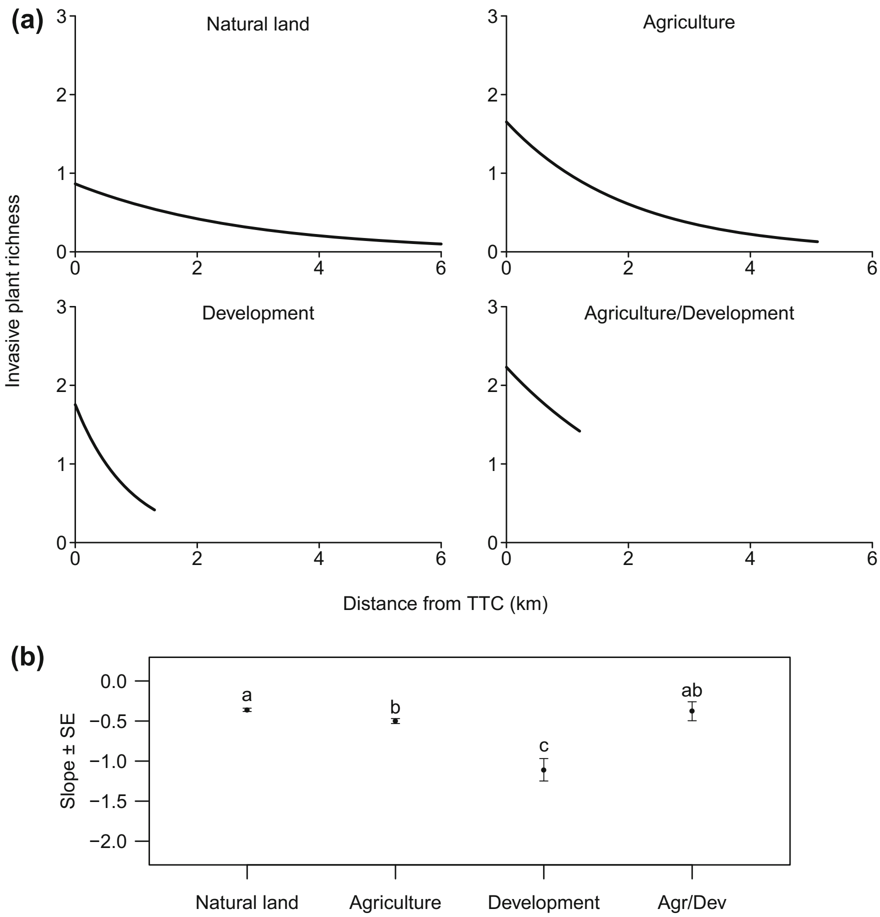

Fig. 3 **a** Invasive plant richness as a function of the interaction of distance from terrestrial transport corridor (TTC) with land use (χ^2_3 = 39.73, $P < 0.0001$; Table 4). Presented with truncated axes and without point clouds, enabling display of the variability among land use types. Lines are only drawn to the distance of the farthest plot within a land use category. For plots with full axes and data points, see Fig. S2.1 in Online Resource 2. Invasive plant data are from USDA Forest Service Forest Inventory and Analysis plots across the eastern USA. **b** Results from Tukey's HSD test comparing slopes presented in panel (**a**) by land use type. *Z*-values and pairwise comparisons are provided in Table S1.4 of Online Resource 1

land use type (distance from TTC × land use: χ^2_3 = 53.00, $P < 0.0001$) as well as regional scale effects from ecological provinces (distance from TTC × ecological province: χ^2_{14} = 326.03, $P < 0.0001$) (Table 6, Fig. 5). Pairwise comparisons of slopes between land use types and ecological provinces in our full model (Fig. 6) yielded similar conclusions to models considering the interactions of each landscape context variable and distance from TTCs separately (i.e., Models 4 and 5 from Table 1). For example, plots associated with natural land and development in M211 were estimated to have 0.4 and 0.7 species, respectively, 10 m away from the nearest TTC compared with 0.2 species on both land use types at 500 m away from the nearest TTC. In province 234, plots associated with natural land and development were estimated to have 0.6 and 1.1 species, respectively, 10 m away from the nearest TTC compared with 0.6 and 0.8 species, respectively, at 500 m away from the nearest TTC.

Some minor differences in pairwise comparisons between ecological provinces were detected, however (Fig. 6b). For example, Province 251 had the slowest decay rates according to Model 6 whereas according to Model 4 Province 234 had the slowest; both provinces exhibited statistically equivalent decay rates to each other in both models (Tukey's HSD: $|Z| < 0.60$, $P > 0.99$). Tukey's HSD tests using the full model

Table 5 Summary statistics from a negative binomial regression with a log link function predicting invasive richness as a function of distance (km) from nearest TTC, ecological province, and distance from TTC × ecological province (Model 5 from Table 1)

Covariate	Estimate	SE	*Z*	*P*
Intercept (211)	0.27	0.06	4.20	< 0.0001
DIST (χ^2_1 = 97.29, $P < 0.0001$)				
Distance from nearest TTC	− 1.50	0.17	− 8.65	< 0.0001
EP (χ^2_{14} = 2739.30, $P < 0.0001$)				
Laurentian Mixed Forest, (212)	− 0.86	0.08	− 10.47	< 0.0001
Eastern Broadleaf Forest, (221)	0.65	0.07	9.10	< 0.0001
Midwest Broadleaf Forest, (222)	0.64	0.08	8.09	< 0.0001
Central Interior Broadleaf Forest, (223)	0.38	0.07	5.40	< 0.0001
Southeastern Mixed Forest, (231)	0.29	0.07	4.45	< 0.0001
Outer Coastal Plain Mixed Forest, (232)	− 0.35	0.07	− 5.26	< 0.0001
Lower Mississippi Riverine Forest, (234)	− 0.39	0.08	− 5.09	< 0.0001
Prairie Parkland-Temperate, (251)	0.09	0.10	0.87	0.38
Prairie Parkland-Sub-Tropical, (255)	− 0.46	0.10	− 4.86	< 0.0001
Everglades, (411)	− 0.68	0.16	− 4.19	< 0.0001
Adirondack-New England Mixed Forest, (M211)	− 1.02	0.14	− 7.49	< 0.0001
Central Appalachian Broadleaf Forest, (M221)	0.15	0.07	2.09	0.0363
Ozark Broadleaf Forest, (M223)	− 0.81	0.13	− 6.45	< 0.0001
Ouachita Mixed Forest-Meadow, (M231)	− 0.36	0.09	− 4.08	< 0.0001
DIST × *EP* (χ^2_{14} = 394.60, $P < 0.0001$)				
Distance × 212	0.78	0.20	3.97	0.0001
Distance × 221	0.31	0.20	1.60	0.11
Distance × 222	0.86	0.22	3.98	0.0001
Distance × 223	0.95	0.19	5.12	< 0.0001
Distance × 231	1.01	0.18	5.70	< 0.0001
Distance × 232	1.18	0.18	6.68	< 0.0001
Distance × 234	1.37	0.18	7.75	< 0.0001
Distance × 251	1.25	0.28	4.42	< 0.0001
Distance × 255	0.76	0.24	3.11	0.0019
Distance × 411	1.27	0.21	5.93	< 0.0001
Distance × M211	− 0.29	0.34	− 0.87	0.39
Distance × M221	0.12	0.19	0.61	0.54
Distance × M223	0.53	0.30	1.78	0.08
Distance × M231	0.54	0.22	2.43	0.0152

For example, invasive richness at one km away from the nearest TTC in forest plots in province 212 was ~ 0.3 ($= e^{0.27 - 0.86 + (-1.50 + 0.78) \times 1 \text{ km}}$). Fit model is displayed graphically in Fig. 4a and pairwise comparisons of slopes within each level of ecological province are provided in Fig. 4b

(Model 6) indicated that decay rates in Province 212 were no longer significantly slower than those in Province 221 ($Z = 1.63$, $P = 0.95$) as they were when conducting such tests using Model 4 ($Z = 3.61$, $P = 0.0241$). Among other minor changes, Province 255 had significantly faster rates than Province M211 according to Tukey's HSD tests when using Model 6 ($Z = 3.43$, $P = 0.0437$), whereas these provinces had statistically equivalent decay rates according to Tukey's HSD tests using Model 4 ($Z = 3.11$, $P = 0.11$), which did not adjust for land use types. For pairwise comparisons between decay rates within land use types and ecological provinces in the full model, see Fig. 6 as well as Table S1.6a and Table S1.6b, respectively, in Online Resource 1.

Discussion

Terrestrial transport corridors promote the spread of invasive plants and increase propagule pressure for adjacent forests (Gelbard and Belnap 2003). By linking forest inventory data from across the eastern USA with TTC, land use, and ecological province data, we found that invasive plant richness was highest on plots nearest to TTCs regardless of landscape context (Fig. 5). At local scales, plots associated with agriculture and/or development had higher invasive richness than those associated with natural land (Table 2), while at regional scales, invasive richness varied significantly between ecological provinces (Table 3). Decay rates in invasive richness were also influenced by land use and ecological province (Figs. 5, 6), with invasive richness declining fastest on plots associated with development (Figs. 3, 6a). Thus, our study indicated that TTCs have facilitated the invasion of forests across the eastern USA, but that the role of TTCs is highly context dependent (Figs. 5, 6).

Invasive richness was highest on plots nearest to TTCs across land use types (Fig. 3) and ecological provinces (Fig. 4). Across all plots, invasive richness declined from ~ 1.4 invasive species per plot adjacent to TTCs to ~ 1.3 species at 100 m (~ 6% decline) and 0.8 species at 1 km (~ 50% decline) (Fig. 2). This percent change in richness with distance from the nearest TTC, although not directly comparable due to differences in sampling and focal ecosystems, was similar to other reports. For example, invasive richness in grasslands ranged from ~ 0.5–2.5 to ~ 0.2–0.4 species per 10 m^2 at 10 and 100 m, respectively, away from TTCs (Barbosa et al. 2010). In mountainous regions of the Greater Yellowstone Ecosystem, invasive richness was ~ 2 and ~ 1 species per 20 m^2 at 1 and 150 m, respectively, away from TTCs, while also declining significantly with increases in elevation (Pollnac et al. 2012). However, rates of decay are often nonlinear (Fig. 5), further complicating comparisons. No significant decay, at least up to 45 m (furthest distance studied) has also been reported (Craig et al. 2010). Indeed, several site- and ecosystem-level factors, in addition to land use types and ecological provinces, mediate spread away from TTCs and likely drive the wide range of invasive richness and estimates therein.

Variability in decay rates across landscape contexts (Figs. 5, 6) is potentially indicative of biotic resistance. Disturbances adjacent to TTCs facilitate invasion (Angold 1997; Forman and Alexander 1998; Gelbard and Belnap 2003; Watkins et al. 2003), whereas decreased light (Brothers and Spingarn 1992), competition (Parendes and Jones 2000), and/or structure and composition of biotic communities (Harper et al. 2005; Flory and Clay 2009) may inhibit spread into forests. The structure of the forest edge, such as the incidence of thinning, can also impact flux of species into forest interiors (Cadenasso and Pickett 2001). Several of these factors likely vary within and between land use types and ecological provinces. However, plots in some areas may not have been invaded owing to spatial heterogeneity in invasion history. That is, plots in the northeast might have been more invaded as a result of their long associations with human activity rather than being attributable to forest invasibility (Theoharides and Dukes 2007; Lodge et al. 2016). Availability of suitable habitat—independent of biotic resistance—could also explain patterns of invasive richness, given that plots associated with development were also associated with the fastest rates of decay (Figs. 3, 6a). These plots likely (1) had less forested area nearby and (2) were confined to areas near TTCs (i.e., developed areas require spatially proximate roads for access), potentially accelerating decay.

We evaluated land use type and ecological province as two aspects of landscape context, but several others remain. Smaller scale variation in landscape features such as fragmentation, traffic volume, and/or type of TTC, may drive rates of decay in invasive richness but were not accounted for in our macroscale analysis. Specific categories of land use within agriculture (e.g., grazing vs. grain production) and development (e.g., commercial vs. residential) likely have unique influences on plant invasion dynamics but were beyond the scope of our study. We also analyzed community level responses, but TTCs and/or landscape context likely have disparate effects on the invasion dynamics of different plant species (González-Moreno et al. 2013). Indeed, species traits can mediate invasion dynamics (Vallet et al. 2010; Nunez-Mir et al. 2019).

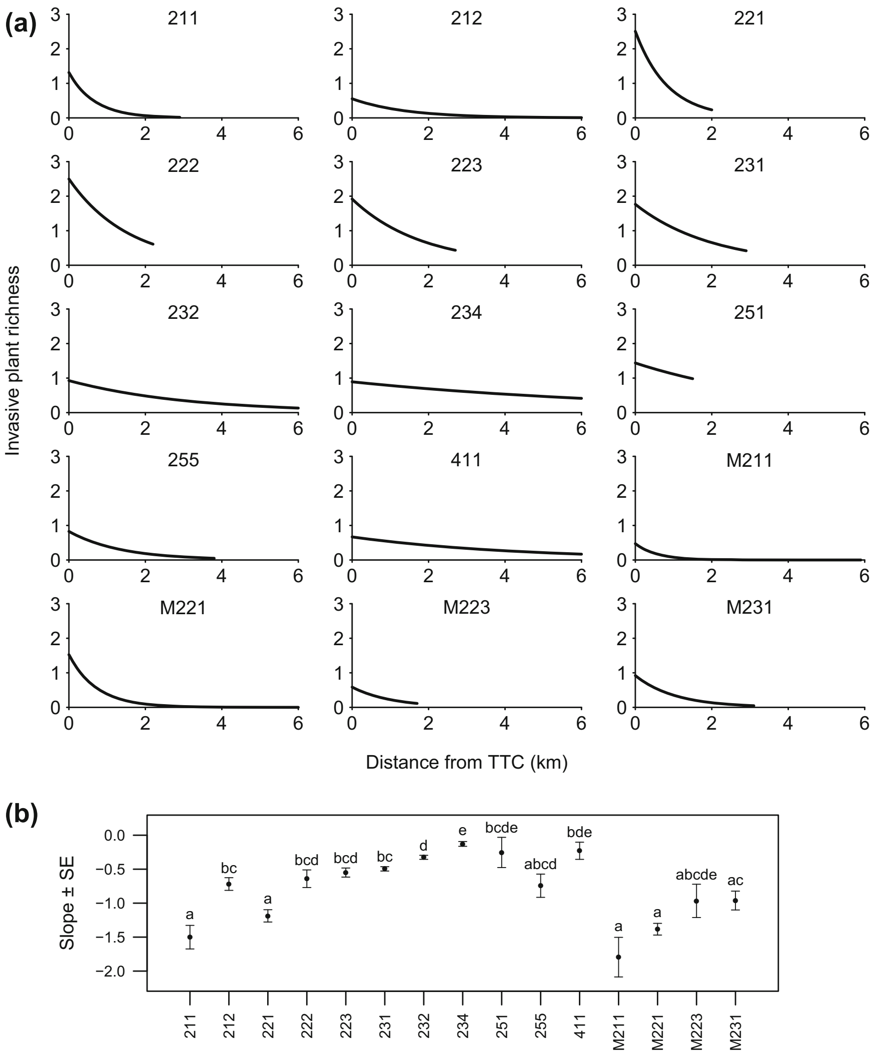

Fig. 4 **a** Invasive plant richness as a function of the interaction of distance from terrestrial transport corridor (TTC) with ecological province ($\chi^2_{14} = 394.60$, $P < 0.0001$; Table 5). Codes for ecological provinces are provided in Fig. 1. Presented with truncated axes and without point clouds, enabling display of the variability among ecological provinces. Lines are only drawn to the distance of the farthest plot within an ecological province. For plots with full axes and data points, see Fig. S2.2 in Online Resource 2. Invasive plant data are from USDA Forest Service Forest Inventory and Analysis plots across the eastern USA. **b** Results from Tukey's HSD test comparing slopes presented in panel (**a**) by ecological province. *Z*-values and pairwise comparisons are provided in Table S1.5 of Online Resource 1

The effects of TTCs on plant invasions can be confounded with other landscape characteristics, such as human population density and associated land development (Riitters et al. 2018). Here, abundances of land use types likely differed across ecological provinces, suggesting that these categorical predictors were not entirely independent. Such correlations among predictors could have influenced some model coefficients and associated test statistics. However, results from models with one or both landscape context variables were highly consistent—having similar signs and effect sizes (Figs. 3b, 4b vs. Figure 6a, b, respectively)—and thus we do not believe this potential issue impacted conclusions.

Table 6 Summary statistics from a negative binomial regression with a log link function predicting invasive richness as a function of distance (km) from nearest TTC, land use, ecological province, distance from TTC × land use, and distance from TTC × ecological province (Model 6 from Table 1)

Covariate	Estimate	SE	Z	P
Intercept (Natural land, 211)	− 0.10	0.06	− 1.52	0.13
DIST (χ^2_1 = 67.11, $P < 0.0001$)				
Distance from nearest TTC	− 1.25	0.17	− 7.26	< 0.0001
LU (χ^2_3 = 1713.44, $P < 0.0001$)				
Agriculture	0.57	0.02	34.55	< 0.0001
Development	0.65	0.03	22.11	< 0.0001
Agriculture/Development	0.81	0.03	30.12	< 0.0001
EP (χ^2_{14} = 2204.97, $P < 0.0001$)				
Laurentian Mixed Forest (212)	− 0.74	0.08	− 9.15	< 0.0001
Eastern Broadleaf Forest (221)	0.54	0.07	7.82	< 0.0001
Midwest Broadleaf Forest (222)	0.40	0.08	5.17	< 0.0001
Central Interior Broadleaf Forest (223)	0.24	0.07	3.49	0.0005
Southeastern Mixed Forest (231)	0.22	0.06	3.32	0.0009
Outer Coastal Plain Mixed Forest (232)	− 0.36	0.07	− 5.50	< 0.0001
Lower Mississippi Riverine Forest (234)	− 0.44	0.07	− 5.93	< 0.0001
Prairie Parkland-Temperate (251)	− 0.15	0.10	− 1.51	0.13
Prairie Parkland-Sub-Tropical (255)	− 0.60	0.09	− 6.45	< 0.0001
Everglades (411)	− 0.60	0.16	− 3.90	0.0001
Adirondack-New England Mixed Forest (M211)	− 0.83	0.14	− 6.12	< 0.0001
Central Appalachian Broadleaf Forest (M221)	0.14	0.07	1.99	0.0470
Ozark Broadleaf Forest (M223)	− 0.84	0.12	− 6.80	< 0.0001
Ouachita Mixed Forest-Meadow (M231)	− 0.22	0.09	− 2.62	0.0087
DIST × *LU* (χ^2_3 = 53.00, $P < 0.0001$)				
Distance ×Agriculture	− 0.19	0.04	− 5.07	< 0.0001
Distance ×Development	− 0.75	0.13	− 5.56	< 0.0001
Distance ×Agriculture/Development	− 0.03	0.11	− 0.23	0.82
DIST × *EP* (χ^2_{14} = 326.04, $P < 0.0001$)				
Distance × 212	0.68	0.19	3.52	0.0004
Distance × 221	0.48	0.19	2.48	0.0131
Distance × 222	0.91	0.21	4.27	< 0.0001
Distance × 223	0.98	0.18	5.35	< 0.0001
Distance × 231	1.07	0.17	6.12	< 0.0001
Distance × 232	1.13	0.17	6.48	< 0.0001
Distance × 234	1.21	0.17	6.94	< 0.0001
Distance × 251	1.26	0.27	4.59	< 0.0001
Distance × 255	0.74	0.24	3.08	0.0021
Distance × 411	1.13	0.21	5.46	< 0.0001
Distance × M211	− 0.40	0.33	− 1.21	0.23
Distance × M221	0.24	0.19	1.27	0.21
Distance × M223	0.57	0.30	1.92	0.05
Distance × M231	0.44	0.22	2.00	0.0460

For example, invasive richness at one km away from the nearest TTC in forest plots associated with agriculture and located in province 212 was $\sim$ 0.4 (= $e^{-0.10\,+\,0.57\,-\,0.74\,+\,(-1.25\,-\,0.19\,+\,0.68)\,\times 1\ \mathrm{km}}$). Fit model is displayed graphically in Fig. 5 and pairwise comparisons of slopes within each level of land use type and ecological province are provided in Fig. 6

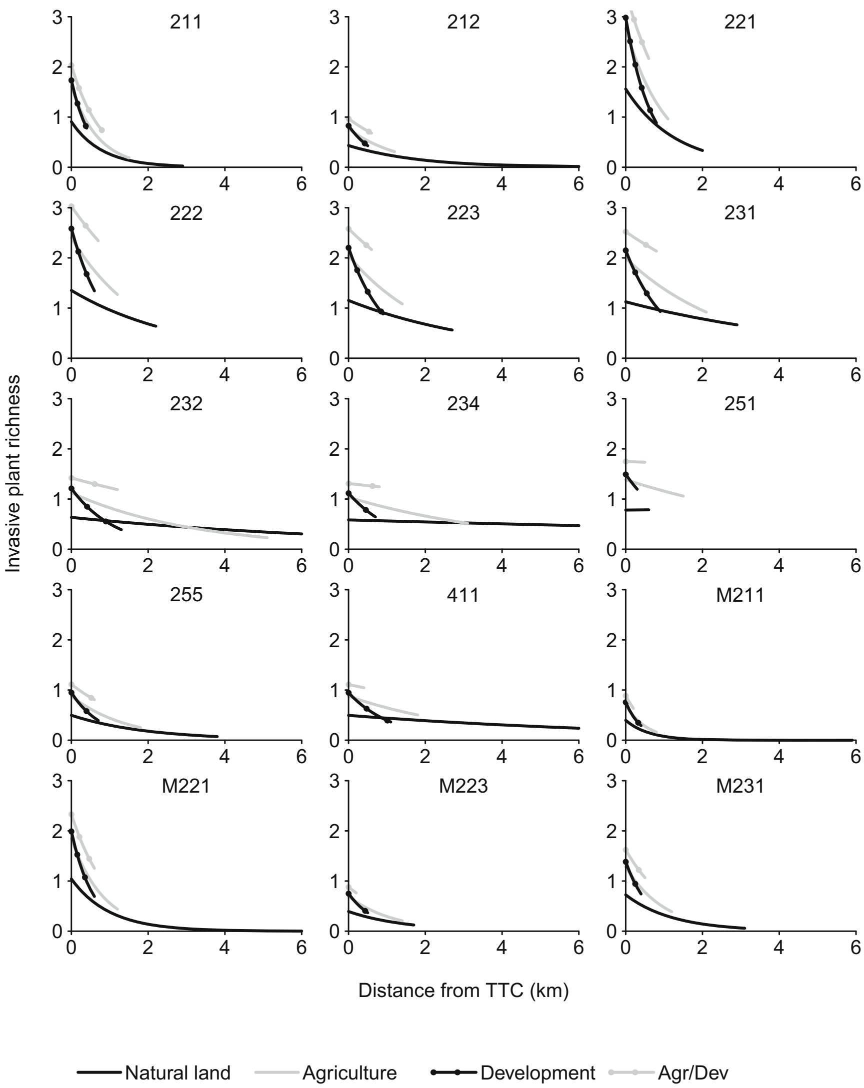

Fig. 5 Invasive plant richness as a function of distance from terrestrial transport corridor (TTC), the interaction of distance from TTC with land use (χ^2_3 = 53.00, $P < 0.0001$), and the interaction of distance from TTC with ecological province (χ^2_{14} = 326.03, $P < 0.0001$). All lines come from a single model (Table 6). Codes for ecological provinces are provided in Fig. 1. Presented with truncated axes and without point clouds, enabling display of the variability among land use × ecological province combinations. Lines are only drawn to the distance of the farthest plot within a land use × ecological province combination. For plots with full axes and data points, see Fig. S2.3 Online Resource 2. Invasive plant data are from USDA Forest Service Forest Inventory and Analysis plots across the eastern USA

We also note that different TTC types (e.g., paved vs. unpaved) can have unique effects on plant invasions (Joly et al. 2011), and analyses with specific TTC categories could potentially unveil disparate effects of such features across our study area. The importance of different types of TTCs can be species-dependent (Lowry et al. 2020), and our approach cannot stand in for more targeted analyses on invasion dynamics of a single species. Nonetheless, landscape-scale analyses conducted here elucidated the role of TTCs in increasing invasive plant richness across a large geographic area and highlighted the importance of landscape context.

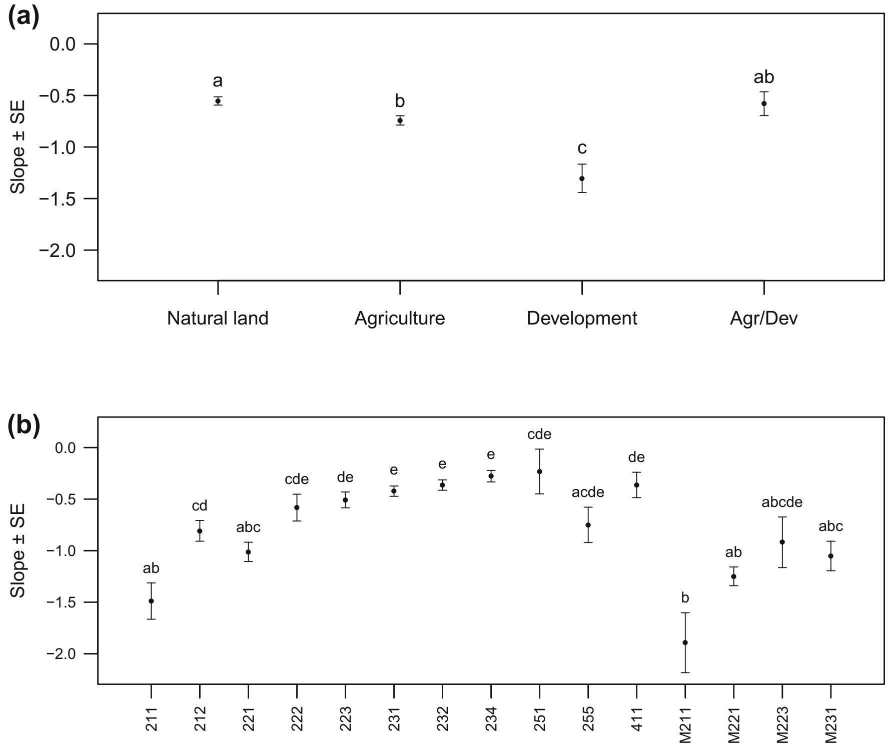

Fig. 6 Results from Tukey's HSD test comparing slopes presented in Fig. 5 by **a** land use type and **b** ecological province. *Z*-values and pairwise comparisons are provided in Table S1.6a and S1.6b of Online Resource 1

Acknowledgements We thank the many Forest Inventory and Analysis employees who collected and compiled data analyzed in this study. We also thank two anonymous reviewers and the handling editor for many insightful comments and suggestions that helped improve the manuscript. This research was supported by National Science Foundation Macrosystems Biology Grant 1638702 and the USDA Forest Service.

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