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Landscape correlates of forest plant invasions: A high-resolution analysis across the eastern United States

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Abstract

Aim: Invasive species occurrence is often related to the anthropogenic context of a given area. Quantifying the effects of roads is of particular interest as roads are a major vector for invasion. Our objective was to further quantify the effects of roads on forest plant invasion through a macroscale, high-resolution investigation to assist effective invasion control and mitigation.

Location: Eastern United States.

Methods: Using invasive plant data from 23,039 forest inventory plots in 13 ecological provinces, we employed logistic regression to relate the odds of invasion to distance from a road, with adjustments for broadscale differences attributable to ecological provinces, and local scale differences in productivity, forest fragmentation and land use.

Results: The overall proportion (P) of invaded plots was 0.58 (0.65 for plots within 50 m of a road), and the highest odds ($P/1 - P$) of invasion were found in relatively more productive, fragmented forest in landscapes with more than 10% agriculture or developed land cover. Wald chi-square statistics indicated the best predictor of the odds of invasion was ecological province, followed by land use, productivity, forest fragmentation and distance from a road. Depending on the province, the adjusted odds of invasion decreased by up to 23% (typically 4%–10%) per 100 m distance from a road. The adjusted probability of invasion approached zero in only three provinces, for the least productive, least fragmented forest that was at least 2,000 m from a road in landscapes with less than 10% agricultural or developed land cover.

Main conclusions: In the eastern United States, the existence of a nearby road is less important than the landscape context associated with the road. A purely road-mediated effect has little practical meaning because anthropogenic activities and roads are pervasive and confounded.

KEYWORDS
fragmentation, invasive species, land use, macroscale, road ecology

1 | INTRODUCTION

Roads pose a significant ecological threat because, among other reasons, their construction, maintenance and use facilitate the establishment and spread of exotic invasive plants (Forman & Alexander, 1998; Trombulak & Frissell, 2000). Invasive forest plants can cause significant and long-term impacts on forested ecosystems (Fei, Phillips, & Shouse, 2014; Martin, Canham, & Marks, 2009) and the services that they provide

(Pejchar & Mooney, 2009). Specifically, invasive plants can alter nutrient cycling, hydrology, fire regimes and energy budgets in native ecosystems (Mack et al., 2000). The concern is warranted in forests of the eastern United States where one-third of the forest area is within 200 m of a road (Riitters & Wickham, 2003) and invasive plants are found on one-half of the forest inventory plots in the region (Oswalt & Oswalt, 2015; Oswalt et al., 2015). While there is little doubt that roads are likely to result in forest plant invasions at local scales, effective resource conservation also requires an understanding of plant invasions at landscape and larger scales, including road effects in relation to other factors that determine propagule pressure and invasibility.

A key question is how much invasion is due to roads *per se*, and how much is due to influences that co-occur with roads, for example non-forest land uses. Invasive species occurrence is often related to the anthropogenic context of a given area (e.g., Catford, Vesk, White, & Wintle, 2011; Kuhman, Pearson, & Turner, 2010), and spatial correlations between roads and other human influences should be expected in most circumstances (Hawbaker, Radeloff, Hammer, & Clayton, 2004). The original forest in the eastern United States was essentially continuous forest land cover. Farms were established where the soil best supported farming, and transportation networks developed to serve the farming enterprise. The existence of roads, railroads and farms were important drivers of further land use changes. We therefore expect that in the geography of the contemporary forest land, the forest that is furthest from roads will be on relatively less productive sites and on land that was too steep or too wet to farm or to build a road. The likelihood of correlated factors created by historical land use patterns makes it difficult to disentangle at landscape scale a road effect from other anthropogenic effects. Similarly, a correlation between site productivity and land development will confound invasibility with propagule pressure in any observational study of invasive plant distribution.

Despite the limitations of observational data, most investigations of the role of roads in invasive plant ecology have used field survey or plot data. Many of those studies have been site-specific (e.g., Barton, Brewster, Cox, & Prentiss, 2004; Parendes & Jones, 2000; Underwood, Klinger, & Moore, 2004) or species-specific (e.g., Cordero, Torchelsen, Overbeck, & Anand, 2016; Davis, Singh, Thill, & Meentemeyer, 2016; Nielsen, Hartvig, & Kollmann, 2008). Survey designs to quantify the effect of distance from a road have included transects perpendicular to a road (e.g., Flory & Clay, 2006; Honu & Gibson, 2006; Pauchard & Alaback, 2004), comparisons of "road" locations with "control" locations (e.g., Christen & Matlack, 2009; González-Moreno, Pino, Gassó, & Vilà, 2013; Hansen & Clevenger, 2005; Yates, Levia, & Williams, 2004) and comparisons of road distance to "found" locations (e.g., Vieira, Finn, & Bradley, 2014; Western & Juvik, 1983). The inconsistency of study objectives and designs has complicated both integration at local scales and generalization over larger areas. As a result, meta-analyses of the distance from a road at which ecosystems are at risk have identified only broad ranges for that distance with the caveat that the actual distance depends on local circumstances (e.g., Forman & Alexander, 1998; Forman 2000; Trombulak & Frissell, 2000).

In recent years, there has been a number of broader scale investigations of plant invasions in relation to anthropogenic influences including roads (e.g., Dark, 2004; Iacona, Price, & Armsworth, 2014; Iannone et al., 2015). With a few exceptions (e.g., Catford et al., 2011; Gavier-Pizarro, Radeloff, Stewart, Huebner, & Keuler, 2010; Lemke, Hulme, Brown, & Tadesse, 2011; Seipel et al., 2012), the broader scale investigations have aggregated measurements of invasive plants and causal factors (roads, land use, etc.) within analysis units such as counties or protected areas. Such aggregation results in a loss of measurement precision, and the assumption of spatial stationarity within analysis units may be tenuous (Jelinski & Wu, 1996). Aggregation also invites less precise specification of exposure to roads. For example, the actual distance from a road is obfuscated by employing alternative measurements such as road density within a unit. Finally, as aggregate road measurements such as road density tend to be correlated with more easily obtained measurements such as human population size, many studies use those alternate variables instead of road measurements. In summary, most previous research which has provided evidence of road effects has been either a local, high-resolution study or a regional, low-resolution study.

The objective of this investigation was to conduct a high-resolution, macroscale analysis of forest plant invasions in the eastern United States (Figure 1). The general goal was to improve understanding of

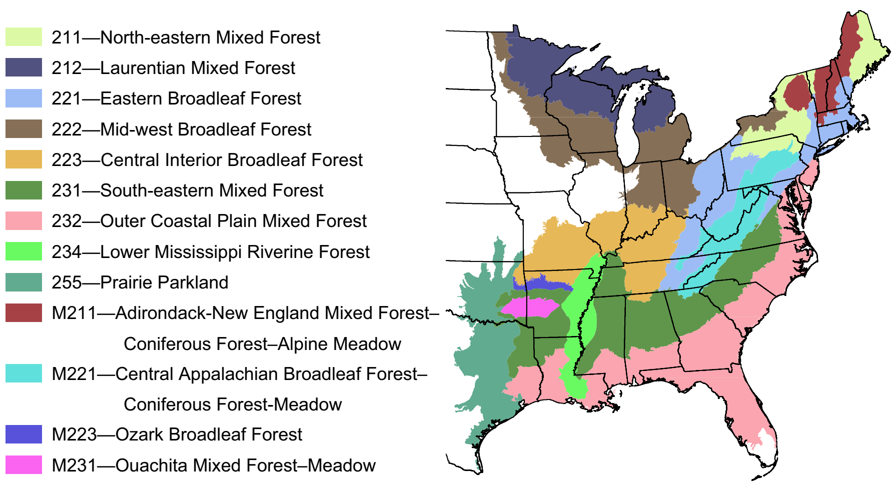

FIGURE 1 The study area was defined by 13 ecological provinces (Bailey, 1995; Cleland et al., 2007) comprising most of the temperate and boreal forestland in the eastern United States. [Colour figure can be viewed at wileyonlinelibrary.com]

forest plant invasions for land management, ecosystem monitoring and risk assessments by clarifying the effects of roads, land use and forest fragmentation, and the spatial scales over which those factors operate. We attempt to bridge the gap between local and regional studies by looking at fine-scale correlates of invasions over a very large region. This investigation also highlights practical limitations of the conceptual model of road-effect zones (Forman & Alexander, 1998) in real landscapes in the eastern United States.

2 | METHODS

2.1 | Data

2.1.1 | Forest plot data

Field observations were obtained from the USDA Forest Service Forest Inventory and Analysis (FIA) database (O'Connell et al., 2015). The inventory uses a permanent, national, systematic, grid-based, equal probability sample design across all land with a sampling intensity of approximately one plot per 2,400 ha (Bechtold & Patterson, 2005). Since 2001, the eastern forest inventory has surveyed invasive plant occurrence and cover on up to four 24 ft (7.3 m) radius subplots at each sampled location (Oswalt & Oswalt, 2015). From that database, we obtained invasive species presence/absence data for 23,039 plot locations (hereafter, "plots") that were surveyed between 2001 and 2011 and classified as a forest land use (i.e., urban and residential forests were excluded). Invasive species "presence" means that at least one invasive plant was observed on a given plot. FIA defines "invasive plants" as exotic plant species of any growth form likely to cause economic or environmental harm (Ries, Dix, Lelmini, & Thomas, 2004). The inventory uses region-specific species lists determined by invasive plant experts (Oswalt et al., 2015). As a result, the inventory may slightly underestimate the overall presence of non-native species. From the database, we also obtained an ordinal measure of site productivity (site index class) which was expressed as a plot-level index of high, medium or low productivity (Table 1). We used the exact plot locations instead of the approximate locations (O'Connell et al., 2015) for geographic analyses.

2.1.2 | Land cover data

A land cover map for the year 2006 was obtained at 0.09-ha spatial resolution from the United States Geological Survey (USGS) National Land Cover Database (NLCD) Program (Fry et al., 2011; USGS, 2014).

TABLE 1 Definition of the independent variables used to model of the odds of forest plant invasion. The symbols used to represent each variable are shown in parentheses. For the categorical variables, the reference class is the class with the lowest observed rate of invasion

Independent variable	Definition
Ecological province (PROV)	Categorical variable derived by spatial overlay of plot locations and the Cleland et al. (2007) map of ecoregions. The thirteen classes are the provinces shown in Figure 1. The reference class is province M211
Productivity (PROD)	Categorical variable derived by condensing the FIA site class code to three productivity classes of high (FIA codes 1 and 2), medium (FIA codes 3, 4 and 5) and low (FIA codes 6 and 7) (O'Connell et al., 2015). The reference class is low. As defined by FIA, the site class code is a measure of relative site productivity for the purpose of growing trees
Forest fragmentation (FRAG)	Categorical variable derived by condensing the value of forest area density in a 15.2 ha neighbourhood (FAD) to three fragmentation classes of low (FAD ≥ 0.9), medium (0.4 ≤ FAD < 0.9) and high (FAD < 0.4). Forest area density is the proportion of a neighbourhood with forest land cover. (Riitters et al., 2002). The reference class is low
Land use (LUSE)	Categorical variable derived by condensing the landscape mosaic class in a 590.49 ha neighbourhood to four land use classes of natural (<10% each of agriculture and developed land cover), agriculture (≥10% agriculture and <10% developed), developed (≥10% developed and <10% agriculture) and agriculture and developed (≥10% each of agriculture and developed). Landscape mosaic is defined by a ternary classification of a neighbourhood according to the proportions of agriculture, developed, and semi-natural land cover in the neighbourhood (Riitters, Wickham, & Wade, 2009). The reference class is natural
Road distance (ROAD)	Continuous variable derived by overlaying plot locations on road maps and measuring the distance (m) from plot centre to the nearest road (USCB (U.S. Census Bureau), 2016). The measurements were divided by 100 so that the unit change of distance was defined as 100 m. "Roads" included all mapped railroad and road features of any type or size, that is, features with MAF/TIGER Feature Class Codes (USCB (U.S. Census Bureau), 2016) that began with the letter "R" or "S."

We measured forest fragmentation and land use in four neighbourhoods surrounding each plot, using neighbourhood sizes of 4.41 ha, 15.21 ha, 65.61 ha and 590.49 ha. The neighbourhood sizes were selected to represent a wide range of measurement scale because fragmentation and land use are naturally scale-dependent and there is no *a priori* "best" measurement scale. As the land cover measurements are necessarily correlated across neighbourhood sizes, we conducted a preliminary analysis to retain for each variable the single neighbourhood size that best explained the odds of invasion (see Appendix S1 in Supporting Information). The best neighbourhood size for fragmentation was 15.2 ha, and the best size for land use was 590.49 ha.

2.1.3 | Road data

A regional analysis of road effects can be only as robust as the accuracy of the road map used in the analysis (Hawbaker & Radeloff, 2004). We obtained the most detailed road and railroad maps available for the study area from the United States Census Bureau (USCB) Geography Program TIGER/Line database (USCB, 2016). We measured the Euclidean distance from each plot centre to the nearest road or railroad of any type and size, including private roads and vehicular trails (Table 1). We included railroads because their potential effects are similar to those of roads.

2.2 | Modelling

The overall objective was to clarify and quantify the importance of road proximity by evaluating the probability of invasion as a function of distance from a road while accounting for broadscale regional differences and several local measures of invasibility and/or propagule pressure (Table 1). We used logistic regression with maximum likelihood estimation (PROC LOGISTIC; SAS, 2012). The principle of maximum likelihood estimation is to choose parameter estimates which, if true, would maximize the probability of obtaining the observed outcomes. We adopted the logit model, in which the dichotomous variable (invaded or not invaded) was presumed to follow a binomial distribution with the parameter *P*. In this model, the "odds" are defined as $P/1 - P$ and the "logit" is defined as log(odds), and the parameter estimates describe changes in the logit associated with the explanatory variables.

Our interest centred on interpreting the effects of each of the independent variables (Table 1) on the likelihood of invasion. However, interpreting the parameter estimates directly is difficult because differences in logits among classes of a variable depend on the values of *p*. For that reason, parameter estimates for categorical variables are easiest to interpret in terms of "odds ratios" which compare classes of the categorical variable to a reference class. For example, suppose there is a model with one categorical variable representing ecological province. Suppose further there are two provinces (*A* and *B*) where the observed rates of invasion (*P*) are $P_A = 0.4$ and $P_B = 0.7$, and let province *A* be the reference province. The odds of invasion in province *A* are 0.4/0.6 = 0.67, while those in province *B* are 0.7/0.3 = 2.33. The odds ratio for province *B* relative to the reference class (province *A*) is 2.33/0.67 = 3.48. The interpretation is that the odds of invasion in province *B* are 3.48 times that in the reference class, or equivalently, the odds are 248% higher ((3.48 − 1)*100%) in province *B* than in the reference class. For comparison, this interpretation differs from statements about the "risk difference" (0.7 − 0.4 = 0.3) or the "relative risk" (0.7/0.4 = 1.75) among the provinces. The effects of continuous variables are easiest to interpret in terms of the change in the odds of invasion per unit change in the explanatory variable. For example, suppose β is the parameter estimate for a continuous variable in a logit model of invasion. As β describes the change in the logit per unit change in distance, the per cent change in the odds of invasion per unit change in distance is (exp(β) − 1)*100%. In our analysis, the distance from a road was divided by 100 so that estimated parameters could be interpreted per 100 m unit change in distance. All regression-based estimates of odds ratios are adjusted for all other terms in the model, using the observed classes of categorical variables and the mean values of continuous variables.

We explored potential interactions among the independent variables as well as models with and without correlated categorical variables. In addition, we explored using fewer or more classes for each of the categorical independent variables. The results (not shown) for models with and without correlated variables suggested that collinearity was not a major problem because it did not result in illogical signs of parameter estimates and it did not change the relative magnitudes of individual class effects for any of the categorical variables. There was a practical trade-off between the maximum number of classes for each categorical variable and the number of interactions in the model, because maximum likelihood estimation is not feasible when too many of the possible combinations of independent variables have no observations. We elected to use more classes per categorical variable because we were interested in evaluating the effects of incremental changes in each variable and because confidence in the model is higher when those incremental changes result in logical and consistent changes in parameter estimates. More complex models would have been called for if there had been inconsistent or illogical parameter estimates, but that outcome was not obtained. Thus, the only interaction term in the model was that between ecological province and distance from a road.

To address the study objectives, we selected a sequence of three models to evaluate the unadjusted effect of distance from a road (Model 1), the regional variation in that effect found among ecological provinces (Model 2) and the adjusted effect of distance from a road with adjustments for productivity, land use and fragmentation (Model 3). In Model 1, the logit was modelled as a function of distance to road (ROAD). Model 2 included a term for ecological province (PROV), and the parameter for distance to road was estimated separately within each province. Model 3 was the same as Model 2 except that it added three terms for productivity (PROD), land use (LUSE) and fragmentation (FRAG). The relative importance of the independent variables was assessed by the Wald (adjusted main effect) chi-square statistics for Model 3 (see Appendix S1).

We assumed the observations were independent because the plots were far apart relative to the scales at which both invasions (Iannone et al., 2016), and many drivers of invasions (Guo, Rejmánek,

& Wen, 2012) were found to be significantly autocorrelated when using similar data (see Appendix S1). We expected collinearity because the independent variables are all spatially correlated to some degree with human activities, but the correlations were generally low (Table 2). As collinearity can affect variance estimates, we conducted a univariate (non-regression) analysis to demonstrate that each variable was by itself a statistically important predictor of the probability of invasion. For that purpose, we used chi-square statistics for the categorical variables, and a *t* statistic for the continuous variable. Appendix S1 contains additional discussion of assumptions.

3 | RESULTS

3.1 | Observed invasion rates

The observed rate of invasion (per cent of plots that were invaded) varied among provinces and with distance from a road within provinces (Table 2). Overall, 58% of the sample plots were invaded, and the invasion rate ranged from 8% for province M211 (the reference province) to 78% for province 231 (the names and locations of ecological provinces are shown in Figure 1). In comparison, 65% of plots within 50 m of a road were invaded, and the rate of invasion for plots within 50 m of a road was higher than the overall province rate except in province 231. Overall, the mean distance from a road was 314 m for invaded plots and 448 m for non-invaded plots, and the mean distance for invaded plots was less than the mean distance for non-invaded plots in all provinces. The chi-square and *t* tests (Table 2) indicated that the observed invasion rates were statistically different ($p < .001$) among provinces, and the mean distance from a road was different ($p < .001$) for invaded versus uninvaded plots.

The observed rate of invasion was higher for high-productivity plots (76%) than low-productivity plots (40%) and for plots with high fragmentation (65%) compared to low fragmentation (46%), and the rates of invasion increased monotonically with both productivity and fragmentation (Table 3). Compared to the rate of invasion in landscapes with natural land use (46%), the rate of invasion was higher in landscapes with anthropogenic land uses (62% to 80%), and the rate for agriculture and developed landscapes was higher than the rate for either developed or agriculture land use alone (Table 3). The chi-square tests indicated all the aforementioned differences were statistically significant ($p < .001$) (Table 3). Spearman rank-order correlations, calculated on a per-plot basis, indicated that the distance to a road was significantly but not highly correlated with land use, productivity and fragmentation (Table 3).

3.2 | Model results

In the logistic regression model with distance from a road as the only explanatory variable, Model 1 predicted a 65% probability of invasion when ROAD = 0 (Figure 2), which was close to the overall observed rate (65%) of invasion for plots within 50 m of a road (Table 2). The estimated odds of invasion decreased by 7.0% per 100 m distance from a road, and the estimated probability of invasion approached zero at a distance of approximately 7,500 m (Figure 2). Model 2 indicated substantial variation in the road effect (i.e., the per cent change in the odds of invasion per unit change in distance among provinces)

TABLE 2 Number of plots, observed rates of invasion and distance from road for invaded and non-invaded plots, by province

Ecological Province	All plots[a]		Plots within 50 m of a road		Mean distance from road[b]	
	Number of plots	Per cent invaded (%)	Number of plots	Per cent invaded (%)	Invaded (m)	Not Invaded (m)
211	163	42	26	35	265	483
212	455	30	29	38	413	794
221	899	65	142	76	227	383
222	201	78	23	78	292	330
223	1,376	71	155	74	294	368
231	8,042	78	999	84	305	400
232	8,276	46	1,024	52	328	403
234	779	43	61	51	643	841
255	482	45	53	57	309	395
M211	158	8	17	18	203	656
M221	1,396	37	205	50	225	454
M223	255	30	23	43	354	462
M231	557	40	66	48	352	531
All	23,039	58	2,823	65	314	448

[a]The chi-square test rejected the null hypothesis that the rate of invasion was the same for all provinces ($\chi^2 = 2,744$; $df = 12$; $p < .0001$).
[b]The *t* test rejected the null hypothesis that the mean difference in mean distance from road for invaded versus non-invaded plots was zero ($t = 5.15$; $df = 12$; $p = .0002$).

TABLE 3 Observed rates of invasion and mean distance from a road for different classes of land use, productivity and fragmentation, for all provinces

Variable	Class	Distribution of sample plots (%)	Per cent invaded[a] (%)	Mean distance from road (m)	Assigned rank[b]
Land use	Natural	49	46	461	1
	Developed	6	62	168	2
	Agriculture	39	69	321	3
	Agriculture and developed	7	80	169	4
Productivity	High	5	76	353	3
	Medium	79	61	358	2
	Low	16	40	436	1
Fragmentation	High	14	65	263	3
	Medium	49	65	294	2
	Low	37	46	515	1

[a]chi-square tests rejected the null hypotheses that the rate of invasion was the same for all classes within each variable (*df* = 2 for productivity and fragmentation; *df* = 3 for land use; $p < .0001$ for all three tests).

[b]For each variable, the assigned ranks for the calculation of Spearman correlations increase with observed per cent invaded. The Spearman (rank-order) correlations (calculated on a per-plot basis) with distance from a road were −.16, −.04 and −.32 for land use, productivity and fragmentation, respectively ($p < .0001$ in all cases). The Spearman partial correlations (adjusted for distance from a road) were 0.00 between land use and productivity ($p = .98$), 0.30 between land use and fragmentation ($p < .0001$) and −0.01 between productivity and fragmentation ($p = .28$).

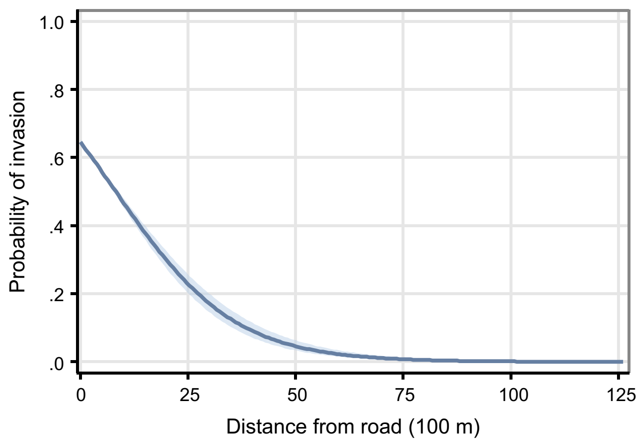

FIGURE 2 From Model 1, the unadjusted probability of invasion decreases with distance from a road. The upper and lower 95% confidence limits from logistic regression are indicated. [Colour figure can be viewed at wileyonlinelibrary.com]

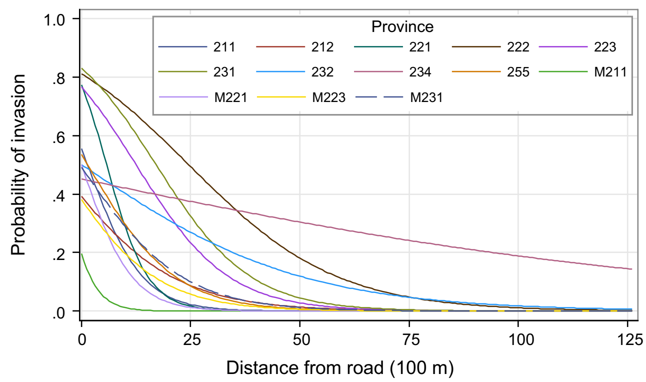

FIGURE 3 From Model 2, the adjusted probability of invasion decreases with distance from a road with substantial variation among ecological provinces. [Colour figure can be viewed at wileyonlinelibrary.com]

(Figure 3 and Table 4). In this case, the predicted probabilities of invasion when ROAD = 0 were close to the observed province rates of invasion for plots within 50 m of a road (Table 1). The apparently large variation in the road effect among provinces in Model 2 was part of the rationale for modelling the interaction between ROAD and PROV in Model 3.

The assessment of the relative importance of variables in Model 3 indicated that that ecological province was the most important single variable explaining the odds of invasion, followed by land use, productivity, fragmentation and distance from a road, in that order (see Appendix S1). Compared to Model 2, the adjustments for land use, productivity and fragmentation in Model 3 reduced the odds of invasion attributable to provinces in 11 of the 12 non-reference provinces (Table 4). Those decreases imply that some of the variation of road-adjusted invasion rates among provinces (Model 2) was explained by province differences in land use, productivity and/or fragmentation. As none of those 12 odds ratios was close to one (1.0) in Model 3, we can infer there is variation among provinces that is not explained by the other variables in Model 3.

Compared to Model 2, the estimated road effect (per cent change in the odds of invasion per 100 m distance from road) decreased for

TABLE 4 Estimated per cent change in province odds ratios and the road effect (per cent change in odds of invasion per 100 m distance from a road) by province before (Model 2) and after (Model 3) adjustment for land use, productivity and fragmentation

	Model 2		Model 3	
Province	Odds ratio	Road effect (%)	Odds ratio	Road effect (%)
211	8.7	−14.7	7.8	−12.0
212	6.1	−7.4	4.8	−4.1
221	19.4	−19.2	14.9	−13.8
222	43.2	−5.8	22.6	−1.7
223	28.9	−9.1	21.3	−5.0
231	43.4	−8.9	26.0	−4.9
232	10.8	−3.9	6.2	−0.9
234	9.8	−1.3	5.0	0.1
255	10.0	−9.6	8.2	−9.5
M211	–[a]	−26.2	–[a]	−22.7
M221	6.6	−16.0	6.1	−10.2
M223	5.5	−8.8	5.7	−4.1
M231	8.8	−8.3	7.7	−5.2

[a]The odds ratio is not applicable for the reference province.

all 13 provinces in Model 3 (Table 4). The decreases are attributable to the correlations between distance from a road and land use, productivity and/or fragmentation (Table 3) and imply that the odds of invasion are less sensitive to distance from a road when those other variables are taken into account. In three provinces (222, 232 and 234), the estimated per cent change in the odds of invasion per 100 m distance from a road was close to zero, implying that the effects of distance from a road were indistinguishable from other confounding variables.

Similarly, the adjusted odds ratios for land use, productivity and fragmentation classes from Model 3 were smaller than the unadjusted odds ratios calculated from the observed invasion percentages (Table 5). The implication is that some of the unadjusted effect of these variables was attributable to differences in those variables among provinces and/or correlations with distance from a road. The relative magnitude of the adjustment was highest for fragmentation and lowest for productivity. While the magnitude of the variable effects was reduced by adjustment, the relative effect of each class within a given variable was the same, and the magnitudes of the adjusted effects were still quite large. In comparison with a plot with natural land use, the adjusted odds of invasion were 58% higher for a plot in a developed landscape, 102% higher for a plot in an agriculture landscape and 223% higher for a plot in an agriculture and developed landscape. The adjusted odds of invasion on a high and medium productivity plot were 363% and 121% higher, respectively, than the odds of invasion on a low-productivity plot. The adjusted odds of invasion for a plot in a landscape with medium to high fragmentation were 64% to 70% higher than the odds of invasion for a plot in a landscape with low fragmentation.

TABLE 5 Observed and adjusted (Model 3) per cent increase in the odds of invasion relative to the reference class of each variable

Variable	Class	Observed (%)	Adjusted (%)
Land use	Natural	–[a]	–
	Developed	88	58
	Agriculture	153	102
	Agriculture and developed	372	223
Productivity	High	371	363
	Medium	135	121
	Low	–[a]	–
Fragmentation	High	121	70
	Medium	118	64
	Low	–[a]	–

[a]The odds ratio is not applicable to the reference class of each variable.

3.3 | Best estimates of road effects

Within the limitations of the data and models we used, the best available estimates of road-mediated invasion risk (i.e., risk attributable to distance from a road alone) come from the estimated probabilities of invasion in relation to distance from a road for the "least risk" plots in each province. The least risk plots are those with low productivity in natural landscapes with low fragmentation. The fitted regression from Model 3 was used to score the probability of invasion and confidence interval for those plots, and the results were plotted in relation to distance from a road for each of the 12 provinces that contained least risk plots (Figure 4). For the least risk plots, there was substantial variation among provinces in the estimated probability of invasion adjacent to roads as well as the rate of decrease in that estimate with increasing distance from a road. The increasing widths of the 95% confidence intervals as distance from road increased reflect the relatively fewer numbers of plots that are far from roads. Within the range of observed distances from a road, the lower confidence limit approached zero in only three provinces (211, 212 and M221).

4 | DISCUSSION

The risk of forest plant invasions cannot be evaluated only on the basis of distance from a road. Forman and Alexander (1998) proposed a conceptual model of a "road-effect zone" to link applied ecology with road engineering in transportation planning. In that model, the existence of a road implies an increased risk of plant invasion, and the width of the zone is determined by the distance from the road at which the incremental risk becomes negligible. They suggested the road-effect zone for invasive plants extends from 200 m to more than 1,000 m from a road. With that definition, we found that the overall road-effect zone in eastern forests extends more than 5,000 m (Figure 2) with substantial differences (approximately 1,000 m to

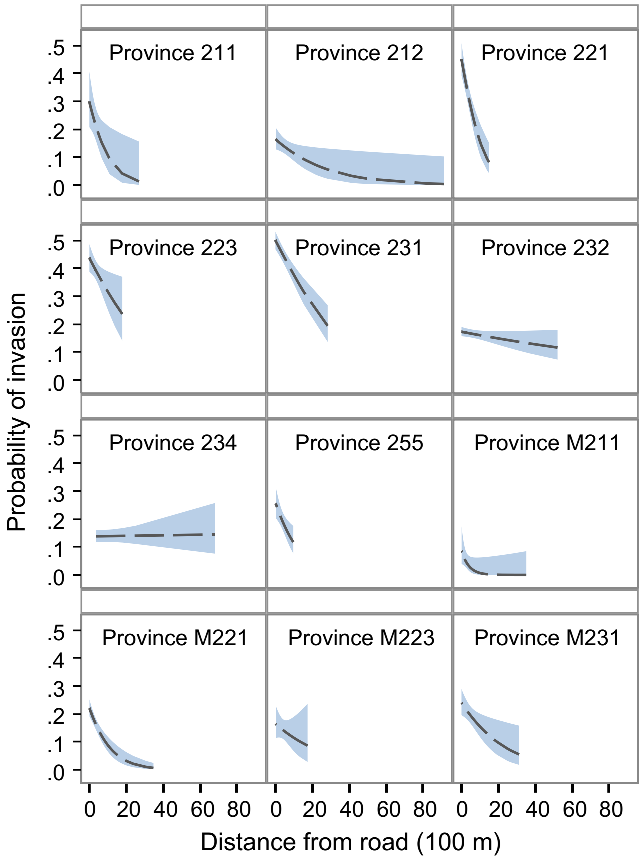

FIGURE 4 From Model 3, the probability of invasion for the least risk plots (i.e., plots with natural land use, low productivity and low fragmentation) typically decreases with distance from a road with substantial variation among ecological provinces. The upper limit on the horizontal axis corresponds to the observed maximum distance from a road in a province. The upper and lower 95% confidence limits are indicated. Province 222 is not shown because there were no least risk plots in that province. [Colour figure can be viewed at wileyonlinelibrary.com]

more than 10,000 m) among ecological provinces (Figure 3). But road-effect zones are determined by natural processes near roads ["nature's directional flows" in Forman and Deblinger (2000)] and road characteristics such as type of surface, traffic volume, land use history near roads and other factors (Forman, 2000). Using Model 3 to account for some of those factors, we found that the road-effect zone for the lowest risk locations still extended at least 2,000 m from a road (Figure 4). One may argue the true road-effect zone subsumes proximate causes (e.g., land uses) because the proximate causes would not occur except for the existence of a road. From another perspective, no matter how far they extend, road effects are simply less important when they are adjusted for differences in land use, productivity and fragmentation.

Precise specification of the width of a road-effect zone may be useful for local transportation planning, and of course the construction of a new road always increases the local risk of plant invasion. After all, invasion rates are demonstrably higher for forest land adjacent to roads (Table 2), and the probability of invasion decreases rapidly with distance from road in relatively less modified landscapes in some provinces (Figure 4). But as a practical matter, only three provinces (211, 212 and M221) in the eastern United States contained least risk plots that were outside of the estimated road-effect zone (Figure 4). Local risks always depend on local circumstances, but a precise regional specification of road-effect zones is unlikely to be informative in the eastern United States where the area at risk of forest plant invasions due to road proximity already encompasses most of the forest area.

The forest inventory data provide a snapshot of conditions which have developed over several centuries. A primary factor determining the current spread of an invasive species is the time since introduction (Liebhold et al., 2013). While an earlier analysis of the forest plant invasion data did not reveal substantial temporal dependence in our study area (Iannone et al., 2015), our higher-resolution analysis may still be confounded by temporal dependence at finer scales. In terms of explaining the odds of forest plant invasions, ecological province was the single most informative variable tested, and distance from a road was the least informative. Province boundaries were originally defined (Bailey, 1995) on the basis of broadscale biophysical patterns. It is plausible that those same patterns are drivers of invasion without human influences, and drivers of the timing and types of human modifications, which together determined the history and patterns of forest plant invasions. The relative unimportance of distance from a road indicates that the type of human activities along roads, and the distance from those activities, may be more important than the simple existence of the road. In other words, "human impact zones" may be more informative than "road-effect zones" when assessing the risk of forest plant invasions; roads are still important, but they can be considered simply as another type of human impact.

The observation that invasion was more likely on higher productivity sites supports the hypothesis that invasibility is directly related to productivity. But that interpretation is somewhat problematic because the earliest land conversions of forest to agriculture very likely occurred at the most productive locations. Given a choice of locations, few farms would be created where productivity is low. Furthermore, the historical road network which was established to connect farms and towns is the basis for the modern road network. We therefore expect that current forest land in high-productivity locations is more likely to be near roads and agriculture. What appears to be evidence in support of the hypothesis that invasibility is directly related to productivity may be an artefact of the confounding of productivity with human influences.

The land use variable was interpreted to indicate invasive species propagule pressure because the adjusted odds of invasion were not the same for all non-reference classes. For example, the odds of invasion for agriculture land use were different from the odds for developed land use, and the combined effect of both together was greater than the sum of both effects alone. The best scale of measurement for the land use variable (590 ha) suggests relatively long-range dispersion of propagules. Compared to natural land cover, the existence of more than 10% of agriculture or developed land within a landscape significantly increased the odds of invasion and the odds increased more for agriculture alone than for developed alone. We can speculate that agriculture had more impact than development because the forest-land plots in the FIA database are generally not near heavily urbanized areas containing higher percentages of invasive ornamental plants. The evidence of synergistic land use effects suggests that different pools of invasive plant species may originate from agricultural and developed land uses, increasing the potential exposure of forested areas within a landscape with both of these land uses compared to forests in landscapes with the presence of only agriculture or only development.

The interpretation of fragmentation in terms of either invasibility or propagule pressure is equivocal. Rapid development of closed-canopy forest may restrict invasion by many introduced plant species (Meiners, Pickett, & Cadenasso, 2002), but there are many shade-tolerant invasive forest plants are unaffected (Martin et al., 2009). Invasibility is difficult to interpret because our neighbourhood measure of fragmentation may not reflect the canopy condition of the forest plot itself, and the importance of propagule pressure cannot be evaluated without knowing the cause of the fragmentation. We found that fragmentation could have been measured as a binary state (fragmented or unfragmented) because the medium and high levels of fragmentation had roughly the same odds of invasion. That may simply indicate the importance of nearby disturbances. As forest conversion in the study area is typically to either agriculture or developed land use, and the best scale to measure fragmentation (15 ha) is small compared to the land use variable, it is also plausible that fragmentation was simply measuring land use at a local scale.

Our models considered the likelihood of invasion by many plant species and therefore our results do not apply to any single invasive species in particular. Furthermore, our results may underestimate the overall impacts of non-native species because the data did not include exotic species that were judged unlikely to cause economic or environmental harm (Ries et al., 2004). We believe it would be a productive exercise to use similar data and models to explore relationships for individual species differing in invader traits. Future work could also consider modelling the degree of invasion (e.g., invasive species cover or diversity) for different forest conditions within different landscape configurations. The expected value of invadedness could then be calculated on a per-plot basis by combining the predicted probability of invasion and the predicted degree of invasion. The expected values could also be extrapolated to regional estimates using the protocols from the FIA sample design, perhaps stratified by other FIA variables such as forest type or ownership. An additional avenue for future work is to apply the models which are developed on a per-plot basis to off-plot locations. That would require new models for off-plot estimation of variables such as site productivity that are normally collected on FIA plots only, but many other variables (e.g., land use, fragmentation and distance from a road) are readily available for off-plot locations. These models would provide wall-to-wall maps of predicted invasive species occurrence or future risk of plant invasions in forest land.

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REFERENCES

Bailey, R. G. (1995) *Descriptions of the ecoregions of the United States*. 2d edn. Misc. Publ. 1391. Washington, DC: U.S. Department of Agriculture Forest Service, 108 p.

Barton, A. M., Brewster, L. B., Cox, A. N., & Prentiss, N. K. (2004). Non-indigenous woody invasive plants in a rural New England town. *Biological Invasions*, *6*, 205–211. https://doi.org/10.1023/B:BINV.0000022139.03833.e5

Bechtold, W. A., & Patterson, P. L. (Eds.) (2005). *The enhanced forest inventory and analysis program – national sampling design and estimation procedures* (p. 85). Asheville, NC: General Technical Report SRS-80, US Department of Agriculture, Forest Service, Southern Research Station.

Catford, J. A., Vesk, P. A., White, M. D., & Wintle, B. A. (2011). Hotspots of plant invasion predicted by propagule pressure and ecosystem characteristics. *Diversity and Distributions*, *17*, 1099–1110. https://doi.org/10.1111/j.1472-4642.2011.00794.x

Christen, D. C., & Matlack, G. R. (2009). The habitat and conduit functions of roads in the spread of three invasive plant species. *Biological Invasions*, *11*, 453–465. https://doi.org/10.1007/s10530-008-9262-x

Cleland, D. T., Freeouf, J. A., Keys, J. E. Jr, Nowacki, G.J., Carpenter, C., & McNab, W. H. (2007) Ecological Subregions: Sections and Subsections of the Conterminous United States [1:3,500,000] [CD-ROM]. Sloan, A.M. (cartog.) Gen. Tech. Report WO-76. Washington, DC: U.S. Department of Agriculture, Forest Service.

Cordero, R. L., Torchelsen, F. P., Overbeck, G. E., & Anand, M. (2016). Analyzing the landscape characteristics promoting the establishment and spread of gorse (*Ulex europaeus*) along roadsides. *Ecosphere*, *7*(3), e01201. https://doi.org/10.1002/ecs2.1201

Dark, S. J. (2004). The biogeography of invasive alien plants in California: an application of GIS and spatial regression analysis. *Diversity and Distributions*, *10*, 1–9. https://doi.org/10.1111/j.1472-4642.2004.00054.x

Davis, A. J. S., Singh, K. K., Thill, J.-C., & Meentemeyer, R. K. (2016). Accounting for residential propagule pressure improves prediction of urban plant invasion. *Ecosphere*, *7*(3), e01232. https://doi.org/10.1002/ecs2.1232

Fei, S., Phillips, J., & Shouse, M. (2014). Biogeomorphic impacts of invasive species. *Annual Review of Ecology, Evolution, and Systematics*, *45*, 69–87. https://doi.org/10.1146/annurev-ecolsys-120213-091928

Flory, S. L., & Clay, K. (2006). Invasive shrub distribution varies with distance to roads and stand age in eastern deciduous forests in Indiana, USA. *Plant Ecology*, *184*, 131–141. https://doi.org/10.1007/s11258-005-9057-4

Forman, R. T. T., & Alexander, L. E. (1998). Roads and their major ecological effects. *Annual Review of Ecology and Systematics*, *29*, 207–231. https://doi.org/10.1146/annurev.ecolsys.29.1.207

Forman, R. T. T. (2000). Estimate of the area affected ecologically by the road system of the United States. *Conservation Biology*, *14*, 31–35.

Forman, R. T. T., & Deblinger, R. D. (2000). The ecological road-effect zone of a Massachusetts (USA) suburban highway. *Conservation Biology*, *14*, 36–46.

Fry, J., Xian, G., Jin, S., Dewitz, J., Homer, C., Yang, L., … Wickham, J. (2011). Completion of the 2006 national land cover database for the conterminous United States. *Photogrammetric Engineering & Remote Sensing*, *77*, 858–864.

Gavier-Pizarro, G. I., Radeloff, V. C., Stewart, S. I., Huebner, C. D., & Keuler, N. S. (2010). Rural housing is related to plant invasions in forests of southern Wisconsin, USA. *Landscape Ecology*, *25*, 1505–1518. https://doi.org/10.1007/s10980-010-9516-8

González-Moreno, P., Pino, J., Gassó, N., & Vilà, M. (2013). Landscape context modulates alien plant invasion in Mediterranean forest edges. *Biological Invasions*, *15*, 547–557. https://doi.org/10.1007/s10530-012-0306-x

Guo, Q., Rejmánek, M., & Wen, J. (2012). Geographical, socioeconomic, and ecological determinants of exotic plant naturalization in the United States: insights and updates from improved data. *NeoBiota*, *12*, 41–55. https://doi.org/10.3897/neobiota.12.2419

Hansen, M. J., & Clevenger, A. P. (2005). The influence of disturbance and habitat on the presence of non-native plant species along transport corridors. *Biological Conservation*, *125*, 249–259. https://doi.org/10.1016/j.biocon.2005.03.024

Hawbaker, T. J., & Radeloff, V. C. (2004). Roads and landscape pattern in northern Wisconsin based on a comparison of four road data sources. *Conservation Biology*, *18*, 1233–1244. https://doi.org/10.1111/j.1523-1739.2004.00231.x

Hawbaker, T. J., Radeloff, V. C., Hammer, R. B., & Clayton, M. K. (2004). Road density and landscape pattern in relation to housing density, land ownership, land cover, and soils. *Landscape Ecology*, *20*, 609–625. https://doi.org/10.1007/s10980-004-5647-0

Honu, Y. A. K., & Gibson, D. J. (2006). Microhabitat factors and the distribution of exotic species across forest edges in temperate deciduous forest of southern Illinois, USA. *Journal of the Torrey Botanical Society*, *133*, 255–266. https://doi.org/10.3159/1095-5674(2006)133[255:MFATDO]2.0.CO;2

Iacona, G. D., Price, F. D., & Armsworth, P. R. (2014). Predicting the invadedness of protected areas. *Diversity and Distributions*, *20*, 430–439. https://doi.org/10.1111/ddi.12171

Iannone, B. V., Oswalt, C. M., Liebhold, A. M., Guo, Q., Potter, K. M., Nunez-Mir, G. C., … Fei, S. (2015). Region-specific patterns and drivers of macroscale forest plant invasions. *Diversity and Distributions*, *21*, 1181–1192. https://doi.org/10.1111/ddi.12354

Iannone, B. V., Potter, K. M., Guo, Q., Liebhold, A., Pijanowski, B. C., Oswalt, C. M., & Fei, S. (2016). Biological invasion hotspots: a trait-based perspective reveals new sub-continental patterns. *Ecography*, *39*, 961–969. https://doi.org/10.1111/ecog.2016.v39.i10

Jelinski, D. E., & Wu, J. G. (1996). The modifiable areal unit problem and implications for landscape ecology. *Landscape Ecology*, *11*, 129–140. https://doi.org/10.1007/bf02447512

Kuhman, T. R., Pearson, S. M., & Turner, M. G. (2010). Effects of land-use history and the contemporary landscape on non-native plant invasion at local and regional scales in the forest-dominated southern Appalachians. *Landscape Ecology*, *25*, 1433–1445. https://doi.org/10.1007/s10980-010-9500-3

Lemke, D., Hulme, P. E., Brown, J. A., & Tadesse, W. (2011). Distribution modelling of Japanese honeysuckle (*Lonicera japonica*) invasion in the Cumberland Plateau and Mountain Region, USA. *Forest Ecology and Management*, *262*, 139–149. https://doi.org/10.1016/j.foreco.2011.03.014

Liebhold, A. M., McCullough, D. G., Blackburn, L. M., Frankel, S. J., Von Holle, B., & Aukema, J. E. (2013). A highly aggregated geographical distribution of forest pest invasions in the USA. *Diversity and Distributions*, *19*, 1208–1216. https://doi.org/10.1111/ddi.12112

Mack, R. N., Simberloff, D., Lonsdale, W. M., Evans, H., Clout, M., & Bazzaz, F. A. (2000). Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications*, *10*, 689–710. https://doi.org/10.1890/1051-0761(2000)010[0689:BICEGC]2.0.CO;2

Martin, P. H., Canham, C. D., & Marks, P. L. (2009). Why forests appear resistant to exotic plant invasions: intentional introductions, stand dynamics, and the role of shade tolerance. *Frontiers in Ecology and Environment*, *7*, 142–149. https://doi.org/10.1890/070096

Meiners, S. J., Pickett, S. T. A., & Cadenasso, M. L. (2002). Exotic plant invasions over 40 years of old field successions: community patterns and associations. *Ecography*, *25*, 215–223. https://doi.org/10.1034/j.1600-0587.2002.250209.x

Nielsen, C., Hartvig, P., & Kollmann, J. (2008). Predicting the distribution of the invasive alien *Heracleum mantegazzianum* at two different spatial scales. *Diversity and Distributions*, *14*, 307–317. https://doi.org/10.1111/j.1472-4642.2007.00456.x

O'Connell, B. M., LaPoint, E. B., Turner, J. A., Ridley, T., Pugh, S. A., Wilson, A. M., … Conkling, B. L. (2015) The Forest Inventory and Analysis Database: Database description and user guide version 6.0.2 for Phase 2. U.S. Department of Agriculture, Forest Service. 748 p. [Online]. Available at: http://www.fia.fs.fed.us/library/database-documentation/.

Oswalt, C., Fei, S., Guo, Q., Iannone, B. V. III, Oswalt, S., Pijanowski, B., & Potter, K. (2015). A subcontinental view of forest plant invasions using national inventory data. *NeoBiota*, *24*, 49–54. https://doi.org/10.3897/neobiota.24.8378

Oswalt, C. M., & Oswalt, S. N. (2015) Invasive plants on forest land in the United States. Chapter 8. In: K. M. Potter & B. L. Conkling (Eds.), *Forest health monitoring: national status, trends, and analysis 2013*. Gen. Tech. Rep. SRS-207. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station, 64 p.

Parendes, L. A., & Jones, J. A. (2000). Role of light availability and dispersal in exotic plant invasion along roads and streams in the H.J. Andrews experimental forest, Oregon. *Conservation Biology*, *14*, 64–75. https://doi.org/10.1046/j.1523-1739.2000.99089.x

Pauchard, A., & Alaback, P. B. (2004). Influence of elevation, land use, and landscape context on patterns of alien plant invasions along roadsides in protected areas of south-central Chile. *Conservation Biology*, *18*, 238–248. https://doi.org/10.1111/j.1523-1739.2004.00300.x

Pejchar, L., & Mooney, H. A. (2009). Invasive species, ecosystem services and human well-being. *Trends in Ecology and Evolution*, *24*, 497–504. https://doi.org/10.1016/j.tree.2009.03.016

Ries, P., Dix, M. E., Lelmini, M., & Thomas, D. (2004). *National strategy and implementation plan for invasive species management*. Washington, D.C.: United States Department of Agriculture, Forest Service.

Riitters, K. H., & Wickham, J. D. (2003). How far to the nearest road? *Frontiers in Ecology and Environment*, *1*, 125–129. https://doi.org/10.1890/1540-9295(2003)001[0125:HFTTNR]2.0.CO;2

Riitters, K. H., Wickham, J. D., O'Neill, R. V., Jones, K. B., Smith, E. R., Coulston, J. W., … Smith, J. H. (2002). Fragmentation of continental United States forests. *Ecosystems*, *5*, 815–822. https://doi.org/10.1007/s10021-002-0209-2

Riitters, K. H., Wickham, J. D., & Wade, T. G. (2009). An indicator of forest dynamics using a shifting landscape mosaic. *Ecological Indicators*, *9*, 107–117. https://doi.org/10.1016/j.ecolind.2008.02.003

SAS (2012). *SAS/STAT software, version 9.4 of the SAS System for Windows*. Copyright © 2012 Cary, NC, USA: SAS Institute Inc.

Seipel, T., Kueffer, C., Rew, L. J., Daehler, C. C., Pauchard, A., Naylor, B. J., … Walsh, N. (2012). Processes at multiple scales affect richness and similarity of non-native plant species in mountains around the world. *Global Ecology and Biogeography*, *21*, 236–246. https://doi.org/10.1111/j.1466-8238.2011.00664.x

Trombulak, S. C., & Frissell, C. A. (2000). Review of ecological effects of roads on terrestrial and aquatic communities. *Conservation Biology*, *14*, 18–30.

Underwood, E. C., Klinger, R., & Moore, P. E. (2004). Predicting patterns of non-native plant invasions in Yosemite National Park, California, USA. *Diversity and Distributions*, *10*, 447–459. https://doi.org/10.1111/j.1366-9516.2004.00093.x

USCB (U.S. Census Bureau) (2016). TIGER/Line shapefiles. U.S. Department of Commerce, U.S. Census Bureau, Geography Division, Spatial Data Collection and Products Branch, Washington DC. http://www.census.gov/geo/maps-data/data/tiger.html (accessed August 9, 2016).

USDA (U.S. Department of Agriculture) Forest Service (2015). Field inventory and analysis national core field guide. Volume I: Field data collection for phase 2 plots. Version 7.0. U.S. Department of Agriculture, Forest Service. 431 p. [Online]. Available at: http://www.fia.fs.fed.us/library/field-guides-methods-proc/docs/2015/Core-FIA-FG-7.pdf

USGS (U.S. Geological Survey) (2014). *NLCD 2006 land cover*, 2011th edn. Sioux Falls, SD, USA: Geological Survey.

Vieira, R., Finn, J. T., & Bradley, B. A. (2014). How does the landscape context of occurrence data influence models of invasion risk? A comparison of independent datasets in Massachusetts, USA. *Landscape Ecology*, *29*, 1601–1612. https://doi.org/10.1007/s10980-014-0080-5

Western, L., & Juvik, J. O. (1983). Roadside plant communities on Mauna Loa, Hawaii. *Journal of Biogeography*, *10*, 307–316. https://doi.org/10.2307/2844740

Yates, E. D., Levia, D. F. Jr, & Williams, C. L. (2004). Recruitment of three non-native invasive plants into a fragmented forest in southern Illinois. *Forest Ecology and Management*, *190*, 119–130. https://doi.org/10.1016/j.foreco.2003.11.008

BIOSKETCH

The research team addresses basic and applied research questions in invasive ecology with a focus on forest plants and applications to macroscale resource modelling and assessment.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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