



Do roads or streams explain plant invasions in forested protected areas?

Melissa K. Daniels · Gwenllian D. Iacona · Paul R. Armsworth · Eric R. Larson

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Abstract Giving land managers the ability to predict invasion patterns can provide planning tools for acquisition and management of protected areas. We compared the effects of roads and streams, two substantial pathways for delivery of invasive plant propagules and sources of disturbance that may facilitate invasions, on the abundance of non-native invasive plants in 27 protected areas in the Appalachian Mountains of the eastern United States. As an extension of our road analysis, we also evaluated specific road type as a predictor of protected area invadedness. We found that road and stream predictors did not improve on a model that included only other covariates (e.g., distance to an urban area, average canopy cover, average slope, edge-to-interior ratio,

percent agricultural land, and percent developed land). In this model, only percent agricultural land was marginally significant in predicting parcel invadedness. However, we found that four-wheel drive (4WD) roads did predict protected area invadedness well relative to other road types (primary, secondary, and local) and better than a covariates-only model. The role of 4WD road density in predicting protected area invadedness may be explained by their relation to recreation, the unmaintained nature of 4WD roads, or the accumulation of mud and plant materials on 4WD vehicles. Although we found overall streams and roads in general to be poor predictors of invadedness of protected areas by invasive plants, we do propose that our finding of a relationship between plant invasions and density of 4WD roads merits further investigation in the future.

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M. K. Daniels · E. R. Larson (✉)
Department of Natural Resources and Environmental
Sciences, University of Illinois at Urbana-Champaign,
Urbana, IL, USA
e-mail: erlarsn@illinois.edu

G. D. Iacona
Center for Biodiversity Outcomes, Arizona State
University, Tempe, AZ, USA

P. R. Armsworth
Department of Ecology and Evolutionary Biology,
University of Tennessee, Knoxville, TN, USA

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Introduction

Protected areas are one of the most important tools for conservation of biodiversity (Rodrigues et al. 2004). In addition, protected areas also provide a variety of ecosystem services, including natural disaster risk reduction and climate regulation (Castro et al. 2015;

Soares-Filho et al. 2010). The many negative ecosystem impacts of invasive plants, such as harm to native plants and animals (Greene and Blossey 2012; Mack et al. 2000) and alterations to the intensity and frequency of disturbances such as fires and floods (Pejchar and Mooney 2009; Brooks et al. 2004), jeopardize benefits provided by protected areas. In order to support the biodiversity conservation and ecosystem services roles of protected areas, a need exists to predict the introduction, establishment, spread, and impacts of invasive plants in protected areas and adequately plan for their management (Lodge et al. 2016).

Invasive species populations are increasing worldwide (Seebens et al. 2017), and many land managers report invasive species management as their highest priority (Kuebbing and Simberloff 2015). Since invasive plant management is costly on protected areas (Iacona et al. 2014) and invasive plants negatively impact their ecosystem services (Castro et al. 2015), organizations that acquire and manage protected areas may be interested in anticipating the current invadedness (proportion invasive cover, Iacona et al. 2014) of parcels being considered for protection. These predictions can help organizations with limited resources avoid acquiring properties susceptible to invasion when all else is equal, or budget to survey or manage invasive plants on acquired properties (Keller et al. 2007).

Transport and introduction of plant propagules is necessary for invasion, and increasing propagule pressure is an important factor in invasion success (Lockwood et al. 2005; Simberloff 2009; Eschtruth and Battles 2009). Roads and streams or rivers (hereafter just streams) are two major sources of transport and introduction for invasive plant propagules in protected areas (DeFerrari and Naiman 1994; Richardson et al. 2007; Mortensen et al. 2009; Christen and Matlack 2009). Streams are corridors for invasive plant propagules, and propagule pressure often increases with increased stream or river discharge (Brown and Peet 2003; Aronson et al. 2017; Nilsson et al. 2010). Stream flooding also causes conditions, such as exposed soil and increased nutrient availability, that may favor the establishment of invasive plants (Hood and Naiman 2000; Richardson et al. 2007). Streams experience many types of recreational activities, including fishing and boat launching, that impact adjacent ecosystems via

shoreline disturbance (Cole and Marion 1988) and introduce invasive plant propagules (Eiswerth et al. 2000; Rothlisberger et al. 2010).

Roads also increase invasive plant propagule pressure through vehicle traffic (Barlow et al. 2017; Taylor et al. 2012; von der Lippe and Kowarik 2007) and human activities along roads such as home building and maintenance (Gavier-Pizarro et al. 2010). Road construction, such as grading and mowing, moves invasive plant propagules and causes disturbance that favors the establishment of invasive plants (Parendes and Jones 2000; Rauschert et al. 2017). Roadside soils experience changes in soil chemistry that favor some invasive plants due to gasoline (Trombulak and Frissell 2000), deicing salts (Skultety and Matthews 2017), vehicle exhaust (Forman and Alexander 1998), and road construction materials (Greenberg et al. 1997).

Road type may also be an important factor in predicting invadedness of a protected area. Typically, areas surrounding paved roads are more invaded than areas surrounding unpaved roads (Gelbard and Belnap 2003; Joly et al. 2011). This relationship has been attributed to factors including changes to soil composition and chemistry by road construction materials (Greenberg et al. 1997) and increased traffic and disturbance (Mortensen et al. 2009; Parendes and Jones 2000). High-use roads (e.g., primary and secondary roads) experience more disturbance than low-use roads [e.g., local and four-wheel drive (4WD) roads] due to vehicle traffic and road maintenance activities and are therefore commonly more invaded (Parendes and Jones 2000). Despite that low-use roads, such as 4WD roads, are frequently found to be less invaded than high-use roads, occurrence of off-road vehicles has been positively associated with invasive plants in some studies (Assaeed et al. 2018; Miller and Matlack 2010). Vehicles driving over plants on unpaved 4WD roads may pick up propagules and disperse them (Veldman and Putz 2010). Vehicles can also disperse plant propagules via mud attached to vehicles, and the unpaved and unmaintained nature of 4WD roads provides substantial opportunities for off-road vehicles to pick up mud and propagules (Zwaenepoel et al. 2006; Rew et al. 2018).

We compare roads and streams as predictors of invadedness of eastern United States (U.S.) forested protected areas using a survey of invasive plants in parcels acquired by The Nature Conservancy (TNC),

the world's largest biodiversity conservation non-profit organization (Armsworth et al. 2012). Since road type may have an effect on invadedness (Gelbard and Belnap 2003; Joly et al. 2011), we also compared road types as predictors of invadedness using density of each road type. We provide, to our knowledge, the first study that has specifically contrasted the role of roads or streams to each other in explaining protected area invadedness. There are various stages of invasion that we could have focused on (e.g., initial establishment or rate of spread), and drivers can differ in importance at different stages. However, here we focused on invadedness (proportion cover), one relevant indicator that has implications for the costs of managing protected areas and ecological benefits protected areas may offer. Determining factors that influence plant invasions will help organizations identify priority areas to focus monitoring and prevention (e.g., roadsides if roads are a significant predictor of invadedness). The ability to predict invadedness may also guide acquisition decisions by allowing conservation organizations to avoid or properly budget for parcels that are likely to be heavily invaded. We test here whether roads or streams can serve as simple landscape-scale predictors of likelihood of plant invasions in protected areas to guide such acquisition, budgeting, and management decisions.

Methods

Study sites

Our study focuses on 27 protected area parcels in the Appalachian Mountains, U.S. (Fig. 1; see Appendices S1 and S2 for site characteristics). The parcels were acquired by TNC between 2000 and 2009 with the goal of protecting forested ecosystems (Armsworth et al. 2018). Some parcels remain under ownership and management of TNC, and others have been transferred to state or federal agencies as wildlife management areas, state parks, or national forest land. Parcel size ranged from a minimum of 10 ha to a maximum of 900 ha with a mean parcel size of 189.2 ha. Minimum and maximum parcel size have been rounded to the nearest ten for confidentiality. Average elevation of the parcels ranged between 181.2 and 1454.4 m. The parcels occur within three TNC-designated ecoregions

(Southern Blue Ridge, Cumberlands and Southern Ridge and Valley, and Central Appalachian Forest) and 10 U.S. states (Fig. 1). TNC acquired all study parcels individually. However, some of these parcels are adjacent to each other, and are managed as a single protected area since TNC acquisition (Armsworth et al. 2018). TNC provides a valuable case study for anticipating invadedness of protected areas because land trusts, including TNC, are highly active in expanding the network of protected areas in the U.S. (Fishburn et al. 2013). We chose to conduct our analyses at the parcel rather than plot scale because these are the units of acquisition by TNC or similar organizations (i.e., land trusts), and our overall goal is to predict invadedness to guide planning and budgeting for both acquisition and management with respect to invasive plants.

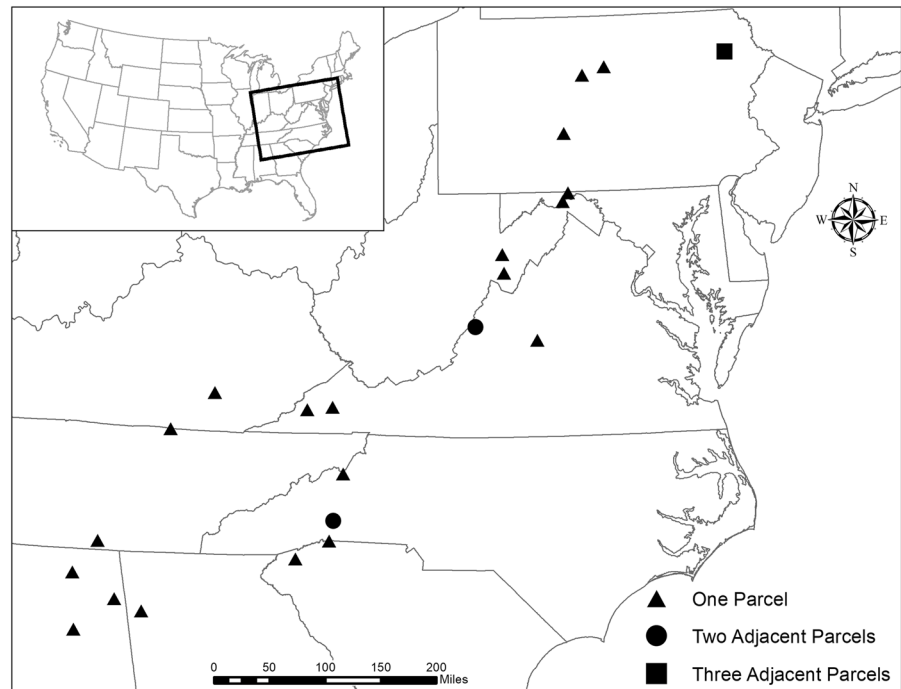
Invasive species data

We collected invasive species between May 30, 2013 and September 24, 2013. We recorded only species listed as highest concern by exotic pest plant councils of the states in which we sampled (Table 1). We established 20 random plots in each parcel: 10 in the parcel edge (within 100 m of property boundary) and 10 in the parcel core. Random points were at least 30 m away from each other. The percent cover within bins (0–5%, 5–25%, 25–50%, 50–75%, 75–95%, 95–100%) was recorded for each non-native invasive plant within a 5 m radius of each plot center. To determine invasive cover of the entire parcel, we calculated the midpoint of cover range for each species at each plot, added the midpoints of all species in each plot, and then averaged the plot sums for all plots in a parcel. For example, in a plot containing species A (0–5%) and species B (50–75%), that plot would be given a percent cover of 65% (2.5% species A + 62.5% species B). This plot would then be averaged with the other 19 plots within its parcel for a total average percent cover for the entire parcel.

Predictors of invadedness

We calculated road and stream variables and five natural and anthropogenic covariates to use in models to predict protected area invadedness (Table 2; see Appendix S1 for summary statistics of model variables). We used upstream length from the most

Fig. 1 Locations of the 27 TNC parcel used to explain forest plant invadedness by streams and roads. The labels of “Two Adjacent Parcels” and “Three Adjacent Parcels” indicate separate parcels that are visible only as one point at the map scale because of geographical proximity



downstream point within a parcel as the stream variable for our model since longer upstream networks are likely to encounter and transport more invasive plant propagules (Nilsson et al. 2010). We used road density within a buffer of the parcel as the road variable since road density accounts for roads standardized by parcel size and is a commonly used metric in invasive plant studies (Barlow et al. 2017; Gavier-Pizarro et al. 2010; Dark 2004).

We acquired stream data from the National Hydrography Dataset (U.S. Geological Survey 2005). We used ArcGIS Utility Network Analyst (Esri 2017) tool to determine upstream length from the downstream-most intersection of streams and parcel boundaries. If a parcel had no streams intersecting the parcel but a stream was on the same elevation as part of the parcel, the downstream-most point was placed on that stream because we assume flood events will carry propagules to the floodplain surrounding the stream. This occurred for one parcel. If no streams intersected a parcel and nearby streams were at a lower elevation, the parcel was given an upstream length of 0.

We used U.S. Census Bureau TIGER roads data for roads analyses (U.S. Census Bureau 2016a). Hawbaker and Radeloff (2004) demonstrated that TIGER

roads data is frequently incomplete. However, TIGER data have the benefit of consistency across the U.S., whereas data from local states, counties, and municipalities are likely to vary in terms of resolution and availability. For each parcel, we calculated road density within multiple buffer distances of the parcel boundary, including roads that lie within the parcel. Road density was calculated as meters of road per buffer area. Forman and Alexander (1998) estimate that the road-effect zone for invasive species is anywhere from 200 to 1000 m when the road is surrounded by less suitable habitat than the roadside itself (e.g. closed canopy forest), so buffer distances were spread around that range at 100 m, 500 m, 1000 m, 1500 m, and 2000 m (but see Riitters et al. 2017 for additional discussion on road buffer distances). We evaluated sensitivity of our model to each buffer distance using information theoretic model competition with AICc (Burnham and Anderson 2002). We selected a 100 m buffer since it had the lowest AICc (all other buffer distance models $\Delta AICc > 0.228$).

For our analysis of road type and parcel invadedness, we used four road categories from TIGER: local, 4WD, secondary, and primary. TIGER generally defines a local road as a paved, non-arterial road with

Table 1 List of all invasive plant species detected at 27 Appalachian protected areas. Each parcel contained 20 plots. We sampled only invasive species listed as high concern by state management agencies in our study region

Species	Plots	Parcels
<i>Ailanthus altissima</i>	9	6
<i>Albizia julibrissin</i>	1	1
<i>Alliaria petiolata</i>	5	3
<i>Berberis thunbergii</i>	16	4
<i>Carduus nutans</i>	1	1
<i>Commelina communis</i>	8	2
<i>Coronilla varia</i>	3	3
<i>Euonymus alata</i>	6	4
<i>Euonymus fortunei</i>	1	1
<i>Polygonum cuspidatum</i>	3	3
<i>Hypericum perforatum</i>	1	1
<i>Ligustrum sinense</i>	17	3
<i>Lonicera japonica</i>	36	7
<i>Lonicera maackii</i>	15	3
<i>Microstegium vimineum</i>	61	14
<i>Paulownia tomentosa</i>	4	3
<i>Polygonum cespitosum</i> Blume var. <i>longisetum</i>	4	1
<i>Polygonum cespitosum</i>	6	4
<i>Polygonum perfoliatum</i>	10	4
<i>Poncirus trifoliata</i>	11	1
<i>Duchesnea indica</i>	8	6
<i>Robinia pseudoacacia</i>	11	1
<i>Rosa multiflora</i>	54	13
<i>Rubus phoenicolasius</i>	4	2
<i>Securigera varia</i>	1	1
<i>Sorghum halepense</i>	4	1
<i>Trifolium pratense</i>	1	1
<i>Dioscorea oppositifolia</i>	1	1

one lane of traffic in each direction (U.S. Census Bureau 2016c). A 4WD road is an unpaved road that is unpassable by typical cars and trucks and requires a 4WD vehicle (U.S. Census Bureau 2016c). Primary and secondary roads are both highways. However, primary roads are divided highways that are typically in the Interstate Highway system, distinguished by having interchanges and no intersections (U.S. Census Bureau 2016c). Secondary roads, on the other hand, are in a U.S. Highway, State Highway, or County Highway system. They may be divided, must have one or more lane in each direction, and usually have intersections with other roads (U.S. Census Bureau 2016c). For each road type, we calculated density within a 100 m buffer, the same buffer distance used for general road models.

We selected model covariates that have a demonstrated relationship with forest plant invasions: distance to an urban area, average canopy cover, average slope, edge-to-interior ratio, percent agricultural land in a buffer, and percent developed land in a buffer. Invadedness frequently increases with proximity to urban areas due to human activities that increase nutrient availability and act as propagule vectors (Skultety and Matthews 2017; León Cordero et al. 2016). Distance to nearest urban area was calculated between parcel centroids and the nearest urban area edge (U.S. Census Bureau 2016b). Decreasing canopy cover increases light availability, which increases resources for plants (Hutchinson and Vankat 1997; Kuhman et al. 2010). We calculated average canopy cover with National Land Cover Database (NLCD)

Table 2 Variables and covariates used in multiple linear regression model and their relationships with parcel invadedness

Variable	Unit	Prediction	Source
Upstream length	m	Positive relationship; longer upstream networks encounter more invasive plant propagule sources	Nilsson et al. (2010)
Road density in a 100 m buffer	m/ha	Positive relationship; roads are corridors for invasive plant propagules, road density standardizes the metric by parcel size	Barlow et al. (2017), Gavier-Pizarro et al. (2010), Dark (2004)
Distance to census-defined urban area	m	Positive relationship; anthropogenic activities increase resource availability and transport vectors	Skultety and Matthews (2017), León Cordero et al. (2016)
Canopy cover	Percent (0–100)	Negative relationship; greater canopy cover decreases light availability for plants	Hutchinson and Vankat (1997), Kuhman et al. (2010)
Slope	Degrees	Negative relationship; microclimatic changes occur with increasing slope	Lemke et al. (2011)
Edge-to-interior ratio	m:ha ratio	Positive relationship; higher edge to interior ratio provides increased points of entry for plant propagules and smaller distance to interior	Yates et al. (2004)
Percent agricultural land in a 500 m buffer	Percent (0–100)	Positive relationship; agriculture increases propagule pressure and disturbances	Moustakas et al. (2018)
Percent developed land in a 500 m buffer	Percent (0–100)	Positive relationship; human development increases propagule pressure and disturbances	Riitters et al. (2017)

2011 data (Homer et al. 2015). The NLCD 2011 Tree Canopy raster contains 30 m cells, where each cell has a value from 0 to 100, which represents percent tree canopy cover of that cell. For each parcel, we averaged all raster cells within the parcel boundary to calculate average canopy cover of the parcel. Invasive plants occur less frequently on steeper slopes due to microclimatic changes as slope increases, such as decreasing soil moisture (Lemke et al. 2011). We calculated average parcel slope with USGS 1/3 arc second digital elevation models (U.S. Geological Survey 2017). We calculated edge-to-interior ratio for each of our protected areas because invadedness may increase as the ratio increases because a larger edge to interior ratio provides more points of entry for invasive plants and a smaller distance to penetrate the interior of a parcel (Yates et al. 2004). Increased developed or agricultural land within a buffer of a protected area may increase parcel invadedness due to increased propagule sources and disturbance (Riitters et al. 2017; Moustakas et al. 2018). Similar to the road density calculation, we calculated percent developed and agricultural land within 100 m, 500 m, 1000 m, 1500 m, and 2000 m of a parcel edge and selected 500 m, the buffer with the lowest AICc, for both land

cover types (all other buffer distance models $\Delta\text{AICc} > 3.023$). We did not consider interactions between covariates because with a relatively small sample size, we felt that adding more variables would risk overfitting our model. We are instead seeking to prioritize parsimony consistent with the information theoretic framework of Burnham and Anderson (2002).

Statistical analyses

We transformed the following variables with plus one natural log in order to accommodate zero values: our response variable (invasive cover), our predictor variables (road density and upstream length), and one covariate (percent agriculture). We used multiple linear regression in R 3.3.3 (R Core Team 2017) to compare the effects of road density and upstream length on invasive plant abundance. We built five models: (1) all covariates and roads, (2) all covariates and streams, (3) all covariates with roads and streams (roads + streams), (4) all covariates with an interaction of roads and streams (roads \times streams), and (5) just covariates. We included the model with an interaction term between roads and streams because

we anticipated parcels with large upstream networks and small adjacent road densities or large adjacent road densities and small upstream networks could differ in their exposure to invasive plant propagules or disturbances that facilitate establishment and spread. We evaluated which was the best performing model using AICc (Barton 2018; Burnham and Anderson 2002). We calculated variance inflation factor (VIF) in R for our most supported model to assess model variables for multicollinearity (Dormann et al. 2012). We used Moran's I to evaluate if our results were affected by spatial autocorrelation between sites (Paradis et al. 2004). This step is especially pertinent because there are some parcels that are adjacent to each other but are considered separate parcels because they were acquired separately by TNC (Fig. 1; Armsworth et al. 2018).

For our road type analyses, we repeated the same statistical analyses with four road type models (local, 4WD, primary, and secondary), along with a covariates only model. We used the same covariates in these models and again transformed the following variables with plus one natural log: the response variable (invasive cover), the predictor variables (road density of all road types), and one covariate (percent agriculture).

Results

Invasive species data

Invasive species were present at 158 of the 540 plots and 20 of the 27 parcels we sampled (Table 1). We recorded a total of 28 invasive species across all parcels visited. The five most common invasive species were *Microstegium vimineum* (61 plots at 14 parcels), *Rosa multiflora* (54 plots at 13 parcels), *Lonicera japonica* (36 plots at 7 parcels), *Ligustrum sinense* (17 plots at 3 parcels), and *Berberis thunbergii* (16 plots at 4 parcels). Half of the species were found in less than five plots.

Road and stream models

Out of the five candidate models, model competition with AICc identified the covariates-only model ($R^2 = 0.271$) as the most supported model (Table 3). This result was insensitive to road buffer distance

used. Percent agriculture within a 500 m buffer was the only predictor among the covariates that was marginally significant ($p = 0.073$; Table 4). Percent agriculture was positively related to parcel invadedness (Fig. 2). We determined that no covariates were too highly correlated for inclusion in this multiple regression analysis ($VIF < 2.249$). The next best performing models were the streams and covariates model ($\Delta AICc = 2.141$, $R^2 = 0.299$) and roads and covariates model ($\Delta AICc = 2.572$, $R^2 = 0.288$; Table 3). We found no evidence of spatial autocorrelation per Moran's I on model residuals from our most supported model ($p = 0.630$).

Road type models

We found that the 4WD roads model had the lowest AICc (Table 5), the covariates-only model had $\Delta AICc > 2$, and the other three road type models had $\Delta AICc > 6$. The 4WD roads model also had the highest R^2 , at 0.405, of the models in our AICc model competition, with the next highest R^2 of all models being 0.271 (Table 5). In the 4WD model, significant predictors were 4WD road density ($p = 0.030$) and edge-to-interior ratio ($p = 0.017$; Table 6). Our model showed a positive relationship between parcel invasive cover and both 4WD road density and edge-to-interior ratio (Fig. 3). We determined that no covariates were too highly correlated for inclusion in this most-supported model ($VIF < 2.281$). Using Moran's I with model residuals, we found no evidence of spatial autocorrelation in the 4WD model ($p = 0.711$).

Discussion

We did not find general streams or roads to be good predictors of invadedness of forest protected areas by invasive plants. Although many other studies have demonstrated a strong positive relationship between both roads and streams and invadedness (Parendes and Jones 2000; Gelbard and Belnap 2003; Richardson et al. 2007), there are many possible explanations for why our overall road and stream variables were poorly supported. Alternatively, we did find a relatively strong positive relationship between density of 4WD roads in and adjacent to our protected areas and plant invasion. This relationship between 4WD roads and parcel invadedness is somewhat surprising because

Table 3 Comparison of candidate models for predicting invadedness of Appalachian protected areas using ΔAICc , AICc weights, R^2 , and variance inflation factor (VIF)

Model	ΔAICc	AIC Weight	R^2	Max VIF
Covariates	0	0.604	0.271	2.249
Streams and covariates	2.141	0.207	0.299	2.562
Roads and covariates	2.572	0.167	0.288	2.422
Roads, streams, and covariates	6.747	0.021	0.275	2.440
Interaction of roads and streams, and covariates	11.628	0.002	0.259	8.698 ^a

The Max VIF value in the table is the highest VIF of all variables in a model. Road variable is road density within a 100 m buffer. Stream variable is upstream length from most downstream point in a parcel. Covariates include distance to an urban area, average parcel slope, edge-to-interior ratio, average canopy cover, percent agricultural land within a 500 m buffer, and percent developed land within a 500 m buffer (Table 4)

^aThis high VIF is due to correlation between the interaction term (roads \times streams) and its parts (roads and streams). In the interaction model, the next highest VIF outside of this interaction is 2.510

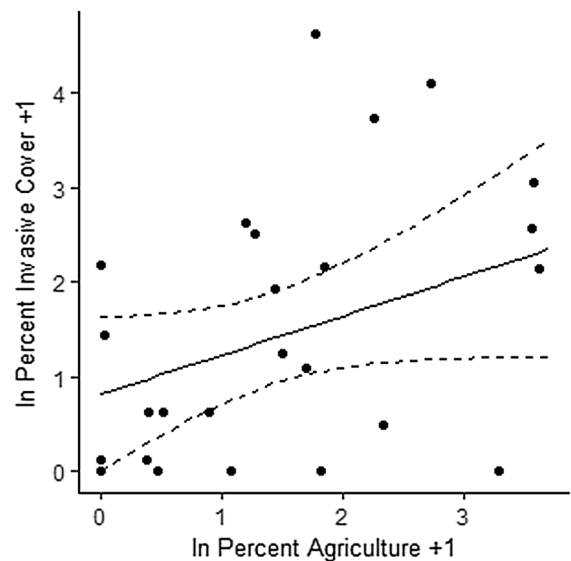
Table 4 Regression table for best model identified by ΔAICc (Table 3)

Variable	Coefficient	p
Distance to urban area	< 0.001 (< 0.001)	0.388
Average slope	0.001 (0.049)	0.979
Edge-to-interior ratio	0.011 (0.007)	0.119
Average canopy cover	0.005 (0.025)	0.839
% agricultural land in buffer	0.414 (0.218)	0.073
% developed land in buffer	0.094 (0.083)	0.268

This model includes only covariates. Numbers in parenthesis indicate standard error

other studies have found unpaved roads to be a less reliable predictor of invadedness than more major paved roads (León Cordero et al. 2016; Gelbard and Belnap 2003), but we believe that this relationship may be due to factors including recreation in and around parcels and the unmaintained nature of 4WD roads.

Streams increase invadedness by increasing propagule pressure to, and disturbance of, natural areas (Hood and Naiman 2000; Parendes and Jones 2000). Streams may have failed to predict protected area invadedness in our study for a variety of reasons. Other studies have noted that although many invasive plants are dispersed along streams, these plants often fail to invade areas surrounding streams and often are constrained to the riparian corridor (Thébaud and Debussche 1991; DeFerrari and Naiman 1994). Von Holle and Simberloff (2005) found that the physical

**Fig. 2** Model-predicted relationship with 95% confidence interval between percent agricultural land and percent invasive cover in covariates model (Tables 3, 4). Percent agriculture and percent invasive cover are plus one natural log transformed to accommodate zero values. The covariates-only model has a relatively low R^2 of 0.271, meaning that percent agriculture may be a weak predictor of percent invasive cover

disturbance of stream flooding had little effect on invasive plant establishment success within our study region, particularly in comparison to propagule pressure. Additionally, the upstream watershed that a stream has flowed through affects the amount of propagules it may carry. A stream that flows through a developed area or highly invaded forest has more opportunity for downstream introduction of invasive

Table 5 Comparison of all candidate road type regression models using Δ AICc, AICc weights, R^2 , and variance inflation factor (VIF)

Model	Δ AICc	AIC Weight	R^2	Max VIF
4WD	0	0.699	0.405	2.281
Covariates only	2.263	0.226	0.271	2.249
Primary	6.547	0.026	0.241	2.300
Local	6.684	0.025	0.235	2.314
Secondary	6.759	0.024	0.237	2.627

The Max VIF value in the table is the highest VIF of all variables in a model. Road density was calculated within a 100 m buffer. Covariates include distance to an urban area, average parcel slope, edge-to-interior ratio, average canopy cover, percent agricultural land within a 500 m buffer, and percent developed land within a 500 m buffer

Table 6 Regression table for most supported road type model identified by AIC

Variable	Coefficient	<i>p</i>
4WD road density	0.570 (0.243)	0.030*
Distance to urban area	< 0.001 (< 0.001)	0.555
Average slope	- 0.014 (0.044)	0.762
Average canopy cover	0.008 (0.023)	0.717
Edge-to-interior ratio	0.017 (0.006)	0.017*
% agricultural land in buffer	0.268 (0.207)	0.211
% developed land in buffer	0.082 (0.075)	0.287

Numbers in parenthesis indicate standard error

*Indicates significance of predictors or covariates at $p < 0.05$

plant propagules than a stream flowing through a relatively uninvaded forest (Richardson et al. 2007). Although our study areas and their upstream watersheds are relatively undeveloped and mostly forested, it is unknown how invaded forests upstream of our protected areas are. This type of information is difficult to integrate into an analysis of our scope because much of the necessary data (e.g., private land invasive plant data) is not readily available, although future work might consider the role of upstream watershed land cover in stream effects on protected area invadedness.

Many of the studies on roads and invadedness focus on the relationship between invadedness and distance from a road (Flory and Clay 2009; Christen and Matlack 2009) since invasive species typically have a

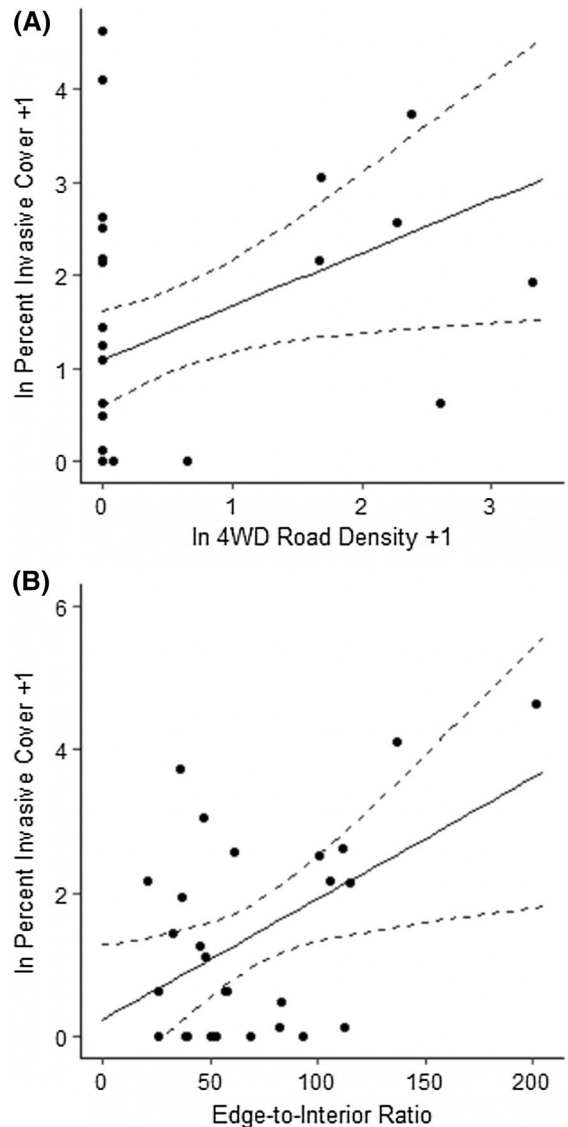


Fig. 3 Model-predicted relationships with 95% confidence intervals between 4WD road density and percent invasive cover (a), and edge-to-interior ratio and percent invasive cover (b), in 4WD roads model (Table 6). 4WD road density and percent invasive cover are plus one natural log transformed to accommodate zero values

higher abundance closer to roads (Watkins et al. 2003; Cadenasso and Pickett 2001). Road density within a buffer of parcels, our road variable choice, should capture this relationship, but it's possible that it did not. Additionally, Riitters et al. (2017) found that road effects are confounded with anthropogenic activity and suggests that road effect zones in eastern U.S. forests can extend more than 5000 m from a road edge,

farther than our largest tested road buffer of 2000 m. These results of Riitters et al. (2017) provide additional possible cause for the weakness of our roads variable as a predictor of invadedness. Although overall road density was a poor predictor of parcel invadedness, we did find a relatively strong relationship between density of 4WD roads and invadedness of our study sites.

We propose three potential reasons for the significance of 4WD roads as a predictor of parcel invadedness. In these protected areas, density of 4WD roads may serve as a proxy for recreation. Many of the protected areas with high 4WD road density in a 100 m buffer have a high prevalence of recreation at or around the parcel (personal observation). Recreation and tourism are associated with invasive plant propagule spread via visitors' vehicles, clothing, and pack animals (Lonsdale and Lane 1994; Pickering et al. 2010) and with disturbance that favors invasive plant establishment (Assaeed et al. 2018). Second, vehicles accumulate plant materials and mud containing plant propagules while traveling on 4WD roads, which may have vegetation growing in the road in addition to in the road verges (Veldman and Putz 2010; Zwaenepoel et al. 2006). Taylor et al. (2012) found that seeds on vehicles were retained for longer distances on unpaved roads than paved roads, indicating that off-road vehicles traveling on unpaved roads may be able to disperse invasive plants relatively large distances. Lastly, the unmaintained nature of 4WD roads could increase invadedness by preventing treatment of existing invasive plant communities (e.g., roadside herbicide spraying by municipalities or departments of transportation; Kohlhepp et al. 1995; Williams and Henderson 2002). 4WD road density as a predictive indicator of parcel invadedness merits further study, as it may guide better parcel acquisition decisions or budgeting to manage for invasive plants.

Several of the covariates we included while comparing the role of roads and streams on parcel invadedness were related to invadedness in our models. We found a marginally significant positive relationship between percent agriculture and invadedness in the covariates-only model in comparison to our general roads and streams models, but the relatively low R^2 (0.271) signifies a low predictive power for this model. Presence of agriculture near a protected area can increase invadedness due to increased propagule pressure and disturbance (Riitters et al. 2017;

Moustakas et al. 2018). The well-supported positive relationship that we found between edge-to-interior ratio and parcel invadedness in the 4WD roads model has been demonstrated in other studies (Yates et al. 2004; Cadenasso and Pickett 2001). As edge length increases relative to the interior area of a parcel, invasive plant propagules have increased points of entry and a shorter distance to travel to the interior of a parcel (Yates et al. 2004). Although these factors were not the primary focus of our study, they may provide additional guidance for conservation organizations looking to predict protected area invadedness.

Our analyses were designed around the question: can conservation organizations, such as TNC, predict and financially plan for the invadedness of a parcel before acquisition based on roads and streams? We specifically chose to contrast roads and streams as landscape-scale predictors of plant invasions because both deliver plant propagules to protected areas that can lead to invasions, and can disturb sites in ways that may influence establishment success and spread. This question could have been addressed at the individual sample plot rather than the overall parcel scale, but we anticipated that parcel scale is likely more relevant for management decisions when choosing to acquire or budgeting to manage land. Another alternative to our analyses would have been to consider individual invasive species as responses, rather than combined as a metric of overall invadedness. We considered species-specific analyses similar to our other regression analyses, but the concept is more narrow than our overall goal of predicting protected area invadedness for land acquisition and management, and preliminary analyses suggested that a species-specific focus would not overturn our results. Similarly, species traits can be an important factor in predictive invasion patterns (Iannone et al. 2016), and future studies might include species traits that account for dispersal mechanism or growth form. We also performed a sensitivity test to evaluate the effect on our model of treating adjacent parcels as single protected areas, but this did not significantly change the results of our analysis.

Past land management practices also play an important role in predicting the invadedness of forested areas (Von Holle and Motzkin 2007). Prior to acquisition by TNC, land use of these parcels ranged from unmanaged forest to managed recreation areas, but unfortunately fine resolution management data, specifically on invasive plant management, prior

to TNC acquisition was unavailable for most of the protected areas in our study. Differences in past or current management could be responsible for some of our unexplained variance around invadedness of these protected areas. It is also important to note that social variables, such as human population size, are important predictors of exotic species richness (Guo et al. 2012). We had only one social variable, distance to an urban area, in our models, and our models could be improved with the inclusion of more social variables. It is possible that parcels are at different stages in the invasion process, but we assume similar exposure to invasion risk given the history of management of and high rate of invasion of eastern U.S. forests, especially in Appalachia (Oswalt and Smith 2014; Oswalt et al. 2015). We did, however, attempt to control for this by including model variables distance to an urban area and percent agricultural land.

Because overall roads and streams were poor predictors of protected area invadedness, neither can be recommended as a predictive rule of thumb for conservation organizations looking to anticipate the invadedness of a protected area for acquisition and management planning. However, 4WD road density and edge-to-interior ratio were relatively good predictors of invasion in our models. Organizations wanting to avoid acquisition of parcels with a high invasion potential or seeking to accurately plan for management costs of newly acquired parcels should consider these factors in the decision-making process (Keller et al. 2007; Iacona et al. 2016). We hypothesize that the relationship between 4WD road density and protected area invadedness may be due to recreation access or lack of roadside management, but this could benefit from further study. Although our findings would benefit from future investigation, they may serve as immediate guidance to organizations that are concerned about invasive plants during the acquisition and management of protected areas, particularly in eastern U.S. deciduous forests. To conserve the abundant benefits of protected areas, it is necessary to address the presence of invasive plants, a major threat to these benefits (Castro et al. 2015; Soares-Filho et al. 2010; Pejchar and Mooney 2009). Invasive species are a costly part of protected area management (Iacona et al. 2014), so to make well-informed and effective management and acquisition decisions, conservation organizations must identify these invasive plant

populations quickly and efficiently (Simberloff et al. 2013; Lodge et al. 2016).

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References

- Armstrong PR, Fishburn IS, Davies ZG, Gilbert J, Leaver N, Gaston KJ (2012) The size, concentration, and growth of biodiversity-conservation nonprofits. *Bioscience* 62:271–281. <https://doi.org/10.1525/bio.2012.62.3.8>
- Armstrong PR, Jackson HB, Cho S, Clark M, Fargione JE, Iacona GD, Kim T, Larson ER, Minney T, Sutton NA (2018) Is conservation right to go big? Protected area size and conservation return-on-investment. *Biol Conserv* 225:229–236. <https://doi.org/10.1016/j.biocon.2018.07.005>
- Aronson MFJ, Patel MV, O'Neill KM, Ehrenfeld JG (2017) Urban riparian systems function as corridors for both native and invasive plant species. *Biol Invasions* 19:3645–3657. <https://doi.org/10.1007/s10530-017-1583-1>
- Assaeed AM, Al-Rowaily SL, El-Bana MI, Abood AAA, Dar BAM, Hegazy AK (2018) Impact of off-road vehicles on soil and vegetation in a desert rangeland in Saudi Arabia. *Saudi J Biol Sci* <https://doi.org/10.1016/j.sjbs.2018.05.001> (in press)
- Barlow KM, Mortensen DA, Drohan PJ, Averill KM (2017) Unconventional gas development facilitates plant invasions. *J Environ Manag* 202:208–216. <https://doi.org/10.1016/j.jenvman.2017.07.005>
- Barton K (2018) MuMIn: multi-model inference. R package version 1.40.4. <https://CRAN.R-project.org/package=MuMIn>. Accessed 12 Feb 2018
- Brooks ML, D'Antonio CM, Richardson DM, Grace JB, Keeley JE, DiTomaso JM, Hobbs RJ, Pellant M, Pyke D (2004) Effects of invasive alien plants on fire regimes. *Bioscience* 54:677–688. [https://doi.org/10.1641/0006-3568\(2004\)054%5b0677:EOIAP0%5d2.0.CO;2](https://doi.org/10.1641/0006-3568(2004)054%5b0677:EOIAP0%5d2.0.CO;2)
- Brown RL, Peet RK (2003) Diversity and invasibility of Southern Appalachian plant communities. *Ecology* 84:32–39. [https://doi.org/10.1890/0012-9658\(2003\)084%5b0032:DAIOSA%5d2.0.CO;2](https://doi.org/10.1890/0012-9658(2003)084%5b0032:DAIOSA%5d2.0.CO;2)
- Burnham KP, Anderson DR (2002) Model selection and multimodal inference. Springer, New York. <https://doi.org/10.1007/b97636>
- Cadenasso ML, Pickett STA (2001) Effect of edge structure on the flux of species into forest interiors. *Conserv Biol* 15:91–97. <https://doi.org/10.1111/j.1523-1739.2001.99309.x>
- Castro AJ, Martín-Lopez B, Lopez E, Plieninger T, Alcaraz-Segura D, Vaughn CC, Cabello J (2015) Do protected areas

- networks ensure the supply of ecosystem services? Spatial patterns of two nature reserve systems in semi-arid Spain. *Appl Geogr* 60:1–9. <https://doi.org/10.1016/j.apgeog.2015.02.012>
- Christen DC, Matlack GR (2009) The habitat and conduit functions of roads in the spread of three invasive plant species. *Biol Invasions* 11:453–465. <https://doi.org/10.1007/s10530-008-9262-x>
- Cole DN, Marion JL (1988) Recreation impacts in some riparian forests of the Eastern United States. *Environ Manag* 12:99–107. <https://doi.org/10.1007/BF01867381>
- Dark SJ (2004) The biogeography of invasive alien plants in California: an application of GIS and spatial regression analysis. *Divers Distrib* 10:1–9. <https://doi.org/10.1111/j.1472-4642.2004.00054.x>
- DeFerrari CM, Naiman RJ (1994) A multi-scale assessment of the occurrence of exotic plants on the Olympic Peninsula, Washington. *J Veg Sci* 5:247–258. <https://doi.org/10.2307/3236157>
- Dormann CF, Elith J, Bacher S, Buchmann C, Carl C, Carré G, García Marquéz JR, Gruber B, Lafourcade B, Leitão PJ, Münkemüller T, McClean C, Osborne PR, Reineking B, Schröder B, Skidmore AK, Zurell S, Lautenbach S (2012) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* 26:27–46. <https://doi.org/10.1111/j.1600-0587.2012.07348.x>
- Eiswerth ME, Donaldson SG, Johnson WS (2000) Potential environmental impacts and economic damages of Eurasian watermilfoil (*Myriophyllum spicatum*) in Western Nevada and Northeastern California. *Weed Technol* 14:511–518. [https://doi.org/10.1614/0890-037X\(2000\)014%5b0511:PEIAED%5d2.0.CO;2](https://doi.org/10.1614/0890-037X(2000)014%5b0511:PEIAED%5d2.0.CO;2)
- Eschstruth AK, Battles JJ (2009) Assessing the relative importance of disturbance, herbivory, diversity, and propagule pressure in exotic plant invasion. *Ecol Monogr* 79:265–280. <https://doi.org/10.1890/08-0221.1>
- Esri (2017) ArcGIS Version 10.5. Environmental Systems Research Institute, Inc., Redlands, CA
- Fishburn IS, Boyer AG, Kareiva P, Gaston KJ, Armsworth PR (2013) Changing spatial patterns of conservation investment by a major land trust. *Biol Conserv* 161:223–229. <https://doi.org/10.1016/j.biocon.2013.02.007>
- Flory SL, Clay K (2009) Effects of roads and forest successional age on experimental plant invasions. *Biol Conserv* 142:2531–2537. <https://doi.org/10.1016/j.biocon.2009.05.024>
- Forman RTT, Alexander LE (1998) Roads and their major ecological effects. *Annu Rev Ecol Syst* 29:207–231. <https://doi.org/10.1146/annurev.ecolsys.29.1.207>
- Gavier-Pizarro GI, Radeloff VC, Stewart SI, Huebner CD, Keuler NS (2010) Housing is positively associated with invasive exotic plant species richness in New England, USA. *Ecol Appl* 20:1913–1925. <https://doi.org/10.1890/09-2168.1>
- Gelbard JL, Belnap J (2003) Roads as conduits for exotic plant invasions in a semiarid landscape. *Conserv Biol* 17:420–432. <https://doi.org/10.1046/j.1523-1739.2003.01408.x>
- Greenberg CH, Crownover SH, Gordon DR (1997) Roadside soils: a corridor for invasion of xeric shrub by nonindigenous plants. *Nat Areas J* 17:99–109
- Greene MT, Blossey B (2012) Lost in the weeds: *Ligustrum sinense* reduces native plant growth and survival. *Biol Invasions* 14:139–150. <https://doi.org/10.1007/s10530-011-9990-1>
- 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>
- Hawbaker TJ, Radeloff VC (2004) Roads and landscape pattern in Northern Wisconsin based on a comparison of four road data sources. *Conserv Biol* 18:1233–1244. <https://doi.org/10.1007/s10530-011-9990-1>
- Homer CG, Dewitz JA, Yang L, Jin S, Danielson P, Xian G, Coulston J, Herold ND, Wickham JD, Megown K (2015) Completion of the 2011 National Land Cover Database for the conterminous United States—Representing a decade of land cover change information. *Photogramm Eng Remote Sens* 81:345–354
- Hood WG, Naiman RJ (2000) Vulnerability of riparian zones to invasion by exotic vascular plants. *Plant Ecol* 148:105–114. <https://doi.org/10.1023/A:1009800327334>
- Hutchinson TF, Vankat JL (1997) Invasibility and effects of amur honeysuckle in Southwestern Ohio forests. *Conserv Biol* 11:1117–1124. <https://doi.org/10.1046/j.1523-1739.1997.96001.x>
- Iacona GD, Price FD, Armsworth PR (2014) Predicting the invadedness of protected areas. *Divers Distrib* 20:430–439. <https://doi.org/10.1111/ddi.12171>
- Iacona GD, Price FD, Armsworth PR (2016) Predicting the presence and cover of management relevant invasive plant species on protected areas. *J Environ Manag* 166:537–543. <https://doi.org/10.1016/j.jenvman.2015.10.052>
- Iannone BV, Potter KM, Guo Q, Liebhold AM, Pijanowski BC, Oswalt CM, 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.01973>
- Joly M, Bertrand P, Gbangou RY, White M, Dubé J, Lavoie C (2011) Paving the way for invasive species: road type and the spread of common ragweed (*Ambrosia artemisiifolia*). *Environ Manag* 48:514–522. <https://doi.org/10.1007/s00267-011-9711-7>
- Keller RP, Frang K, Lodge DM (2007) Preventing the spread of invasive species: economic benefits of intervention guided by ecological predictions. *Conserv Biol* 22:80–88. <https://doi.org/10.1111/j.1523-1739.2007.00811.x>
- Kohlhepp PF, Sanders TG, Tackett CC, Walters RW (1995) Roadside vegetation management. Colorado Department of Transportation. <https://www.codot.gov/programs/research/pdfs/1996/roadsidevegetation.pdf>. Accessed 13 Oct 2018
- Kuebbing SE, Simberloff D (2015) Missing the bandwagon: nonnative species impacts still concern managers. *NeoBiota* 25:73–86. <https://doi.org/10.3897/neobiota.25.8921>
- Kuhman TR, Pearson SM, Turner MG (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. *Landsc Ecol* 25:1433–1445. <https://doi.org/10.1007/s10980-010-9500-3>

- Lemke D, Hulme PE, Brown JA, Tadesse W (2011) Distribution modelling of Japanese honeysuckle (*Lonicera japonica*) invasion in the Cumberland Plateau and Mountain Region, USA. For Ecol Manag 262:139–149. <https://doi.org/10.1016/j.foreco.2011.03.014>
- León Cordero R, Torchelsen FP, Overbeck GE, Anand M (2016) Analyzing the landscape characteristics promoting the establishment and spread of gorse (*Ulex europaeus*) along roadsides. Ecosphere 7:1–14. <https://doi.org/10.1002/ecs2.1201>
- Lockwood JL, Cassey P, Blackburn T (2005) The role of propagule pressure in explaining species invasions. Trends Ecol Evol 20:223–228. <https://doi.org/10.1016/j.tree.2005.02.004>
- Lodge DM, Simonin PW, Burgiel SW, Keller RP, Bossenbroek JM, Jerde CL, Kramer AM, Rutherford ES, Barnes MA, Wittmann ME, Chadderton WL, Apriesnig JL, Beletsky D, Cooke RM, Drake JM, Egan SP, Finnoff DC, Gantz CA, Grey RK, Hoff MH, Howeth JG, Jensen RA, Larson ER, Mandrak NE, Mason DM, Martinez FA, Newcomb TJ, Rothlisberger JD, Tucker AJ, Warziniack TW, Zhang H (2016) Risk analysis and bioeconomics of invasive species to inform policy and management. Annu Rev Environ Resour 41:453–488. <https://doi.org/10.1146/annurev-environ-110615-085532>
- Lonsdale WM, Lane AM (1994) Tourist vehicles as vectors of weed seeds in Kakadu National Park, Northern Australia. Biol Conserv 69:277–283. [https://doi.org/10.1016/0006-3207\(94\)90427-8](https://doi.org/10.1016/0006-3207(94)90427-8)
- Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions: causes, epidemiology, global consequences, and control. Ecol Appl 10:689–710. [https://doi.org/10.1890/1051-0761\(2000\)010%5b0689:BICEGC%5d2.0.CO;2](https://doi.org/10.1890/1051-0761(2000)010%5b0689:BICEGC%5d2.0.CO;2)
- Miller NP, Matlack GR (2010) Population expansion in an invasive grass, *Microstegium vimineum*: a test of the channelled diffusion model. Divers Distrib 16:816–826. <https://doi.org/10.1111/j.1472-4642.2010.00690.x>
- Mortensen DA, Rauschert ESJ, Nord AN, Jones BP (2009) Forest roads facilitate the spread of invasive plants. Invasive Plant Sci Manag 2:191–199. <https://doi.org/10.1614/IPSM-08-125.1>
- Moustakas A, Voutsela A, Katsanevakis S (2018) Sampling alien species inside and outside protected areas: does it matter? Sci Total Environ 625:194–198. <https://doi.org/10.1016/j.scitotenv.2017.12.198>
- Nilsson C, Brown RL, Jansson R, Merritt DM (2010) The role of hydrochory in structuring riparian and wetland vegetation. Biol Rev 85:837–858. <https://doi.org/10.1111/j.1469-185X.2010.00129.x>
- Oswalt SN, Smith WB (2014) U.S. Forest Resource Facts and Historical Trends (Report No. FS-1035). Washington, D.C.: U.S. Forest Service. https://www.fia.fs.fed.us/library/brochures/docs/2012/ForestFacts_1952-2012_English.pdf. Accessed Dec 2018
- Oswalt CM, Fei S, Guo W, Iannone BV III, Oswalt SN, Pijanowski BC, Potter KM (2015) A subcontinental view of forest plant invasions. NeoBiota 24:49–54. <https://doi.org/10.3897/neobiota.24.4526>
- Paradis E, Claude J, Strimmer K (2004) APE: analyses of phylogenetics and evolution in R language. Bioinformatics 20:289–290. <https://doi.org/10.1093/bioinformatics/btg412>
- Parendes LA, Jones JA (2000) Role of light availability and dispersal in exotic plant invasion along roads and streams in the H. J. Andrews Experimental Forest, Oregon. Conserv Biol 14:64–75. <https://doi.org/10.1046/j.1523-1739.2000.99089.x>
- Pejchar L, Mooney HA (2009) Invasive species, ecosystem services and human well-being. Trends Ecol Evol 24:497–504. <https://doi.org/10.1016/j.tree.2009.03.016>
- Pickering CM, Hill W, Newsome D, Leung Y (2010) Comparing hiking, mountain biking and horse riding impacts on vegetation and soils in Australia and the United States of America. J Environ Manag 91:551–562. <https://doi.org/10.1016/j.jenvman.2009.09.025>
- Rauschert ESJ, Mortensen DA, Bloser SM (2017) Human-mediated dispersal via rural road maintenance can move invasive propagules. Biol Invasions 19:2047–2058. <https://doi.org/10.1007/s10530-017-1416-2>
- Rew LJ, Brummer TJ, Pollnac FW, Larson CD, Taylor KT, Taper ML, Fleming JD, Balbach HE (2018) Hitching a ride: seed accrual rates on different types of vehicles. J Environ Manag 206:547–555. <https://doi.org/10.1016/j.jenvman.2017.10.060>
- Richardson DM, Holmes PM, Esler KJ, Galatowitsch SM, Stromberg JC, Kirkman SP, Pyšek P, Hobbs RJ (2007) Riparian vegetation: degradation, alien plant invasions, and restoration prospects. Divers Distrib 13:126–139. <https://doi.org/10.1111/j.1366-9516.2006.00314.x>
- Riitters K, Potter K, Iannone BV III, Oswalt C, Fei S, Guo Q (2017) Landscape correlates of forest plant invasions: a high-resolution analysis across the eastern United States. Divers Distrib 24:274–284. <https://doi.org/10.1111/ddi.12680>
- Rodrigues ASL, Akçakaya HR, Andelman SJ, Bakarr MI, Boitani L, Brooks TM, Chanson JS, Fishpool LDC, Da Fonseca GAB, Gaston KJ, Hoffmann M, Marquet PA, Pilgrim JD, Pressey RL, Schipper J, Sechrest W, Stuart SN, Underhill LG, Waller RW, Watts MEJ, Yan X (2004) Global gap analysis: priority regions for expanding the global protected-area network. Bioscience 54:1092–1100. [https://doi.org/10.1641/0006-3568\(2004\)054%5b1092:GGAPRF%5d2.0.CO;2](https://doi.org/10.1641/0006-3568(2004)054%5b1092:GGAPRF%5d2.0.CO;2)
- Rothlisberger JD, Chadderton WL, McNulty J, Lodge DM (2010) Aquatic invasive species transport via trailered boats: what is being moved, who is moving it, and what can be done. Fisheries 35:121–132. <https://doi.org/10.1577/1548-8446-35.3.121>
- R Core Team (2017) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>. Accessed Sept 2017
- Seebens H, Blackburn TM, Dyer EE, Genovesi P, Hulme PE, Jeschke JM, Pagad S, Pyšek P, Winter M, Arianoutsou M, Bacher S, Blasius B, Brundu G, Capinha C, Celesti-Grappo L, Dawson W, Dullinger S, Fuentes N, Jäger G, Kartesz J, Kenis M, Kreft H, Kühn I, Lenzner B, Liebhold A, Mosena A, Moser D, Nishino M, Pearman D, Pergl J, Rabitsch W, Rojas-Sandoval J, Roques A, Rorke S, Rosinelli S, Roy HE, Scalera R, Schindler S, Štajerová K, Tokarska-Guzik B, van Kleunen M, Walker K, Weigelt P,

- Yamanaka T, Essl F (2017) No saturation in the accumulation of alien species worldwide. *Nat Commun* 8:1–9. <https://doi.org/10.1038/ncomms14435>
- Simberloff D (2009) The role of propagule pressure in biological invasions. *Annu Rev Ecol Evol Syst* 40:81–102. <https://doi.org/10.1146/annurev.ecolsys.110308.120304>
- Simberloff D, Martin J, Genovesi P, Maris V, Wardle DA, Aronson J, Courchamp F, Galil B, García-Berthou E, Pascal M, Pyšek P, Sousa R, Tabacchi R, Vilà M (2013) Impacts of biological invasions: what's what and the way forward. *Trends Ecol Evol* 28:58–66. <https://doi.org/10.1016/j.tree.2012.07.013>
- Skultety D, Matthews JW (2017) Urbanization and roads drive non-native plant invasion in the Chicago Metropolitan region. *Biol Invasions* 19:2553–2566. <https://doi.org/10.1007/s10530-017-1464-7>
- Soares-Filho B, Moutinho P, Nepstad D, Anderson A, Rodrigues H, Garcia R, Dietzsch L, Merry F, Bowman M, Hissa L, Silveirini R, Maretti C (2010) Role of Brazilian Amazon protected areas in climate change mitigation. *Proc Natl Acad Sci USA* 107:10821–10826. <https://doi.org/10.1073/pnas.0913048107>
- Taylor K, Brummer T, Taper ML, Wing A, Rew LJ (2012) Human-mediated long-distance dispersal: an empirical evaluation of seed dispersal by vehicles. *Divers Distrib* 18:942–951. <https://doi.org/10.1111/j.1472-4642.2012.00926.x>
- Thébaud C, Debussche M (1991) Rapid invasion of *Fraxinus ornus* L. along the Hérault River system in Southern France: the importance of seed dispersal by water. *J Biogeogr* 18:7–12. <https://doi.org/10.2307/2845240>
- Trombulak SC, Frissell CA (2000) Review of ecological effects of roads on terrestrial and aquatic communities. *Conserv Biol* 14:18–30. <https://doi.org/10.1046/j.1523-1739.2000.99084.x>
- U.S. Census Bureau (2016a) Roads National Geodatabase. Suitland, Maryland, U.S. <https://www.census.gov/geo/maps-data/data/tiger-geodatabases.html>. Accessed Nov 2017
- U.S. Census Bureau (2016b) Cartographic Boundary Shapefiles—Urban Areas. Suitland, Maryland, U.S. https://www.census.gov/geo/maps-data/data/cbf/cbf_ua.html. Accessed Nov 2017
- U.S. Census Bureau (2016c) MTFCC Codes for 2016 and earlier TIGER Products. Suitland, Maryland, U.S. <https://www.census.gov/geo/reference/mtfcc.html>. Accessed Nov 2017
- U.S. Geological Survey (2005) National Hydrography Dataset Plus V2. Reston, Virginia, U.S. <https://www.usgs.gov/core-science-systems/ngp/national-hydrography>. Accessed Nov 2017
- U.S. Geological Survey (2017) National Elevation Dataset. Reston, Virginia, U.S. <https://lta.cr.usgs.gov/NED>. Accessed Nov 2017
- Veldman JW, Putz FE (2010) Long-distance dispersal of invasive grasses by logging vehicles in a tropical dry forest. *Biotropica* 42:697–703. <https://doi.org/10.1111/j.1744-7429.2010.00647.x>
- von der Lippe M, Kowarik I (2007) Long-distance dispersal of plants by vehicles as a driver of plant invasions. *Conserv Biol* 21:986–996. <https://doi.org/10.1111/j.1523-1739.2007.00722.x>
- Von Holle B, Motzkin G (2007) Historical land use and environmental determinants of nonnative plant distribution in coastal southern New England. *Biol Conserv* 136:33–43. <https://doi.org/10.1016/j.biocon.2006.10.044>
- Von Holle B, Simberloff D (2005) Ecological resistance to biological invasion overwhelmed by propagule pressure. *Ecology* 86:3212–3218. <https://doi.org/10.1890/05-0427>
- Watkins RZ, Chen J, Pickens J, Brososke KD (2003) Effects of forest roads on understory plants in a managed hardwood landscape. *Conserv Biol* 17:411–419. <https://doi.org/10.1046/j.1523-1739.2003.01285.x>
- Williams WH, Henderson K (2002) Tree and brush control for county road right-of-way. Iowa Department of Transportation. https://www.tallgrassprairiecenter.org/sites/default/files/Tech_Manual/roadside_brush_control_manual.pdf. Accessed 13 Oct 2018
- Yates ED, Levia DF Jr, Williams CL (2004) Recruitment of three non-native invasive plants into a fragmented forest in southern Illinois. *For Ecol Manag* 190:119–130. <https://doi.org/10.1016/j.foreco.2003.11.008>
- Zwaenepoel A, Roovers P, Hermy M (2006) Motor vehicles as vectors of plant species from road verges in a suburban environment. *Basic Appl Ecol* 6:83–93. <https://doi.org/10.1016/j.baec.2005.04.003>

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