PREDICTING INVADEDNESS OF FORESTED PROTECTED AREAS IN RELATION TO NATURAL AND ANTHROPOGENIC DISTURBANCES

BY

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THESIS

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ABSTRACT

Protected areas are essential for biodiversity conservation and ecosystem services such as natural disaster risk reduction and climate regulation. However, invasive plants threaten these benefits of protected areas by negatively impacting native plants and animals and altering ecosystem structure and function. Natural and anthropogenic disturbances create conditions that may favor establishment and spread of invasive plants. In order to manage invasive plants and mitigate their effects on forested protected areas, it is important to be able to predict how disturbances affect invasive plant populations. My thesis includes two studies that address the effects of natural and anthropogenic disturbances on invasive plant abundance in protected areas. In Chapter 1, I outlined a general background on the ecological and economic impacts of invasive plants, and management responses to the four stages of the invasion process. In Chapter 2, I explored the effects of roads and streams on invadedness of 27 Appalachian protected areas. I focused on roads and streams as predictors of invadedness since both roads and streams deliver invasive plant propagules and are sources of disturbance that can favor establishment of invasive plants. Having a reliable predictor of protected area invadedness would meaningfully help land management organizations avoid acquiring heavily invaded protected areas or accurately plan for their management costs. In Chapter 3, I used a time series of windstorms in southern Illinois to determine whether windstorm-disturbed forests are significantly more invaded than areas of undisturbed forest. I expected forest blowdown areas to be more heavily invaded than undisturbed forest since a decrease in tree canopy provides increased resources, such as light, to invasive plants. I then sought to determine the effects of time since disturbance and disturbance magnitude on invadedness of blowdown areas. Knowing the factors that affect the invadedness

of blowdowns will allow land managers to preferentially allocate funding to management of invasive plants in specific blowdown areas.

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CHAPTER 1: GENERAL BACKGROUND

Invasive plants are pervasive in the United States and globally. 39% of U.S. forests are invaded by non-native plants, and when the eastern U.S. is considered alone, that estimate rises to 46% (Oswalt et al. 2015). The impacts of invasive plants are multifaceted, and a single species can have multiple wide-ranging effects. Spotted knapweed (*Centaurea maculosa*), for example, is an invasive plant in the United States that causes many economic, environmental, and societal impacts. Spotted knapweed is particularly problematic in the western U.S., where it causes millions of dollars per year in economic losses (Hirsch and Leitch 1996). It decreases forage for animals such as elk and cattle (Thompson 1996; Hirsch and Leitch 1996), reduces native vegetation (Hirsch and Leitch 1996), and alters fire regimes (Grace et al. 2001; Harrod and Reichard 2001). Spotted knapweed is also detrimental to soil and water resources as presence of spotted knapweed increases surface runoff and sediment yield (Lacey et al. 1989).

Invasive plants have a significant negative impact on native plants (Greene and Blossey 2012) and can decrease their health by depleting resources typically used by native plants, hybridizing with natives, and suppressing regeneration of natives (Mack et al. 2000). In some ecosystems, native seedlings experience more herbivory damage than non-natives (Flory and Clay 2009). Invasive plants can also be detrimental to native wildlife by providing poor habitat and forage (Mack et al. 2000; Pimentel et al. 2005). They can reduce the health of fish (Pejchar and Mooney 2009) and alter invertebrate communities (Lecerf et al. 2011).

Invasive plants are detrimental to human livelihood and recreation. They reduce crop yields at estimates up to 12% per year (Pimentel et al. 2005) and by billions of dollars per year (Pejchar and Mooney 2009). Invasive plants reduce livestock forage and in some cases are toxic to livestock (Pimentel et al. 2005; Pejchar and Mooney 2009). The reduction in fish health caused by invasive plants has the potential to reduce recreational and commercial fishing opportunities (Eiswerth et al. 2000). Invasive aquatic plants clog waterways and restrict boat movement (Pimentel et al. 2005), which reduces opportunities for recreational boating and swimming (Eiswerth et al. 2000). These losses in recreational opportunities are economically significant because the loss of visitors negatively impacts surrounding communities that provide visitor services (Pejchar and Mooney 2009).

Negative environmental and ecological impacts of invasive plants include changes in soil nutrient composition (Mack et al. 2000), increased erosion (Pejchar and Mooney 2009), and increased air pollution (Hickman et al. 2010). One of the most destructive environmental impacts of invasive plants is their ability to change fire regimes. Although many invasive plants alter fire regimes (Brooks et al. 2004; Mack et al. 2000), cheatgrass (*Bromus tectorum*) is perhaps the best-documented example of this. Cheatgrass, which can quickly dominate rangeland, causes increased fire risk, frequency, and intensity (Link et al. 2006; Knapp 1996). Cheatgrass significantly shortens fire recurrence intervals and is 10 to 500 times more likely to burn than native bunchgrasses (Knapp 1996). From 1980 to 1992, the estimated cost of fires attributed to cheatgrass in the Great Basin region (Nevada, U.S.) was about $10 million per year (Knapp 1996). Riparian and aquatic invasive plants cause substantial hydrological impacts, including narrowing of stream channels, increased sedimentation, changes in water flow, and increased flood risk (Fall et al. 2004; Birken and Cooper 2006; Pejchar and Mooney 2009). Riparian invasive plants can decrease water availability by using significantly more water than native species or by increasing water loss due to higher rates of evapotranspiration (Zavaleta 2000; Pejchar and Mooney 2009; Gebauer et al. 2016).

Although it is difficult to determine a concrete figure of economic cost of invasive plants that encompasses every aspect of every plant, the current limited estimates are considerable. Pimentel et al. (2005) estimated that the economic cost of invasive plants in the U.S. is $27 billion annually, but it is probable that this figure is not a complete picture. Economic impacts of single species alone can reach up to tens of millions of dollars annually in the United States. Yellow star thistle (*Centaurea solstialis*), for example, costs California's ranching industry $17.1 million dollars annually (Eagle et al. 2007). In four U.S. states (Montana, North Dakota, South Dakota, and Wyoming), direct economic impacts of leafy spurge (*Euphorbia esula*) on stock growers, landowners, and agribusiness firms are estimated at approximately $37 million annually, and secondary impacts on the regional economy are estimated at approximately $83 million (Leistritz et al. 2004). While economic costs are important in conceptualizing the impact of invasive plants, is it important to consider that there are impacts, such as the loss of habitat and forage for native animals, that extend beyond market value costs and can be challenging or controversial to frame economically (Costanza et al. 2014; Small et al. 2017).

Negative impacts of invasive plants are substantial even in protected areas that are typically slightly less invaded than other land use types (Moustakas et al. 2018), but funding for invasive plant management in protected areas is decreasing in many places, including U.S. public lands (U.S. National Park Service 2017; U.S. Forest Service 2017). The Natural Resource Stewardship program of the U.S. National Park Service (NPS) manages invasive plants on NPS land and will have a 7.5% decrease from fiscal year (FY) 2017 to FY 2018 (U.S. National Park Service 2017). The U.S. Forest Service FY 2018 budget includes a 16% decrease in invasive species research and development and projects a 54.5% decrease in the amount of federal land treated for invasive plants and other pests from FY 2016 to FY 2018 (U.S. Forest Service 2017).

These decreases are happening as management of invasive species remains the highest priority for many land managers (Kuebbing and Simberloff 2015) and as rates of spread of invasive plants continue to increase (Seebens et al. 2017). With decreasing funds available in some of the most vulnerable areas in the U.S., it will become increasingly more important for land managers to effectively budget and anticipate funding needs for protected areas by identifying where invasive species are most likely to be introduced, establish, spread, and have severe impacts (Lodge et al. 2016).

Invasive plant management options can target any of the stages of invasion (Lodge et al. 2016). Introduction is movement of propagules to a new location, and management options involve propagule pressure reduction, such as screening of seed stocks or public education on planting nonnatives (Theoharides and Dukes 2007; Lodge et al. 2016). Establishment is the development of a self-sustaining, expanding population and is filtered by abiotic (e.g., temperature, disturbance regime, resource availability) and biotic (e.g., plant competition, pathogens and herbivores) factors (Theoharides and Dukes 2007). Management focused on the establishment stage includes controlling existing populations (Lodge et al. 2016). Management may also include using restoration to create a plant community resistant to invasion (Funk et al. 2008; Bakker and Wilson 2004), although the predictability and reliability of biotic resistance are inconsistent and change with scale (Levine 2004; Fridley et al. 2007). The spread of a species across a landscape is controlled by biotic (e.g., dispersal ability) and abiotic (e.g., landscape connectivity) factors (Theoharides and Dukes 2007; Lodge et al. 2016). Valuable management strategies at this stage include reducing propagule vectors (e.g., vehicles and people traveling through invaded areas), identification of susceptible sites near invaded sites, and treatment of invaded sites (Pyšek and Richardson 2010; Theoharides and Dukes 2007; Lodge et al. 2016).

Management at impact, the final stage of invasion, is aimed at control and adaptation and can involve the development of new chemical, mechanical, and genetic control methods (Lodge et al. 2016).

Control of existing invasive plant populations costs the U.S. billions of dollars per year (Pimentel et al. 2005), but these control costs can be significantly minimized by preventing the introduction and spread of invasive plants (Lodge et al. 2016; Mack et al. 2000). Prevention is economically more cost-effective than controlling established populations of invasive species (Leung et al. 2002) and typically results in more net benefits (Lodge et al. 2016). Prevention practices at the introduction and spread stages include isolating invasions (Davies and Sheley 2007; Lodge et al. 2016), public education about invasive plants (Simberloff et al. 2013), and careful inspection and cleaning of vectors such as seed mixes (Theoharides and Dukes 2007), boats (Rothlisberger et al. 2010), and vehicles (Davies and Sheley 2007). Understanding the factors that contribute to invasibility, such as the significance of different propagule vectors, will facilitate determination of where to focus prevention efforts to maximize limited protected area funding.

In both of my studies in this thesis, I explored the effects of natural and anthropogenic disturbances on invasive plant populations in forested protected areas. Both chapters relied heavily on geographic information systems (GIS), including remote sensing of satellite imagery, for data creation and analysis. In Chapter 2, the first study, I sought to answer the question: can land management organizations predict the invadedness of protected areas using the presence of roads and streams for acquisition and management decisions? I approached this question using a survey of 27 protected areas acquired by The Nature Conservancy, the world’s largest biodiversity conservation non-profit organization (Armsworth et al. 2012). My results provide guidance to land management organizations wanting to avoid acquiring heavily invaded parcels. My results also assist organizations in planning for parcel management costs by providing a rule of thumb that may realistically predict parcel invadedness. In Chapter 3, I surveyed blowdowns caused by three windstorms in three protected areas in southern Illinois to investigate the effects of windstorm canopy disturbance on invasive plant populations. I proposed three hypotheses: 1) blowdown areas will be more invaded than undisturbed forest because of increased resources, 2) invadedness will decrease with time since disturbance as canopy regrowth decreases light availability, and 3) invadedness will increase with increased magnitude of canopy disturbance because of increased light availability.

CHAPTER 2: DO ROAD OR STREAM NETWORKS EXPLAIN PLANT INVASIONS IN FORESTED PROTECTED AREAS?

2.1 Abstract

Giving land managers the ability to predict invasion patterns may allow for planning of prevention, outreach, and early detection efforts for invasive plants when acquiring and managing protected areas. We compared the effects of roads and streams, two significant 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 (U.S.). 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 networks 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 stream and road networks 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.

2.2 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, and spread 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) or potential for future invasion of a parcel. These predictions can help organizations with limited resources avoid acquiring properties susceptible to invasion when all else is equal, or budget to survey or eradicate invasive plants (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). 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, the 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. 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.

2.3 Methods

Study Sites

Our study focuses on 27 protected area parcels in the Appalachian Mountains, U.S. (Fig. 2.1). 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 11.6 ha to a maximum of 891.3 ha with a mean parcel size of 189.2 ha. Average elevation of the parcels ranged between 181.2 m to 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. 2.1). 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 considerably 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

Invasive species data were collected between May 30, 2013 and September 24, 2013. 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 network variables and five natural and anthropogenic covariates to use in models to predict protected area invadedness (Table 2.1). We used upstream length from the most 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 Hydrology 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 zero.

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 m 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. We evaluated sensitivity of our model to each buffer distance using information theoretic model competition with AICc (Burnham & Anderson 2002). We selected a 100 m buffer since it had the lowest AICc (all other buffer distance models ΔAICc>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 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) 2011 data (Homer et al. 2015). The NLCD 2011 Tree Canopy raster contains 30m 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 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 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 ΔAICc>3.023).

Statistical Analyses

We log-transformed 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 × 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 & 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. 2.1; 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 log-transformed the response variable (invasive cover), the predictor variables (road density of all road types), and one covariate (percent agriculture).

2.4 Results

Invasive Species Data

Invasive species were present at 158 of the 540 plots and 20 of the 27 parcels we sampled. 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 at 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 2.2). Percent agriculture within a 500 m buffer was the only predictor among the covariates that was marginally significant (p=0.073; Table 2.3). Percent agriculture was positively related to parcel invadedness (Fig. 2.2). 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 (ΔAICc=2.141, R^2=0.299) and roads and covariates model (ΔAICc=2.572, R^2=0.288; Table 2.2). 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 2.4), the covariates-only model had ΔAICc>2, and the other three road type models had ΔAICc>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 2.4). In the 4WD model, significant predictors were 4WD road density (p=0.030) and edge-to-interior ratio (p=0.017; Table 2.5). Our model showed a positive relationship between parcel invasive cover and both 4WD road density and edge-to-interior ratio (Fig. 2.3). 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).

2.5 Discussion

We did not find general stream or road networks 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 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 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 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 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 higher abundance closer to roads (Watkins 2003; Cadenasso and Pickett 2003). Road density within a buffer of parcels, our road variable choice, should capture this relationship, but it's possible that it did not. 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. 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 2004; Cadenasso and Pickett 2003). 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 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 road and stream networks? This analysis could have been conducted 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. 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.

Because overall road and stream networks 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 networks, edge-to-interior ratio, and agricultural land in a buffer were 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 networks 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).

2.6 Tables

Table 2.1 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 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

Table 2.2 Comparison of candidate models for predicting invadedness of Appalachian protected areas using ΔAICc, AICc weights, and R^2. 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 2.3).

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

Table 2.3 Regression table for best model identified by ΔAICc (Table 2.2). This model includes only covariates. Numbers in parenthesis indicate standard error.

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

Table 2.4 Comparison of all candidate road type regression models using ∆AICc, AICc weights, and R^2. 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.

Model	∆ AICc	AIC Weight	R^2
4WD	0	0.699	0.405
Covariates only	2.263	0.226	0.271
Primary	6.547	0.026	0.241
Local	6.684	0.025	0.235
Secondary	6.759	0.024	0.237

Table 2.5 Regression table for most supported road type model identified by AIC. Numbers in parenthesis indicate standard error. * indicates significance of predictors or covariates at p<0.05.

Variable	Coefficient	p
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

2.7 Figures

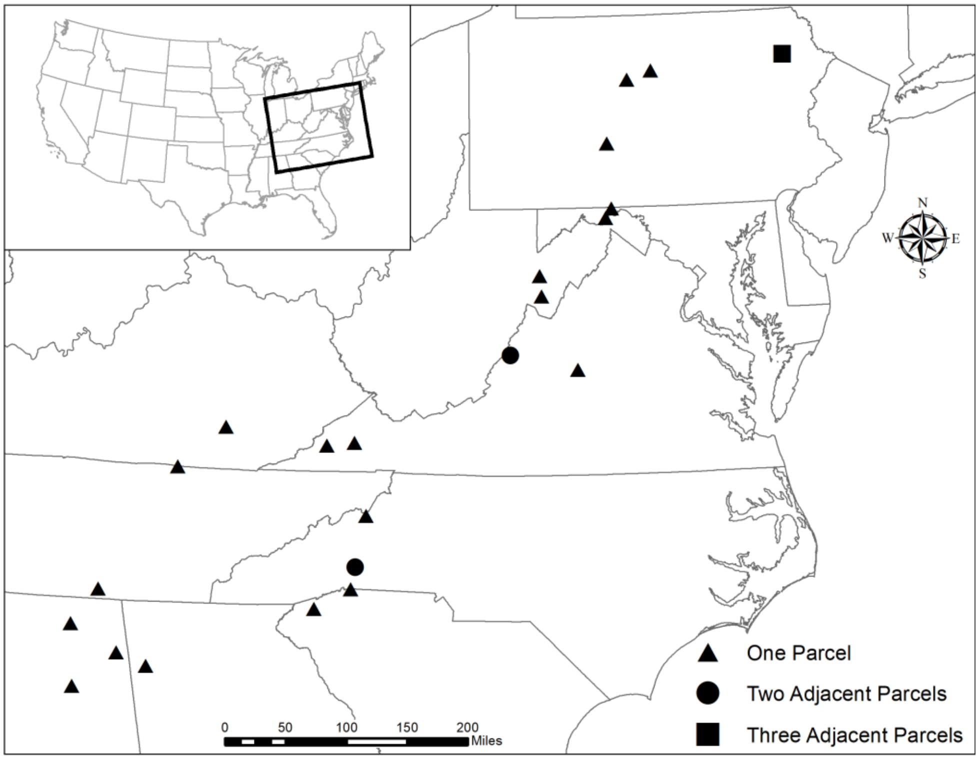

Fig. 2.1 Locations of the 27 TNC parcel used to explain forest plant invadedness by stream and road networks. The labels of “Two Adjacent Parcels” and “Three Adjacent Parcels” indicate separate parcels that are visible only as one point at the map scale because of geographical proximity.

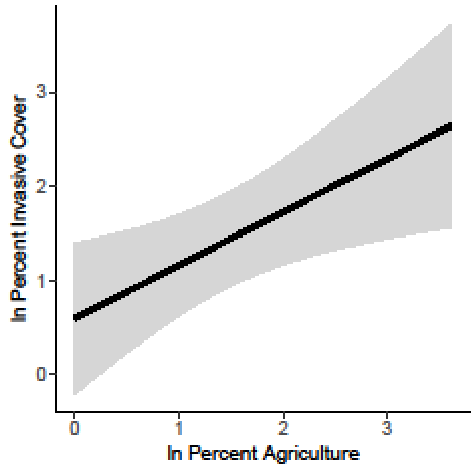

Fig. 2.2 Relationship between percent agricultural land and percent invasive cover in covariates model (Table 2.2, Table 2.3). Black line indicates regression line, and grey shading represents 95% confidence interval. Percent agriculture and percent invasive cover are natural log transformed.

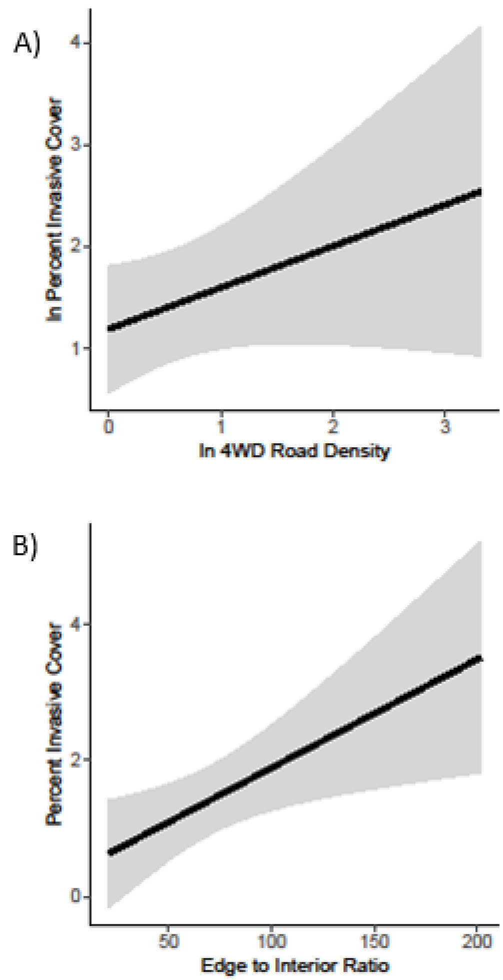

Fig. 2.3 Relationship between 4WD road density and percent invasive cover (A), and edge to interior ratio and percent invasive cover (B), in 4WD roads model (Table 5). Black line indicates regression line, and grey shading represents 95% confidence interval. 4WD road density and percent invasive cover are natural log transformed.

CHAPTER 3: INVASIVE PLANT RESPONSE TO WINDSTORM FOREST CANOPY DAMAGE

3.1 Abstract

Invasive plant populations respond positively to light increase from windstorm-caused canopy damage but are typically outcompeted over time as the tree canopy recovers. Some invasive plants have the ability to slow or even completely prevent canopy regrowth. It is important to understand invasive plant dynamics in windstorm blowdowns to inform effective forest management. We hypothesize that blowdown areas are more invaded than unaffected forest and that invadedness of a blowdown will decrease with increasing time since disturbance and increase with disturbance magnitude. We used Landsat imagery to identify 31 blowdowns caused by one of three storms in southern Illinois of the United States: 2006 tornado, 2009 derecho, or 2017 tornado. We statistically matched these blowdowns to areas of unaffected forest based on slope, aspect, elevation, distance to a road, and distance to a trail. We surveyed blowdown and unaffected units for invasive plants in summer 2018. Disturbance magnitude was measured in two ways: percent change in normalized difference vegetation index (NDVI) and area of blowdown. Overall, blowdown areas were more invaded than their statistically matched areas. Invadedness of blowdown areas decreased with increasing time since disturbance, indicating that the blowdowns are recovering as tree canopy regrowth shades out invasive plants. Percent change in NDVI was not a supported predictor of blowdown invadedness, but invadedness was strongly positively related to blowdown size. Larger blowdowns recover more slowly than smaller units due to different recovery pathways, providing more time and opportunity for the spread and establishment of invasive plants. Our findings suggest that although blowdown areas contain higher cover of invasive plants than forest unaffected by

windstorms, invasive plants are responding negatively to canopy regrowth. Land managers should prioritize treatment of invasive plants in larger and more recent blowdown areas.

3.2 Introduction

As global non-native plant invasion rates show no sign of slowing down (Seebens et al., 2017), invasive plants continue to negatively impact valuable forest ecosystems economically and ecologically (Pimentel et al., 2005; Flory and Clay, 2010). Invasive plants significantly alter structure and function of forest ecosystems by reducing growth and survival of native plants (Greene & Blossey, 2012), providing poor habitat for native animals (Mack et al., 2000), and altering soil nutrient cycling processes (Ehrenfeld, 2003; Vilà et al., 2011). Forest disturbances such as windstorms can accelerate existing invasions or change the relative abundance of invasive plants (Horvitz et al., 1998). Invasive plants establish in windstorm blowdown areas from the soil seed bank, existing individuals, or seeds dispersed into the area (Runkle, 1985; Honu et al., 2009; Greenberg et al., 2001) and respond positively to increased canopy disturbance and light levels (Parendes & Jones, 2000; Greenberg et al., 2001; Burnham & Lee, 2010; Gagnon & Platt, 2008). Although disturbance is not always a reliable predictor of invadedness (Moles et al., 2012), canopy disturbance or gaps is a more consistent predictor of invadedness than some other disturbance types (Eschtruth & Battles, 2009; Greenberg et al., 2001; Gagnon & Platt, 2008; Burnham & Lee, 2010). Because time since disturbance is an important factor in predicting invadedness (DeFerrari & Naiman, 1994), investigating a time series of disturbances can help explain the dynamics of invasive plant populations as forest gaps regenerate and whether invasive plants can alter that process. We build here on the narrow body of literature about invasive plants in windstorm blowdowns by developing a novel study that uses remote sensing-derived disturbance variables, surveys the entire community of management-relevant invasive plants, and investigates multiple characteristics of blowdown areas across a time series of windstorms.

A single windstorm can cause forest canopy mortality comparable to one to three decades of baseline mortality (Woods, 2004). Windstorms cause canopy gaps by knocking down, debranching, and defoliating trees (Everham & Brokaw, 1996), altering forest successional patterns (Woods, 2004). Canopy gaps increase light availability to understory plants (Canham et al., 1990; Collins et al., 1985; Carlton & Bazzaz, 1998). In general, light availability increases with gap size (Collins et al., 1985), but light regime (e.g., ratio of direct to diffuse radiation, sunfleck duration, incidence angle) changes with gap size and forest type (Canham et al., 1990). Canopy gap regrowth depends on many factors, including species composition and gap size (Martin & Ogden, 2006; Everham & Brokaw, 1996). Thus, predicting forest responses can be difficult. Total understory cover of shrubs and herbs typically increases in blowdown gaps due to increased resource availability (Meigs & Keeton, 2018). However, if understory shrubs and herbs are present and are unaffected by a disturbance, there may be little effect on species' spatial patterns (Hughes & Fahey, 1991).

The presence of invasive species in blowdown gaps can significantly alter forest recovery pathways. Closing of a canopy gap may prevent growth of shade-intolerant invasive plants, but if shade-tolerant invasive plants, such as Japanese stiltgrass (*Microstegium vimineum*) or Japanese knotweed (*Fallopia japonica*), establish in the blowdown gap, they can persist under forest canopy and spread into surrounding forests (Martin et al., 2009). Invasive plants can significantly impede or even prevent closure of canopy gaps by competitively suppressing or preventing tree growth, regeneration, and recruitment (Kneeshaw & Prévost, 2007; Fagan & Peart, 2004;

Merriam & Feil, 2002) and increasing seedling mortality and herbivory (Gorchov & Trisel, 2003; Meiners, 2007). In blowdown gaps, herb and shrub populations increase rapidly due to increased light availability, but eventually herb populations decline as tree seedlings establish and dominate the canopy (Peterson & Pickett, 1995). However, the ability of invasive plants to suppress native tree regeneration and possibly prevent canopy closure has important implications for forest management, as it would underscore the importance of treating invasive plants in blowdown areas. Even if eventual canopy regrowth could completely suppress establishment and growth of invasive plants over time, initial treatment of invasive plants after blowdowns is crucial to preventing spread into surrounding areas, especially when shade-tolerant species are present (Martin et al., 2009) or when a propagule corridor, such as a road or trail, intersects the blowdown gap (Miller & Matlack, 2010).

If invasive plants establish in gaps, studying blowdown gaps over a time series will indicate which of the pathways discussed above is being followed in the gaps: trees shading out invasive plants over time or invasive plants continuing to thrive in the gap. The lack of a decline of invasive plants in blowdown gaps over time would highlight the importance of treating invasive plants in those gaps to promote native canopy tree regeneration. Our study uses a time sequence of three major windstorms in southern Illinois (IL) of the United States (U.S.) between 2006 and 2017. We hypothesize that 1) blowdown areas will be more invaded than undisturbed forest because of increased resources, 2) invadedness will decrease with time since disturbance as canopy regrowth decreases light availability, and 3) invadedness will increase with increased magnitude of canopy disturbance because of increased light availability. Our study uniquely uses a time series of windstorms and multiple measures of disturbance severity to investigate the abundance of invasive plants in blowdown areas over time and in response to disturbance intensity.

3.3 Methods

Study Sites

Study sites included blowdown areas in three protected areas in southern Illinois: Shawnee National Forest (NF), Giant City State Park (SP), and Crab Orchard National Wildlife Refuge (NWR). This region has a humid continental climate (Chagnon, 1985) with mean annual precipitation of 113.2 cm (National Oceanic and Atmospheric Administration, 2010). Elevation of the study sites ranges from 104.4 m to 240.0 m. These protected areas are within two U.S. Environmental Protection Agency (EPA)-designated ecoregions: Interior Plateau, characterized by open hills, irregular plains and tablelands, with primary vegetation being oak-hickory forest; and Interior River Valleys and Hills, characterized by flat-bottomed terraced valleys, forested slopes, and dissected glacial till plains, with primary vegetation being deciduous and swamp forests in bottomlands and oak-hickory and mixed oak forests in uplands (U.S. Environmental Protection Agency, 2013).

Our study focused on blowdown gaps caused by three different windstorms: tornadoes in 2006 and 2017 and a derecho in 2009. On September 22, 2006, an F2 tornado (peak wind speed estimated at 241 km h^{-1}) hit Jackson County, IL (National Oceanic and Atmospheric Administration, 2006), and on February 28, 2017, an EF3 tornado (peak wind speed estimated at 233 km h^{-1}) hit Jackson County, IL (National Oceanic and Atmospheric Administration, 2017). On May 8, 2009, a derecho hit southern Illinois, producing winds of 148-167 km h^{-1} (Weisman et al., 2013). Derechos are convectively induced windstorms that occur in the U.S. east of the Rocky Mountains characterized by wide swaths of straight-line winds (Bentley & Mote, 1998; Weisman et al., 2013).

Blowdown Delineation

We used Landsat imagery stacks to calculate change in canopy cover in blowdown areas (Fig. 3.1; U.S. Geological Survey, 2018). We considered using more high-resolution remote sensing data but found that it would have no significant effect on our analyses (see Appendix A). For change detection for the September 2006 tornado, we used Landsat TM data from July 31, 2006 and June 16, 2007. For the May 2009 derecho, we used Landsat TM data from July 20, 2008 and a cloud-free mosaic of two images from summer 2009: June 5 (85.4% of mosaic) and May 20 (14.6% of mosaic). For the February 2017 storm, we used Landsat OLI data from June 8, 2016 and July 15, 2017. All Landsat data were Level-2 surface reflectance data, which have been radiometrically and atmospherically corrected. We calculated normalized difference vegetation index (NDVI) for each year, and then calculated percent change in NDVI for each pair. From conversations with land managers at the three management agencies, we identified likely blowdown areas and then used the percent change rasters to hand-delineate blowdown areas. We detected ten blowdown areas for the 2006 tornado, but five were excluded for possible interaction with the 2009 derecho. We detected eight blowdown areas for the 2017 tornado, but three were excluded because they had been salvaged for timber. We detected 101 blowdown areas for the 2009 derecho, and 21 were randomly selected for inclusion. All 2006 and 2017 units are in Shawnee NF (Fig. 3.2). Four 2009 derecho units were within Giant City SP, six were within Crab Orchard NWR, and 11 were within Shawnee NF (Fig. 3.2).

Unit Matching

For each unit, we used Mahalanobis distance (Land Facet Corridor Designer; Jenness & Beier, 2013) in ArcMap 10.5 (Esri, 2017) to establish a comparative unit in unaffected forest that is similar to the blowdown unit in terms of elevation, slope, aspect, distance to a road, and distance to a trail (Table 3.1). We acquired trail shapefiles from personal communications with each agency (Shawnee NF, Giant City SP, and Crab Orchard NWR) and road shapefiles from the U.S. Census Bureau TIGER database (U.S. Census Bureau, 2016a). We calculated distance rasters with roads or trails using a Euclidean distance tool in ArcMap (Esri, 2017). We chose distance to a road and distance to a trail as matching variables because roads and trails represent delivery mechanisms for invasive plant propagules (Pickering et al., 2010; Christen & Matlack, 2009). We used slope, elevation, and aspect as matching variables because these abiotic factors cause microclimatic variation (e.g., light and moisture) that can favor or hinder establishment of invasive plants (Lemke et al., 2011; Kuhman et al., 2010; Bennie et al., 2006).

Comparative units were also matched in terms of forest type (e.g., deciduous forest to deciduous forest, and mixed deciduous and coniferous forest to mixed forest). Comparative units were placed within either Shawnee NF, Crab Orchard NWR, or Giant City SP, but could be placed in different land ownership than the windstorm-affected unit. Comparative units were the exact same size and shape as the blowdown units they were matched to. We matched four blowdown units in areas with prescribed fire to areas that had a prescribed burn within two years of the blowdown unit burn. To maintain independence, the smallest distance between paired units was 2.94 km, and the average distance between paired units was 39.87 km. Comparative units were ground-truthed for similarity to study units.

Plant Surveys

We created 12 randomly distributed plots in each affected and comparative unit (Fig. 3.1). Plots were at least 10 m from each other. At each plot, we recorded percent cover of each invasive species in a 5 m radius to the nearest interval of 5% and used a densiometer to measure canopy cover. Surveys were conducted from May 30 to July 20, 2018. We surveyed for all non-native invasives identified by local land managers as species of concern.

Statistical Analyses

To address the first hypothesis, whether blowdown areas are more invaded than undisturbed areas, we used a Wilcoxon signed-rank test in R version 3.3.3 (R Core Team, 2017) for each disturbance year to make a plot-level comparison between invadedness of blowdown areas and invadedness of their unaffected matches. To address the second and third hypotheses, the effects of time since disturbance and magnitude of canopy disturbance on invadedness, we used AICc model selection with plot-level linear mixed models in R (Burnham & Anderson 2002). The response variable in these models was the plot-level difference between percent invasive cover of blowdown areas and the percent invasive cover of their matched areas, to account for the variables already used in the statistical matching of units. Fixed effects in these models were time since disturbance (years), blowdown unit area (as delineated with Landsat change detection; ha), percent change in NDVI (plot-level), and field canopy cover (estimated with densiometer at the plot-level; %). To account for possible differences in baseline forest NDVI changes across the region, the percent change in NDVI value used was the percent change in NDVI at the blowdown plot minus the percent change in NDVI at the paired unaffected plot. Blowdown unit area and percent change in NDVI are both considered measures of canopy disturbance magnitude. Random effects in these models were land management agency (Shawnee NF, Giant City SP, or Crab Orchard NWR) and if the unit has the same land management agency as its unaffected match (0 or 1).

We included the two random effects (land management agency and difference in land management agency between matched pairs) because we expect that past land management practices vary widely between agencies. Invasive shrubs, such as *Rosa multiflora* and *Elaeagnus umbellata*, were historically planted in the eastern United States for uses including hedges (Steavenson, 1946; Anderon & Edminster, 1954) and wildlife conservation (Allan & Steiner, 1972). Local land managers believe that invasive shrubs were historically planted at Giant City SP and Crab Orchard NWR in the mid-to-late-1900s but likely not at our study areas in Shawnee NF (personal communications, Dan Wood, 22 Oct 2018).

We used AICc model selection on models containing all possible combinations of the four fixed effects: field canopy cover, time since disturbance, unit area, and percent change in NDVI. All models contained both random effects. Model selection also included a model containing only random effects. We chose a plot-level analysis instead of an aggregated unit-level analysis in order to preserve the association of fine scale plot-level variables: plot invasive cover, field canopy cover, and percent change NDVI. We recognize that our plot-level analysis could be interpreted as pseudoreplication (Hurlbert, 1984), but we did not want to further complicate our models with a third random effect for unit. Instead, we compared our plot-level analysis with a unit-level analysis and found that our results are largely insensitive to scale (plot vs. unit) of these models (see Appendix B).

3.4 Results

Average plot-level percent change in NDVI was -8.38% for the 2006 tornado, -13.53% for the 2009 derecho, and -6.05% for the 2017 tornado. The smallest blowdown unit area was 1.25 ha, the largest unit area was 40.45 ha, and the average unit area was 8.94 ha.

We recorded 16 invasive plant species at our study units. Invasive plants were detected in 54.3% of blowdown plots and 15.3% of unaffected plots. Invasives were detected at 96.8% of blowdown units and 35.5% of unaffected units. By number of plot occurrences, the five most abundant invaders, in order, were *Lonicera japonica*, *Elaeagnus umbellata*, *Rosa multiflora*, *Lonicera maackii*, and *Celastrus orbiculatus*. By percent cover, that list changes to, in order, *Lonicera japonica, Elaeaganus umbellata, Celastrus orbiculatus, Rosa multiflora,* and *Lonicera maackii*. Four invasives were recorded at only one plot.

Wilcoxon signed-rank tests for all disturbance years demonstrated a significant difference between invadedness of blowdown units and their unaffected match paired units ($p<0.001$; Fig. 3.3). The best performing mixed model from our AICc analysis included only time since disturbance and unit area as fixed effects (Table 3.2). In this model, time since disturbance was strongly negatively related to plot invasive cover (Table 3.3; Fig. 3.3), whereas unit area was strongly positively related to invasive cover (Fig. 3.4). The next best performing model was 1.03 ΔAICc from the best performing model (Table 3.2). This model similarly included both time since disturbance and unit areas as fixed effects, and additionally included field canopy cover, which had a weakly negative effect on invasive cover (Table 3.3). All other models were >2 ΔAICc from the best performing model.

3.5 Discussion

We found that windstorms have significantly altered southern Illinois forest plant communities and that dynamics of invasive plant communities in blowdowns can be predicted by blowdown size and age. Overall, blowdown areas were more invaded than the statistically matched unaffected areas. Within these blowdown units, invadedness in our best performing model was positively related to area of the unit (one measure of disturbance magnitude) and negatively related to time since disturbance. The two other model fixed effects, percent change NDVI (another measure of disturbance magnitude) and field canopy cover measurements, were not included in the best performing model. Our results support all three hypotheses: 1) disturbed units will be more invaded than undisturbed forest, 2) invadedness will decrease with increasing time since disturbance, and 3) invadedness will increase with increasing disturbance magnitude. To our knowledge, this is the first demonstration of the roles of both time since disturbance and disturbance intensity in forest blowdown plant invasion using field and remote-sensed variables.

For the time series of three windstorms from 2006 to 2017, blowdown areas were significantly more invaded than matched unaffected units (Fig. 3.3). A previous study in this region found no effect of windstorm canopy disturbance on plant invasions (Romano et al., 2013) but did not include a time series of storms and used unit-scale estimates of canopy disturbance intensity at intervals of 25%. Further, our results are consistent with many other studies that demonstrate the positive response of invasive plants to forest canopy disturbance (Eschtruth and Battles 2009; Greenberg et al. 2001). Light availability increases in blowdown gaps immediately after disturbance, and this increased light availability can persist in the gap for years after the disturbance (Carlton & Bazzaz, 1998). An increase in light from canopy disturbance releases invasive plants already present in the understory (Greenberg et al., 2001). These findings demonstrate that land managers should indeed be concerned about invasive plants establishing in blowdown areas.

More recent blowdowns were more invaded than older blowdown areas. This indicates that these southern Illinois blowdowns are recovering such that the tree canopy shades out invasive plants over time (Peterson & Pickett, 1995). Although this also suggests that the invasives growing in these blowdowns are not significantly preventing canopy regeneration, it is possible that the invasives present may be slowing canopy regeneration (Flory & Clay, 2010; Stinson et al., 2006). Our results, however, still signal a need for management of invasive plants in blowdown areas. In the time it takes for the canopy to recover, invasive plants that establish in blowdown areas can spread to surrounding forest, especially if the species present are shade tolerant (Martin et al., 2009) or if there are road or trails traversing the blowdown (Miller & Matlack, 2010).

We measured disturbance magnitude in several ways: percent change NDVI and blowdown unit area, and a field measure of canopy openness with a densiometer. Percent change NDVI, representing disturbance of the tree canopy at a specific plot, was not included in our most supported models. Our field measure of canopy openness was supported in one of our two most supported, equivalent models, but the effect of this variable on invadedness was relatively weak in comparison to other fixed effects (Table 3.3). We found, however, that larger blowdown units were more invaded than smaller blowdown units (Fig. 3.4). In smaller canopy gaps, the canopy can regenerate relatively quickly via lateral growth of trees surrounding the gap (Everham & Brokaw, 1996). In larger gaps, canopy regeneration requires growth of surviving seedlings or recruitment of new individuals, which takes more time than lateral growth of existing trees (Everham & Brokaw, 1996). This longer recovery time gives more opportunity for the establishment and spread of invasives, indicating that land management agencies looking to prioritize treatment of invasive plants in blowdowns should focus on relatively large blowdowns.

Forest disturbances are complex and multifaceted (Martin & Ogden, 2006; Everham & Brokaw, 1996), and it is difficult to create a model that includes all factors affecting forest plant communities. It's possible that these disturbances were marginally compounded by additional forest disturbances (e.g., ice storms, pests, or disease; Changnon & Kristovich, 2009). However, since overall change in canopy cover is measured by our remote sensing methods, it should not matter if there was an additional minor mechanism of canopy damage. Besides increased light availability due to decreased canopy cover, blowdowns cause many other microclimatic changes that can affect invasive species populations, such as creation of new microhabitats (e.g., pits and mounds) (Runkel, 1985; Carlton & Bazzaz, 1998), changes in soil temperature and moisture (Collins et al., 1985), and increased nutrient availability due to increased litter (Collins et al., 1985). Measurements of these factors were outside the scope of our study.

Windstorms are capable of causing significant, lasting impacts to forest plant communities (Woods, 2004; Meigs & Keeton, 2018). In this system in southern Illinois, we found that while blowdown areas from 2006 to 2017 are overall significantly more invaded than unaffected forest, invasive plant response within these blowdown areas was best predicted by time since disturbance and area of the blowdown patch. Land managers concerned about invasive plants establishing in blowdown areas and spreading into surrounding unaffected forests should focus monitoring and treatment efforts on blowdown areas that are recent or relatively large. We recommend that future studies include older windstorm disturbances to determine recovery time required for invasive plant communities to be comparable to unaffected forest, or explore these relationships in forests in other regions to ascertain whether our hypothesis are supported in different systems. An extension of our study could also evaluate spread of invasive plants from blowdown areas over a similar time series since disturbance and over gradients of disturbance magnitude.

3.6 Tables

Table 3.1 Average and standard deviation of variables used in Mahalanobis distance matching of 31 blowdown units to their comparative units. Distance to a trail and distance to a road are calculated from Euclidean distance rasters in which the value of each raster cell is the straight-line distance from that cell to the nearest trail or road, respectively. Northness is a cosine transformation of aspect, in which values range from -1 (south-facing) to 1 (north-facing; Kumar et al., 2006). Eastness is a sine transformation of aspect that ranges from -1 (west-facing) to 1 (east-facing; Kumar et al., 2006).

		Blowdown Units	Comparative Units
Distance to a Trail (m)	Mean	1493.2	1640.4
	SD	84.6	87.7
Distance to a Road (m)	Mean	278.9	321.2
	SD	70.3	72.9
Northness	Mean	0.01	0.01
	SD	0.71	0.71
Eastness	Mean	0.01	0.01
	SD	0.71	0.70
Slope (degrees)	Mean	11.5	14.5
	SD	5.2	5.8
Elevation (m)	Mean	161.5	169.7
	SD	10.6	10.8

Table 3.2 Best performing plot-level linear mixed models in AICc model selection. Both models contained two random effects: a categorical variable for land management agency of the blowdown unit and a binary variable representing whether the blowdown unit and its matched unit are managed by the same agency. Model selection included all possible combinations of the four fixed effects, including a null model containing only random effects. All other models not displayed in this table were > 16 ΔAICc from best performing model. Canopy: field canopy cover, NDVI: percent change NDVI, Time: time since disturbance, Area: blowdown unit area.

Model	K	AICc	ΔAICc	AIC weight	R^2
Time + Area	6	3806.12	0	0.47	0.47
Canopy + Time + Area	7	3807.15	1.03	0.28	0.48
NDVI + Time + Area	7	3808.28	2.17	0.16	0.48
Canopy + NDVI + Time + Area	8	3809.31	3.19	0.09	0.49

Table 3.3 Coefficients and standard error of fixed effects in plot-level mixed models with ΔAICc < 2 (Table 3.2). Models contained two random effects: a categorical variable for land management agency of the blowdown unit and a binary variable representing whether the blowdown unit and its matched unit are managed by the same agency. Canopy: field canopy cover, NDVI: percent change NDVI, Time: time since disturbance, Area: blowdown unit area. Number in parenthesis indicates standard error. A dash (-) indicates that a particular fixed effect was not included in a model.

Model	Field Canopy Cover	Percent Change NDVI	Time Since Disturbance	Unit Area
Time + Area	-	-	-4.88 (0.68)	1.19 (0.27)
Canopy + Time + Area	-0.37 (0.28)	-	-4.40 (0.77)	1.18 (0.27)

3.7 Figures

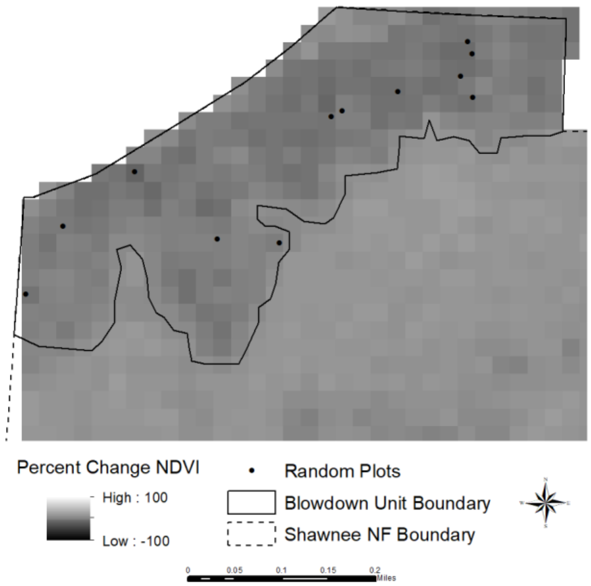

Fig. 3.1 Example of blowdown delineation from Landsat change detection and random plot distribution. Percent change NDVI is the difference between NDVI in the summer before the windstorm and the summer after the windstorm, in this case from July 20, 2008 to June 5, 2009. Blowdown areas were delineated by hand using the percent change raster. Decreasing negative NDVI represents increasing canopy disturbance. Random plots were required to be at least 10 m from each other.

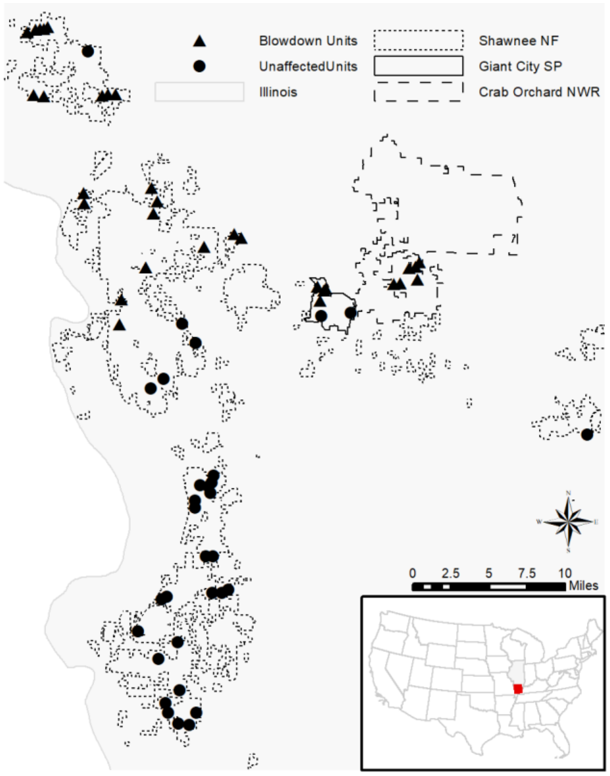

Fig. 3.2 Locations of blowdown units and their comparative, statistically matched unaffected unit. Units are in forest managed by one of three southern Illinois land management agencies: Shawnee National Forest (NF), Giant City State Park (SP), or Crab Orchard National Wildlife Refuge (NWR). 12 random plots in all blowdown and comparative units were surveyed for invasive plants between May 20 and July 20, 2018 (Fig. 3.1).

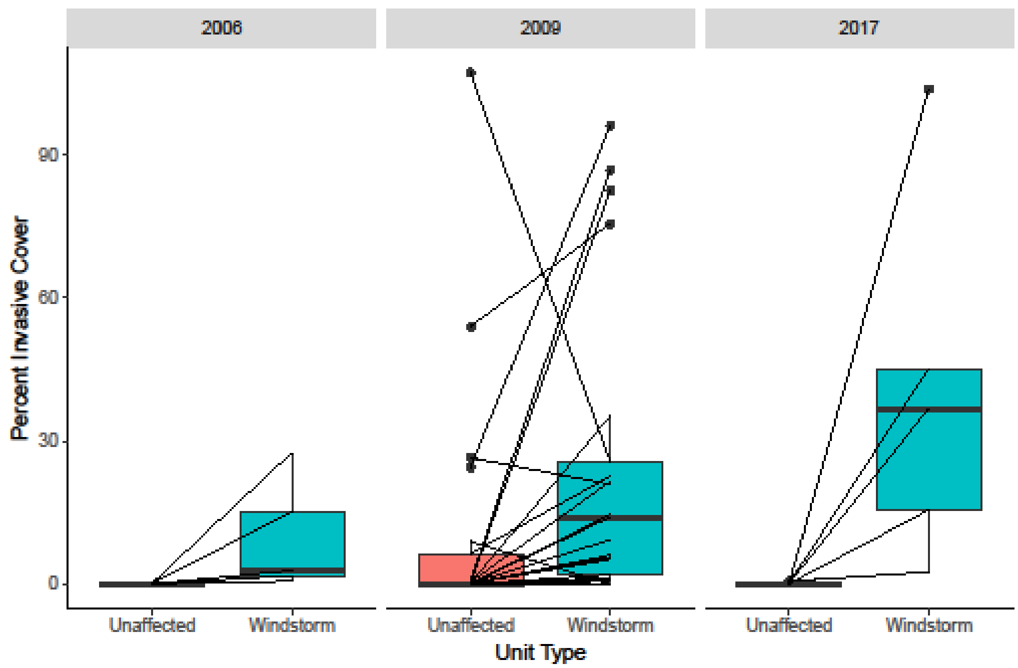

Fig. 3.3 Boxplots displaying unit-level invasive cover data for blowdown areas from three storms: 2006 tornado, 2009 derecho, and 2017 tornado. This figure includes data from all land management agencies (Shawnee NF, Giant City SP, and Crab Orchard NWR). The y-axis label "Percent Invasive Cover" is the average percent invasive cover of all plots within a unit. Figure uses unit-level invasive cover data rather than plot-level invasive cover data to simplify visualization. Lines between points are connecting blowdown units with their statistically matched unit in forest unaffected by the respective storms.

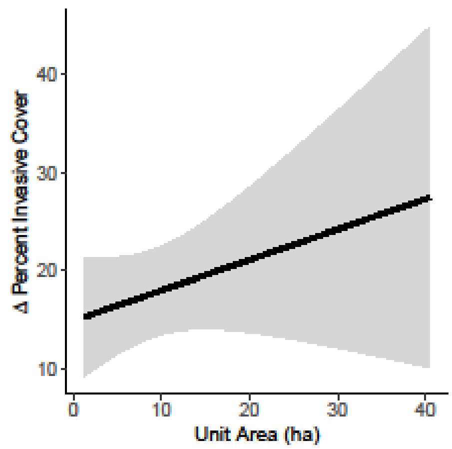

Fig. 3.4 Relationship between plot-level Δ percent invasive cover and blowdown unit area in linear mixed model (Table 3.2). Black line indicates regression line, and grey shading represents 95% confidence interval. Δ percent invasive cover is the plot-level difference between blowdown unit invasive cover and comparative unit invasive cover.

CHAPTER 4: SUMMARY

In my thesis, I present two studies that aimed to assist land managers seeking to predict the invadedness of protected areas in response to anthropogenic and natural disturbances. Invasive plants are a high priority for land managers (Kuebbing and Simberloff 2015), and these studies address practical and realistic questions that land managers may ask when attempting to prevent the establishment and spread of invasive plants, or when planning for land acquisition. Both studies involved exploring the effects of natural disturbances on invasive plant abundance: streams in the Appalachian protected areas study and windstorms in the southern Illinois blowdown study. The Appalachia study also included roads, a source of anthropogenic disturbance, in the analyses. In both studies, I identified significant predictors of invasive plant abundance, which can serve as guidelines for land managers looking to predict invadedness of protected areas and plan management responses.

In the Appalachian protected areas study (Chapter 2), I sought to determine if road and stream networks could be used as predictors of invadedness, based on 27 forested protected areas acquired by The Nature Conservancy (TNC). Although general road and stream networks were not reliable predictors of parcel invadedness, I found that four-wheel-drive (4WD) road density specifically was a significant predictor of invadedness. I also found a marginally significant positive relationship between percent agricultural land in a buffer and parcel invadedness, and a significant positive relationship between edge-to-interior ratio and parcel invadedness. Land management organizations such as TNC concerned about invasive plants should either plan for high management costs or be cautious of acquiring parcels with high 4WD road density in and around the parcel, especially when recreation activities are present. They also may want to apply these considerations to parcels with a high edge-to-interior ratio or a relatively large amount of agricultural land in and around the parcel.

In the southern Illinois blowdown study (Chapter 3), I answered the questions: 1) Are windstorm-disturbed forest areas more invaded than similar undisturbed areas? 2) What are the effects of time since disturbance and disturbance magnitude on the invadedness of windstorm-disturbed areas? I found that windstorm-disturbed forested areas were significantly more invaded than statistically matched areas of undisturbed forest. Within blowdown areas, I found that the most reliable predictors of invadedness were time since disturbance and unit area. My results indicate that 1) southern Illinois blowdowns are recovering such that as the forest canopy is regrowing over time, invasive plants are being shaded out, and 2) that larger blowdowns are recovering more slowly due to different, more time-intensive recovery mechanisms required in larger areas. Despite evidence that invasive plants are being shaded out over time, land managers should be concerned about invasive plants that establish in blowdowns spreading to surrounding forest and therefore should focus treatment efforts on recently disturbed areas and relatively large blowdowns.

My research demonstrates the ability of specific natural and anthropogenic disturbances to accelerate forest plant invasions. As these invasive plants continue to cause substantial ecological and economic impacts (Pejchar and Mooney 2009, Pimentel et al. 2005), having reliable predictors of invadedness will assist protected area managers in budgeting for and managing invasive plants. My results from Chapter 2 provide general guidelines that can be used in the process of acquiring of forested protected areas. Although neither overall road nor stream networks are reliable predictors of forest invadedness, the presence of a high density of 4WD roads may signal increased invadedness in Appalachian protected areas. I believe that my conclusions about 4WD roads merit further investigation. My results in Chapter 3 provide guidance for a later stage in the land acquisition and management process: predicting how a windstorm may affect invasive plant populations in an existing protected area. Although forests affected by windstorm may experience an increase in invasive plants, these invasive plants populations should decrease over time as the forest canopy recovers. Land managers looking to control invasive plant populations in windstorm-disturbed forests should prioritize relatively large and recent blowdowns. Together, both of my thesis chapters provide practical and valuable recommendations that will assist land managers in the processes of acquiring and managing protected areas.

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APPENDIX A: HIGH-RESOLUTION ANALYSIS

Landsat is a useful imagery source for change detection because it has a fine temporal resolution and no cost. However, it comes at a tradeoff of relatively course spatial resolution (30m). Sources of high-resolution imagery (e.g., Planet Labs' SkySat and PlanetScope or DigitialGlobe's WorldView-2 and WorldView-3) would be more ideal for forest windstorm change detection but are not available for the 2006 tornado or 2009 derecho. For the February 2017 tornado blowdown areas, we compared calculations of a model variable, percent change in NDVI, from Landsat OLI analyses to calculations of the same variable from PlanetScope imagery (3m). The literature on this topic contains conflicting results about whether spatial resolution has a significant effect (Rocchini 2007; McCarthy et al. 2015; Hou 2018). We hypothesized that finer detection of canopy damage would allow for more realistic estimates of change in canopy cover and may more accurately explain invasive plant response to windstorm damage.

We selected PlanetScope as a source of imagery for this analysis because of their generous Education and Research Program. At 3 m resolution, it has 10 times finer resolution than Landsat. We calculated plot-level percent change in NDVI from the summer before the storm to the summer after the windstorm, and compared these values to the plot-level values calculated from the Landsat analyses. The mean percent change NDVI calculated from Landsat was -5.94%, and the mean percent change NDVI calculated from PlanetScope was -5.16%. For each plot, we calculated the percent difference between the Landsat-derived percent change NDVI and PlanetScope-derived percent change NDVI. The average of all plot-level percent differences was 0.66%. A paired Wilcoxon signed-rank test found no significant difference between plot-level Landsat and PlanetScope percent change NDVI values ($p=0.093$).

An ideal analysis would compare differences in mixed model results used in the main analysis using Landsat and then using PlanetScope. However, this high-resolution data analysis was only able to be carried out on the 2017 units, all of which are on land managed by Shawnee NF. A recreation of our mixed model with these data would therefore require the removal of three variables (time since disturbance, land management agency, and whether the blowdown unit and matched unit are managed by the same agency) and would no longer be the same analysis.

Although we found no difference in plot-level percent change NDVI values between Landsat and PlanetScope, we believe that a finer-scale analysis would have been beneficial in more accurately delineating blowdown unit boundaries. Imposing the unit boundaries delineated from Landsat analysis onto the percent change NDVI raster calculated from PlanetScope data shows that our delineation process was reasonably accurate enough for this analysis (Fig. A1). However, the coarser resolution Landsat analysis may have caused inclusion of small pieces of less disturbed areas into blowdown units (see bottom right corner of unit pictured in Fig. A1) or exclusion of small slivers of relatively more disturbed areas (see top boundary of unit pictured in Fig. A1). We believe that these small errors are negligible and likely did not have a large effect on our analyses.

We conclude that in the context of this study, using high spatial resolution satellite imagery would not have improved our model or our ability to predict invasive plant response to windstorm forest canopy damage. Since high-resolution imagery can come at a very high cost, this is an important implication for similar analyses carried out at the same scale. In the context of research with a limited budget and a similar scope, using Landsat's 30 m resolution imagery should be sufficient and should not compromise the quality of the research.

Appendix A References

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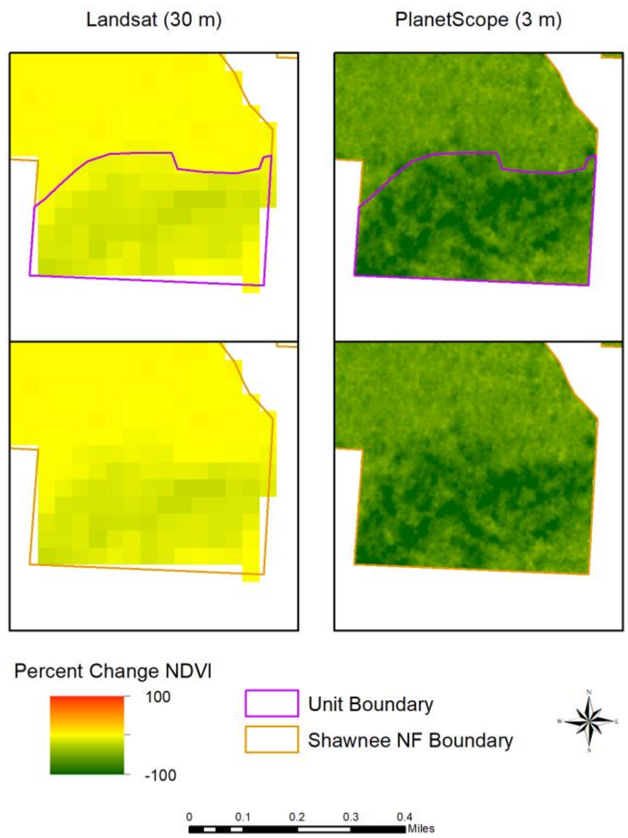

Fig. A1 The left two frames display percent change NDVI from June 8, 2016 to July 15, 2017 using we used Landsat OLI imagery. The right two frames display percent change NDVI from July 21, 2016 to July 22, 2017 using PlanetScope imagery. Percent change NDVI is used as a measure of tree canopy disturbance. The tornado causing this disturbance happened on February 28, 2017.

APPENDIX B: UNIT-LEVEL AICc ANALYSIS

Table B1 Best performing unit-level linear mixed models in AICc model selection, for comparison to plot-level models reported in the main text (Table 2). All models contained two random effects: a categorical variable for land management agency of the blowdown unit and a binary variable representing whether the blowdown unit and its matched unit are managed by the same agency. Model selection included all possible combinations of the four fixed effects, including a null model containing only random effects. All other models not displayed in this table were > 2 ΔAICc from best performing model. Canopy: field canopy cover, NDVI: percent change NDVI, Time: time since disturbance, Area: blowdown unit area. Unit-level AICc analysis had more equivalent models (ΔAICc < 2) than plot-level AICc analysis. However, in both analyses, the most supported model had the same fixed effects, time since disturbance and blowdown unit area, with similar coefficients for both variables (Table 3; Table B3). Additionally, in both analyses, time since disturbance was included in all well-supported models (Table 2).

Model	K	AICc	ΔAICc	AIC weight	R^2
Time + Area	6	302.239	0	0.167	0.514
Canopy + Time + Area	7	302.594	0.355	0.139	0.510
Time	5	302.874	0.635	0.121	0.427
Canopy + Time	6	302.932	0.693	0.118	0.419
NDVI + Time + Area	7	303.377	1.138	0.094	0.517
NDVI + Time	6	303.661	1.422	0.082	0.450
Canopy + NDVI + Time	7	303.922	1.683	0.072	0.446
Canopy + NDVI + Time + Area	8	303.971	1.732	0.070	0.517

Table B2 Coefficients and standard error of fixed effects of all unit-level mixed model with ΔAICc < 2 (Table B1) for comparison to plot-level models in the main text (Table 3). All models contained two random effects: a categorical variable for land management agency of the blowdown unit and a binary variable representing whether the blowdown unit and its matched unit are managed by the same agency. Canopy: field canopy cover, NDVI: percent change NDVI, Time: time since disturbance, Area: blowdown unit area. Number in parenthesis indicates standard error. A dash (-) indicates that a particular fixed effect was not included in a model. Parameter estimates are broadly similar to plot-level analyses used in the main text.

Model	Field Canopy Cover	Percent Change NDVI	Time Since Disturbance	Unit Area
Time + Area	-	-	-4.56 (1.67)	1.11 (0.66)
Canopy + Time + Area	0.34 (1.78)	-	-5.01 (2.93)	1.12 (0.68)
Time	-	-	-3.57 (1.62)	-
Canopy + Time	0.09 (1.84)	-	-3.69 (2.92)	-
NDVI + Time + Area	-	0.07 (1.23)	-4.53 (1.78)	1.11 (0.68)
NDVI + Time	-	0.27 (1.25)	-2.47 (1.71)	-
Canopy + NDVI + Time	0.18 (1.90)	0.29 (1.29)	-3.69 (2.97)	-
Canopy + NDVI + Time + Area	0.37 (1.84)	0.11 (1.27)	-5.01 (2.98)	1.12 (0.69)