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Patterns of invasive plant abundance in disturbed versus undisturbed forests within three land types over 16 years

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Abstract

Aim: Long-term monitoring of forest understorey species was used to describe changes in native and invasive exotic plant abundances over time within different disturbed or undisturbed forest types. This information was then used to determine the predictive invasion model (passenger/opportunist, driver or back-seat driver).

Location: Cheat Ranger District of the Monongahela National Forest, West Virginia, USA.

Methods: Understorey vegetation of mature and clear-cut forests was sampled every 5–6 years for 16 years. Stands were stratified across three land types following a moisture gradient. Invasive plant richness, frequency and abundance were evaluated across land type and disturbance type with general linear mixed models. Change in richness, diversity and abundance of both native and invasive non-native plants was evaluated as a measure of impact.

Results: The mesic mature stands had the greatest invasive plant richness, frequency and abundance. The moderately mesic clear-cut stands initially showed the greatest invasive plant richness, frequency and abundance, but over time these values became greater for the drier clear-cuts. The mature forests showed no change in native species abundance in response to invasion. Clear-cut-drier stands showed a decrease, while the more mesic stands showed an increase in native plant richness, diversity and abundance in response to invasion. The drier clear-cuts, with increasing invasions and negative native species impacts, were indicative of the back-seat driver model. The hitchhiker model, a new term, described increasing plant invasions with no measurable impacts.

Main Conclusions: The drier clear-cut stands exhibit a lack of biotic resistance to invasion, unlike the mesic clear-cut stands. Increasing invasion in the mature forests suggests that a threshold may be reached that results in impacts on the native vegetation, but with no increase in native plant abundance to help alleviate these effects.

KEYWORDS

biotic resistance, disturbance, ecological land type, forest management, invasion model, invasion patterns, invasive plants, long-term monitoring, moisture gradient, restoration

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1 | INTRODUCTION

Long-term monitoring of plant invasions in forests differing by type and disturbance history may reveal patterns of invasion longevity (stage) and direction (drivers or passengers of change) that lead to more informed restoration efforts. The lag-time effect noted for several invasive species is generally thought to be the time between introduction and invasion (Pyšek & Hulme, 2005; Richardson et al., 2000; Williamson et al., 2005). Longer lag times associated with intact forests may be due to large time intervals between disturbances (Martin et al., 2009) and dispersal limitations of propagules due to fewer nearby sources (Von Holle & Simberloff, 2005). Such lag effects make forest invasions difficult to document if not monitored over time or compared with archaeophytes or pre-1500 alien plant species (Essl et al., 2012), the latter of which does not apply well to New World forests. In contrast, residence time of an invasive plant starts from the first record in the wild until present; longer residence times are associated with faster spread rates at the regional scale and larger invaded ranges (Pyšek et al., 2009; Williamson et al., 2009). Several invasive plant species share long residence times and expansive ranges with long lag times in forested areas, giving the appearance that forests are less vulnerable to invasion (Martin et al., 2009). Nonetheless, there may be patterns of forest invasion associated with environmental and landscape factors such as soil, climate, land use and anthropogenic disturbances (Huebner & Tobin, 2006; Richardson & Pysek, 2012). The relationship between likelihood of invasion and resource availability has been well-established (Davis et al., 2000), showing higher likelihood of an invasive species being found in disturbed areas and areas with more resources, such as more mesic and nutrient-rich sites (Catford et al., 2012; Huebner & Tobin, 2006). In addition to resource availability, biotic interactions among native plants and other exotic plants are expected to play an important role in forest invasions (Blumenthal et al., 2009).

There are several invasive models in the literature used to define the mechanisms behind plant invasions and to predict the success of any subsequent restoration. Invasive plants may be passengers of disturbance, opportunists of a lack of system resiliency, active drivers of plant compositional change (Chabrerie et al., 2008; Didham et al., 2005) or back-seat drivers of compositional change (Bauer, 2012). As passengers, once the disturbance is removed or alleviated, the abundance of the invasive plant and impact on native species are expected to decrease over time. Both native and invasive species respond positively to the disturbance (White et al., 2013). Opportunistic invasive plants take advantage of negative effects of disturbances or a lack of system resilience, both of which negatively impact the native community, but do not directly benefit the invasive species (Chabrerie et al., 2008). Removal of the disturbance(s) benefits the native species, resulting in a decrease in invasive species over time. The combined synergistic effect of a lack of resiliency due to multiple stressors (e.g. deer, climate, harvesting) and invasion has been termed the "back-seat driver effect," in which impacts on native species are in response to both the disturbance and the invasion, and recovery of native species is only possible with both removal of the invasive species and the disturbance (Bauer, 2012). In contrast, drivers of change would have a negative effect on native species with or without a disturbance or a lack of system resilience (Bauer, 2012; Chabrerie et al., 2008; Didham et al., 2005; White et al., 2013). A key aspect of each model is that it predicts potential impacts on native species if the disturbance and/or the invasive plant were removed. The most suitable invasion model may change with the invasion stage (introduction, establishment, spread) or length of presence at a site (Banerjee & Dewanji, 2017; Colautti & MacIsaac, 2004; Radosevich et al., 2003; Richardson et al., 2000; Williamson, 2006) and may depend on how multiple invasive species interact with each other, the environment and native species (Kuebbing et al., 2013).

For practical reasons, invasive plant management takes place at the stand scale, even if the species in question are regionally invasive. Local management of common, regionally expansive, invasive plants is a problem shared by many landowners and managers, and local solutions are potentially more important than macroscale range expansion rate estimates; hence, this article focuses on local-scale spread.

The purpose of this study was to compare local long-term invasion patterns of invasive plant species in disturbed (clear-cut harvest) and undisturbed mixed-mesophytic eastern forests across different ecological land types that follow a moisture gradient. The goal in making this comparison is to determine the invasion model associated with these forests, which have been monitored for 16 years. This information will enable forest managers to prioritize management and restoration efforts based on disturbance history and land type and associated invasion patterns and impacts on native plants over time. We address the following two questions: (a) How have the invasive plant richness, frequency and abundance changed over 16 years within mature versus clear-cut forests and do these measures differ with land type or landscape features, such as distance to roads? And (b) which invasion model do these forests follow and is there a pattern associated with disturbance type, land type or landscape features?

2 | METHODS

2.1 | Study area and site selection

The study area was in a mixed-mesophytic forest within the Allegheny Mountain Section of the Unglaciated Allegheny Plateau in the Cheat Ranger District of the Monongahela National Forest in Tucker and Randolph Counties, West Virginia (approximately 39°03´ N and 79°41´ E; Figure 1). Selected stands were part of a long-term study started in 2001 in which 24 sites were randomly selected from each of two forest ages: (a) 80-year or older mature second-growth stands and (b) 15-year-old clear-cuts (cut between 1985 and 1989) and stratified across three ecological land types (Huebner & Tobin, 2006). Ecological land types (ELTs) were defined according

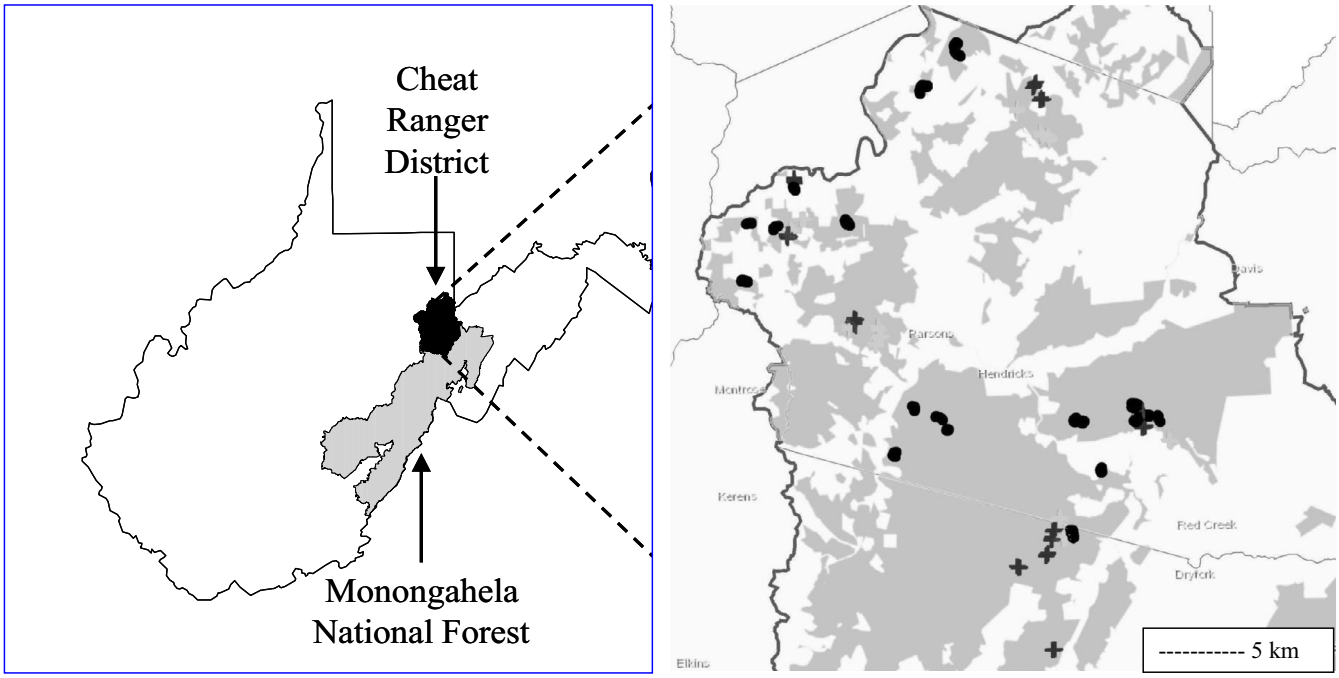
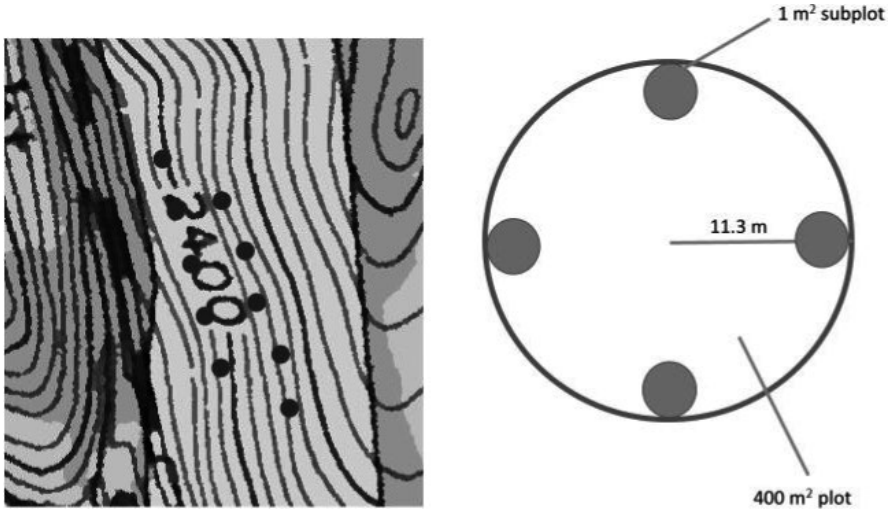


FIGURE 1 Study area showing state, Monongahela National Forest, Cheat Ranger District boundaries, and the 23 mature stands (circle) and 12 clear-cut stands (+)

FIGURE 2 Example stand schematic showing systematic set-up of plots about every 0.4 ha and an example of a plot and the four subplots



to Barnes et al. (1982), Russell and Jordan (1991), Hurst (1994), and Host et al. (1996) and include (a) ELT 220, more mesic and fertile, represented by *Acer saccharum* Marshall and *Tilia americana* L. and also containing *Laportea canadensis* (L.) Wedd. and/or *Caulophyllum thalictroides* (L.) Michx. in the understorey; (b) ELT 230, intermediate, represented by *A. saccharum* and *Quercus rubra* L. and *L. canadensis* and/or *C. thalictroides* in the understorey; and (3) ELT 300, less mesic and fertile, represented by *Q. rubra* and *Vaccinium* L. sp. and/or *Kalmia latifolia* L. in the understorey.

The mature forest stands were first sampled in June 2001, again in June 2006, 2012 and 2017. The number of mature stands was reduced to 23 because one stand was harvested prior to the second sample date, leaving six in the ELT 220, eight in ELT 230 and nine in ELT 300. Clear-cut stands were sampled starting in June 2002, again in June 2007, 2013 and 2018. The number of clear-cut stands was reduced to 12 because nine of the sites were no longer accessible due to wind damage and excessively poor road conditions in 2012 and an additional crop-tree release was administered in 2011 to three of the remaining 15 stands. The remaining clear-cut stands had four per ELT. Only the remaining 23 mature and 12 clear-cut stands are included in this study, though a few comparisons are made with the three clear-cut stands that had a crop-tree release.

2.2 | Sampling design

A systematic, nested plot design was used with four 1-m^2 subplots per plot (400 m^2) and one plot every 0.4 ha for each site (Figure 2).

Number of plots per stand was dependent on stand size and varied between 7–20 plots; previous analyses confirm that stand size or plot number did not affect likelihood of invasion (Huebner & Tobin, 2006). Nonetheless, all analyses, except for a comparison of native plant cover change in invaded subplots, averaged subplot data within plots and averaged plot data within stands; therefore, the individual stands represent independent replicates. The total number of stands used in this study was 35, with 23 mature and 12 clear-cut stands, and no fewer than 4 stands per ELT (Table 1).

In years 2001/2002 and 2006/2007, per cent cover of all herb, shrub and vine species, and per cent cover and density of all tree seedlings under 1 m in height were measured. Relative cover was

TABLE 1 Stands by disturbance type, replicate, ecological land type (ELT), number of plots and number of invaded subplots

Stand	Replicate	ELT	Number of plots	Subplots for native/invasive change analysis (2012/2013–2001/2002)	Crop-tree release
Mature 1	3	300	20	0	
Mature 2	2	230	10	0	
Mature 3	1	220	10	1	
Mature 4	2	230	12	0	
Mature 5	3	300	18	0	
Mature 6	2	230	8	0	
Mature 7	3	300	10	0	
Mature 8	2	230	7	0	
Mature 9	2	230	7	6	
Mature 10	3	300	16	1	
Mature 11	2	230	12	4	
Mature 12	3	300	10	0	
Mature 13	1	220	11	0	
Mature 14	2	230	10	0	
Mature 15	2	230	10	0	
Mature 16	1	220	17	1	
Mature 17	1	220	10	13	
Mature 18	1	220	10	0	
Mature 19	3	300	10	0	
Mature 20	3	300	10	0	
Mature 21	2	230	8	0	
Mature 22	3	300	10	0	
Mature 23	1	220	16	7	
Clear-cut 1	6	300	11	4	
Clear-cut 2	6	300	11	0	
Clear-cut 3	5	230	18	0	
Clear-cut 4	5	230	14	19	X
Clear-cut 5	5	230	14	12	
Clear-cut 6	4	220	10	0	X
Clear-cut 7	6	300	18	12	
Clear-cut 8	4	220	13	14	X
Clear-cut 9	5	230	12	0	
Clear-cut 10	5	230	17	0	
Clear-cut 11	4	220	12	2	
Clear-cut 12	4	220	14	0	
Clear-cut 13	4	220	14	2	
Clear-cut 14	4	220	10	0	
Clear-cut 15	6	300	10	3	

Replicate = random effect.

used to calculate importance values of the herbs, shrubs and vines; relative density and relative cover were summed and divided by two to determine the importance values of the tree seedlings. These importance values were used to calculate the Shannon and Simpson diversity indices. Average total cover of all native plant species per plot as defined by the four subplots was also calculated. The plots were walked for presence-only data of all herb, shrub, vine and tree species.

In 2013, it became evident in the clear-cuts that adding a cover estimate within the plots in addition to the cover estimates collected in the subplots would help document spread of invasive exotic species. All exotic species within the 400-m^2 area (all forest strata) were estimated for cover as follows. If the shape of the patch was more circular, the largest diameter was measured and a circular area was calculated, and if the shape of the patch was more rectangular, the longest width and length were measured, and the area was calculated. The plot was divided into quarters for larger infestations (greater than 25% of 400-m^2 plot), and cover was initially estimated as a per cent of the quarter covered; these areas were totalled for the full plot. Total areas per species were summed for each plot and averaged for each stand. These plot estimates for all invasive non-native species were continued for the clear-cuts in 2018 and were started for the mature sites in 2017. All non-native species cover was estimated this way.

Also starting in 2013, due to a lack of botanically trained staff, the sampled subplots were limited to those with an invasive non-native plant in or within 0.5 m of the subplot edge in the current or any previous sample year. For instance, if a subplot had no invasive plants in or near it in 2017/2018 but it did in 2012/2013 (or any previous sample year), it was still sampled as were all subplots that currently had an invasive plant species in or within 0.5 m. Thus, the final year of sampling would yield as many or more (but not less than) subplots than previous years. The intent was to focus on direct impacts of invasion on native plant cover, evaluating only subplots that had an invasive plant present in or near them during any sample year.

Invasive exotic species were defined conservatively by several flora (Fernald, 1970; Gleason & Cronquist, 1993; Rhoads & Block, 2000; Strausbaugh & Core, 1977) and by being included as a severe threat on at least two Mid-Atlantic state exotic invasive species lists (Harmon, 1999; Invasive Plant Council of New York, 2003; Maryland Invasive Plant List, 2019; McAvoy, 2001; Native Plant Society of New Jersey, 2003; Pennsylvania Department of Conservation & Natural Resources, 2000; Virginia Department of Conservation & Recreation & Virginia Native Plant Society, 2014). Nomenclature for all species follows the Integrated Taxonomic Information System (ITIS; http://www.itis.gov). The goal was to evaluate common invasive plants known to be invasive regionally, because these plants were more likely to be found in forested areas than less common non-native plants. All non-native plants that were not included on these invasive species lists were also tracked in our surveys. These data were not included in the analyses for this study but may be included in future analyses if their abundances increase or their status is changed to invasive.

Landscape features that served as a surrogate measure of sources of invasive species propagules included distance to the nearest (a) river or body of water, (b) paved road, (c) gravel road, (d) open (non-forested) public land area, (e) open private land and (f) all (general) private land. Measurements were determined from digital 7.5´ series quadrangles, 1:24,000 topographic maps. Private land, especially land with open area, is often associated with current or historic housing or agricultural land use all of which have been correlated with the presence of invasive plants (Gavier-Pizarro et al., 2010; Holmes & Matlack, 2019).

2.3 | Statistical analyses

The following three dependent variables were used as measures of vegetation change: (a) number of invasive plant species (richness) over time averaged per plot for each stand for each year, (b) frequency of invaded plots per stand for each year and (c) cover per plot for the most recent years (2017 for the mature stands and 2013 and 2018 for the clear-cut stands). Models included disturbance type (cut vs. mature), ELT (220, 230 or 300) and year (2001/2002, 2006/2007, 2012/2013 and 2017/2018) and their interactions as independent variables (fixed effects). Stand (defined by ELT and disturbance type) was the random effect. A general linear mixed model (Proc GLIMMIX; SAS 9.4) with a lognormal distribution and identity link function having the best fit was used. All data were increased by 1 to remove zeroes. A Tukey adjusted post hoc comparison of the least square means was conducted for multiple comparisons. Also, multiple comparisons of all levels of one fixed factor (ELT or disturbance type) were compared at a single level of the other fixed factor (ELT or disturbance type) using a SLICEDIFF statement as an option within the LSMEANS statement (Proc GLIMMIX; SAS 9.4). A random statement for year with a AR(1) variance function was used to address the repeated nature of yearly measures using stand as the random effect. Though models with ELT, disturbance type and year together converged, the G matrix was not a positive definite. Consequently, we run the models separately across years for ELT and disturbance type.

Using the same three dependent variables, the six landscape features were run as independent variables in regression models after log-transforming distance to the nearest gravel road, open private area and general private area to meet normality assumptions. The simple regression models were run with both disturbance types together and separately.

The six landscape features were also run as dependent variables with the two disturbance types and three ELTs as independent variables or fixed effects. Stand (number per ELT within disturbance type) was the random effect. Proc GLIMMIX with lognormal distribution and identity link function showed the best fit for distance to nearest gravel roads, open private land and general private land, whereas Proc GLIMMIX using a gaussian distribution and identity link function was used for distance to nearest paved roads, open public land and river.

A change in cover (increase or decrease) of both native and invasive non-native plants and change in richness and diversity (Shannon and Simpson indices calculated in PC-ORD v. 5, MjM Software Design) for the native plants within the subplots were determined by focusing on years 2001/2002 and 2017/2018 for both mature and clear-cut stands. Any subplots with invasive plants in or near them in 2001/2002 were included even if the same subplot did not have an invasive plant in or near it in 2017/2018. Thirty-three subplots in the mature stands, 35 subplots in the clear-cut stands that had no crop-tree release and 33 subplots in the clear-cut stands with crop-tree release met these criteria (Table 1). The change in cover of native and invasive non-native plants within the clear-cut stands was further evaluated using a nonparametric Kruskal–Wallis test (within Proc NPAR1WAY in SAS 9.4) because normality assumptions could not be met, and no other distribution could be fit. The subplots in the three mature stands, 12 clear-cut stands and three clear-cut stands with a crop-tree release were evaluated separately. Changes in native species richness and diversity were also compared with the Kruskal–Wallis test.

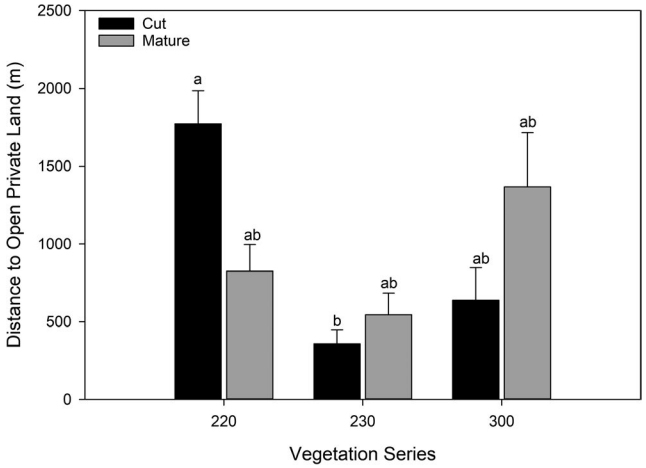


FIGURE 3 A comparison of means and standard errors of distance to nearest general (open or forested) privately owned land by land type (ELT 220, ELT 230 and ELT 300) and disturbance type (cut vs. mature) using a general linear mixed model with a lognormal distribution and identity link function. Variables with different letters are significantly different at a *p*-value of .05

3 | Results

3.1 | Landscape features and invasive plant richness, frequency and abundance

The landscape features were not correlated with invasive species richness, frequency of plots invaded or area covered by invasive plants when the two disturbance types were evaluated together and separately. All regression models had adjusted R^2 values below .02.

None of the landscape features differed significantly when looking only at disturbance type in the GLIMMIX models. However, including ELT and the interaction between disturbance type and ELT as independent variables revealed a significant ($F = 3.62$, $p = .040$) effect of ELT on distance to the nearest open private land, with ELTs 230 and 300 in the clear-cut stands being closer to private land than ELT 220 with ELT 230 clear-cut stands being significantly different from ELT 220 clear-cut stands ($t = 2.56$, $p = .041$). There is a notable trend of the drier ELTs within the clear-cut stands and the more mesic ELTs of the mature stands being closer to open privately owned land (Fig. 3).

3.2 | Most recent invasive plant richness, frequency and abundance values

The mature and clear-cut-stand invasive species that were documented at least once in one or more sample years were *Rosa multiflora* Thunb., *Berberis thunbergii* DC., *Lonicera morrowii* A. Gray, *Elaeagnus umbellata* Thunb., *Microstegium vimineum* (Trin.) A. Camus and *Ailanthus altissima* (Mill.) Swingle. *Rosa multiflora* and *B. thunbergii* were present each year since 2001 (Table 2). Four other exotic species found in growing consistency in the mature and clear-cuts stands that were not defined here as invasive, because they did not make multiple lists, were *Glechoma hederacea* L., *Persicaria posumbu* (Buch.-Ham. ex D. Don) H. Gross, *Stellaria media* (L.) Vill. and *Veronica officinalis* (L.). Analyses that included these additional exotic species for both mature and clear-cut stands did not change the observed patterns or results. All invasive species found in the clear-cuts were also found in the mature forests, but the clear-cuts had greater richness per stand on average (approaching four different invasive species, while mature stands had just above two different species), greater frequency and much higher cover values (Figure 4a–c).

There was an insignificant trend for the drier ELTs in the clear-cut stands to have greater invasive plant richness and the drier ELTs in the mature stands to have lower invasive plant richness. There was a significant interaction ($F = 3.57$, $p = .045$) between ELT and disturbance type for frequency of invaded plots, and disturbance type was marginally significant ($F = 3.84$, $p = .062$). The frequency of invaded plots differed significantly in terms of disturbance type evaluated by ELT with the mature stands showing lower frequency values than the clear-cut stands, only within ELT 300 ($t = 2.16$, $p = .045$). ELT 300 in the mature stands showed lower frequency values than both ELTs 220 ($t = 2.65$, $p = 0.037$) and 230 ($t = 2.50$; $p = .051$). The clear-cut stands had significantly ($F = 6.23$, $p = .021$) more area infested with invasive plants than the mature stands but only for ELT 300 ($t = 2.26$, $p = .034$). The ELTs did not differ significantly in terms of invaded area per plot within each disturbance type (Figure 4a–c).

3.3 | Invasive plant richness, frequency and abundance within disturbance type across ecological land types and over five sampling periods (16 years)

Within the mature stands, invasive plant species richness differed significantly in terms of year ($F = 10.97$, $p = <.0001$) such that 2001

TABLE 2 Invasive plant species documented (marked with an X) in this study by disturbance type, ecological land type (ELT) and year

		Year	*Ailanthus altissima*	*Berberis thunbergii*	*Elaeagnus umbellata*	*Lonicera morrowii*	*Microstegium vimineum*	*Rosa multiflora*
		First USA Record	1784	1864-1879	1873	1894	1919	1886
Disturbance	ELT	First WV Record	1921	1926	1963	1938	1956	1940
Mature	220	2001		x				x
Mature	230	2001		x				x
Mature	300	2001		x				
Mature	220	2006				x	X	x
Mature	230	2006				x		x
Mature	300	2006						x
Mature	220	2012		x			X	x
Mature	230	2012		x	x		X	x
Mature	300	2012		x			X	x
Mature	220	2017		x			X	x
Mature	230	2017	x	x	x	x	X	x
Mature	300	2017		x			X	x
Clear-cut	220	2002		x				x
Clear-cut	230	2002	x	x		x		x
Clear-cut	300	2002		x				x
Clear-cut	220	2007		x				x
Clear-cut	230	2007	x	x				x
Clear-cut	300	2007		x				x
Clear-cut	220	2013		x	x			x
Clear-cut	230	2013	x	x				x
Clear-cut	300	2013		x			X	x
Clear-cut	220	2018		x				x
Clear-cut	230	2018	x	x			X	x
Clear-cut	300	2018	x	x	x		X	x

Estimated years of introduction into the United States and West Virginia are included and derived from a variety of herbaria sources (iDiGBio, 2020, SERNEC, 2020 and Huebner, 2003).

and 2006 both differed from 2012 and 2017. Though ELT did not differ significantly, there was an evident trend of the most mesic ELT (220) having the greatest invasive plant species richness for all years and the driest ELT (300) being the least rich (Figure 5a). Within the clear-cut stands, invasive plant species richness differed significantly in terms of year ($F = 8.85$, $p = .0002$), such that 2002 differed from that in 2013 and 2018; invasive plant species richness in 2007 differed significantly from that in 2018. However, there was a significant interaction with ELT ($F = 2.62$, $p = 0.033$); the richness for ELT 300 surpassed that of the other two ELTs in 2018 (Figure 5b). Evaluating disturbance type separately, the mature stands' frequency of invaded plots differed significantly by year ($F = 15.60$, $p = <.0001$) and ELT ($F = 3.81$, $p = .026$), with the most mesic ELT (220) having the greatest frequency of invaded plots, and year, with the frequency in 2017 being significantly greater than that in 2001 and 2006. The frequency in 2001 was also significantly lower than the frequency in 2012 (Figure 6a). Years differed significantly ($F = 8.73$; $p = .0002$). The year 2002 for clear-cut stands had a lower frequency of invaded plots from frequencies in 2013 and 2018. Though not significant, there was a similar switch in frequencies as there was for richness in 2013 for ELT 300, which surpassed the other two ELTs (Figure 6b).

Because cover was not measured in the mature forest plots in multiple years, increases or decreases in cover cannot be determined at the plot level. Increases were becoming evident in some of the more mesic land types in 2017, when plot-level estimates began. The presence/absence and subplot data show this increase is primarily associated with one ELT 220 mature stand (Figure 7a) in which *M. vimineum* appeared for the first time in 2006 (*M. vimineum* was not found in the clear-cuts until 2013). *Microstegium vimineum* was then documented in subsequent years in all three ELTs of the mature forests, but more frequently in ELT 220, and manifested greater spread than any other invasive plant in the mature stands, with as much as 80 m^2 per 400 m^2

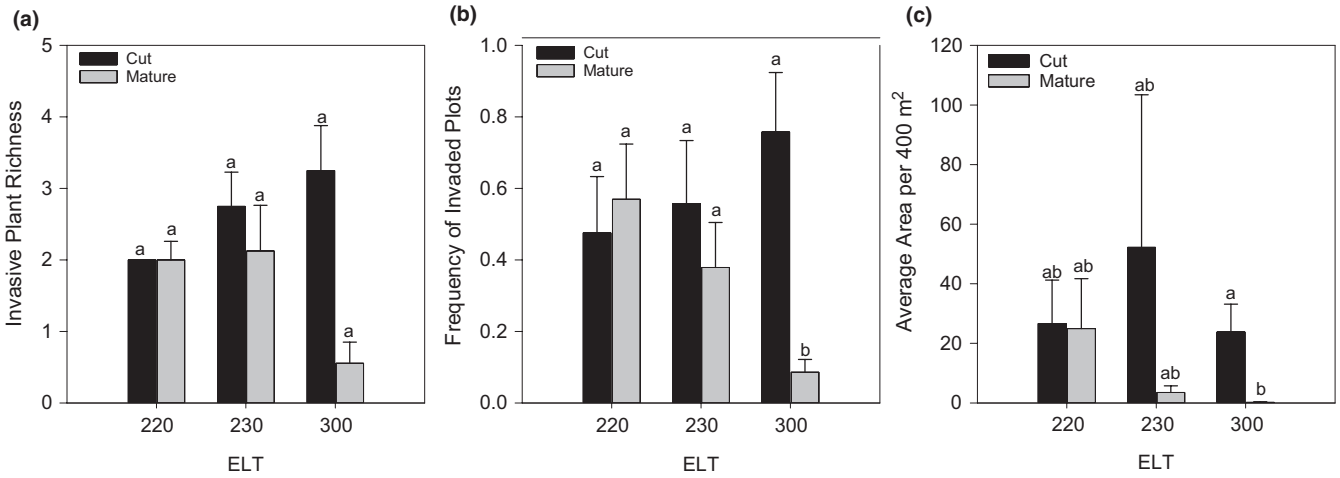


FIGURE 4 A comparison of means and standard errors of invasive plant species (a) richness, (b) frequency and (c) cover by disturbance type (cut vs. mature) and land type (ELT 220, ELT 230 and ELT 300) using a general linear mixed model with a lognormal distribution (increasing all values by 1 to remove any zeroes) and identity link function. Values shown are prior to data transformation. Variables with different letters are significantly different at a *p*-value of .05

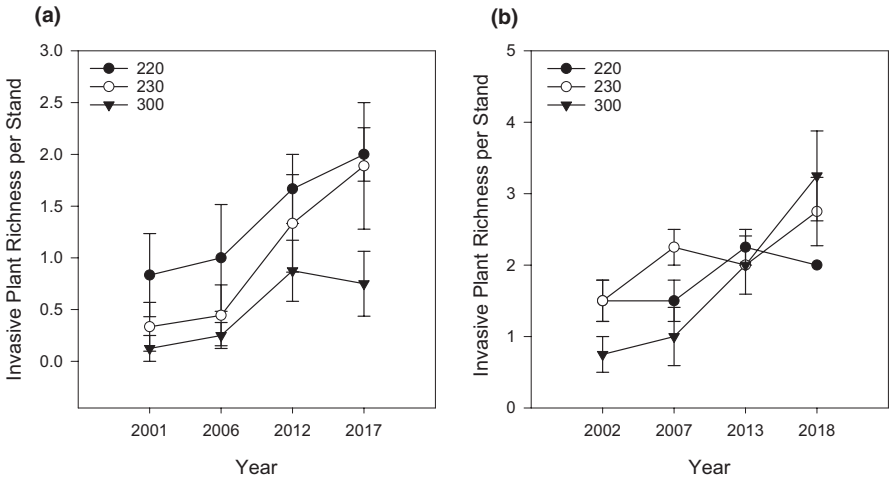


FIGURE 5 A comparison of means and standard errors of invasive plant species richness in (a) mature stands and (b) clear-cut stands by land type (ELT 220, ELT 230 and ELT 300) and time using a general linear mixed model with a lognormal distribution (increasing all values by 1 to remove any zeroes) and identity link function. Values shown are prior to data transformation. A random statement for year with a AR(1) variance function was used to address the repeated nature of yearly measures. Significantly different variables are not shown because of the complexity of the graphs but are stated in the text

plot cover. Invasive plant cover within the clear-cut stands was significantly ($F = 22.33$, $p = .0002$) greater in 2018 than 2013 for all land types. Comparing clear-cut cover with available mature stand data after including year showed the same greater abundance of invasive plants in clear-cuts for ELTs 230 and 300, but not the more mesic 220 (Figure 7a). The effect of crop-tree release was to increase invasive plant cover 4–5 times compared to stands without crop-tree release and about 10 times between 2013–2018 (Figure 7b).

3.4 | Impacts on native plant species

An evaluation of the subplots showed that none of the 23 mature stand subplots that also had an invasive exotic present showed a change in native species cover between 2001 and 2017 (33 subplots had invasives; Table 1). Within the 12 clear-cut stands (35 subplots had invasives), 31% of the subplots that also had an invasive exotic plant present in or within 0.5 m showed a decrease in native plant species cover, 2% showed no change, and 67% showed an increase in native plant species cover between 2002 and 2018. In the three clear-cut stands (none of which were ELT 300) that also had a crop-tree removal, all the subplots (33 total) with an invasive exotic had an increase in native plant species cover. The native species showing increases in the 12 clear-cut understories were not all early-successional ruderal species, though *Rubus* spp. was among the top five species in cover. The native species showing the greatest increase in cover between 2002 and 2018 in order from greatest to least were *Laportea canadensis* (L.) Wedd., *Thelypteris noveboracensis*

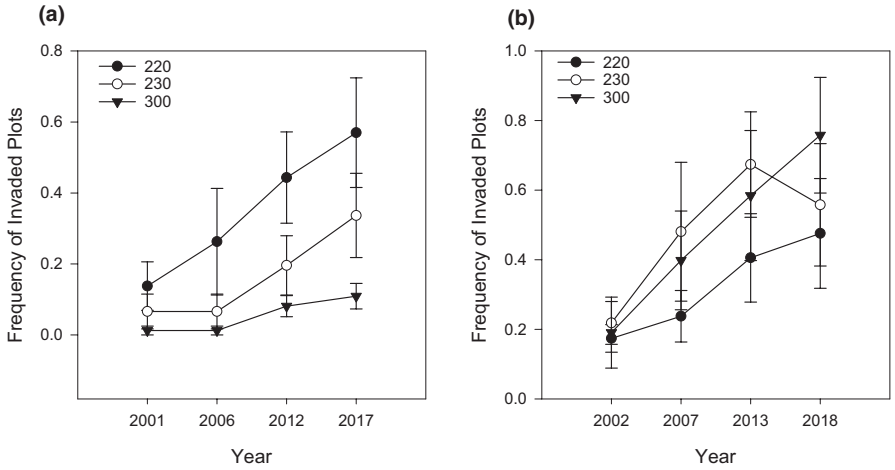


FIGURE 6 A comparison of means and standard errors of invasive plant species frequency in (a) mature stands and (b) clear-cut stands by land type (ELT 220, ELT 230 and ELT 300) and time using a general linear mixed model with a lognormal distribution (increasing all values by 1 to remove any zeroes) and identity link function. Values shown are prior to data transformation. A random statement for year with a AR(1) variance function was used to address the repeated nature of yearly measures. Significantly different values are not shown because of the complexity of the graphs but are stated in the text

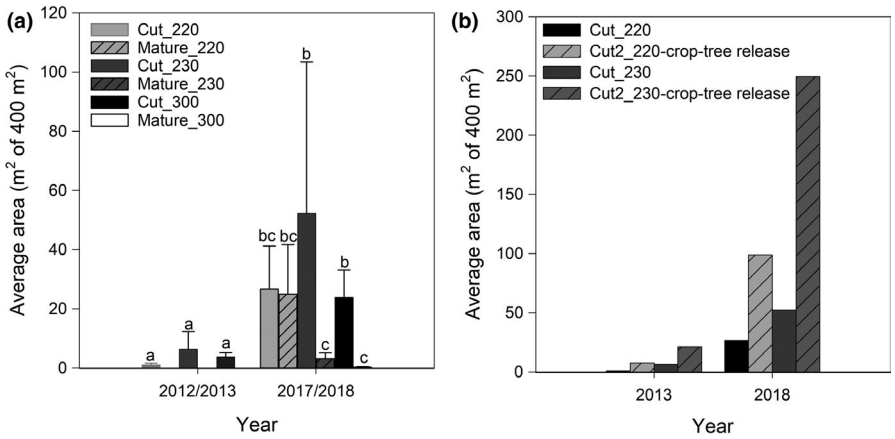


FIGURE 7 A comparison of invasive plant species cover in (a) mature stands and (b) clear-cut stands by land type (ELT 220, ELT 230 and ELT 300) and time using a general linear mixed model with a lognormal distribution (increasing all values by 1 to remove any zeroes) and identity link function. Values shown are prior to data transformation. A random statement for year with a AR(1) variance function was used to address the repeated nature of yearly measures. Variables with different letters are significantly different at a *p*-value of .05

(L.) Nieuwl. *Rubus* L. spp., *Viola pubescens* Aiton., *Polystichum acrostichoides* (Michx.) Schott and *Stellaria pubera* Michx. These changes reflect a response to increasing overstorey cover and decreasing light reaching the understorey. ELTs did not differ significantly in terms of native plant species richness or diversity between the two time periods for either the mature or clear-cut subplots that had been invaded, but richness and diversity increased for ELTs 220 and 230 and decreased for the driest ELT 300, a trend shared with native species cover. The decrease in native species cover and richness noted in ELT 300 stands included small changes in cover of many different species.

Within the clear-cut stands without any crop-tree release, there was a trend for the drier ELTs to show a greater increase in invasive non-native plants than the native plants; the driest ELT showed a decrease in native plant cover (Figure 8a). Both ELTs 220 ($\chi^2 = 6.99$; $p = .0082$) and 230 ($\chi^2 = 12.4$, $p = .0004$) in the stands with crop-tree release had significantly greater increases in native plant cover than invasive non-native plant cover (Figure 8b).

4 | DISCUSSION

4.1 | Question 1

The invasive plants in the mature forests are increasing in species number and frequency over time, and the increase in invasive plants in the mature stands is most notable in the more mesic ELTs, which are closer to private land. Patches of intact forest may be more susceptible to invasion if near a propagule source (Chapman et al., 2015; Gavier-Pizarro et al., 2010). Increases in abundance are

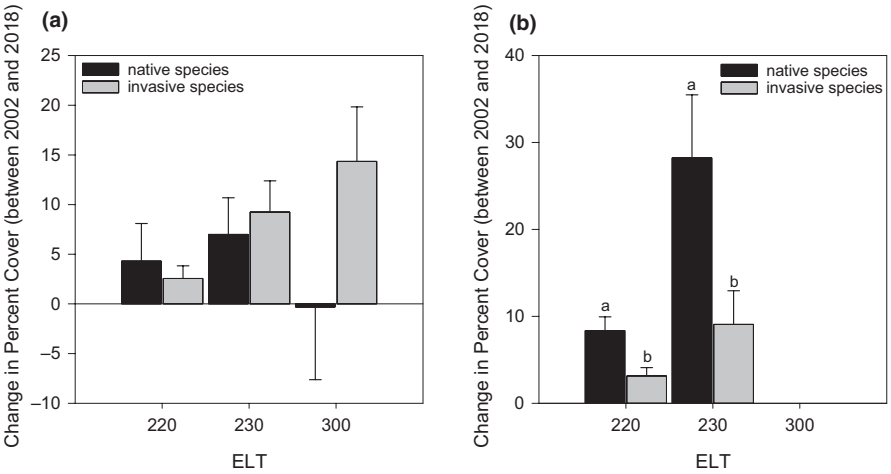


FIGURE 8 A comparison of the change in invasive and native plant species cover between 2002–2018 in (a) clear-cut stands without crop-tree release and (b) clear-cut stands with crop-tree release using a nonparametric Kruskal–Wallis test. Variables with different letters are significantly different at a *p*-value of .05

not yet documented, though presence/absence data from 2001 plots and the large cover estimates support likely cover increases at least in some ELT 220 mature stands. Based on these findings, the invaded mature stands are in early stages of invasion at the management scale, with evident self-perpetuating populations (Richardson et al., 2000).

The differences among the ELTs should not be under-rated. In the final sample year of the mature stands, ELT 220 and ELT 230 have 4x greater invasive plant richness and 4-6x higher invaded plot frequency with the rate of increase being greater in both richness and frequency than the drier ELT 300 stands. ELT 220 stands have 20x greater invasive species cover than both ELT 230 and ELT 300 stands. Though mature ELT 300 stands are furthest from general private land, ELT 230 is closest. Thus, nearness to private land only partly explains the greater invasive plant richness, frequency and abundance manifested by ELT 220 compared with both ELT 230 and ELT 300. The increasing invasion rates provide evidence that invaded mature forests should not be ignored, though there is more time to act. Prioritization of the more mesic invaded mature stands may be a sound management strategy.

Like the mature stands, the clear-cut stands are in early stages of invasion. The rates of invasion are higher than those in the mature stands, but only in ELTs 230 and 300. Both ELT 230 and ELT 300 clear-cut stands are also closer to privately owned land than clear-cut ELT 220 stands, which may explain, in part, the greater richness, frequency and abundance in these clear-cut stands in year 2018, but does not explain why the values are not also greater than ELT 220 stands in prior years. The moderate ELT 230 stands show the greatest invasive plant richness and frequency of invaded plots, but invasive plant richness and frequency in the ELT 300 stands consistently increase in all years at a rate greater than that found for ELT 220 in the mature stands. Invasion rates in ELT 220 clear-cut stands are less than that found for the mature stands, and invasion richness and frequency rates in the ELT 230 clear-cut stands decrease over time. This switch in response to environmental conditions may be due to changing environmental conditions as succession takes place, the growing importance of biotic interactions or both. Decreasing light due to canopy closure in these now 31-year-old clear-cuts is supported by the increases in shade-tolerant understorey native species abundance.

The interactions between native and invasive plants appear to be increasing with time rather than decreasing as predicted by Iacarella et al. (2015), which shows declines in impact starting at longer time periods (50 years or more) than this study (31 years if we assume the clear-cuts were first invaded during the harvest). In this study, cover of invasive plants increases the most for ELT 230 stands, suggesting resource availability may still play a role in invasion success in the clear-cut stands (Funk & Vitousek, 2007; Heberling & Fridley, 2013; Ordonez & Olff, 2013), but the more shade-tolerant native species also continue to benefit relative to the invasive plant cover in the more productive stands. Thus, ELT 220 and ELT 230 stands, which are both more productive with higher species diversity than ELT 300 (Huebner & Tobin, 2006), are exhibiting signs of biotic resistance. Such a response by native species may help keep invasive plants in check, following stochastic and/or neutral niche theory (Gaston & Chown, 2005; Hubbell, 2005; Kennedy et al., 2002; Stohlgren et al., 2008; Tilman, 2004) via competition or coexistence (Aarssen, 1983; Chesson & Warner, 1981; MacDougall et al., 2009; Piglotti & Cencini, 2010).

Conversely, the decrease in native plant abundance in ELT 300 clear-cut stands in response to increasing invasive plant abundance may indicate a growing superior competitive ability of the invasive plants in a more stressful environment. Though harsh sites are generally less invaded (Zefferman et al., 2015) which this article's data support, once these relatively harsh environments are invaded, there are greater negative impacts on native plants, also supported by this research. Environments that may promote invasive plant establishment are not necessarily the same as those that give invasive plants a superior competitive edge over native plants (Brewer & Bailey, 2014).

Based on the most common invasive species found in both the mature and clear-cut forests, this increase is not simply associated with increases in well-known shade-tolerant invasive plants (e.g. *M. vimineum*) (Martin et al., 2009), showing forests are not immune to invasion by shade-intolerant plants as well. However, the shade-tolerant *M. vimineum* shows the greatest cover estimates of

all invasive plants in 2017 in the mature stands, suggesting that with light limitations, shade-tolerant invasive plants may be at an advantage. In contrast, *R. multiflora*, which is shade-intolerant even compared with other relatively shade-intolerant woody invasive species (Heberling & Fridley, 2016), has the greatest cover of all invasive plants in 2018 in the clear-cuts. Many invasive species have higher specific leaf area, leaf-nitrogen content and photosynthetic capacity than native species when grown under the same conditions (Funk & Vitousek, 2007; Heberling & Fridley, 2013, 2016; Ordonez & Olff, 2013), but native forest understorey species also benefit from high resource environments and could be at an advantage over shade-intolerant invasive plants in those environments (Funk & McDaniel, 2010). In studies comparing native and non-native plants, the native species are often selected from the same genus or a pre-defined shared-functional niche or plant traits (Heberling & Fridley, 2013; Ordonez & Olff, 2013; Yannelli et al., 2017) rather than selecting the dominant native species likely to colonize the specific invaded area in question (Gooden & French, 2015). Though the most abundant natives (*L. canadensis* and *T. noveboracensis*) increasing in abundance in the clear-cuts are notably shade-tolerant Kruger & Tabone, 1990)), *L. canadensis* does respond to moderate increases in light, such as found in canopy gaps, with taller and larger plants (Menges, 1987); however, *T. noveboracensis* does not (Hill & Silander, 2001).

The evident interactions with native plants shown in this research indicate that invasion models will be informative. However, given the differences in invasive plant invasion rates between the mature and clear-cut stands and across land types, the use of any single invasion model is likely inadequate (Catford et al., 2009).

4.2 | Question 2

Though increasing invasive plant abundance, frequency and richness are evident, there are still no measurable impacts on native species in all mature forest land types and some land types of the clear-cut forests. There is no invasion model that reflects increasing abundance of invasive plant (with no additional disturbance) without apparent impacts. This condition is tentatively termed the "hitchhiker model," because the invasive plants benefit but the native plant community is not harmed after associating with the invader and is heading in the same direction or successional trajectory.

In terms of management implications, successful restoration of the stands defined by the hitchhiker model would require a continued absence of disturbance or stressors and may also require removal or reduction in the invasive plants at least to a level at which any increases continue to result in no impacts. Time and further increases in invasive plants may eventually result in levels reaching a threshold that transforms these stands into systems that meet the driver (mature stands) or back-seat driver (clear-cut stands) model criteria. It is also possible that the measures of impact in this study are not sensitive enough; additional 1-m^2 subplots per plot may improve detection of impacts on native species, but would also require more time and effort, which are limited commodities in land management.

In contrast, impacts are evident for the clear-cut, drier land types, which follow the back-seat driver model. Restoration success of these stands would, in theory, require a continued absence of disturbance, addressing conditions of a non-resilient forest and removal of the invasive plants (D'Antonio & Chambers, 2006; Gaertner et al., 2014; Hobbs, 2007; Prior et al., 2018; Reid et al., 2009). Because these more stressful sites are least likely to be invaded initially, likelihood of re-invasion in response to disturbing the site again by removing the invasive plant is likely to be moderate (Gabler & Siemann, 2012). Existing biotic resistance in the drier stands is low either due to the low productivity associated with a more stressful site or possibly due to another stressor such as deer herbivory. Though there was no evidence that ELT 300 clear-cuts were any more impacted by deer than the other stands, it is possible regrowth of native vegetation after the harvest in the ELT 300 clear-cuts (oak-dominated) was preferred by deer (Bugalho et al., 2013; Huebner et al., 2018), resulting in a deficit of native vegetation adapted to the site.

Management priorities may be best focused on removing invasive plants from the mature forests (hitchhiker model), especially the more mesic land types, and the drier clear-cut forests (back-seat driver model). The management of the invasive plants in the clear-cut forests following the hitchhiker model (the more mesic ELTs showing similar increases in native plant cover) may be more challenging. In many of these stands, it may be possible to suppress invasive plants to smaller patches on a plot-by-plot basis, perhaps giving the increasing native species an advantage; eradication is not a reasonable goal and may not be needed for recovery (Prior et al., 2018; Reid et al., 2009). However, electing to do nothing with any of the hitchhiker model forests now may ensure a transition to the driver/back-seat driver invasion models in which restoration may be less likely.

This study cannot yet tell us what threshold of invasion must be met before impacts on native species occur. Currently, the productive more mesic clear-cuts show a corresponding increase in native species cover in response to disturbance that appears to quell the effects of the invaders. Also, the lower light-level characteristic of the mature forests may keep abundance low for both native and invasive plant species such that impacts on native species may not be evident until invasive plant abundance reaches similar levels as found in the clear-cut stands.

5 | CONCLUSIONS

A lack of biotic resistance in the drier disturbed stands may explain the apparent impact on native plant species abundance, placing these stands in the back-seat driver invasion model. All other stands fall into the newly suggested hitchhiker invasion model. Increasing invasion in the mature forests may indicate that a threshold could eventually be reached that will result in impacts on the native vegetation, because an increase in native

plant abundance is not likely to accompany this threshold event. Consequently, the drier clear-cut stands and all the mature stands are a priority for restoration. However, the management of the invasions of more mesic clear-cut stands should also be attempted as resources allow, perhaps by reducing local spread from more invaded plots to less invaded plots.

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PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data used in these analyses are available in the Forest Service Research Data Archive (RDA): https://doi.org/10.2737/RDS-2020-0004.

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BIOSKETCH

Cynthia D. Huebner is interested in how invasive and native plant species interact in response to changing environmental conditions and disturbances. This article is one of several studies that fulfil her research mission focused on the effects of invasive plants on forest ecosystems and how best to ameliorate their impacts.

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