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RESEARCH ARTICLE

Functional form and interactions of the drivers of understory non-native plant invasions in northern US forests

Marina Golivets[1,2] | Christopher W. Woodall[3] | Kimberly F. Wallin[1,4]

[1]Rubenstein School of Environment and Natural Resources, University of Vermont, Burlington, VT, USA

[2]Department of Community Ecology, Helmholtz-Centre for Environmental Research – UFZ, Halle, Germany

[3]Northern Research Station, USDA Forest Service, Durham, NH, USA

[4]Northern Research Station, USDA Forest Service, Burlington, VT, USA

Correspondence
Marina Golivets
Email: maryna.golivets@ufz.de

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Abstract

1. The number and rate of non-native plant invasions in forests have been steadily increasing over the last century with profound consequences for the composition, structure and functioning of these ecosystems. While multiple regional, landscape and local environmental factors are known to drive the spread of non-native invasive plant species (NNIPS) into forests, such factors have rarely been analysed within a unified analytical framework allowing for the assessment of their relative importance, possible non-linear behaviour and interactions. Obtaining such knowledge would improve the understanding and allow prediction of forest plant invasions and help prioritize actions for effective NNIPS control and mitigation.
2. We used boosted regression trees and Bayesian non-linear regression to analyse forest inventory data spanning 14 northern US states in combination with data on climate, land use and disturbance. Within each framework, we assessed the magnitude, direction and functional form of the effects of 18 regional to local environmental factors and their interactions on the probability of presence and richness of NNIPS in the forest understory, while controlling for sampling intensity, data collection time and spatial autocorrelation.
3. The studied drivers together captured nearly 50% of the variation in NNIPS occurrence and richness and were sufficient to obtain sensible predictions. Most drivers exhibited monotonic non-linear individual effects and several drivers showed non-additive combined effects. Temperature and landscape openness were the two major determinants of NNIPS presence and richness, but their effects were to a different degree moderated by elevation, climatic and topographic wetness, and stand age. Stand age was a more important predictor of NNIPS invasion than stand productivity. Deer density tended to be positively associated with NNIPS, whereas gypsy moth outbreaks possibly have increased resistance to plant invasions.
4. *Synthesis and applications*. To optimize non-native invasive plant species (NNIPS) control efforts in forests, it is important to explicitly account for the functional form and interactions among the factors operating across spatial and temporal scales. Increasing the average stand age at the landscape and regional levels is

essential for buffering against further invasions. Recurrent canopy disturbance likely slowed down NNIPS invasion previously, yet whether this holds under higher propagule pressure remains unknown.

KEYWORDS
Bayesian, biological invasions, boosted regression trees, drivers of invasion, forest understory, non-native plants, spatial scale

1 | INTRODUCTION

Forest interiors have been traditionally perceived as highly resistant to invasion of non-native vascular plants due to intense light competition and strong biological inertia (Brothers & Spingarn, 1992; Von Holle, Delcourt, & Simberloff, 2003). However, the growing number of non-native plant species invading forest ecosystems locally and globally suggests that our understanding of how novel plant species establish and thrive in forests is incomplete (Fridley, 2008; Martin, Canham, & Marks, 2009). Forests of the northern US have been particularly prone to non-native plant invasions (Iannone et al., 2015; Schulz & Gray, 2013). These forests harbour a globally distinct suite of non-native plant species (Fridley, 2008; Wavrek, Heberling, Fei, & Kalisz, 2017), many of which have had serious impacts on forest species composition, functioning and productivity (Fagan & Peart, 2004; Mascaro & Schnitzer, 2011; Peebles-Spencer, Gorchov, & Crist, 2017; Rodgers, Wolfe, Werden, & Finzi, 2008). While several historical and contemporary factors are known to have facilitated the spread of non-natives into northern US forests (e.g. land-use history: Mosher, Silander, & Latimer, 2009; logging: Lee & Thompson, 2012; novel disturbance regimes: Dávalos, Nuzzo, & Blossey, 2015), their effects have largely been examined independently at small spatial scales. As a result, a general consensus on which factors, at what spatial scales and to what extent promote plant invasion in these ecosystems has not been reached. Without this knowledge, it is difficult to accurately predict current and future non-native plant invasions and develop targeted scale-specific strategies for their control.

Invasion success within and across species is determined by an interplay of multiple ecological and socio-economic factors acting simultaneously or consecutively at different spatial scales and potentially exhibiting non-linear effects (Pauchard & Shea, 2006). Thus, obtaining full understanding of the invasion process requires a unified and flexible analytical framework that allows one to account for cross-time and cross-scale interactions among potential drivers and nonlinearity (Higgins & Richardson, 1998; Milbau, Stout, Graae, & Nijs, 2009). Although such an approach is demanding in terms of data quality and quantity, using it to understand the drivers of non-native plant invasions in northern US forests is much needed and feasible for at least two reasons. First, standardized non-native plant data from national forest inventories and high-quality environmental data have recently become available for this region, which solves the data limitation problem. Second, as many non-native species in these forests are at their late stage of invasion – and thereby approaching equilibrium within their environment – it is possible to discern propagule pressure from habitat invasibility, reliably assess the importance of individual drivers of invasion and accurately predict patterns of non-native plant invasion (Jones, 2012).

In addition to the high contextuality and dispersion of the evidence regarding the factors promoting non-native plant invasions in northern US forests, some potentially important invasion drivers have received disproportionally little attention from researchers. Remarkably, we do not know whether the spread of non-native plants into these forests is associated with non-native invasive insect disturbance, a major agent of forest succession in the region (Morin & Liebhold, 2015). It has been hypothesized that such disturbance may facilitate the establishment and further spread of non-native plants via increased resource availability and altered resource competition dynamics (Gandhi & Herms, 2010; McEwan, Rieske, & Arthur, 2009). Indeed, an increase in non-native plants richness and abundance following non-native insect outbreaks has been reported for some systems (e.g. Eschtruth & Battles, 2009; Hoven, Gorchov, Knight, & Peters, 2017). More generally, however, this relationship is likely contingent upon the type and intensity of disturbance and propagule availability. For instance, when the system is able to recover quickly after disturbance, the opportunity window may be simply too short for non-native plants to respond. Alternatively, post-outbreak conditions may be, contrary to common logic, less favourable for non-native plants due to intensified competition with native understory species, nutrient leaching or translocation, or increased rates of insect and pathogen attacks. Clearly, as insect outbreaks are becoming more common and intense (Dukes et al., 2009; Weed, Ayres, & Hicke, 2013), more research into their consequences for the spread of other non-native organisms is warranted.

Here we perform a comprehensive assessment of climate, land use, topography, disturbance and stand characteristics as the drivers of understory non-native plant species invasions in northern US forests within a unified analytical framework. We model georeferenced, plot-level non-native invasive plant species (NNIPS) presence–absence and richness data spanning 14 northern US states as a function of all the drivers and develop models with highest possible predictive accuracy, based on which we assess the magnitude, direction and functional form of the drivers of NNIPS invasion and their interactions. The results of this study refine our understanding of the multiple drivers of forest plant invasions and provide a set of statistical models which can be used to develop plant invasion

predictions to prioritizing scale-specific NNIPS management decisions under current and future environmental conditions.

2 | MATERIALS AND METHODS

2.1 | Data collection

We obtained NNIPS data from the USDA Forest Service's Forest Inventory and Analysis (FIA) Program database v.1.7.2.00 (FIADB; Forest Inventory & Analysis Database, 2018). The FIA Program conducts a three-phase inventory of forest attributes on permanent plots across the country (Bechtold & Patterson, 2005). In Phase 2, plots (one plot per 2,428 ha) consisting of four circular 168.3 m^2 subplots are visited on the ground where detailed tree and forest stand data, along with topographic site information, are collected. Since 2007, data on the presence and per cent cover of 44 NNIPS have been additionally collected on a subset of Phase 2 plots in the northern US (Kurtz, 2013). These data are provided at the subplot level for each forest condition class (defined based on land use and vegetation) present. We aggregated NNIPS data at the condition class level and used data only for the dominant (i.e. comprising largest area or, in cases of a tie, the condition at the centre of subplot one) condition class. We determined NNIPS presence–absence and richness (i.e. total number of species) for each selected condition and used these two metrics as response variables in our analyses. We restricted our dataset to field-visited plots where all four subplots were surveyed using the national plot design and where accessible forest land was present in at least one subplot, excluding exotic tree plantations. For plots that were surveyed twice between 2007 and 2016, we used the most recent data.

For all FIA plots, we assembled data on climate, land use, topography, disturbance and stand characteristics along with the area sampled and year of the FIA measurement, all of which were used as predictor variables in our models (Table 1). Our final dataset comprised observations from 5,624 FIA plots sampled between 2007 and 2016 (Figure 1).

2.2 | Data analysis

We independently modelled NNIPS presence–absence and richness as functions of all potential predictors using two distinct modelling techniques, boosted regression trees (BRT) and Bayesian non-linear regression. BRT offer an efficient way of developing a predictive framework in the presence of high number of predictor variables and complex interactions among them, whereas Bayesian non-linear regression allows to have more control over the relationships and correlative structures in the data but also requires more prior knowledge and computational resources. The models for NNIPS presence–absence had a Bernoulli error distribution and a logit link function and the models for NNIPS richness had a Poisson error distribution and a logarithmic link function. Prior to analyses, we ensured that predictors were not highly correlated (|Pearson's r| < .7) and, upon preliminary analyses, excluded per cent forested areas from regression models because we could not estimate it reliably due to high correlation with per cent open areas (r = .65). All analyses were performed in R v.3.5.0 (R Core Team, 2018).

2.2.1 | Boosted regression trees

Boosted regression trees are an ensemble technique that combines regression trees and boosting algorithms to provide an additive model in which individual terms are regression trees, fitted in a forward, stagewise fashion (De'ath, 2007). BRT do not require prior data transformation, are not sensitive to outliers, can accommodate nonlinearities and complex interactions, and are suited for both inferential and predictive modelling (Elith, Leathwick, & Hastie, 2008). We used the packages *gbm* (Ridgeway, 2017) and *dismo* (Hijmans, Phillips, Leathwick, & Elith, 2017) to fit BRT models. We initially fitted models with different combinations of tree complexity (tc), bag fraction (bf) and learning rate (lr) using the function *'gbm.step'* in *dismo*. The models comprising less than 1,000 trees (nt) were then discarded as those that did not meet the recommended BRT model size (Elith et al., 2008) and the remaining models were compared against their predictive performance. To account for the stochasticity component of BRT, we re-fitted final models 100 times and calculated the median and the range (the minimum and maximum values) of the 100 model runs for all outputs. When detected, residual spatial autocorrelation was modelled using the residual autocovariate (RAC) approach (Crase, Liedloff, & Wintle, 2012; see Appendix S1 in Supporting Information for more details).

We evaluated predictive performance of BRT models based on 10-fold cross-validation (CV) using the area under the receiver operating curve (AUC_{CV}; only for presence–absence data), the proportion of deviance explained (DE_{CV}) and correlation between observed and predicted values (r_{CV}) calculated across held-out CV folds. AUC provides an aggregate measure of classification performance across all possible thresholds; AUC of 0.5 means that a classifier performs not better than a random coin toss and AUC of 1 indicates a perfect classifier. DE_{CV} was calculated as the ratio of the null deviance minus the residual deviance to the null deviance. Predictive potential of individual predictors was assessed by calculating their relative importance, which was based on the number of times a given predictor was selected for tree splitting, weighted by the deviance reduction at each split, averaged over all trees (Friedman, 2001). We explored the interactions between predictor variables using the *gbm.interactions* function in *dismo*. The form of the relationship between individual predictors and the response variable was evaluated by visualizing marginal (i.e. averaged over the effects of other predictors) effects calculated with the package *pdp* (Greenwell, 2017).

2.2.2 | Bayesian non-linear regression

We performed full Bayesian statistical inference using the Hamiltonian Monte Carlo sampling algorithm implemented in the modelling software Stan (Carpenter et al., 2017) via the function

TABLE 1 Description of the studied drivers of understory non-native vascular plant invasions in northern US forests

Predictor	Definition	Measurement scale	Value range	Measurement unit	Spatial scale	Spatial resolution	Source
Area surveyed	Total area of the surveyed condition (i.e. sampling effort)	Continuous	4.7 to 673.3	m^2	Local	Condition	FIADB
Basal area	Basal area of all live trees ≥2.54 cm DBH sampled in the condition	Continuous	0.1 to 80.0	m^2/ha	Local	Condition	FIADB
Canopy defoliation	Occurrence of the gypsy moth (*Lymantria dispar* (L.)) canopy defoliation (1970–2015)	Categorical	Not defoliated (*N* = 4,199); defoliated (*N* = 1,425)	Unitless	Local	Varying	See Supplemental Methods
Deer density	White-tailed deer (*Odocoileus virginianus* Zimmerman) density (2001–2005)	Ordinal	1 (<5.8 deer/km^2) to 4 (>17.4 deer/km^2)	Unitless	Landscape	County	Walters, Woodall, and Russell (2016)
% Developed areas	Per cent developed areas in the landscape (2-km radius)	Continuous	0 to 86.9	%	Landscape	30 m	NLCD 2006 (Fry et al., 2011), NLCD 2011 (Homer et al., 2015)
Distance to road	The straight-line distance from plot centre to the nearest improved road	Ordinal	1 (≤30 m) to 9 (≥8,047 m)	Unitless	Landscape	Plot	FIADB
Disturbance	An indicator of whether abiotic, biotic or anthropogenic disturbance occurred since the last inventory or within the last 5 years	Categorical	Undisturbed (*N* = 4,965); disturbed (*N* = 659)	Unitless	Local	Condition	FIADB
Elevation	The distance the plot is located above sea level	Continuous	0 to 1,048.5	m	Local	Plot	FIADB
% Forested areas	Per cent forested areas in the landscape (2- and 5-km radii)	Continuous	10 to 100	%	Landscape	30 m	NLCD 2006, NLCD 2011
Forest type	A broad forest type category	Categorical	AsBr – aspen and birch (*N* = 419); ElAsh – elm and ash (*N* = 498); Mp – maple and other broadleaves (*N* = 1,893); OkPn – oak and pine (*N* = 173); Ok – oak-dominated (*N* = 1,841); Pn – pine (*N* = 418); Sp – spruce (*N* = 482)	Unitless	Local	Condition	derived from FIADB
MAT	Mean annual temperature	Continuous	2.1 to 14.3	°C	Regional	1 km	WorldClim (Fick & Hijmans, 2017)
% Open areas	Per cent open areas in the landscape (2- and 5-km radius)	Continuous	0 to 84.2	%	Landscape	30 m	NLCD 2006, NLCD 2011
Slope	The angle of slope	Continuous	0 to 70	%	Local	Plot	FIADB

(Continues)

TABLE 1 (Continued)

Predictor	Definition	Measurement scale	Value range	Measurement unit	Spatial scale	Spatial resolution	Source
Stand age	Average age of a subset of dominant and co-dominant trees on a plot	Continuous	19 to 150	Years	Local	Condition	FIADB
Stand origin	An indicator of whether a stand was artificially regenerated	Categorical	Natural; planted	Unitless	Local	Condition	FIADB
Summer precipitation	Precipitation of warmest quarter	Continuous	208 to 399	mm	Regional	1 km	WorldClim
TAP	Total annual precipitation	Continuous	700 to 1,481	mm	Regional	1 km	WorldClim
Temperature seasonality	Temperature seasonality (standard deviation derived from monthly temperature values)	Continuous	8.4 to 11.9	°C	Regional	1 km	WorldClim
Topographic wetness	The general effect of land form, topographical position and soil on moisture available to trees	Ordinal	1 (xeric) to 3 (moist)	Unitless	Local	Condition	FIADB
Year	The year of FIA survey	Continuous	2007 to 2016	Unitless	Local	Plot	FIADB

'*brm*' in the package *brms* (Bürkner, 2017). For NNIPS presence–absence and richness, we independently developed global models that included main effects for all predictors and ecologically plausible two-way interactions between predictors. Non-linear relationships were modelled by including spline-based smooth terms into the models using the functions '*s*' and '*t2*' from the package *mgcv* (Wood, 2017). Prior to analyses, we log-transformed per cent developed areas and zero-centred and scaled continuous predictors to improve model fitting and facilitate variable selection. Predictors measured on an ordinal scale were modelled using monotonic transformation as implemented in *brms*.

To identify the most parsimonious model with highest predictive accuracy, we first fitted multiple reduced models following a combination of stepwise backward and forward variable selection and compared their performances using the approximate leave-one-out CV as implemented in the package *loo* (Vehtari, Gabry, Yao, & Gelman, 2018). We used the LOO information criterion (LOOIC), LOO-corrected *AUC* (AUC_{LOO}) and R^2 (R^2_{LOO}) as the measures of predictive performance. We assessed and accounted for spatial autocorrelation in the posterior means of the residuals of the model with lowest LOOIC using the same methods as in BRT analyses. We report posterior distributions as posterior means and 95% posterior credible intervals. We considered an effect significant if its 95% posterior credible interval did not contain zero and assessed its magnitude and functional form based on its marginal effect. Other details on model specification and evaluation are provided in Appendix S1.

3 | RESULTS

3.1 | NNIPS presence

Non-native plant species were recorded in 2,563 (45.6%) plots (Figure 1). The final models exhibited good predictive performance, with a slight advantage of the BRT model (BRT: AUC_{CV} = 0.9; DE_{CV} = 42.3%–43.2%, r_{CV} = 0.71; regression: AUC_{LOO} = 0.83; R^2_{LOO} = 0.50) and provided overall agreeing results. The BRT model contained all predictors except stand origin and recent disturbance, which were removed as non-informative, and its residuals were not spatially autocorrelated. The regression model did not include stand origin, recent disturbance, forest type and deer density and was somewhat improved after residual spatial autocorrelation was accounted for (Δ LOOIC = 51.3 ± 15.7 *SE*). Other discrepancies between the models concerned the magnitude and, in some cases, functional form of marginal effects (e.g. MAT and elevation had a non-monotonic effect in the BRT but not in the regression model; Figures 2 and 3) as well as the number of interaction terms (Figures S1 and S2).

In the BRT model, landscape openness (i.e. per cent open areas) and MAT were, by far, the two major predictors of NNIPS presence (Figure 2; predictors' relative contributions are shown in the X-axis titles). The marginal effect of landscape openness steeply increased in the range 0%–20% and reached a plateau; under the average conditions, c. 12% open areas was sufficient to

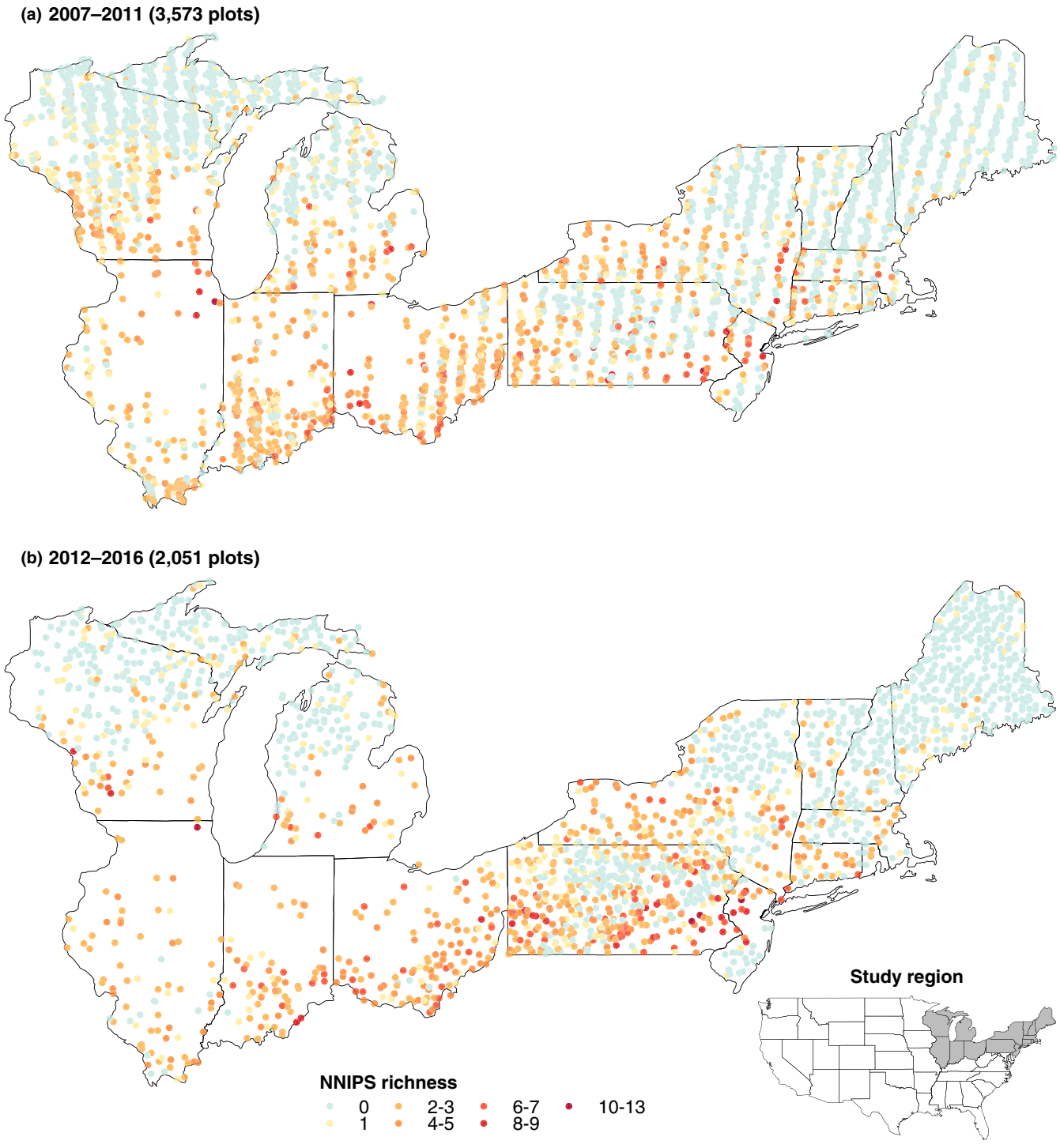

FIGURE 1 Geographical location of and non-native invasive plant species (NNIPS) richness in the Phase 2 USDA Forest Service's Forest and Inventory Analysis Program plots (N = 5,624). NNIPS richness for the dominant forest condition class is shown. The study region includes 14 US states (CT, IL, IN, MA, ME, MI, NH, NJ, NY, OH, PA, RI, VT and WI). In compliance with the FIA Program confidentiality requirements, a perturbation was applied to plot geographical coordinates prior to plotting

increase the probability of NNIPS presence over 0.5 (Figure 2a). MAT exhibited a positive effect for the most part of its range, with the marginal probability of NNIPS presence reaching 0.83 at 10.6°C (Figure 2b), and interacted with elevation, temperature seasonality, landscape openness, summer precipitation, soil wetness and stand age (Figure S1). The probability of NNIPS presence increased over time and was further enhanced by higher per cent developed areas, summer precipitation, topographic wetness, sampling effort and deer density. Meanwhile, several factors were negatively associated with NNIPS presence, with stand age being the most influential. Temperature seasonality had a non-monotonic relationship and in addition to MAT, interacted with the FIA

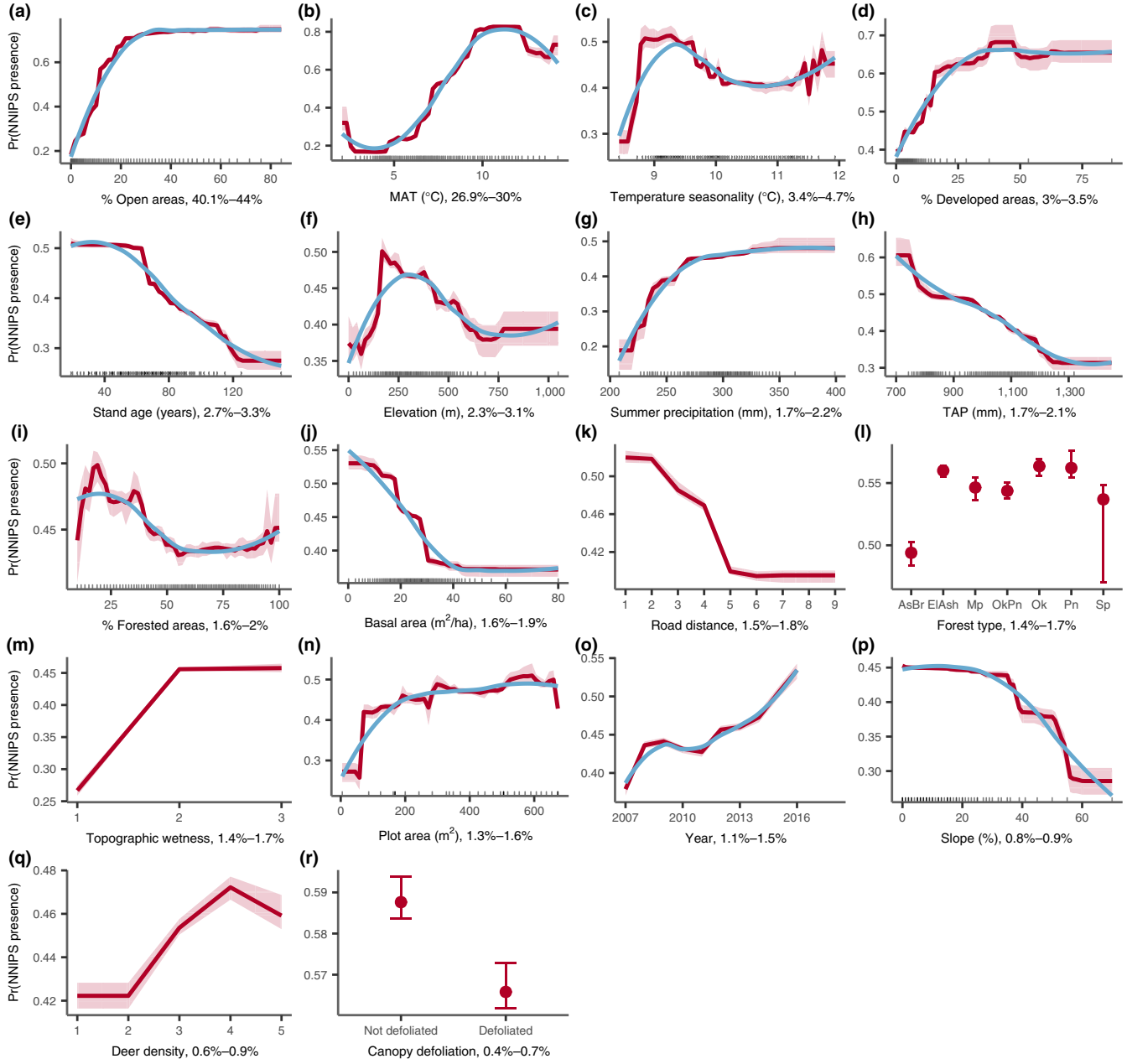

FIGURE 2 Marginal effects of the predictors of non-native invasive plant species (NNIPS) presence in the final boosted regression tree model (tc = 5, lr = 0.015, bf = 0.7, nt = 1,000–1,550). Red lines/points and their bands/error bars indicate the median and the range, respectively, and blue lines indicate the smoothed average for 100 model runs. Relative contributions (% range) of individual predictors are provided in the X-axis titles. Rug plots on the inside of the X-axes show the distributions of the data points along individual predictor gradients, in percentiles. Note the different scales of the Y-axes. For information on the predictors, see Table 1

survey year (Figure S1i). Finally, aspen-birch forests and previously defoliated stands were less likely to contain NNIPS.

In the regression model, the strongest associations were with MAT, TAP, summer precipitation and RAC, followed by landscape openness and temperature seasonality (Figure 3).

3.2 | NNIPS richness

NNIPS richness was on average 1.19 ± 1.76 *SD* (Figure 1). Accounting for spatial autocorrelation in residuals improved the predictive accuracy of both BRT (ΔDE_{CV} = 0.8%–1%) and Bayesian regression models (ΔLOOIC = 236.8 ± 34.7 *SE*). Both models showed similar predictive performance (BRT: DE_{CV} = 55.9%–56.3%, r_{CV} = 0.72–0.73; regression: R^2_{LOO} = 0.54). All predictors except stand origin and canopy defoliation were retained in the final BRT, whereas the regression model did not contain slope, stand origin, recent disturbance, forest type and deer density. Meanwhile, the regression model included more interaction terms than the BRT model (Figures S3 and S4). The model agreed as regard to the functional form of the predictors in common except for RAC, which had a

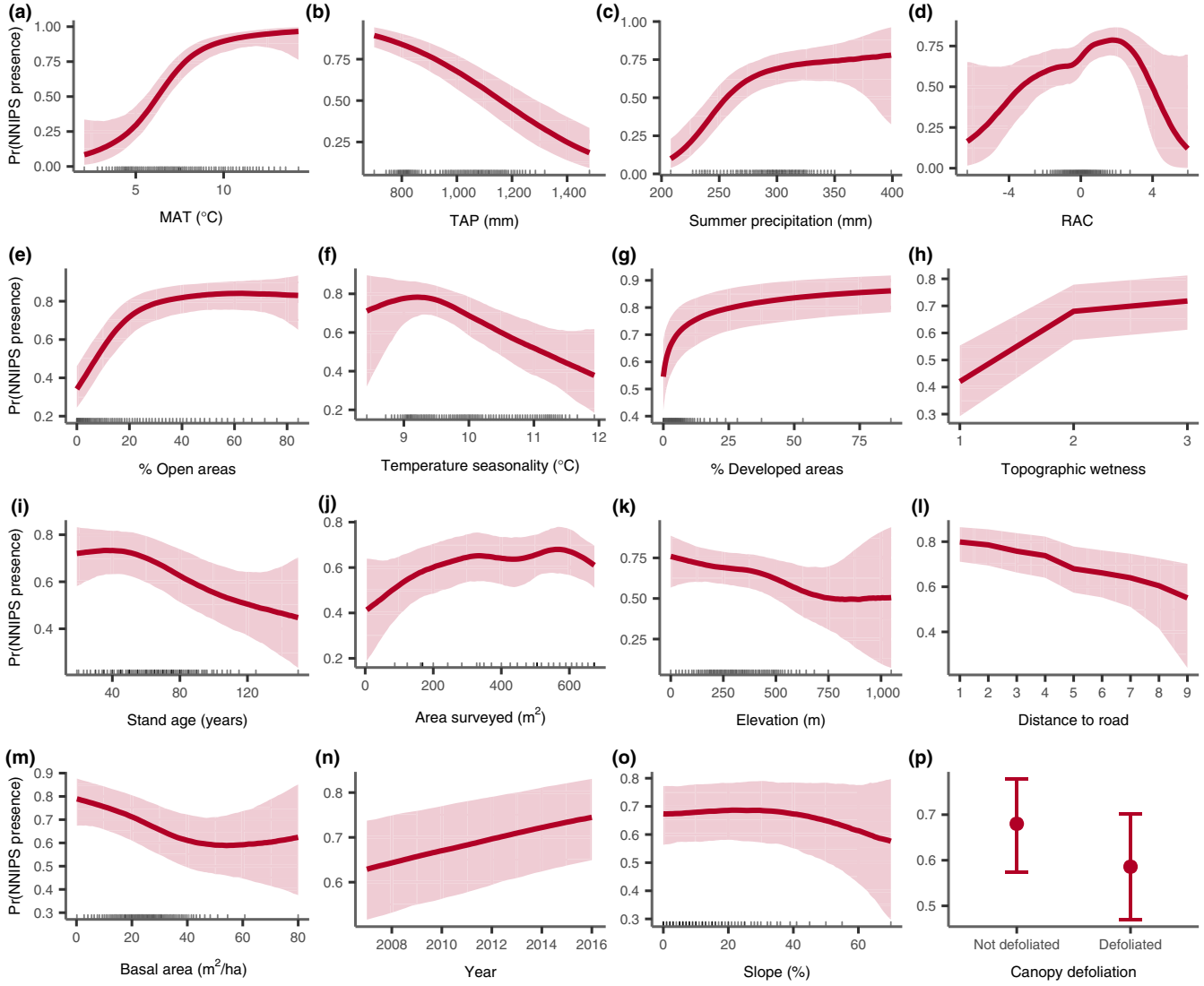

FIGURE 3 Marginal effects of the predictors of non-native invasive plant species (NNIPS) presence in the final Bayesian regression model. Lines/points indicate posterior means and bands/error bars indicate posterior 95% credible intervals. Other details are as in Figure 2

unimodal effect in the BRT and a nearly linear effect in the regression (Figures 4 and 5).

Compared to the presence–absence model, the relative contributions of the individual drivers in the species richness BRT model were more balanced, although there still was a clear hierarchy, with MAT, per cent open and developed areas, stand age and temperature seasonality being the top five predictors (Figure 4). Per cent open and developed areas each exhibited close to linear effect on NNIPS richness, and high proportion of either of them in the landscape guaranteed the presence of one additional NNIPS on average. Other associations were similar to those in the presence–absence model.

In the regression model, NNIPS richness was most strongly associated with MAT, TAP, per cent open and developed areas, and summer precipitation (Figure 5). The regression model also depicted several significant interactions, which were absent from the BRT model: the effect of developed areas was more pronounced as summer precipitation and plot area increased; the effect of landscape openness was on dry sites at close proximity to roads (Figure S4). Moreover, the negative effect of canopy defoliation became stronger as forest age increased (Figure S4g), potentially suggesting that forests with higher cumulative defoliation severity are less favoured by NNIPS (Figure S5).

4 | DISCUSSION

In this study, we coupled forest inventory data and high-resolution environmental information collected over a large spatial extent within a unified analytical framework, which allowed us to accurately quantify the importance and function of the 18 drivers of non-native plant invasions in northern US forest understories. All the drivers excluding stand origin explained the patterns of NNIPS presence and richness to a varying degree and jointly provided sensible predictions. By considering all the drivers simultaneously, we not only untangled their individual effects, which were often nonlinear (Figures 2–5), but also revealed multiple interactions among

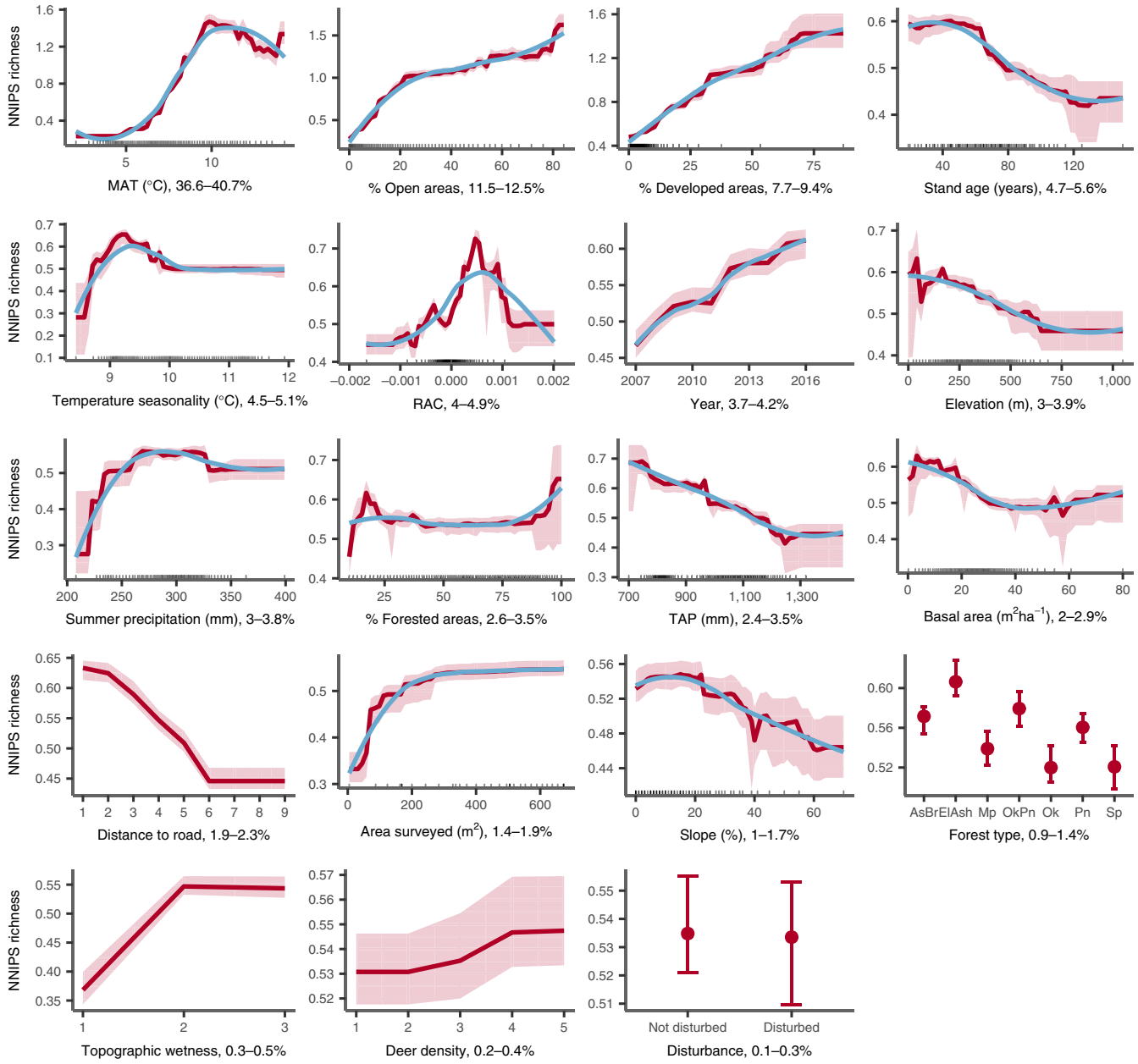

FIGURE 4 Marginal effects of the predictors of non-native invasive plant species (NNIPS) richness in the final boosted regression tree model (tc = 10, bf = 0.7, lr = 0.015, nt = 1,000–1,150). Other details as in Figure 2

them (Figures S1–S4). Although both BRT and Bayesian non-linear regression proved to be suitable for revealing the complex behaviour of the invasion drivers and provided largely agreeing results, there were differences regarding the magnitude and functional form of the effects of individual predictors and their interactions. The presence–absence models resulting from the two approaches were more similar to each other than the species richness models, which might be at least partially due to the fact that we explicitly did not model interactions between RAC and other predictors in the regression models, while in the BRT we could not control which interactions were modelled. Given the complexity and multidimensionality of the invasion process, we tend to consider BRT a more reliable and efficient way to infer about the drivers of invasion in the presence of sufficient amount of data, yet we believe that the issue of appropriately accounting for residual spatial autocorrelation in BRT deserves further discussion.

We also showed that, despite some redundancy in the species presence and richness analyses due to the high number of zeroes in the data, individual drivers ranked differently in terms of their predictive importance for NNIPS presence and richness and, in some cases, also had different functional relationships with these two invasion measures. For example, in the BRT analyses, per cent developed areas was only slightly less important for predicting NNIPS richness than per cent open areas (Figure 3b,c), whereas for NNIPS presence, landscape openness was clearly the most important driver (Figure 2). Additionally, the effects of per cent open and developed

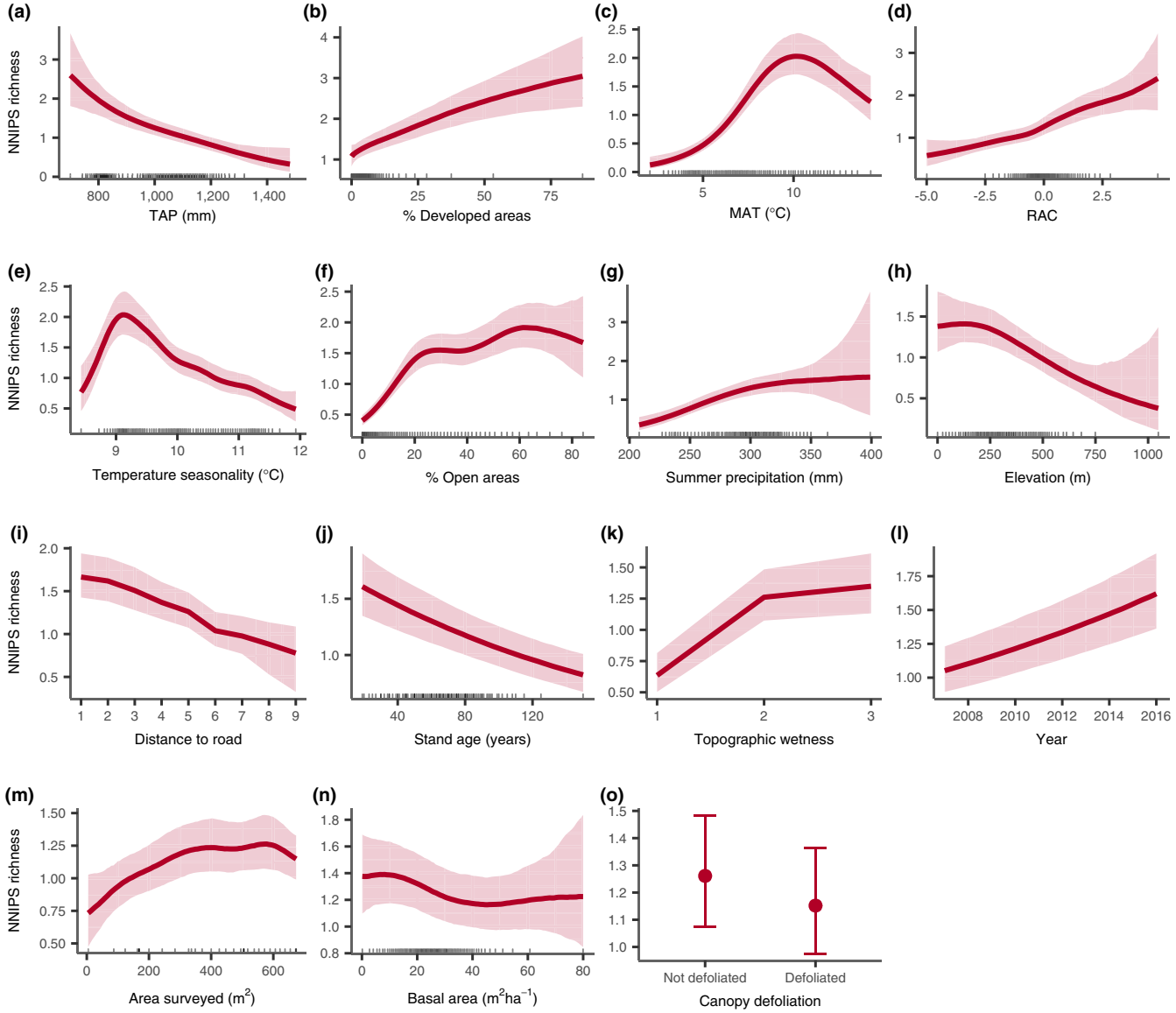

FIGURE 5 Marginal effects of the predictors of non-native invasive plant species (NNIPS) richness in the final Bayesian regression model. Lines/points indicate posterior means and bands/error bars indicate posterior 95% credible intervals. Other details are as in Figure 2

areas on NNIPS presence both quickly saturated, while their effects on NNIPS richness were close to linear. This suggests that different facets of plant invasion may be determined by distinct sets of factors, and therefore multiple measures of invasion should be preferably incorporated into analyses and NNIPS management strategies. Moreover, we demonstrated the need to control for sampling effort, data collection time and residual spatial autocorrelation to obtain unbiased inference about the process of plant invasion. Overall, in addition to corroborating and refining the findings of the previous studies (Bartuszevige, Gorchov, & Raab, 2006; Flory & Clay, 2006; Iannone et al., 2015; Ibáñez, Silander, Allen, Treanor, & Wilson, 2009; Riitters et al., 2018; Vila & Ibáñez, 2011), our study has successfully incorporated several previously overlooked sources of complexity into our understanding of plant invasions in the forest.

As expected, given the large geographical extent of our study region, macroclimatic variables altogether explained the majority of the variation in the invasion measures, and MAT was the most or second most influential predictor in our models, in line with the existent evidence for the temperate forest biome (Ibáñez et al., 2009; Ohlemüller, Walker, & Wilson, 2006; Pyšek, Jarošík, & Kučera, 2002). Despite the overall dominance of the macroclimatic effect, several individual landscape- and local-scale drivers also showed strong associations with NNIPS presence and richness. In fact, for NNIPS presence the BRT analysis revealed that landscape openness was even more important than MAT, whereas stand age was among the five most influential predictors (Figures 2 and 4). Likewise, the amount of developed areas had larger influence on NNIPS richness than all microclimatic variables except MAT (Figure 4). These results undoubtedly suggest that incorporating landscape- and local-level information into macroscale assessments of forest plant invasions is as important as accounting for macroclimatic gradients. High-context dependency of the

invasion drivers' effects, as depicted by multiple significant interactions in our final models (Figures S1–S4), further underlines the necessity of developing management strategies to tackle forest plant invasions that would be based on high-quality data and explicit understanding of how invasion drivers operate across spatial scales.

Interestingly, the effect of biotic disturbance on NNIPS was agent dependent. Deer density had a positive but very weak association with NNIPS, thus only partially supporting the previous evidence of direct and indirect NNIPS facilitation by overabundant deer (Knight, Dunn, Smith, Davis, & Kalisz, 2009). It is worth noting, however, that the spatial resolution and precision of deer density data were quite low, and this might have caused inability to quantify the effect of deer density more precisely. Meanwhile, contrary to what has been suggested (Gandhi & Herms, 2010; McEwan et al., 2009), past canopy defoliation resulting from gypsy moth outbreaks was negatively associated with NNIPS presence and richness, indicating that these disturbances may have created less favourable conditions for NNIPS establishment and spread. Increased canopy openness may have boosted the growth of native understory plants (Collins, 1961; Jedlicka, Vandermeer, Aviles-Vazquez, Barros, & Perfecto, 2004), intensifying resource competition and making it more difficult for non-natives to establish. The negative long-term effect of defoliation on non-native plants could also be attributed to decreased nitrogen availability due to its leakage, microbial immobilization and/or redistribution in the system (Christenson, Lovett, Mitchell, & Groffman, 2002). For NNIPS richness, we also detected a significant interaction between defoliation occurrence and stand age, although only in the regression model (Figure S4g). As stand age correlated with the total number of defoliation events (Figure S5), this finding further suggests that gypsy moth canopy disturbance enhances forest resistance for NNIPS. Future inquiries into this question would benefit from explicitly accounting for the timing and severity of defoliation events and incorporating additional data (e.g. native plant and soil data) into analyses, as well from undertaking experimental and/or time-series study approach.

Although our set of predictors of non-native plant invasion was sufficient to obtain realistic predictions, it is not final or exhaustive. Depending on the level of precision required for meeting specific management goals, this list can be further extended or reduced. In particular, detection of strong residual spatial autocorrelation when modelling NNIPS points out that either certain important predictors may have been omitted or local NNIPS spread needs to be modelled explicitly. In the presented analyses, we did not fully embrace the land-use and forest management history, both of which facilitated plant invasions in the study region in the past and may continue to do so (Beauséjour, Handa, Lechowicz, Gilbert, & Vellend, 2015; Mosher et al., 2009). Moreover, we did not account for soil characteristics and other potentially important biotic factors (e.g. the presence of non-native invasive earthworms), yet these factors can potentially alter forest susceptibility to plant invasions (Dávalos et al., 2015). Importantly, we observed an increase in the level of NNIPS invasion over time, which is indicative of the ongoing plant invasion in northern US forests but also might reflect an increase in species detection due to additional training and experience obtained each year. As more FIA plots are re-surveyed, time-series analysis is a promising next step towards predicting future trends of NNIPS invasions in the region.

5 | CONCLUSIONS

Our study provided a detailed assessment of the drivers of forest plant invasions that operate at different spatial scales. We demonstrated that environmental factors often showed non-linear associations and jointly exhibited non-additive effects on the probability of NNIPS presence and NNIPS richness. We also showed that across the multiple environmental gradients captured in our data, stand age was consistently the most important indicator of forest resistance to plant invasions. Additionally, we highlighted the need to account for data collection time in macroscale analyses of plant invasions, even for relatively short time frames as ours. Finally, we detected a negative association between invasive insect canopy defoliation and understory NNIPS, which broadens our understanding of the role of disturbance in promoting plant invasions in forests.

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AUTHORS' CONTRIBUTIONS

M.G. conceived the idea and designed methodology; M.G. and C.W.W. collected the data; M.G. analysed the data and wrote the first draft of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository http://doi.org/10.5061/dryad.h8b6vs2 (Golivets, Woodall, & Wallin, 2019).

ORCID

Marina Golivets https://orcid.org/0000-0003-1278-2663

REFERENCES

Bartuszevige, A. M., Gorchov, D. L., & Raab, L. (2006). The relative importance of landscape and community features in the invasion of an exotic shrub in a fragmented landscape. *Ecography*, *29*, 213–222. https://doi.org/10.1111/j.2006.0906-7590.04359.x

Beauséjour, R., Handa, I. T., Lechowicz, M. J., Gilbert, B., & Vellend, M. (2015). Historical anthropogenic disturbances influence patterns of non-native earthworm and plant invasions in a temperate primary forest. *Biological Invasions*, *17*, 1267–1281. https://doi.org/10.1007/s10530-014-0794-y

Bechtold, W. A., & Patterson, P. L. (2005). *The enhanced forest inventory and analysis program: National sampling design and estimation procedures* (Vol. *80*). Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station.

Brothers, T. S., & Spingarn, A. (1992). Forest fragmentation and alien plant invasion of central Indiana old-growth forests. *Conservation Biology*, *6*, 91–100. https://doi.org/10.1046/j.1523-1739.1992.610091.x

Bürkner, P.-C. (2017). brms: An R package for Bayesian multilevel models using Stan. *Journal of Statistical Software*, *80*, 1–28. https://doi.org/10.18637/jss.v080.i01

Carpenter, B., Gelman, A., Hoffman, M. D., Lee, D., Goodrich, B., Betancourt, M., … Riddell, A. (2017). Stan: A probabilistic programming language. *Journal of Statistical Software*, *76*, https://doi.org/10.18637/jss.v076.i01

Christenson, L. M., Lovett, G. M., Mitchell, M. J., & Groffman, P. M. (2002). The fate of nitrogen in gypsy moth frass deposited to an oak forest floor. *Oecologia*, *131*, 444–452. https://doi.org/10.1007/s00442-002-0887-7

Collins, S. (1961). Benefits to understory from canopy defoliation by gypsy moth larvae. *Ecology*, *42*, 836–838. https://doi.org/10.2307/1933521

Crase, B., Liedloff, A. C., & Wintle, B. A. (2012). A new method for dealing with residual spatial autocorrelation in species distribution models. *Ecography*, *35*, 879–888. https://doi.org/10.1111/j.1600-0587.2011.07138.x

Dávalos, A., Nuzzo, V., & Blossey, B. (2015). Single and interactive effects of deer and earthworms on non-native plants. *Forest Ecology and Management*, *351*, 28–35. https://doi.org/10.1016/j.foreco.2015.04.026

De'ath, G. (2007). Boosted trees for ecological modeling and prediction. *Ecology*, *88*, 243–251. https://doi.org/10.1890/0012-9658(2007)88[243:BTFEMA]2.0.CO;2

Dukes, J. S., Pontius, J., Orwig, D., Garnas, J. R., Rodgers, V. L., Brazee, N., … Ehrenfeld, J. (2009). Responses of insect pests, pathogens, and invasive plant species to climate change in the forests of northeastern North America: What can we predict? *Canadian Journal of Forest Research*, *39*, 231–248. https://doi.org/10.1139/X08-171

Elith, J., Leathwick, J. R., & Hastie, T. (2008). A working guide to boosted regression trees. *Journal of Animal Ecology*, *77*, 802–813. https://doi.org/10.1111/j.1365-2656.2008.01390.x

Eschtruth, A. K., & Battles, J. J. (2009). Assessing the relative importance of disturbance, herbivory, diversity, and propagule pressure in exotic plant invasion. *Ecological Monographs*, *79*, 265–280. https://doi.org/10.1890/08-0221.1

Fagan, M. E., & Peart, D. R. (2004). Impact of the invasive shrub glossy buckthorn (*Rhamnus frangula* L.) on juvenile recruitment by canopy trees. *Forest Ecology and Management*, *194*, 95–107. https://doi.org/10.1016/j.foreco.2004.02.015

Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, *37*, 4302–4315. https://doi.org/10.1002/joc.5086

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

Forest Inventory and Analysis Database. (2018). St. Paul, MN: U.S. Department of Agriculture, Forest Service, Northern Research Station. [Available only on internet]. Retrieved from http://apps.fs.fed.us/fiadb-downloads/datamart.html

Fridley, J. D. (2008). Of Asian forests and European fields: Eastern US plant invasions in a global floristic context. *PLoS ONE*, *3*, e3630. https://doi.org/10.1371/journal.pone.0003630

Friedman, J. H. (2001). Greedy function approximation: A gradient boosting machine. *Annals of Statistics*, *29*, 1189–1232. https://doi.org/10.1214/aos/1013203451. Retrieved from https://www.jstor.org/stable/2699986

Fry, J., Xian, G., Jin, S., Dewitz, J., Homer, C., Yang, L., … Wickham, J. (2011). Completion of the 2006 National Land Cover Database for the Conterminous United States. *Photogrammetric Engineering and Remote Sensing*, *77*, 858–864.

Gandhi, K. J., & Herms, D. A. (2010). Direct and indirect effects of alien insect herbivores on ecological processes and interactions in forests of eastern North America. *Biological Invasions*, *12*, 389–405. https://doi.org/10.1007/s10530-009-9627-9

Golivets, M., Woodall, C. W., & Wallin, K. F. (2019). Data from: Functional form and interactions of the drivers of understory non-native plant invasions in northern US forests. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.h8b6vs2

Greenwell, B. M. (2017). pdp: An R package for constructing partial dependence plots. *The R Journal*, *9*, 421–436. Retrieved from https://journal.r-project.org/archive/2017/RJ-2017-016/index.html

Higgins, S. I., & Richardson, D. M. (1998). Pine invasions in the southern hemisphere: Modelling interactions between organism, environment and disturbance. *Plant Ecology*, *135*, 79–93. https://doi.org/10.1023/A:100976051

Hijmans, R. J., Phillips, S., Leathwick, J., & Elith, J. (2017). dismo: Species distribution Modeling. R package version 1.1-4. Retrieved from https://CRAN.R-project.org/package=dismo

Homer, C. G., Dewitz, J. A., Yang, L., Jin, S., Danielson, P., Xian, G., … Megown, K. (2015). Completion of the 2011 National Land Cover Database for the conterminous United States-Representing a decade of land cover change information. *Photogrammetric Engineering and Remote Sensing*, *81*, 345–354.

Hoven, B. M., Gorchov, D. L., Knight, K. S., & Peters, V. E. (2017). The effect of emerald ash borer-caused tree mortality on the invasive shrub Amur honeysuckle and their combined effects on tree and shrub seedlings. *Biological Invasions*, *19*, 2813–2836. https://doi.org/10.1007/s10530-017-1485-2

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

Ibáñez, I., Silander, J. A. Jr, Allen, J. M., Treanor, S. A., & Wilson, A. (2009). Identifying hotspots for plant invasions and forecasting focal points of further spread. *Journal of Applied Ecology*, *46*, 1219–1228. https://doi.org/10.1111/j.1365-2664.2009.01736.x

Jedlicka, J., Vandermeer, J., Aviles-Vazquez, K., Barros, O., & Perfecto, I. (2004). Gypsy moth defoliation of oak trees and a positive response of red maple and black cherry: An example of indirect interaction. *The American Midland Naturalist*, *152*, 231–236. https://doi.org/10.1674/0003-0031(2004)152[0231:GMDOOT]2.0.CO;2

Jones, C. C. (2012). Challenges in predicting the future distributions of invasive plant species. *Forest Ecology and Management*, *284*, 69–77. https://doi.org/10.1016/j.foreco.2012.07.024

Knight, T. M., Dunn, J. L., Smith, L. A., Davis, J., & Kalisz, S. (2009). Deer facilitate invasive plant success in a Pennsylvania forest understory. *Natural Areas Journal*, *29*, 110–116. https://doi.org/10.3375/043.029.0202

Kurtz, C. M. (2013). *An assessment of invasive plant species monitored by the Northern Research Station Forest Inventory and Analysis Program, 2005 through 2010 [Gen. Tech. Rep. NRS-109]* (70 pp). Newtown Square, PA: US Department of Agriculture, Forest Service, Northern Research Station.

Lee, T. D., & Thompson, J. H. (2012). Effects of logging history on invasion of eastern white pine forests by exotic glossy buckthorn (*Frangula alnus* P. Mill.). *Forest Ecology and Management*, *265*, 201–210. https://doi.org/10.1016/j.foreco.2011.10.035

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

Mascaro, J., & Schnitzer, S. A. (2011). Dominance by the introduced tree *Rhamnus cathartica* (common buckthorn) may limit aboveground carbon storage in Southern Wisconsin forests. *Forest Ecology and Management*, *261*, 545–550. https://doi.org/10.1016/j.foreco.2010.11.005

McEwan, R. W., Rieske, L. K., & Arthur, M. A. (2009). Potential interactions between invasive woody shrubs and the gypsy moth (*Lymantria dispar*), an invasive insect herbivore. *Biological Invasions*, *11*, 1053–1058. https://doi.org/10.1007/s10530-008-9316-0

Milbau, A., Stout, J. C., Graae, B. J., & Nijs, I. (2009). A hierarchical framework for integrating invasibility experiments incorporating different factors and spatial scales. *Biological Invasions*, *11*, 941–950. https://doi.org/10.1007/s10530-008-9306-2

Morin, R. S., & Liebhold, A. M. (2015). Invasions by two non-native insects alter regional forest species composition and successional trajectories. *Forest Ecology and Management*, *341*, 67–74. https://doi.org/10.1016/j.foreco.2014.12.018

Mosher, E. S., Silander, J. A., & Latimer, A. M. (2009). The role of land-use history in major invasions by woody plant species in the northeastern North American landscape. *Biological Invasions*, *11*, 2317–2328. https://doi.org/10.1007/s10530-008-9418-8

Ohlemüller, R., Walker, S., & Wilson, J. B. (2006). Local vs regional factors as determinants of the invasibility of indigenous forest fragments by alien plant species. *Oikos*, *112*, 493–501. https://doi.org/10.1111/j.0030-1299.2006.13887.x

Pauchard, A., & Shea, K. (2006). Integrating the study of non-native plant invasions across spatial scales. *Biological Invasions*, *8*, 399–413. https://doi.org/10.1007/s10530-005-6419-8

Peebles-Spencer, J. R., Gorchov, D. L., & Crist, T. O. (2017). Effects of an invasive shrub, *Lonicera maackii*, and a generalist herbivore, white-tailed deer, on forest floor plant community composition. *Forest Ecology and Management*, *402*, 204–212. https://doi.org/10.1016/j.foreco.2017.05.053

Pyšek, P., Jarošík, V., & Kučera, T. (2002). Patterns of invasion in temperate nature reserves. *Biological Conservation*, *104*, 13–24. https://doi.org/10.1016/S0006-3207(01)00150-1

R Core Team. (2018). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from https://www.R-project.org/

Ridgeway, G., with contributions from others. (2017). gbm: Generalized boosted regression models. R package version 2.1.3. Retrieved from https://CRAN.R-project.org/package=gbm

Riitters, K., Potter, K., Iannone, B. V. III, Oswalt, C., Fei, S., & Guo, Q. (2018). Landscape correlates of forest plant invasions: A high-resolution analysis across the eastern United States. *Diversity and Distributions*, *24*, 274–284. https://doi.org/10.1111/ddi.12680

Rodgers, V. L., Wolfe, B. E., Werden, L. K., & Finzi, A. C. (2008). The invasive species *Alliaria petiolata* (garlic mustard) increases soil nutrient availability in northern hardwood-conifer forests. *Oecologia*, *157*, 459–471. https://doi.org/10.1007/s00442-008-1089-8

Schulz, B. K., & Gray, A. N. (2013). The new flora of northeastern USA: Quantifying introduced plant species occupancy in forest ecosystems. *Environmental Monitoring and Assessment*, *185*, 3931–3957. https://doi.org/10.1007/s10661-012-2841-4

Vehtari, A., Gabry, J., Yao, Y., & Gelman, A. (2018). loo: Efficient leave-one-out cross-validation and WAIC for Bayesian models. R package version 2.0.0. Retrieved from https://CRAN.R-project.org/package=loo

Vila, M., & Ibáñez, I. (2011). Plant invasions in the landscape. *Landscape Ecology*, *26*, 461–472. https://doi.org/10.1007/s10980-011-9585-3

Von Holle, B., Delcourt, H. R., & Simberloff, D. (2003). The importance of biological inertia in plant community resistance to invasion. *Journal of Vegetation Science*, *14*, 425–432. https://doi.org/10.1111/j.1654-1103.2003.tb02168.x

Walters, B. F., Woodall, C. W., & Russell, M. B. (2016). White-tailed deer density estimates across the eastern United States, 2008. Retrieved from the Data Repository for the University of Minnesota. https://doi.org/10.13020/D6G014

Wavrek, M., Heberling, J. M., Fei, S., & Kalisz, S. (2017). Herbaceous invaders in temperate forests: A systematic review of their ecology and proposed mechanisms of invasion. *Biological Invasions*, *19*, 3079–3097. https://doi.org/10.1007/s10530-017-1456-7

Weed, A. S., Ayres, M. P., & Hicke, J. A. (2013). Consequences of climate change for biotic disturbances in North American forests. *Ecological Monographs*, *83*, 441–470. https://doi.org/10.1890/13-0160.1

Wood, S. N. (2017). *Generalized additive models: An introduction with R* (2nd ed.). Boca Raton, FL: Chapman and Hall/CRC.

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