Climbing vines and forest edges affect tree growth and mortality in temperate forests of the U.S. Mid-Atlantic States

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ABSTRACT

In tropical forests, climbing vines are known to affect forest structure, composition, and processes, but the role of climbing vines in temperate forests is less well understood. In the tropics, climbing vine abundance appears to be increasing in most forest ecosystems, and a key driver of this trend is forest fragmentation and the creation of edge habitat. In this paper, we use a forest vegetation dataset collected in National Park Service units in the Mid-Atlantic region of the United States to ask how climbing vines affect tree growth and mortality. Many of the most successful exotic plant invasions in the Mid-Atlantic region have been climbing vine species, and exotic plant abundance is often positively related to edge habitat. Therefore, we also examined how forest edges influence temporal and spatial patterns in vine recruitment to trees and compared patterns for native and exotic vines.

We found that both the proportion of trees with vines and the average number of vine species on each tree is increasing in our study area, and that recruitment of climbing vines on trees is greatest near forest edges. Trees are more likely to recruit a new native vine species than they are to recruit a new exotic vine species, although this is likely due to native vines being more widespread and abundant at the start of this study. Recruitment of both exotic and native vines is highest near forest edges, although compared to native vines, recruitment of exotic vines is constrained to a narrower zone near forest edges. Finally, climbing vines in a tree's crown reduce tree growth, particularly for large trees, and vines in the crown reduce tree survivorship particularly near forest edges. Given that the proportion of trees with vines is increasing, even small impacts of vines on tree demographics are likely to result in long-term changes in forest structure, composition, and process. Over time, the greater recruitment of climbing vines and higher tree mortality observed near forest edges may result in receding edges and diminishing size of remnant forest patches, posing grave threats to small urban forests. Active management of climbing vines near forest edges may mitigate these threats.

Published by Elsevier B.V.

1. Introduction

Climbing vines are known as an integral component of tropical forest ecosystems. They compete with trees for above- and below-ground resources (Schnitzer et al., 2005; Toledo-Aceves and Swaine, 2008; Alvarez-Cansino et al., 2015) and can affect tree growth, mortality, and fecundity (Phillips et al., 2002; Campanello et al., 2007; Ingwell et al., 2010). Through these direct effects on individual trees, vines can influence forest composition and structure (Allen et al., 2007), carbon sequestration (Duran and Gianoli, 2013; van der Heijden et al., 2013), and the availability of food resources for wildlife (Schnitzer and Bongers, 2002). Vines

have been well-studied in tropical forests, where their abundance, measured as basal area or density, appears to be increasing (Phillips et al., 2002; Wright et al., 2004; Ingwell et al., 2010; Schnitzer and Bongers, 2011; Laurance et al., 2014; and many others), possibly driven by large-scale environmental changes, such as elevated CO_2 (Mohan et al., 2006), warmer winter temperatures (Schnitzer, 2005), and increased forest fragmentation and disturbance (Laurance et al., 2001; Schnitzer and Bongers, 2002; Londre and Schnitzer, 2006). Regardless of the mechanism, if vine abundance continues to increase in tropical forests, competition between trees and vines will increase as well, leading to stronger effects of vines on tree demography and on forest structure and function (Toledo-Aceves, 2015).

In contrast to tropical systems, vines and their ecology have often been overlooked in the temperate zone, perhaps because

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they contribute less to forest biomass and diversity than they do in tropical forests (Schnitzer and Bongers, 2002). The native vine flora of the Mid-Atlantic region of the United States, for example, is relatively depauperate: vines account for ~4% of the plant taxa occurring in Virginia and Maryland (USDA NCRS, 2015), whereas vines can account for 25% or more of plant species in some tropical forests (Leicht-Young, 2014; Campbell et al., 2015). As a result of limited research, the temporal trend in vine abundance is not well understood in temperate forests, and the few studies conducted in eastern North American forests have not found a consistent pattern: vine density increased over a 12-year period in South Carolina (Allen et al., 2007) and over a 50-year period in New Jersey (Ladwig and Meiners, 2010), whereas vine abundance and basal area did not increase over a 45-year period in Wisconsin (Londre and Schnitzer, 2006). Despite disagreement on the temporal trend, however, each of these studies found that vine abundance was positively related to forest disturbance and edge habitat.

In the eastern U.S., forests are becoming increasingly fragmented, a process driven in large-part by a growing human population (Ritters et al., 2012). In particular, exurban development (i.e., the conversion of rural landscapes into low-density residential development) is a major contributor to forest fragmentation in and around urban centers; in the Washington, DC region of the Mid-Atlantic U.S., exurban development averaged 6.1% per year between 1986 and 2009 (Suarez-Rubio et al., 2012). If climbing vines in the Mid-Atlantic region respond to forest fragmentation and edge creation similarly to vines in tropical forests, it is likely that vine abundance is increasing in these temperate areas as well, despite relatively low native vine diversity. An influx of non-native vine species, many of which have been very successful in eastern North America (Leicht-Young and Pavlovic, 2015), may augment changes in vine abundance. To date, there has been limited research examining what effect these climbing vines have on trees in fragmented temperate forests (but see Dillenburg et al., 1993; Ladwig and Meiners, 2009; Horton and Francis, 2014).

In this study, we use a forest monitoring dataset collected in the Mid-Atlantic region of eastern North America to examine the temporal and spatial distribution of vines in relation to forest edges. We then explore how climbing vines affect their tree hosts. Specifically, we asked the following questions: (1) Are climbing vines on trees increasing in Mid-Atlantic forests? Is the pattern consistent for native and exotic species? (2) Are climbing vines more likely to spread to new trees if the tree is located near a forest edge? (3) Do climbing vines on trees affect tree growth and mortality?

2. Methods

2.1. Study area

The study area includes eleven National Park units in three Mid-Atlantic States (Maryland, Virginia, and West Virginia) and the District of Columbia (DC) (Fig. 1). The National Park Service (NPS) Inventory and Monitoring Division (IMD) conducts natural resource monitoring in NPS units throughout the U.S., and these eleven units constitute IMD's National Capital Region Network (NCRN). Forest is the most common land cover, accounting for ~70% of the total area of the NCRN parks (Fry et al., 2011), and the NCRN conducts a long-term forest vegetation monitoring programs in these parks. Much of the Mid-Atlantic region was logged or cultivated at some point, and most of the parks' forests are second-growth patches of various sizes. Parks in the DC metro area are characterized by forested patches surrounded by urban development; these patches range in size from ~150 ha in Rock Creek

Park to small stands of less than a hectare. Outside of the highly developed urban area, some parks are characterized by relatively large, contiguous forested landscapes (e.g., >1000 ha patches in Catoctin Mountain Park and Prince William Forest Park), whereas others include smaller forest patches in an agricultural landscape (e.g., Manassas National Battlefield Park and Antietam National Battlefield). This mix of landscapes provides an ideal setting to examine temporal and spatial trends in temperate vine species presence and to explore interactions between climbing vines, trees, and forest edges in a temperate ecosystem. We expect that a better understanding of how vine recruitment to trees is affected by landscape-level forest structure and how climbing vines affect tree growth and mortality will aid in natural resource management decision-making, particularly for parks in an urbanized or urbanizing landscape.

2.2. Field sampling

Our dataset includes 403 permanent forest vegetation plots, which were randomly located within forested areas of NCRN parks using a generalized random tessellation stratified sampling procedure (Stevens and Olsen, 2004; Schmit et al., 2014). Each plot is sampled once every four years. Approximately one-hundred plots visited each growing season; a full sample of all plots takes four years. Plots are circular, with a 15 m radius. In each plot, all trees ⩾10 cm diameter at breast height (dbh) are tagged with a unique identification number. At each sampling event and for each tagged tree, we identified the tree to species, record tree status (i.e., living or dead) and dbh, and for living trees only, vine species climbing the trunk and the presence of vines in the tree's crown. 'Vines' includes both lianas and herbaceous vines. We record vines species climbing a tree's trunk to track the spread of vine species and presence of vines in a tree's crown to assess the effect climbing vines on individual trees. For this study, we use the four year sample completed in 2010 (referred to as "the 2010 sample"), and the subsequent full sample, completed in 2014 (referred to as "the 2014 sample").

Note that we do not tag or otherwise track the number, growth, recruitment, or mortality of individual vines, only the presence of vine species on each tree. Therefore, throughout this paper we examine the only impacts of the presence and number of vine species on trees and not impacts related to vine abundance and biomass. While vine species can vary in their effects on trees (e.g. Ichihashi and Tateno, 2011), it is beyond the scope of this paper to contrast the impacts of different vine species.

2.3. Landscape variables

For each plot, we calculated distance (in meters) to forest edge as the distance from plot center to a non-forested cover class using the 2011 National Land Cover Database (NLCD) land cover map (Homer et al., 2015). Thirty-one plots did not map to one of the four NLCD classes we considered forest (i.e., 41 - Deciduous forest, 42 - Evergreen Forest, 43 - Mixed Forest, and 90 - Woody Wetlands). For these plots, distance to forest edge was recorded as 0. Distances were calculated in ArcMap 10.2.

2.4. Temporal patterns of vine richness

We counted the number of climbing vine species observed on each tree and summed this value across all trees in each plot to create a plot-level "summed vine richness index" (SVRI) for the 2010 and 2014 samples. To determine if the SVRI was different in the two sampling events, we fit a mixed effects negative binomial model to the data using the glmmadmb() function in the glmmADMB package (version 0.8.0; Skaug et al., 2014). We first
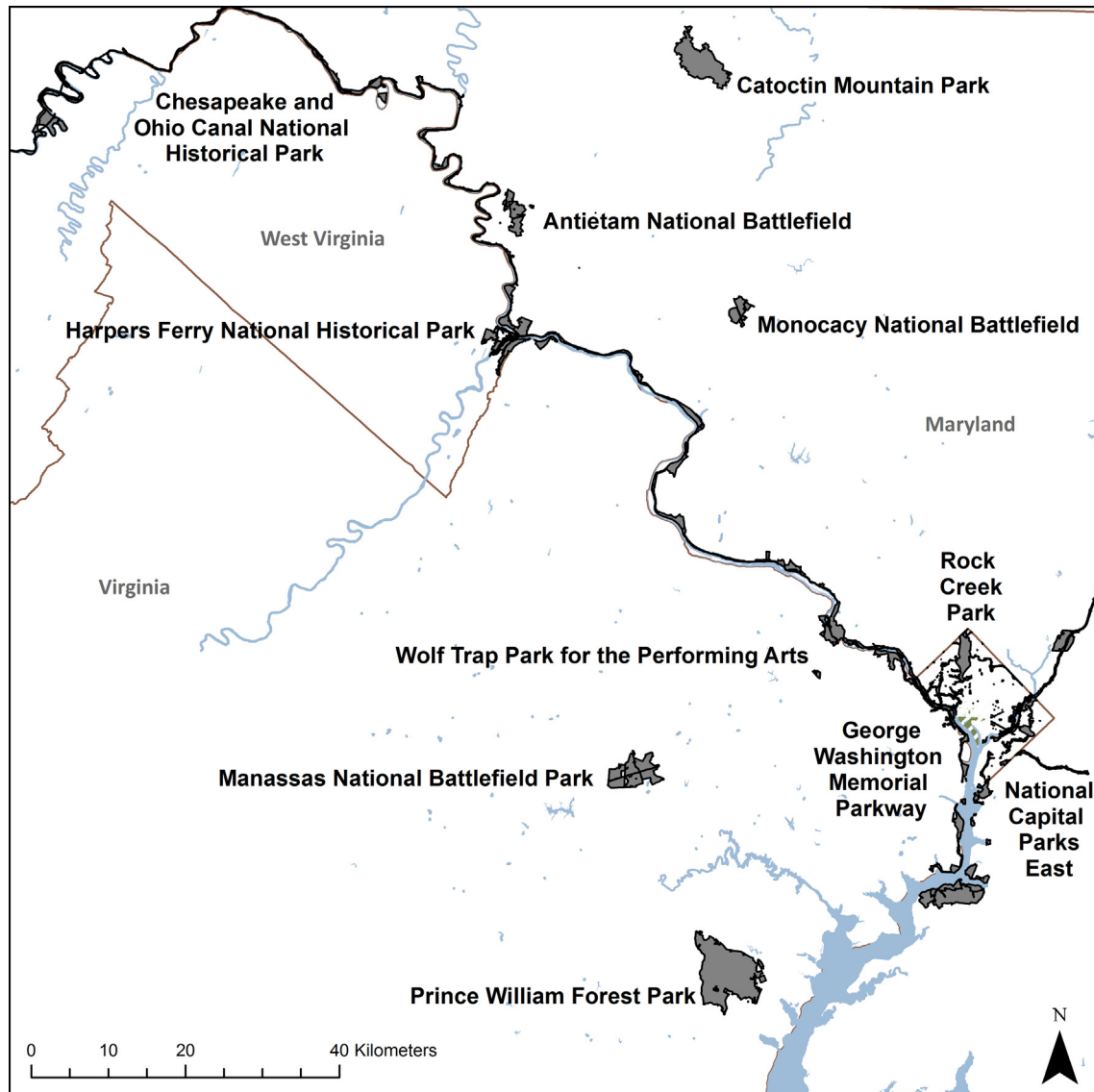
Fig. 1. National Park Service units in the National Capital Region Network. Units are: Antietam National Battlefield; Catoctin Mountain Park; Chesapeake and Ohio Canal National Historic Park; George Washington Memorial Parkway; Harpers Ferry National Historic Park; Manassas National Battlefield Park; Monocacy National Battlefield; National Capital Parks East; Prince William Forest Park; Rock Creek Park; and Wolf Trap Park for the Performing Arts.

fit a model with the SVRI as the dependent variable and sample event as the independent variable. To assess model fit, we then fit a null model with no predictors and compared relative support for the alternative models using Akaike's information criterion (AIC) (Burnham and Anderson, 2002). To assess whether SRVI of native and exotic vine species varied with sample event (e.g. 2010 vs. 2014 sample), we then fit two additional models: one with the SVRI calculated using only native vines, and another with the SVRI based on exotic vines. In both cases the SVRI was the dependent variable and sample event was the independent variable (model fits were also assessed by comparison with the appropriate null model).

In all models involving SVRI, we included plot ID as a random effect to account for repeated observations at each plot (e.g., the 2010 and the 2014 sample). SVRI is inherently a count and is constrained by the abundance of trees present at each plot. For data such as this, the preferred method of dealing with variation in tree abundance is to include the log of the number of trees at each plot as an offset in the model (Hilbe, 2011).

2.5. Edge effects on vine recruitment

To assess if trees located near a forest edge were more likely to recruit a new climbing vine species than trees located in the forest interior, we fit a mixed effects binomial model with a binary response variable representing whether or not a tree recruited a new climbing vine species at the 2014 sample. We did not distinguish between trees that recruited one species and trees that recruited multiple species. Trees that were alive at both samples were included in this analysis (n = 10,615). Distance to forest edge was included in these models as a predictor variable, and plot ID was included as a random effect to account for the spatial clustering of trees in plots. To assess model fit, we fit a null model with no predictors, and compared relative support for the alternative models using AIC. Similar to our approach in the analysis of temporal patterns of SVRI (described in the preceding paragraph), we then fit models with response variables representing the recruitment of new native vine species and the recruitment of new exotic vine species to see if recruitment patterns differed depending upon vine

nativity. Models were fit using the glmer() function in the lme4 package (version 1.1-7; Bates et al., 2014).

2.6. Vine and edge effects on tree growth and mortality

We fit linear mixed models to analyze tree growth, measured as annual diameter growth rate (DGR = $dbh_2 - dbh_1$/time). Only trees that were alive at both samples were included in this analysis. To limit the influence of outlier observations resulting either from measurement error or extreme situations, we excluded trees whose DGR was less than −0.275 cm and greater than 1.075 cm (i.e., the 1st percentile and 99th percentile of DGR values). We also excluded multi-stemmed trees. For these trees the NCRN protocol records the dbh of each stem, but does not individually tag each stem. Therefore for multi-stemmed trees observed across time periods, we can only reliably track the tree's total basal area, not the dbh of individual stems. After filtering, the dataset comprised 9330 tree records. Models were fit with the lmer() function in the lme4 package, with annual diameter growth rate as the response and presence or absence of vines in the tree's crown, and distance to forest edge as predictors. Tree initial size (basal area) was included in the models as a co-variate, since tree growth rates may vary with initial tree size (Bowman et al., 2013). We included two random effects in the model: plot, to account for spatial autocorrelation, and tree species, to account for species-specific variation in growth rates. We constructed 12 candidate models with different combinations of predictor variables, including all possible combination of two-way interaction terms and main effects, and we compared relative support for the alternative models using AIC. Models were fit using maximum-likelihood estimation instead of restricted maximum-likelihood (REML) estimation because REML estimates are not comparable among models with different fixed effects (Bolker et al., 2009).

To determine the effects of climbing vines on the probability that individual trees would die between 2010 and 2014, we used generalized linear mixed models implemented with the glmer() function of the lme4 package. We fit binomial models, with tree status at the 2014 sample (e.g., alive or dead) as the response variable and the presence or absence of vines in the crown at the 2010 sample and distance to forest edge as predictors. Since tree size has been shown to influence survivorship (de Toledo et al., 2011; Wang et al., 2012), tree basal area was included as a co-variate in the model. The dataset include 11,308 trees that were alive at the 2010 sample and dead or alive at the 2014 sample. Again, we constructed 12 candidate models with different combinations of predictor variables and compared support among mortality models using AIC. We included two random effects in each model: plot, to account for spatial autocorrelation, and tree species, to account for species-specific variation in mortality rates.

All analyses were conducted in R 3.1.2 (R Core Team, 2014).

3. Results

3.1. Temporal patterns in summed vine richness index (SRVI)

There were 11,346 living trees at the 2010 sample and 11,420 living trees at the 2014 sample. In 2010, the SVRI summed across all 403 plots was 3414 (8.5 per plot, 0.30 per tree). Of these, 856 vine observations were attributed to exotic vine species and 2558 to native vine species. In 2014, the SVRI summed across all plots was 4359 (10.8 per plot, 0.38 per tree). Of these, 1333 were attributed to exotic species and 3026 were native vine species. A complete list of vine species, their nativity, and the number of trees on which they were found is provided in Appendix A. Sample event was a significant predictor of SVRI; the negative coefficient associ-

Table 1
Parameter estimates from the negative binomial models fitted to the plot-level SVRI. The negative coefficients associated with the *Sample (2010)* terms indicates that the SVRI was smaller in the 2010 sample.

Model	Source	Estimate	SE	Z	Sig.
All vines	Intercept	−2.6671	0.1379	−19.34	<0.001
	Sample (2010)	−0.2571	0.0288	−8.92	<0.001
Native vines	Intercept	−2.8990	0.1319	−21.98	<0.001
	Sample (2010)	−0.1658	0.0277	−5.99	<0.001
Exotic vines	Intercept	−8.272	0.567	−14.58	<0.001
	Sample (2010)	−0.690	0.101	−6.84	<0.001

ated with the "*Sample (2010)*" term indicates that the SVRI was significantly lower in the 2010 sample (Table 1). When native and exotic vines are examined separately, the pattern for each is the same (i.e., lower SVRI in the 2010 sample), but the effect size is larger for exotic vines than for native vines, indicating that exotic SVRI increased more than the native vine SVRI between the two samples.

3.2. Edge effects on vine recruitment

Out of 10,615 individually tagged trees recorded as living at both samples, 1697 trees (16%) recruited a new climbing vine species between the 2010 and 2014 samples and 2668 (25%) had at least one climbing vine species at the 2014 sample. Of the trees that recruited a new climbing vine species, 699 (41%) were previously vine free. Trees that were located near a forest edge were more likely to recruit a new climbing vine species than trees located in interior forest (Table 2). In particular, trees located within 150 m of a forest edge were much more likely to recruit a new climbing vine species (Fig. 2). This edge effect was evident for both native and exotic vine species, although the likelihood of a tree recruiting a new exotic vine species was less than that of recruiting a new native vine species, regardless of a tree's distance to an edge. Further, exotic vine recruitment was more constrained to forest edges: the probability of recruiting an exotic vine decreased to almost 0 within 50 m from a forest edge, whereas the probability of recruiting a new native vine didn't approach 0 until ca. 150 m from a forest edge (Fig. 2).

3.3. Effects on tree growth rates and mortality

The most highly supported tree growth model (Akaike weight (*w*) = 0.66) included distance to forest edge, vines in a tree's crown (VIC), and initial basal area as predictor variables, as well as terms representing interactions between basal area and VIC and between basal area and distance to forest edge (Table 3). The second most highly ranked model (*w* = 0.28) included the same predictors as the top-ranked model, as well as an interaction term between VIC and distance to forest edge. Since the coefficient estimates

Table 2
Parameter estimates from the binomial models describing probability of a tree recruiting a new climbing vine species. The negative coefficient associated with the *Distance* term in the models indicates that vine recruitment was negatively related to distance to forest edge.

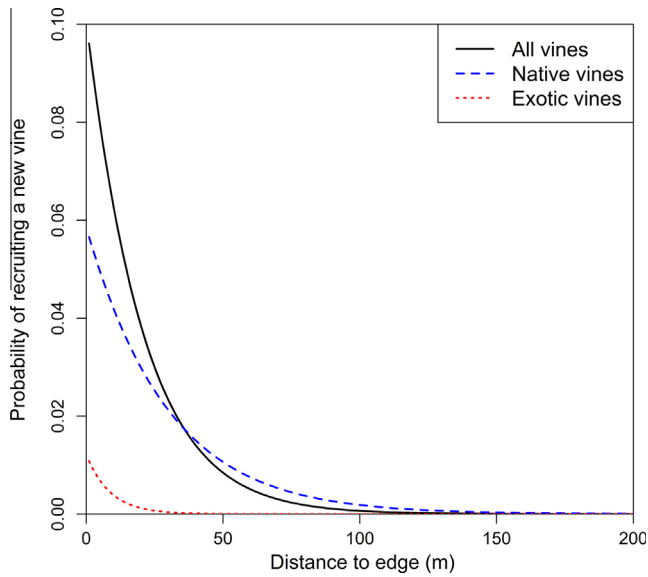| Model	Source	Estimate	SE	Z	Sig.
All vines	Intercept	−2.1897	0.2132	−10.269	<0.001
	Distance	−0.0515	0.0083	−6.206	<0.001
Native vines	Intercept	−2.7781	0.2038	−13.630	<0.001
	Distance	−0.0351	0.0077	−4.583	<0.001
Exotic vines	Intercept	−4.3991	0.4744	−9.273	<0.001
	Distance	−0.1158	0.0190	−6.121	<0.001

Fig. 2. Predicted probability of a tree recruiting a new climbing vine species as a function of distance to forest edge (m), based on the equation estimated from the binomial model (Table 2).
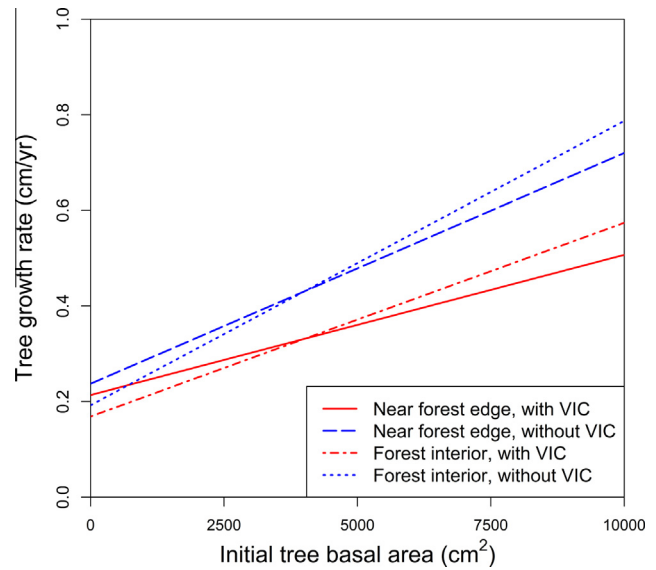

Fig. 3. Predicted tree growth rate (cm/year) as a function of initial basal area (cm²), based on the equation estimated from the linear model (Table 4). The solid red line represents predicted growth rates for trees near the forest edge (55 m) and with VIC. The dashed blue line represents predicted growth rates for trees near the forest edge without VIC. The dashed and dotted red line represents predicted growth rates for trees in interior forest (300 m from the forest edge) with VIC. The dotted blue line represents predicted growth rates for trees in interior forest without VIC.

Table 3
Comparison of candidate models describing tree growth. Variables listed in table include: BA, tree basal area; Distance, distance to forest edge; and VIC, presence/absence of vines in the tree's crown. Column heading are: AIC, Akaike's information criterion; ΔAIC, change in AIC value from model with the lowest AIC value; w, Akaike weight (weighted estimate of relative strength of model). ∗ indicates interaction between variables. Highly ranked models discussed in the text are in bold font.

	Model[a]	K	AIC	ΔAIC	w
1	**VIC ∗ BA + BA ∗ Distance**	**9**	**−5226.07**	**0.00**	**0.66**
2	**VIC ∗ BA + VIC ∗ Distance + BA ∗ Distance**	**10**	**−5224.36**	**1.71**	**0.28**
3	VIC + BA ∗ Distance	8	−5220.52	5.55	0.04
4	VIC ∗ Distance + BA ∗ Distance	9	−5218.69	7.38	0.02
5	VIC ∗ BA + VIC ∗ Distance	9	−5210.00	16.08	0.00
6	VIC ∗ BA + Distance	8	−5211.65	14.42	0.00
7	VIC + Distance + BA	7	−5203.43	22.64	0.00
8	VIC ∗ Distance + BA	8	−5201.64	24.44	0.00
9	BA	5	−5160.21	65.86	0.00
10	Distance	5	−4691.17	534.90	0.00
11	VIC	5	−4668.42	557.65	0.00
12	Intercept only	4	−4658.96	567.11	0.00

[a] Plot and tree species were treated as random effects in all models.

were similar in both models (i.e., consistent direction of effects and similar effect sizes), we focus our discussion and interpretation on the most highly supported model (which was also the more parsimonious model). Trees with larger initial basal area had higher growth rates, whereas the presence of vines in a tree's crown decreased tree growth rates (Table 4; Fig. 3). The effect of VIC, however, interacted with initial basal area, such that the negative

Table 4
Parameter estimates from the best-fit model describing tree growth (model 2, Table 3). Variables listed in table include: BA, tree basal area; Distance, distance to forest edge; and VIC, presence/absence of vines in the tree's crown.

Source	Estimate	SE	t-value
Intercept	0.2462542	0.0144605	17.029
BA	0.0460398	0.0030196	15.247
VIC	−0.0235576	0.0095571	−2.465
Distance	−0.0017961	0.0002873	−6.251
VIC ∗ BA	−0.0189463	0.0068907	−2.750
BA ∗ Distance	0.0004483	0.0001106	4.055

effect of VIC on tree growth was greater for large trees than it was for small trees. For example, at the forest edge, VIC causes a small 10 cm DBH tree to suffer an 11% drop in growth, whereas a larger 100 cm DBH tree suffers a 28% drop in growth with VIC. The strength of the effect of initial basal area on tree growth was dependent on distance to forest edge; the positive effect of increasing initial BA on tree growth rates was stronger for trees growing in the forest interior than it was for trees growing near a forest edge (e.g., in Fig. 3, the slope of the lines representing trees in the forest interior is greater than the slope of the lines representing trees near the forest edge). The main effect of distance to forest edge is negative, but the effect of distance to edge was also dependent on initial basal area (Table 4). For small trees, growth rates near a forest edge are higher than in the forest interior (Fig. 3), but larger trees are the opposite, with higher growth rates in the interior than at the edge. Interestingly, unlike initial basal area, the distance from the edge has little effect on the decrease in growth due to VIC. When measured as a percentage, trees suffered a similar decline in growth rate, regardless of their proximity to an edge.

Between the 2010 and 2014 samples, 693 of 11,308 trees (6.1%) died. Our analysis identified four competing models that were essentially equivalent in terms of small ΔAIC values (models 1, 3, 4, and 7; Table 5). Each of these models included a significant VIC by distance to forest edge interaction term, and three models included additional two-way interaction terms (models 1, 3, and 4). However, none of the p-values associated with the additional interaction terms were significant ($P < 0.05$), and the direction and magnitude of the coefficients for all other terms remained consistent among the three candidate models. As such, we focused our interpretation on model 7, the most parsimonious of the three candidate models. Trees with vines in the crown were less likely to survive between sampling events than trees without vines in the crown, and larger trees were more likely to survive than smaller trees (Table 6). However, the detrimental effect of having a vine in the crown was stronger for trees located near the forest edge than it was for trees located in the forest interior (Fig. 4): for trees near the edge, having a vine in the crown approximately doubles

Table 5
Comparison of candidate models describing tree mortality. Variables listed in table include: BA, tree basal area; Distance, distance to forest edge; and VIC, presence/absence of vines in the tree's crown. Column heading are: AIC, Akaike's information criterion; ΔAIC, change in AIC value from model with the lowest AIC value; w, Akaike weight (weighted estimate of relative strength of model). ∗ indicates interaction between variables. Highly ranked models discussed in the text are in bold font.

	Model[a]	K	AIC	ΔAIC	w
1	**VIC ∗ BA + VIC ∗ Distance + BA ∗ Distance**	**9**	**4746.38**	**0.00**	**0.28**
2	**VIC ∗ BA + VIC ∗ Distance**	**8**	**4746.52**	**0.14**	**0.26**
3	**VIC ∗ Distance + BA**	**7**	**4746.55**	**0.16**	**0.25**
4	**VIC ∗ Distance + BA ∗ Distance**	**8**	**4747.48**	**1.09**	**0.16**
5	VIC ∗ BA + BA ∗ Distance	8	4752.10	5.72	0.02
6	VIC ∗ BA + Distance	7	4752.24	5.86	0.01
7	VIC + Distance + BA	6	4752.63	6.24	0.01
8	VIC + BA ∗ Distance	7	4753.45	7.06	0.01
9	BA	4	4766.00	19.62	0.00
10	VIC	4	4768.43	22.05	0.00
11	Distance	4	4774.36	27.98	0.00
12	Intercept only	3	4777.36	30.97	0.00

[a] Plot and tree species were treated as random effects in all models.

Table 6
Parameter estimates from the most-parsimonious model describing tree mortality (model 7, Table 6). Variables listed in table include: BA, tree basal area; Distance, distance to forest edge; and VIC, presence/absence of vines in the tree's crown.

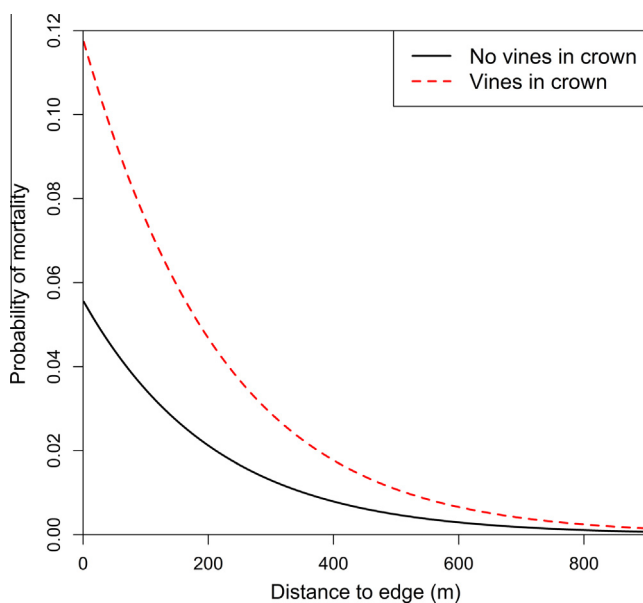| Source	Estimate	SE	P
Intercept	2.8304	0.1934	<0.001
VIC	−0.8172	0.1754	<0.001
Distance	0.0050	0.0031	0.102
BA	0.2141	0.0574	<0.001
VIC ∗ Distance	0.0339	0.0128	0.008

Fig. 4. Predicted probability of mortality as a function of distance to forest edge (m) and presence or absence of vines in a tree's crown, based on the equation estimated from the binomial model (Table 6).

the probability of mortality, whereas the effect of vines in the crown was much smaller for trees in the forest interior. Of the 3667 trees located within 100 m of the forest edge, 271 (7.4%) died between the 2010 and 2014 sample, whereas 10 of the 285 trees (3.5%) located 500–600 m from a forest edge died.

4. Discussion

Climbing vines are common in temperate forests of the Mid-Atlantic region, occurring on a quarter of the trees sampled in this study. This value is somewhat lower than what has been previously reported in other temperate forests (e.g., 45% of trees in Massachusetts and 68% of trees in New Jersey; Buron et al., 1998; Ladwig and Meiners, 2009), but even across the short observation period examined here (i.e., 4 years in between sample events), we found that vines are becoming more common, as demonstrated by the summed vine richness index. Forest fragmentation and the corresponding creation of forest edges are likely important drivers of a forest's SVRI in the Mid-Atlantic region, as trees located near a forest edge were more likely to recruit a new climbing vine species than trees located in interior forests. Given that forest fragmentation and other large-scale environmental changes that may increase vine abundance (e.g., elevated CO_2 and warmer winter temperatures) are on-going, SVRI is likely to continue increasing in these forests.

Forest edges are characterized by abiotic and biotic conditions distinct from interior forests. Low height, small diameter woody plants are often more common in edge habitats and provide an ideal ladder for climbing vines to invade forest canopies (Pavlovic and Leicht-Young, 2011). Further, vines may be better suited than other woody species to take advantage of the altered forest edge environment through rapid stem elongation (Schnitzer and Bongers, 2002) and diverse dispersal pathways (e.g., vegetative dispersal, lateral growth from intact forests, dispersal by birds; Londre and Schnitzer, 2006; Schnitzer and Bongers, 2011). For similar reasons (e.g., high propagule pressure and competitive advantages in altered environmental conditions), exotic plant species are often found in greater abundance near forest edges (Weber and Gibson, 2007; Fridley et al., 2009); as such, we expected that exotic vine recruitment would be more common than native vine recruitment near edges. While we did find that the exotic SVRI is increasing more rapidly than that for native species, we also found that the probability of an edge tree recruiting a new native vine was greater than the probability of it recruiting a new exotic vine. This may be due to native vine species, as a group, being more abundant and widespread on the contemporary landscape than the exotic vine species (e.g. of the total climbing vine SVRI observed in the 2014 sample, 30% was attributed to exotic species, whereas 70% was attributed to native species); as exotic vines continue to spread and become more abundant in Mid-Atlantic forests, these recruitment patterns may change. In addition, our monitoring methods may have resulted in an underestimate of exotic vine recruitment. Our analysis of vine recruitment was limited to trees living at both samples, since we do not record climbing vines on dead trees; however, exotic vine recruitment was more constrained to forest edges, where we also observed the highest tree mortality. Exotic vine recruitment on dead trees near forest edges would have been excluded by our methodology.

Interestingly, the reduction in recruitment due to distance to the edge is more severe for exotic vines than native vines. The probability of a tree recruiting a new exotic vine declined nearly to zero within 50 m of an edge, whereas the probability of recruiting a new native vine species approached zero at 150 m from the forest edge (Fig. 2). This pattern might be a result of exotic vines simply not having had as much time to successfully invade interior forests as their native competitors. Alternatively, exotic vines may be more competitive in the high light environment of forest edges, and unable to compete in the more shaded interior forest environment. Finally, vines exhibit a wide range of climbing mechanisms, each of which may be best adapted to colonizing different forest

successional stages (DeWalt et al., 2000; Schnitzer and Bongers, 2002). We did not address climbing mechanisms here, but if the distribution of climbing mechanisms among exotic vine species is different than among the native, we might expect a different suite of species to dominate forests of different ages or structural stages.

4.1. Effects on tree growth rates and mortality

In Mid-Atlantic forests, climbing vines that have infested a tree's crown (vines in the crown; VIC) reduce tree dbh growth, but this effect was stronger for larger trees than it was for smaller trees. Above-ground competition for light may explain this interaction: for larger trees, whose canopies receive full overhead light, crown infestation by vines is more likely to reduce direct light exposure from above than it would for smaller trees, whose canopies are more likely to be shaded from above by larger neighboring trees and are more reliant on diffuse light rather than direct overhead light (i.e. crown infestation of smaller trees has less of an effect on overall light exposure). Ingwell et al. (2010) described a similar pattern in Panamanian tropical forests, where crown infestation by lianas reduced growth for trees with sun-exposed canopies, but had no effect on trees with shaded canopies. In the present study, we cannot tease apart above- and below-ground competition; however, below-ground root competition for water and nutrients between vines and their tree hosts has also been shown to decrease tree growth rates and may contribute to the reduced tree growth observed here (Dillenburg et al., 1993; Schnitzer et al., 2005). In addition to the effect of vines on growth, we also found an interaction effect between initial size and distance to forest edge on tree growth: growth rates generally declined at greater distances from the forest edge for small trees, but larger trees had higher growth rates in the interior. This pattern, again, may be related to light competition; smaller trees are likely to access more light, both direct overhead and diffuse, near the forest edge than they are in a shaded forest interior.

Vines in a tree's crown increased the probability of tree mortality. Climbing vines likely put considerable mechanical stress on a host tree and have been shown to increase host susceptibility to wind damage (Allen et al., 2007) and winter storm and ice loading (Siccama et al., 1976). In Panamanian forests, liana infestation doubled tree mortality (Ingwell et al., 2010), similar to the magnitude of the effect observed here. In the present study, however, the effect of vines in the crown (VIC) was strongest near forest edges, where the probability of mortality for trees with VIC was more than twice that of trees without VIC (Fig. 3). It is well-known that forest edges are more stressful environments than forest interiors (e.g., increased wind exposure and subsequent wind throw; greater moisture demand from higher evapotranspiration rates; sudden exposure to high light levels), and that these conditions often result in higher tree mortality, at least in the short-term (Harper and Macdonald, 2002; Jonsson et al., 2007). Vine infestations may exacerbate this edge effect by putting additional stress on trees in an already stressful environment. Vines may increase the impacts of wind throw, for example, by increasing the surface area of the tree's canopy and by connecting multiple tree canopies, so that when one tree breaks, canopies of other trees are affected as well.

Our dataset didn't include the identity of the vine species infesting a tree's crown; as such, we were unable to distinguish between the effects of exotic and native vines on tree growth and mortality. Previous work, however, has suggested that exotic vine species may have a stronger effect on tree growth than native species do. The common Mid-Atlantic weed *Lonicera japonica*, for example, suppressed tree growth in eastern Maryland forests more than the native vine, *Parthenocissus quinquefolia*, as a result of more intense below-ground competition (Dillenburg et al., 1993). Additionally, many of the most abundant exotic vine species in the Mid-Atlantic have longer growing seasons than their native counterparts (e.g., due to longer autumn leaf phenology; Fridley, 2012), giving them a competitive edge.

4.2. Management implications

We have shown a variety of edge effects on Mid-Atlantic forests, ranging from greater vine recruitment near forest edges to elevated growth rates of small trees near edges and increased mortality risk of edge trees with climbing vines in their crown. As forest fragmentation becomes more prevalent, even small changes in the proportion of trees with vines may have substantial effects on regional forest structure, composition, and processes. Over time, the greater recruitment of climbing vines and higher tree mortality observed near forest edges may result in receding edges and diminishing area of remnant forest patches (see Gascon et al., 2000). Vine-mediated effects of forest fragmentation, ranging from receding edges to changes in forest C-storage, are likely already occurring in highly urbanized landscapes, where forest patches are smaller and have more edge habitat.

In these urban areas, active management of vines near forest edges may mitigate their impacts. Since vines in the crown suppress tree growth and increase tree mortality, edge trees in fragmented urban forests are likely to respond well to management practices that reduce their vines. This is not to say that vines do not play important ecological roles in forests; many native vine species (e.g., *Smilax* and *Vitis* spp.), for instance, are important resources for native wildlife (McCarty et al., 2002). For a variety of reasons (e.g., exotic vines appear to be increasing more rapidly than native vines; exotic vine recruitment is more constrained to forest edges; some exotic vine species have stronger effects on trees than native vines), vine management near forest edges might best target exotic vine species over natives.

5. Conclusion

We have shown that many of the vine patterns first described in tropical forests are also evident in the temperate forests of the Mid-Atlantic region. Climbing vines are common in these forests, particularly near forest edges, and the SVRI in our study area is increasing. Further, the presence of vines in a tree's crown affects growth and mortality of the host tree. Similar to expectations in the tropical zone, we anticipate that continued increases in vines in this region are likely to result in stronger effects of vines on individual trees and on forest structure and function.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2016.05.005.

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