



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.

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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 CO₂ (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 Catocin 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 vine 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

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