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Laura Ladwig
Eastern Illinois University

Scott J. Meiners
Eastern Illinois University, sjmeiners@eiu.edu

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Spatiotemporal dynamics of lianas during 50 years of succession to temperate forest

LAURA M. LADWIG¹ AND SCOTT J. MEINERS

Eastern Illinois University, Department of Biological Sciences, 600 Lincoln Avenue, Charleston, Illinois 61920 USA

Abstract. Although they are important components of forest communities, the general ecology and spatiotemporal patterns of temperate lianas during forest regeneration are largely unknown. The dependence of lianas on other plants for physical support makes them a potentially important driver of community dynamics. We examined 50 years of vegetation data from an old-field succession study to determine the dynamics and community controls on liana expansion within the Piedmont region of New Jersey, USA. Four lianas, *Lonicera japonica*, *Parthenocissus quinquefolia*, *Toxicodendron radicans*, and *Vitis* spp., occurred in enough abundance for detailed analyses. In general, liana cover peaked during mid-succession (20–30 years post-abandonment) when community composition was mostly herbaceous with scattered trees and shrubs. Liana cover began to decrease as trees became dominant and the canopy closed. Temporal patterns of cover dynamics of abundant species indicated three early- and one late-successional liana species within the community. In contrast to cover, frequency of lianas increased throughout succession, indicating that liana populations persisted despite dramatic declines in cover for the three early-successional species. Temporal dynamics between native and nonnative lianas were similar but spatially distinct as cover of native species dispersed and expanded near the forest edge while the nonnative species preferentially grew far from the forest. These dynamics indicate that successional processes may ultimately lead to the decline of most lianas. However, the persistence of lianas as high numbers of suppressed individuals suggests that they may rebound quickly following canopy disturbance.

Key words: Buell-Small Succession Study (BSS); community and population dynamics; lianas; long-term data; *Lonicera japonica*; old-field succession; *Parthenocissus quinquefolia*; Piedmont region, New Jersey, USA; *Toxicodendron radicans*; *Vitis* spp.

INTRODUCTION

Lianas (woody vines) are an integral but often overlooked component of forest ecology (Putz and Mooney 1991, Clark 1994, Schnitzer and Bongers 2002, Leicht-Young et al. 2007, Selaya and Anten 2008). Well known for their weedy growth habit and reliance on other plants for support, lianas are capable of quickly colonizing disturbed areas, lowering diversity, and retarding forest regeneration (Putz and Holbrook 1991, Fike and Niering 1999, Schnitzer et al. 2000, Yurkonis and Meiners 2004). Due to the inherent diversity of morphological and anatomical characteristics of lianas as a life form, they are adapted to a broad range of environmental conditions, often benefiting from environmental perturbations (Rowe and Speck 2005). Worldwide, both native and nonnative liana species have become problematic, leading to costly eradication and forest restoration efforts (Gerwing 2001, Pérez-Salicrup et al. 2001). Lianas compose 9% of the invasive

plant species of the eastern United States (Barger et al. 2003) and represent some of the region's most problematic invaders (e.g., *Lonicera japonica*, *Celastrus orbiculatus*). As liana densities increase with disturbance (Boring and Monk 1981, Putz 1984b, Hegarty and Caballé 1991, Buron et al. 1998, Schnitzer et al. 2000, Schnitzer and Carson 2001, Ibarra-Manríquez and Martínez-Ramos 2002, Londré and Schnitzer 2006) and with increasing CO₂ levels (Granados and Korner 2002, Mohan et al. 2006), information regarding the underlying ecology and spatiotemporal dynamics of lianas is crucial to understanding regeneration in temperate forests.

During all phases of forest regeneration, lianas compete with trees for aboveground resources. In the tropics, lianas can contribute 5% of forest basal area while occupying 30% of the canopy (Putz 1983). Young lianas often grow along the soil surface in search of a host and may create a dense ground layer. This cover reduces light availability for germination and physically blocks growth of understory vegetation, including young trees (Putz 1984b, Dillenburg et al. 1995, Royo and Carson 2006). Compared to trees, lianas do not need to produce a supportive trunk, which allows allocation of resources to competitive strategies including rapid growth, high leaf area:biomass ratios, and

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¹ Present address: Department of Biology, MSC03 2020, University of New Mexico, Albuquerque, New Mexico 87131 USA. E-mail: lladwig@unm.edu

extended growing seasons (Putz and Windsor 1987, Gerwing and Farias 2000, Selaya and Anten 2008). Once in the canopy, lianas can overtop the highest layer of tree leaves, reducing light availability for both canopy trees and plants on the forest floor (Dillenburg et al. 1993, Avalos et al. 1999, Pérez-Salicrup 2001). Lianas can also physically alter tree growth by constricting vascular tissue within trunks and removing bark, shoots, and buds (Lutz 1943, Stevens 1987). Lianas often increase damage levels and wind throw risk to established trees (Siccama et al. 1976, Putz 1984b).

In addition to aboveground competition, lianas and trees compete intensively belowground. Liana and tree root systems differ in morphology since liana roots do not need to provide stabilization of stems. This constraint on trees allows liana roots to be longer, with more surface area and to potentially obtain water and nutrients unavailable to trees (Putz 1991, Pérez-Salicrup and Barker 2000). Lianas also alter nutrient concentrations in trees, reducing the nitrogen content of tree leaves with belowground liana competition (Dillenburg et al. 1993, 1995, Lewis and Tanner 2000). While separate processes, above- and belowground competition between lianas and trees occur concurrently and are difficult to tease apart (Lewis and Tanner 2000, Pérez-Salicrup and Barker 2000, Schnitzer et al. 2005).

The community impacts of lianas vary with forest age and composition. In the tropics, growth of late-successional tree species is typically more reduced by lianas than early-successional trees, possibly because pioneer tree species have faster growth rates comparable to lianas and can escape canopy competition (Clark and Clark 1990, Schnitzer et al. 2000). Differential impacts of lianas on tree seedlings impact the assemblage of later communities by acting as a selective filter that reduces the success of some species (Pérez-Salicrup 2001). Similarly, through their dense growth, lianas may stall gap regeneration and create unpredictable successional pathways in both temperate and tropical systems (Fike and Niering 1999, Schnitzer et al. 2000). With increasing time since disturbance and the shift from early- to late-successional communities, total liana abundance decreases (Lutz 1943, Putz 1984a, b, DeWalt et al. 2000, Schnitzer and Carson 2001). Therefore, impacts of lianas on forest regeneration would be expected to be more prevalent in early- to mid-successional communities, when their abundance is highest and when late-successional trees are establishing.

Lianas are distributed heterogeneously across forest types and within landscapes. At a global scale, liana species richness increases with decreasing latitude and mean annual precipitation (Gentry 1991, Avalos et al. 1999, Schnitzer 2005, Jiménez-Castillo et al. 2007). At local scales, the distribution of individual liana species may be influenced by abiotic (elevation and nutrient and moisture levels) as well as biotic conditions (host tree architecture) (Balfour and Bond 1993, Collins and Wein 1993, Ibarra-Manríquez and Martínez-Ramos 2002).

Following disturbance, such as treefalls or anthropogenic canopy reduction, lianas may recolonize faster than trees (Boring and Monk 1981, Hegarty and Caballé 1991). Within forest patches, edges are optimal locations for lianas due to increased light levels, greater variety in structural supports, and occurrence of frequent disturbances to allow establishment (Ibarra-Manríquez and Martínez-Ramos 2002). Although it is well-documented that lianas are more abundant along forest edges and gaps (Putz 1984b, Hegarty and Caballé 1991, Buron et al. 1998, Schnitzer and Carson 2001, Londré and Schnitzer 2006), the population responses that generate this spatial association are largely unstudied.

Despite their potential importance, our understanding of the fundamental dynamics of liana populations in reestablishing forest communities in the temperate zone is limited. Most of our knowledge about lianas as components of forests comes from tropical systems and may not directly reflect processes within temperate communities. Additionally, studies examining impacts of lianas are often short-term, noncontinuous, or employ space-for-time substitutions that might not provide accurate depictions of liana colonization and impacts on community dynamics (Dillenburg et al. 1995, Schnitzer et al. 2000, Londré and Schnitzer 2006). Successional communities are particularly useful for studying liana dynamics because the cover of lianas, and therefore their presumed impacts, are greatest in young forests (Boring and Monk 1981, Hegarty and Caballé 1991, Schnitzer et al. 2000).

This project examined a 50-year record of secondary succession in a temperate forest to document liana dynamics and place them in a community context. The objectives of this research were to: (1) evaluate liana population patterns through succession, (2) determine community controls on liana expansion, (3) examine the spatiotemporal response of liana population dynamics to forest edges, and (4) compare the population dynamics of native and nonnative species.

METHODS

Study site

The study was conducted in the Piedmont region of New Jersey, USA, at the William L. Hutcherson Memorial Forest Center (HMFC; 40°18'00" N, 74°19'48" W), a land preserve owned and maintained by Rutgers University. It contains an old-growth forest and communities in various stages of succession, ranging from recently abandoned agricultural fields to second-growth forests. Bard (1952) documented succession in the area surrounding HMFC but gave only limited information about the lianas. Within this land preserve is the Buell-Small Succession Study (BSS), a continuous, long-term study of old-field succession. The BSS consists of 10 agricultural fields located adjacent the old-growth forest where farming was experimentally ceased and the resulting vegetation patterns of secondary succession documented for the past 50 years (from 1958 to 2008). From 1958 to

1966, pairs of fields were abandoned in alternate years, each containing 48 permanent, 1-m² quadrats for vegetation surveys. Plots were located in uniform rows to effectively represent the entire area of fields, which range from 0.5 to 1 ha. Fields were surveyed annually until 1979 when surveying switched to alternate years, with five fields surveyed each year. At each sampling, the percent cover of each species present was recorded. Care was taken to accurately account for the summed coverage of lianas in both the canopy and subcanopy. Surveys were conducted in late July when vegetation was at peak cover. Since fields were abandoned in different years, data analysis was based on time since abandonment rather than calendar year. Due to the staggered abandonment of the fields, in 2008 field ages ranged from 42 to 50 years; therefore older ages had fewer datapoints. Additionally, after 1979, when surveys switched to alternate years, sample size was reduced from 480 to 240 plots for each year. For more background information about the BSS see Pickett (1982).

Study organisms

The liana species that are most abundant in the BSS and were the focus of this research are: *Parthenocissus quinquefolia* (Virginia creeper; Vitaceae), *Toxicodendron radicans* (poison ivy; Anacardiaceae), *Vitis* spp. (grape, including *V. aestivalis*, *V. labrusca*, *V. riparia*, *V. palmata*, and *V. vulpina*; Vitaceae), and *Lonicera japonica* (Japanese honeysuckle; Caprifoliaceae). Within the BSS, understory *Vitis* plants were initially identified to species, but once in the canopy correct species identification became difficult and plants were identified to genus only. Less abundant liana species located within the BSS, *Celastrus orbiculatus* (oriental bittersweet; Celastraceae), *Hedera helix* (English ivy; Araliaceae), *Smilax* spp. (greenbriers; Smilacaceae), and *Clematis virginiana* (Ranunculaceae), could not be analyzed independently due to low cover.

Although the four most abundant lianas share the common fundamental characteristics of lianas, the species vary in morphology, climbing mechanisms, origin, and invasiveness. *Parthenocissus quinquefolia* is native and abundant in mid- to late-successional communities throughout eastern and midwestern North America. It is dispersed by birds, and rapid growth follows establishment. Specialized tendrils ending with adhesive discs allow *P. quinquefolia* to climb nearly any structure large enough to support its mass (Gleason and Cronquist 1991). *Toxicodendron radicans* is also dispersed by birds and is native to eastern North America. Characteristic aerial rootlets produced along the stem attach *T. radicans* to woody stems as it climbs into the canopy (Mitch 1995). *Vitis* spp. are native to North America, climb by means of tendrils, and commonly occur later in succession (Fike and Niering 1999, Londré and Schnitzer 2006). Fruits of *Vitis* spp. are dispersed by both birds and mammals. *Lonicera japonica* is native to Asia and climbs via twining stems. Once established,

plants become highly invasive in eastern and southern North America (Schweitzer and Larson 1999, Schierenbeck 2004). *Lonicera japonica* is dispersed by birds, but seed production in North America is limited due to lack of suitable pollinators (Larson et al. 2002).

Data analysis: controls on liana expansion

Dynamics of all liana species were examined collectively (hereafter referred to as total lianas) in addition to individual species analysis. We examined the percent cover and frequency (number of plots occupied) of lianas through succession. To determine local controls on liana population growth, an eight-year time window during greatest liana increase in cover and frequency was chosen for each liana and total lianas. Since liana species expanded at different successional ages, the start time of expansion windows varied among species, but the length of the period was held constant (Fig. 1). For total lianas and three of the dominant species (*L. japonica*, *P. quinquefolia*, and *T. radicans*) the analysis window was from 10 to 18 years post-abandonment. The expansion of *Vitis* spp. occurred later in succession, with a corresponding analysis window from 30 to 38 years post-abandonment. Expansion rates were calculated as the change in liana cover between the end (T_2) and start (T_1) of each expansion window ($T_2 - T_1$) for each plot. Though expansion rate would be negative if liana cover decreased during this period, the majority were positive since a time window during population growth was chosen. Plots where lianas did not occur during the expansion window were dropped from analysis (Meiners et al. 2004). Expansion rates were tested for an association with cover of other life forms (trees, shrubs, perennials, annuals, and grasses) to evaluate whether liana expansion was associated with particular vegetation types. Cover of dominant tree species, other lianas, and the 15 most abundant species (which sometimes included trees and lianas) during the expansion windows were also tested for association with liana expansion rates using stepwise regressions (SAS 9.1; SAS Institute, Cary, North Carolina, USA). Individual stepwise regressions were run for total lianas and each dominant liana.

Data analysis: spatiotemporal influence of the forest edge

Spatial patterns of liana dynamics in relation to the old-growth forest edge were examined throughout the continuous 50 years of vegetation data. Distances between the plots and the edge of the bordering old-growth forest ranged from 3 to 74 m. Liana population dynamics within five fields that bordered old-growth forest on one edge were examined to test for an association between liana cover dynamics within each plot to landscape position relative to distance from the edge of the forest through succession. To do this, the 50-year data set was split into four-year increments and the change in liana cover between each four-year increment ($T_2 - T_1$) was related to distance from the old-growth

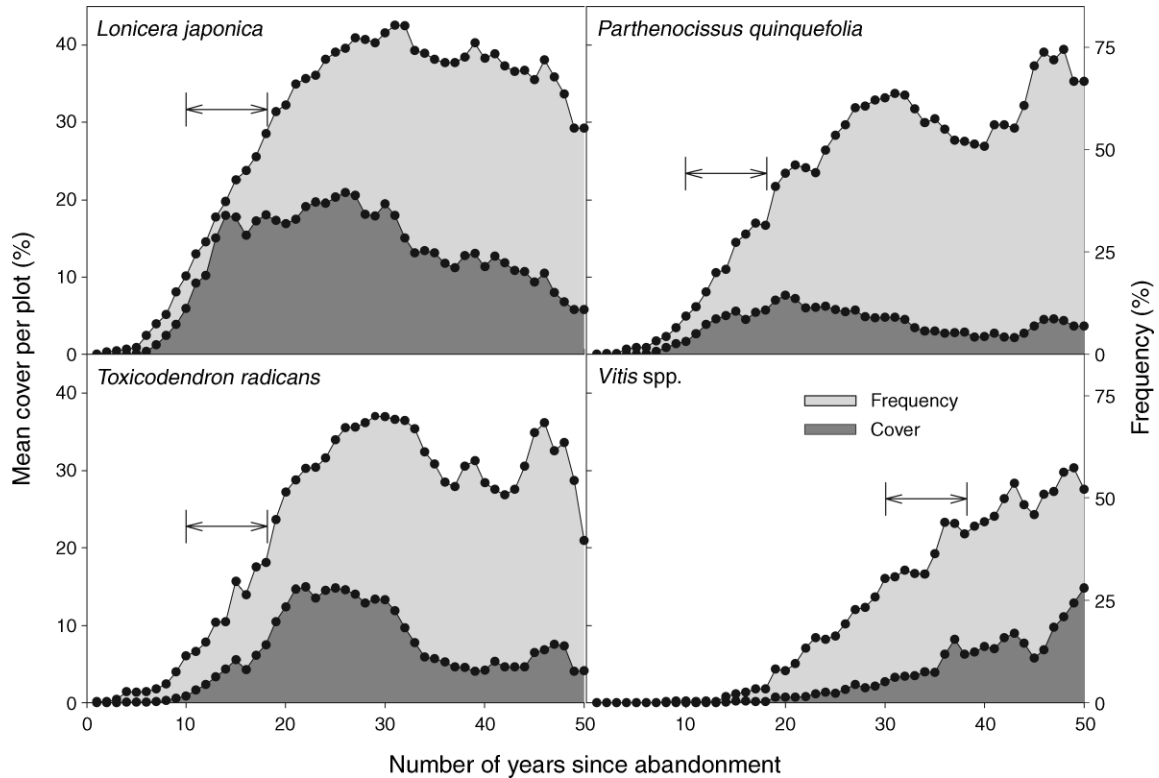


FIG. 1. Change in cover (left axis) and frequency (right axis) of the four dominant liana species during 50 years of old-field succession. Mean absolute percent cover per plot of each species is indicated in dark gray. Frequency, or the percentage of the total plots in which the species occurred, is indicated in light gray. Brackets and arrows indicate the window of expansion analyzed for each species. The study was conducted in the Piedmont region of New Jersey, USA, at the William L. Hutcheson Memorial Forest Center.

forest edge using Pearson correlations. We started time windows at year 8 due to low liana abundance early in succession and ended at year 40 to allow all windows full field replication. Because we were looking for broad population trends through time and the test is relatively weak, we did not correct for multiple comparisons. This analysis was conducted on total liana cover and each species individually.

RESULTS

Lianas in 50 years of succession

Cover of total lianas was low early in succession and started to increase at approximately seven years post-abandonment. Lianas continued increasing until absolute cover peaked at year 27, when total liana cover per plot reached 46%, representing 25% of the relative cover. The peak in total liana cover corresponded with a shift in community dominance from herbaceous to woody species (Fig. 2). Lianas were most abundant when herbaceous cover began to decline and trees were small and scattered. Similar to total lianas, three of the dominant liana species, *L. japonica*, *T. radicans*, and *P. quinquefolia*, peaked during mid-succession (peak cover at years 27, 22, and 20, respectively; Fig. 1). Of these three species, *L. japonica* had the highest peak cover, followed by *T. radicans* and *P. quinquefolia* (22%, 15%,

and 8% cover, respectively). Highest cover of the fourth liana, *Vitis* spp., reached 15% at year 50, but its cover has continued to increase with succession, showing no sign of decrease (Fig. 1).

Temporal patterns of liana frequency showed remarkably different dynamics from liana cover. Despite the pronounced decrease in cover of *L. japonica*, *P.*

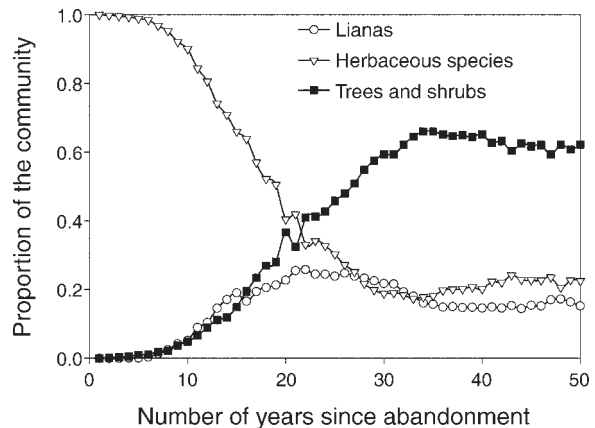


FIG. 2. Relative cover of life forms over 50 years of succession. Data are means of all 10 Buell-Small Succession Study (BSS) fields.

quinquefolia, and *T. radicans* late in succession, frequency (the number of plots occupied by lianas) remained relatively high for most species (Fig. 1). Total liana frequency nearly reached 100% at 30 years post-abandonment and remained high through the rest of succession (Fig. 3). Likewise, *L. japonica*, *P. quinquefolia*, and *T. radicans* each peaked in frequency at approximately year 30 and maintained high frequency. *Vitis* spp. frequency reached 60% at year 50 and is expected to continue increasing during succession. Mean species richness of lianas per plot increased consistently until year 30 post-abandonment and remained at two to three species until year 50 (Fig. 3).

Controls on liana expansion

Despite large amounts of variation in the system, cover expansion rates of lianas showed clear relationships to changing structural attributes of the community. The total liana expansion rate (all species combined) was correlated positively with cover of all herbaceous perennials, the annual grass *Bromus racemosus*, and the legume *Trifolium pratense* and negatively correlated with cover of the mid-successional goldenrod *Euthamia graminifolia* (Table 1). *Lonicera japonica*, *P. quinquefolia*, and *T. radicans* all shared the same expansion window (10–18 years post-abandonment) but each had slightly different interactions with the surrounding community. Increase in *L. japonica* cover was positively correlated with cover of all herbaceous perennials and *T. pratense*. *Parthenocissus quinquefolia* cover expansion had a positive relationship with the cover of *T. pratense* and *Solidago canadensis*, a mid-successional goldenrod. Increasing *T. radicans* cover was positively correlated with the cover of the herbaceous vine *Calystegia sepium* and annual grasses. Expanding cover of *Vitis* spp., which occurred later than the other liana species, was positively associated with cover of the tree *Fraxinus americana* and negatively associated with the conifer *Juniperus virginiana* and the liana *Lonicera japonica*.

Influence of the forest edge on spatiotemporal patterns

While total liana expansion showed no spatiotemporal patterns, the dynamics of individual species throughout the 50-year data set showed various relationships with distance from the edge of the bordering old-growth forest (Table 2). Ten to 25 years into succession, *P. quinquefolia* and *T. radicans* expansion was negatively related with distance from the forest as both species increased more along the edge. In contrast, *L. japonica* expansion was positively correlated with distance from the forest as the cover increase was greatest farther from the forest (Table 2). *Vitis* spp. expansion showed no relationship with distance to the forest during any time period (Table 2). Thirty to 40 years into succession, as liana cover declined, *P. quinquefolia* and *T. radicans* decrease in cover became positively correlated with distance from the forest and *L. japonica* negatively correlated with distance from the edge of the forest

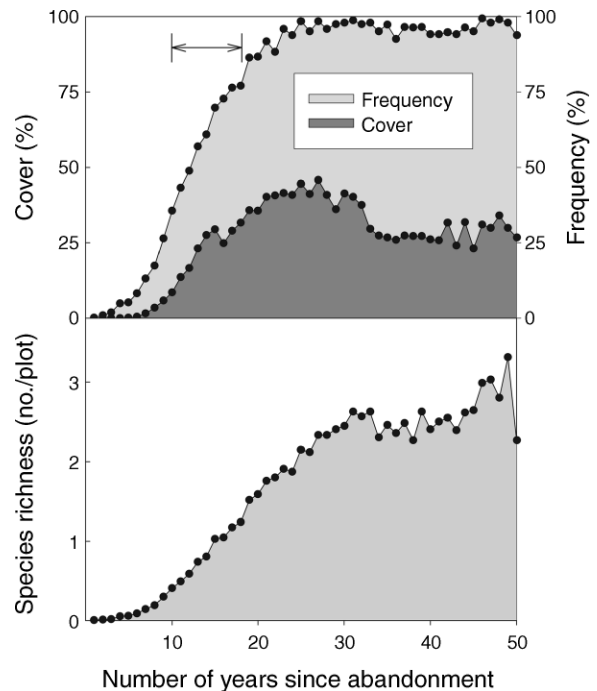


FIG. 3. Mean cover (left axis) and frequency (right axis) of all lianas (top) and mean liana species richness (bottom) during 50 years of old-field succession. Bracket and arrow indicate the window of expansion analyzed.

(Table 2). The switch between negative and positive relationships with distance from the forest were mostly due to population declines at sites of initial expansion and not increased growth at other locations.

DISCUSSION

Successional dynamics of lianas

Many factors contributed to the dynamics of lianas during forest regeneration. Liana cover in this system increased for the first 27 years of succession, leveled off, and then slowly declined. This pattern is supported by other research indicating that liana abundance initially increases following disturbance and then decreases with greater time since disturbance (Putz 1984b, Hegarty and Caballé 1991). While liana abundance is often lower in mature forests, biomass is often similar to disturbed environments as the remaining individuals are quite large (Hegarty and Caballé 1991, Laurance et al. 2001). We do not know how liana biomass has changed in this system.

The relationship between lianas and trees changed with successional stage. During tree establishment, the peak in total liana cover corresponded with the transition from a herbaceous- to woody-dominated community (Fig. 2) when young trees and shrubs would have provided support structures for lianas. As canopy closure occurred, increased tree cover would have reduced understory light availability and inhibited those lianas that had not made it into the forest canopy.

TABLE 1. Results from stepwise regressions indicating relationships between liana expansion and community variables (cover of other species, life forms, and distance from the edge of the old-growth forest).

Community variable	r^2	df	F/t	β	P
Total liana					
Model	0.1107	4, 396	12.33		<0.0001
Perennial		1	4.87	0.2203	<0.0001
<i>Bromus racemosus</i>		1	5.14	0.5513	<0.0001
<i>Euthamia graminifolia</i>		1	-2.13	-0.2928	0.0340
<i>Trifolium pratense</i>		1	3.07	0.5098	0.0023
<i>Parthenocissus quinquefolia</i>					
Model	0.076	3, 179	4.93		0.0026
Distance from edge		1	-2.07	-0.1226	0.0403
<i>Solidago canadensis</i>		1	2.12	0.4547	0.0352
<i>Trifolium pratense</i>		1	2.22	0.4017	0.0278
<i>Toxicodendron radicans</i>					
Model	0.2182	3, 209	19.54		<0.0001
Distance from edge		1	-2.39	-0.1339	0.0176
<i>Calystegia sepium</i>		1	3.82	0.5722	0.0002
Annual grass		1	5.81	0.41848	<0.0001
<i>Lonicera japonica</i>					
Model	0.1028	2, 290	16.62		<0.0001
Perennial		1	5.24	0.2371	<0.0001
<i>Trifolium pratense</i>		1	3.15	0.4994	0.0018
<i>Vitis</i> spp.					
Model	0.0715	3, 260	6.68		0.0002
<i>Faxinus americana</i>		1	2.18	0.1725	0.0305
<i>Juniperus virginiana</i>		1	-2.36	-0.1318	0.0189
<i>Lonicera japonica</i>		1	-2.30	-0.1646	0.0220

Notes: Regression coefficients (β) and significant tests for overall model (F) and each individual model term (t) are presented. The study was conducted in the Piedmont region of New Jersey, USA, at the William L. Hutcheson Memorial Forest Center.

The dynamics of individual species indicated that both early- and late-successional lianas occurred within the system. *Lonicera japonica*, *T. radicans*, and *P. quinquefolia* cover increased within the early-successional herbaceous community and decreased with canopy closure (Fig. 1). Following a different trajectory, the cover of *Vitis* spp. increased later in succession, around the same time trees became abundant, and showed no sign of population decline after 50 years of succession (Fig. 1).

The timing of liana expansion was expected to correspond with climbing characteristics and shade tolerance of each species. Coilers and twiners are often

early-successional species due to the need for small-diameter climbing supports and reduced shade tolerance. Lianas with specialized growth structures, including tendrils, adhesive disks, or aerial roots, are often late-successional species that can climb larger hosts and are more shade tolerant (Carter and Teramura 1988, Hegarty and Caballé 1991). Temporal separation of lianas based on climbing strategy has been examined in tropical systems but only hypothesized in temperate communities (Carter and Teramura 1988, Hegarty and Caballé 1991). In the BSS, some liana species followed this pattern: *L. japonica*, the most abundant twiner,

TABLE 2. Results from Pearson correlations between amount of liana expansion and distance from the edge of the old-growth forest during eight time windows through succession.

Time window (yr)	<i>Vitis</i> spp.		<i>Toxicodendron radicans</i>		<i>Parthenocissus quinquefolia</i>		<i>Lonicera japonica</i>		Total liana	
	r	P	r	P	r	P	r	P	r	P
8-12	-0.014	0.856	-0.134	0.045*	-0.12	0.076	0.189	0.003*	-0.001	0.985
12-16	0.008	0.917	-0.04	0.553	-0.133	0.050*	0.191	0.003*	0.097	0.134
16-20	-0.013	0.171	-0.049	0.47	0.017	0.801	-0.079	0.222	-0.081	0.212
20-24	-0.139	0.064	-0.093	0.166	0.125	0.064	0.224	0.001*	0.113	0.082
24-28	-0.093	0.215	0.177	0.008*	0.128	0.058	-0.129	0.047*	0.042	0.515
28-32	-0.029	0.696	0.137	0.041*	0.045	0.510	0.005	0.944	0.055	0.397
32-36	0.047	0.533	-0.024	0.725	0.172	0.011*	-0.169	0.009*	-0.046	0.479
36-40	-0.039	0.607	0.174	0.009*	0.071	0.295	-0.129	0.047*	-0.044	0.497

Notes: Negative relationships indicate greater liana expansion in plots closest to the edge of the forest.

* $P < 0.05$.

peaked early in forest succession and *Vitis* spp., with specialized tendrils for climbing, were late successional. This general separation between early- and late-successional species based on climbing strategy and shade tolerance was not seen for all species. *Parthenocissus quinquefolia* and *T. radicans* should be late-successional species because they have specialized climbing structures (adhesive disks and aerial rootlets) and high shade tolerance (Carter and Teramura 1988), but they peaked early in succession. Also, *Celastrus orbiculatus*, a nonnative twining liana increasing at the site, would be expected to occur in early-successional communities but the population did not begin to increase until much later.

A better separation between early- and late-successional lianas in this system might be their dependency on woody supports. *Lonicera japonica*, *P. quinquefolia*, and *T. radicans* grow well in high light conditions with little structural support. *Parthenocissus quinquefolia* and *T. radicans* commonly grow as ground cover in the absence of supports and can be quite dominant in herbaceous communities. The small twining stems of *L. japonica* can climb relatively small supports, such as upright mid-successional herbs. *Vitis* spp., however, depend on larger woody hosts for support and do not commonly persist as a ground cover. Instead of spreading along the ground, *Vitis* spp. spread once in the forest canopy and require a closed canopy for maximum expansion. Therefore, expansion of *Vitis* spp. occurred later in succession when trees were well-established with almost complete canopy closure. Similar species-specific population patterns were seen by Londré and Schnitzer (2006) as *T. radicans* populations decreased and *Vitis* spp. increased in temperate forests over a 45-year period.

Despite the ultimate declines in cover of most species, lianas remained present in the vast majority of plots during the last 25 years of succession. As lianas presumably spread into the canopy as tree cover increased, cover per plot decreased as plants remaining in the understory declined. However, lianas persisted in the young forest as either a few large canopy individuals or as suppressed individuals in the forest understory. Lianas appear to employ a “sit and wait” strategy by spreading to new sites on the ground and persisting at low cover for an extended time until opportunities, such as treefall gaps, initiate growth and allow access to the canopy (Putz and Holbrook 1991, Baars and Kelly 1996, Greenberg et al. 2001, Selaya and Anten 2007). This strategy allows for potential liana population explosions when suitable conditions arise, such as following disturbance. As liana species richness peaked at two to three species per plot, any gap would be colonized by multiple species, increasing the likelihood of a liana entering the canopy.

Controls on liana expansion

Change in the cover of liana species exhibited a variety of associations with the resident plant community. Lianas thrived in high light conditions following

disturbance, and we observed greatest liana expansion in plots with a suite of early successional grasses and broadleaved perennials, possibly due to the high light levels associated with these plots. The success of liana expansion within herbaceous-dominant plots was probably related to microclimate characteristics rather than direct interaction with individual species within the plot. However, *L. japonica* (see Plate 1) and *P. quinquefolia* expansion was greatest in plots with higher cover of *Trifolium pratense*, possibly indicating that lianas benefited from the nitrogen-fixing qualities of the legume in addition to high light.

The relationship between trees and lianas was contingent on the age of the community and individual liana species. Expansion rates of total lianas and the three dominant lianas that shared the same expansion window (*L. japonica*, *P. quinquefolia*, *T. radicans*) were unrelated to tree cover, either collectively or as individual tree species. Later in succession, *Vitis* spp. expansion was positively associated with *Fraxinus americana* and negatively associated with *Juniperus virginiana*. The low expansion rate of *Vitis* spp. in areas dominated by *J. virginiana* could reflect the requirement of *Vitis* spp. for suitably sturdy hosts for growth. The numerous small branches of *J. virginiana* might not support large, heavy *Vitis* spp. stems. The dense lower branches of *J. virginiana* may also limit light levels to reduce growth of young *Vitis* spp. climbing the trunk. *Vitis* spp. appear better suited for growth on canopy trees with fewer, larger branches, such as *Fraxinus americana*. Once in the canopy, expanding *Vitis* spp. can use small-diameter branches to spread between tree canopies. This tree-to-tree spread likely explains why *Vitis* spp. expansion was greatest as the forest canopy closed.

Interactions between liana species also appeared later in succession as *Vitis* spp. expansion was negatively associated with *L. japonica* cover. The overall morphology of these lianas differs as *L. japonica* typically has multiple small stems and *Vitis* spp. produce one main stem. Appropriate hosts for *L. japonica* might not be suitable for *Vitis* spp., and this may lead to a spatial separation of the two species. However, this association may also result from direct interaction early in seedling development. Young *L. japonica* was observed twining around and completely shading understory herbs and saplings. If the two liana species initially colonized the same support, fast-growing *L. japonica* stems may have twined around and smothered slower growing *Vitis* spp. stems, lowering growth and survivorship of *Vitis* spp. in *L. japonica*-dominated areas.

Influence of the forest edge

Although the temporal dynamics of *T. radicans*, *L. japonica*, and *P. quinquefolia* were similar, their spatio-temporal dynamics associated with the forest edge varied. Populations of *P. quinquefolia* and *T. radicans* were most dynamic in plots closest to the forest edge,



PLATE 1. Numerous stems of *Lonicera japonica* climbed *Juniperus virginiana* trees. Appropriate host trees for lianas varied between liana species. Photo credit: L. M. Ladwig.

where initial expansion occurred. Thirty to 40 years into succession, the greatest decreases in cover also occurred in these plots. *Toxicodendron radicans* also began increasing in plots farthest from the old-growth forest during this period, contributing to the spatial association. *Parthenocissus quinquefolia* and *T. radicans* appear to have initially dispersed from the old-growth forest and were able to thrive close to the forest edge because tree cover was low, creating adequate light conditions for establishment. As trees colonized the fields, the old-growth forest edge became shaded and only individuals that had reached the canopy continued growing. As tree abundance increased, the functional edge of the forest expanded farther into the fields and so too did liana populations (Myster and Pickett 1992). Liana cover close to the old-growth forest began declining, while dispersal into the less forested areas further from the edge increased, shifting expansion patterns.

Lonicera japonica dynamics followed a similar pattern over time, but had the opposite spatial response to the forest edge compared to *P. quinquefolia* and *T. radicans*. *Lonicera japonica* expansion was initially greatest in plots farthest from the old-growth forest. During expansion, *L. japonica* was the only liana species with a positive relationship with herbaceous perennials, around which it often twines. As perennials dominated the community, the dense cover would have competed

intensively with *T. radicans* and *P. quinquefolia*, which grew mainly as ground covers during this time. Meanwhile, a dense perennial community would be ideal for *L. japonica*, as it could easily escape light competition by climbing erect perennials. As the advancing front of trees expanded into the fields, plots farthest from the old-growth forest became shaded and cover of *L. japonica* eventually declined.

Native vs. nonnative species

Native species are often perceived as part of the plant community while nonnative invasive species are expected to perform differently and dominate the community (Dreyer et al. 1987, Baars and Kelly 1996, Van Clef and Stiles 2001, Leicht-Young et al. 2007). However, we did not see dramatic differences among native and nonnative liana species in the BSS based on population dynamics. Comparisons between native and nonnative species were based on only four species, three native (*T. radicans*, *P. quinquefolia*, *Vitis* spp.) and one nonnative (*L. japonica*), since other species present were not abundant enough for statistical analysis. The regionally problematic *L. japonica* is an invasive nonnative with several potential advantages over native species, including greater morphological plasticity, specialized circumnutation behavior of the central shoot axis, and extended leaf phenology (Dillenburg et al. 1993, Schweitzer and Larson 1999, Larson 2000). While the nonnative liana had greater cover than other species for most of succession, the basic population trajectory of *L. japonica* did not differ from the two mid-successional natives, *T. radicans* and *P. quinquefolia* (Fig. 1). All three species peaked at mid-succession and decreased ultimately to ~5% cover per plot. Similarly, frequency steadily increased for all dominant liana species, and at 50 years post-abandonment each species occupied ~60% of plots in each field (Fig. 1). The greater peak cover achieved by *L. japonica* did not appear to give it an advantage over the native species. Similar dominance patterns of lianas of different origins within the BSS further support Meiners' (2007) finding of similar dynamics of native and nonnative species during succession. Despite the potential mechanisms of competitive superiority noted for *L. japonica*, native and nonnative lianas appear to play equivalent successional roles, with no inherent benefit to the invader. Commonalities between lianas of different origin were also seen by Fike and Niering (1999), who found that both native *Vitis labrusca* and nonnative *Celastrus orbiculatus* exhibited similar invasive tendencies in a regenerating forest.

Conclusions

Impacts of increasing worldwide deforestation and forest fragmentation are well documented, while increasing agricultural abandonment is resulting in old-field succession and reforestation in some areas (Foster 1992). As documented by Brown (2003), a decrease in agricultural land resulted in an increase in forest cover,

~15% from 1970 to 1990. Although the successional sequence of climbing mechanisms based on tropical lianas did not hold up in this temperate forest, the dynamics of lianas in successional areas should ultimately lead to decreases in at least some liana species as succession proceeds. As even late-successional lianas depend on canopy openings for regeneration, the abundance of these species may also decrease as succession proceeds. However, the continued persistence of lianas in the understory may allow them to increase rapidly following treefalls or other disturbances. The high disturbance rates associated with many fragmented forests may maintain lianas as an important forest component. With sufficient disturbance rates, lianas may increase locally, even in mature forests, and may pose significant challenges to forest regeneration. The combination of morphological plasticity, known invasiveness, and potential responses to global climate change make lianas an increasing threat to temperate deciduous forests. As such, much more information on the regeneration and impacts of lianas within temperate forests is needed.

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