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Pavlovic, N. B. and S. A. Leicht-Young (U.S. Geological Survey, 1100 N. Mineral Springs Rd., Porter, IN 46304). Are temperate mature forests buffered from invasive lianas? J. Torrey Bot. Soc. 138: 85–92. 2011.—Mature and old-growth forests are often thought to be buffered against invasive species due to low levels of light and infrequent disturbance. Lianas (woody vines) and other climbing plants are also known to exhibit lower densities in older forests. As part of a larger survey of the lianas of the southern Lake Michigan region in mature and old-growth forests, the level of infestation by invasive lianas was evaluated. The only invasive liana detected in these surveys was *Celastrus orbiculatus* Thunb. (Celastraceae). Although this species had only attached to trees and reached the canopy in a few instances, it was present in 30% of transects surveyed, mostly as a component of the ground layer. Transects with *C. orbiculatus* had higher levels of soil potassium and higher liana richness than transects without. In contrast, transects with the native *C. scandens* had higher pH, sand content, and soil magnesium and lower organic matter compared to transects where it was absent. *Celastrus orbiculatus* appears to be a generalist liana since it often occurs with native lianas. *Celastrus orbiculatus* poses a substantial threat to mature forests as it will persist in the understory until a canopy gap or other disturbance provides the light and supports necessary for it to ascend to the canopy and damage tree species. As a result, these forests should be monitored by land managers so that *C. orbiculatus* eradication can occur while invasions are at low densities and restricted to the ground layer.

Key words: *Celastrus orbiculatus*, *Celastrus scandens*, deciduous forests, invasive plants, Lake Michigan, lianas.

Invasive exotic plant species most often are dependent on disturbance to infiltrate native plant communities. These disturbances can come in many forms, such as removal of vegetation (Huebner and Tobin 2006, Burnham and Lee 2010, Hausman et al. 2010), disturbance of the soil (McNab and Loftis 2002, Hausman et al. 2010), creation and management of rights of way (Flory and Clay 2006, Mortensen et al. 2009), and past land use (Lundgren et al. 2004, DeGasperis and Motzkin 2007, Mosher et al. 2009). The increase in light, creation of avenues for propagule dispersal, and decrease in competition allow for invasion of these habitats (Brothers and Spingarn 1992, Flory and Clay 2006, Eschtruth and Battles 2009). Thus, mature and old-growth forests that have low light levels and minimal human disturbance, are thought to be buffered against many invasive species (Brothers and Spingarn 1992, McCarthy et al. 2001, Weber and Gibson 2007, Mosher et al. 2009), although this hypothesis has been relatively untested (but see Flory and Clay 2009).

Lianas (woody vines), like invasive species are most commonly thought of as disturbance-dependent species that reach their peak densities in early successional habitats such as regenerating forests and canopy gaps (DeWalt et al. 2000, Schnitzer et al. 2000, Schnitzer and Carson 2001, Letcher and Chazdon 2009, Schnitzer and Carson 2010). These habitats are ideal for liana colonization due to the availability of low, small diameter woody saplings, poles, and shrub supports that allow for infiltration of the canopy (Putz 1984, Hegarty 1991, Hegarty and Caballé 1991, Balfour and Bond 1993). Lianas, however, are also present in mature forests although the distribution of lianas in mature and old-growth forests is not well studied in temperate areas (but see Talley et al. 1996, Webb et al. 2000, Allen et al. 2005, Allen et al. 2007). Lianas can cause damage to trees through girdling (Lutz 1943), increasing sus-

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ceptibility to ice damage (Siccama et al. 1976), decreasing growth (Ladwig and Meiners 2009), and interrupting succession (McNab and Meeker 1987, Schnitzer et al. 2000, Schnitzer and Carson 2010). To better understand the impacts of invasive lianas in temperate forests, we asked how common exotic lianas are in mature and old-growth forests.

We examined the presence and abundance of exotic lianas and herbaceous vines in the ground layer and canopies of temperate mature and old-growth forests in the southern Lake Michigan lake plain region. This research was part of a study to examine climber community ecology in temperate mature forests (Leicht-Young et al. 2010). Climbers were defined as both lianas and herbaceous vines. We predicted that these mature forests would not contain high numbers of invasive liana species due to low levels of disturbance, resulting in a lack of suitable supports and low light availability for liana colonization. The results of this study will assist managers of mature forests in preventing the further establishment of damaging invasive liana species into these high-quality habitats.

Materials and Methods. STUDY SITES. We surveyed native and exotic climbers in 69 transects at 20 different sites in the southern Lake Michigan lake plain (Table 1; see Leicht-Young et al. 2010). We focused our efforts on mature forests with low amounts of disturbance although many sites were selectively logged 100–150 years ago (Cook and Jackson 1978). However, only Warren Woods was an uncut old-growth forest dominated by *Fagus grandifolia* Ehrh. and *Acer saccharum* Marsh. (Table 1; Cain 1935). We also examined the successional dune forests (*Quercus velutina* Lam. and *Pinus banksiana* Lamb.) of this region as a reference community that has had minimal human disturbance similar to the mature and old-growth forests, but represents an earlier successional stage. Habitats included were successional dune forests, mature dune forests, oak savanna, oak-hickory forests, and beech maple forests. Here, we will primarily report on the extent of exotic invasion in these habitats. Nomenclature follows the USDA PLANTS database (USDA NRCS 2011).

SURVEY METHODS. At each of 20 sites we established three or six 60 m transects separated by at least 50 m for a total of 69 transects (Table 1; see Leicht-Young et al. 2010 for detailed methods). Larger natural areas such as Ogden Dunes, Furnessville, Heron Rookery, and Warren Woods and Dunes could accommodate two sets of three transects with each set differing in forest type while smaller sites such as Wintergreen Woods and the Pinhook Bog uplands could only fit three. Because our goal was to survey relatively intact forested areas, we located all transects at least 40 m away from any forest or trail edges to minimize their influence on the plant community (Matlack 1994, Londré and Schnitzer 2006, Flory and Clay 2009). Along these transects, we used three survey techniques to quantify species and types of climbers. Presence of climbers was assessed along a 2 m wide by 60 m strip transect (120 m^2 per transect). Climber density in the ground layer was estimated by counting stems of climbers under 1 m tall in 1 m^2 quadrats every 15 m along the transect (N = 5 points for a total of 5 m^2 $transect^{-1}$). Finally, we used point-quarter methods at the same 15 m points (Cottam and Curtis 1956, Mitchell 2007) to survey the trees and climbers that were physically climbing on them (N = 20 trees per transect). At each point we used a spherical densiometer to determine canopy cover and took soil moisture readings with the Delta-T moisture meter (Delta-T Devices 1998) to characterize the environments at each transect. We also collected samples of the upper 10 cm of soil at each point and combined them by transect for analysis of soil chemistry to determine whether exotic liana abundance varied with soil nutrient levels (e.g., sand versus moraine soils). Samples were analyzed for percent organic matter, total phosphorous (ppm), potassium (% and ppm), magnesium (% and ppm), calcium (% and ppm), pH, cation exchange capacity (CEC; meq 100 g^{-1}), nitrate (ppm), ammonium (ppm), and the percentage of sand, silt, and clay (A & L Great Lakes Laboratories, Inc., Fort Wayne, IN).

DATA ANALYSES. Since there was only one invasive liana species detected (*Celastrus orbiculatus* Thunb.) we decided to compare the environmental attributes separately in transects where it and its native congener, *C. scandens* L. were present in comparison to where each was absent. To do this, we used *t*-

Table 1. Site name, number of transects, forest community type, and liana abundance statistics by *Celastrus* species for forest sites having *Celastrus* spp. Abundance variables are number of transects with liana present, ground layer density, and climbing stems per transect. The habitats are as follows: Mixed RmRo = Mixed red maple (*Acer rubrum*)/red oak (*Quercus rubra*) forest; Red oak df = Red oak dune forest; 3 = Oak (*Quercus* spp.)/hickory (*Carya* spp.); Beech-maple = Beech (*Fagus grandifolia*)/sugar maple (*A. saccharum*); BoJp = Black oak (*Q. velutina*)/jack pine (*Pinus banksiana*). Names in bold are landholders for the sites.

			C. orbiculatus			*C. scandens*		
Site Name[1]	Transects (*N*)	Forest community type	Presence (Transects Site^{-1})	Density (Stems m^{-2})	Stems (transect^{-1})	Presence (Transects Site^{-1})	Density (Stems m^{-2})	Stems (transect^{-1})
INDNP								
Moraine Nature Preserve	3	Beech-maple	1			0		
Indiana Dunes State Park	3	Mixed RmRo	1			0		
Pinery (Indiana Dunes S.P.)	3	Mixed RmRo	2			0		
INDU								
Furnessville Woods	6	Mixed RmRo, Red oak df	6	0.5 ± 0.3	0.2 ± 0.2			
Headquarters Woods	3	Oak hickory	2			0		
Keiser Woods	3	Mixed RmRo	3	0.1 ± 0.1		0		
Learning Center Woods	3	Oak hickory	3	0.7 ± 0.4		0		
Ogden Dunes	6	Red oak df, BoJp	1	0.3 ± 0.2	0.7 ± 0.7	4	0.1 ± 0.1	14.3 ± 10.5
West Beach	3	Red oak df	2	0.1 ± 0.1		0		
MIDNR						0		
Warren Dunes	6	Red oak df, BoJp	0			3	0.1 ± 0.1	9.67 ± 9.67

[1] Sites without *Celastrus* included Indiana Department of Natural Resources (INDNR) properties Ambler Flatwoods and Moraine Nature Preserve, Indiana Dunes National Lakeshore (INDU) properties Hobart Prairie Grove, Heron Rookery, Miller Woods, and Pinhook Bog, LaPorte County Parks (LCP) properties Red Mill and Wintergreen Woods, and Michigan Department of Natural Resources (MIDNR) Warren Woods property.

tests followed by a Benjamini-Hochberg adjustment for the p-values to avoid Type-I error from multiple tests (Benjamini and Hochberg 1995). We used NMS ordination (Sørenson distance measure) with climber presence/absence data to determine whether there were relationships between climbers and environmental factors (i.e., canopy cover, moisture, soil type; McCune and Mefford 2006). Mean density of climbers per species in the ground layer was calculated on a site basis. For tree data collected using the point-quarter method, we calculated total number of tree species, total absolute density, and total mean basal area (BA) of all tree species for each transect following the methods in Mitchell (2007).

Results. Only one invasive liana species, *Celastrus orbiculatus* (oriental bittersweet), was found in nine of 20 mature forest sites, representing 45% of the sites (Table 1). Out of the 69 transects, this species was present in 21 transects overall, in 10 transects in density plots, and only in two transects physically attached to trees, respectively representing 30%, 14%, and 3% of the total transects. On a transect basis, mean stem density ranged from 0.2–1.6 stems m^{-2} with averages per site ranging from 0.1 to 0.7 stems m^{-2} (Table 1). At the two sites where *C. orbiculatus* was growing in trees, the mean number of vines per transect ranged from 0.2 to 0.7 vines per transect (Table 1). In comparison, the native congener of *C. orbiculatus*, *C. scandens* (American bittersweet), only occurred at Ogden and Warren Dunes and had on average 14 and 10 climbing stems per transect respectively (Table 1). The only exotic herbaceous vine found was *Solanum dulcamara* L. from a transect at the Pinery in Dunes State Park.

In transects with *Celastrus orbiculatus*, levels of phosphorous were significantly higher ($t_{67} = 3.0$, $P < 0.01$) and there was significantly greater liana species richness ($t_{67} = 5.1$, $P < 0.001$) overall (Table 2). In transects with *C. scandens*, pH ($t_{67} = -5.4$, $P < 0.001$) and % sand ($t_{60} = -8.5$, $P < 0.001$) were significantly higher compared to plots without this species. These transects also had significantly lower canopy cover ($t_6 = 2.5$, $P = 0.04$), organic matter ($t_{67} = 2.3$, $P = 0.03$), K ($t_{47} = 10.1$, $P < 0.001$), ammonium ($t_{67} = 2.2$, $P = 0.03$), % silt ($t_{49} = 8.4$, $P < 0.001$), % clay ($t_{67} = 7.0$, $P < 0.001$), total absolute density ($t_{67} = 3.8$, $P < 0.001$) and mean basal area ($t_{67} = 2.9$, $P = 0.004$) of trees compared to transects without *C. scandens* (Table 2).

Three-dimensional NMS ordination showed that occurrence of the invasive *Celastrus orbiculatus* (black circles in Fig. 1) was mostly central in the climber ordination space in mature forests often co-occurring with the majority of native liana species (Fig. 1). Climber presence/absence was highly correlated along axis 1 with climber species richness ($r = 0.71$) whereas pH ($r = 0.74$) and percent magnesium ($r = 0.66$) were highly correlated along axis 2 in the opposite direction compared to organic matter ($r = -0.61$) and canopy cover ($r = -0.64$) (Leicht-Young et al. 2010). The mature forests where *C. orbiculatus* occurs represent more neutral and richer soils supporting forests with high canopy cover compared to the successional dunes where *C. scandens* occurs (gray diamonds and see biplot vectors in Fig. 1).

Discussion. In the mature forests of the southern Lake Michigan region, we only detected one invasive liana species, *Celastrus orbiculatus*, being present in 30% of the transects. While established juvenile plants of C. *orbiculatus* were present in 14% of transects, larger plants had reached the tree canopy at only 3% of transects in mature forests. These mature forest habitats also had higher overall liana species diversity. These habitats had higher phosphorous, likely related to the fact that *C. orbiculatus* was not as prominent in the very sandy dune habitats that are inherently low in phosphorous (Maun and Sun 2002). Thus, the combination of conditions that make an area favorable to native lianas may also be favorable to exotic lianas such as *C. orbiculatus*. Therefore, our prediction about mature forests being buffered from invasive lianas was not supported.

The two sites where *Celastrus orbiculatus* was actively climbing trees were very different. One was a mature, probably selectively logged forest of mixed northern hardwoods such as *Acer rubrum* L., *Quercus rubra* L., and *Q. alba* L. with a high richness of ground layer flora (Furnessville Woods, Table 1; Pavlovic and Leicht-Young, unpublished data) and the other a dune forest on the lee side of a high sand dune with *Fraxinus americana* L., *Pinus strobus* L., *Q. rubra* and *Tilia americana* L. (Ogden Dunes, Table 1). At the former site, *C. orbiculatus* was concentrated in canopy gaps

Table 2. Mean (± SE) values of environmental and biological traits for transects with and without *Celastrus orbiculatus* and *C. scandens*. Superscript letters indicate significant differences in variable between the presence and absence of each species separately at the $\alpha = 0.05$ level.

	C. orbiculatus present	*C. orbiculatus* absent	*C. scandens* present	*C. scandens* absent
Canopy Cover (%)	89.5 ± 2.6	84.5 ± 3.0	53.4 ± 14.1^{A}	89.6 ± 1.5^{B}
Moisture (%)	15.0 ± 3.1	9.2 ± 1.3	4.8 ± 1.1	11.6 ± 1.4
Organic Matter (%)	4.6 ± 0.9	4.0 ± 0.4	1.6 ± 0.7^{A}	4.4 ± 0.4^{B}
P (ppm)	18.6 ± 4.0^{A}	10.7 ± 1.2^{B}	4.1 ± 0.8^{A}	14 ± 1.6^{B}
K (ppm)	58.8 ± 6.7	48.2 ± 4.0	14.3 ± 2.1^{A}	55.5 ± 3.4^{B}
Mg (ppm)	120.8 ± 15.6	109.8 ± 9.9	112.1 ± 23.4	113.1 ± 9
pH	5.9 ± 0.2	5.9 ± 0.1	7.4 ± 0.2^{A}	5.8 ± 0.1^{B}
CEC (meq/100g)	6.0 ± 0.7	6.2 ± 0.5	4.7 ± 1.2	6.3 ± 0.4
Nitrate (ppm)	3.6 ± 1.7	5.2 ± 1.5	1 ± 0	5.2 ± 1.3
Ammonium (ppm)	13.4 ± 1.6	12.8 ± 1.2	6.9 ± 1.3^{A}	13.6 ± 1^{B}
Sand (%)	71.0 ± 5.7	71.8 ± 2.9	94.3 ± 1.3^{A}	69 ± 2.7^{B}
Silt (%)	20.7 ± 4.0	19.9 ± 2.0	3.4 ± 1.1^{A}	22 ± 1.9^{B}
Clay (%)	8.5 ± 1.8	8.2 ± 1.0	2.3 ± 0.3^{A}	9 ± 0.9^{B}
Total Tree Species	5.8 ± 0.4	6.0 ± 0.3	5.1 ± 0.5	6 ± 0.3
Total Absolute Density (trees/ha)	380.2 ± 31.9	316.7 ± 21.1	152.4 ± 52^{A}	355.7 ± 17.2^{B}
Total Mean BA (cm^2)	1008.2 ± 119.7	1024.5 ± 73.7	502.3 ± 146.9^{A}	1078.2 ± 63.5^{B}
Liana Species	6.2 ± 0.4^{A}	3.3 ± 0.3^{B}	4.3 ± 1.1	4.6 ± 0.3

and was making its way through the understory, even "laddering" up nearby *Vitis* spp. vines to ascend towards the canopy (Putz 1995). Since *C. orbiculatus* is a stem twiner, it needs smaller diameter supports to wrap around in order to reach the canopy of mature forests (Putz 1984, DeWalt et al. 2000). Canopy gaps serve as areas of tree and liana regeneration and provide the conditions necessary for readily available supports (Schnitzer

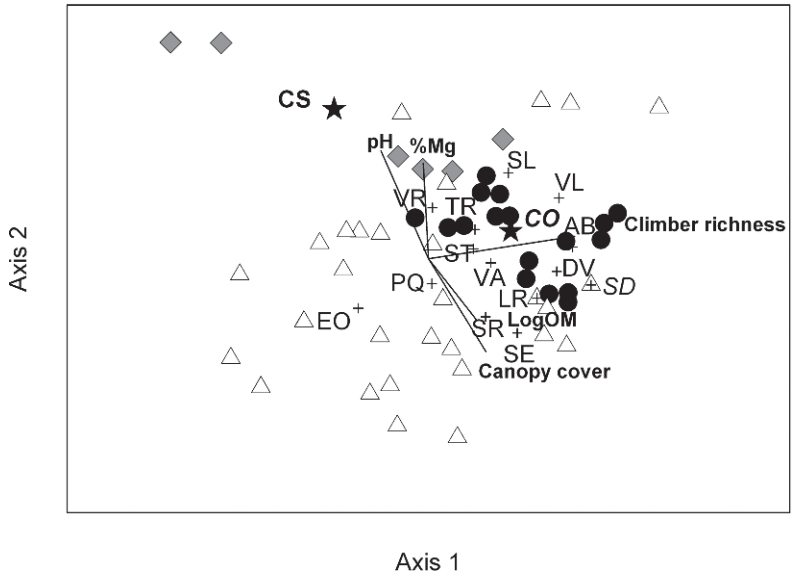

FIG. 1. Liana and herbaceous vine presence/absence ordination (NMS) showing 69 transects and species centroids (plus symbols). Exotic species are italicized, *Celastrus* species are bolded, and native species are in plain text. Centroid of *C. orbiculatus* (CO) and C. scandens are stars; transects are open triangles; transects with *C. orbiculatus* present are black circles; and transects with *C. scandens* present are gray diamonds. Species codes are AB = *Amphicarpea bracteata* (L.) Fernald, CS = *Celastrus scandens*, DV = *Dioscorea villosa* L., EO = *Euonymus obovatus* Nutt., LR = *Lonicera reticulata* Raf., PQ = *Parthenocissus quinquefolia* (L.) Planch., SE = *Smilax ecirrhata* (Engelm. ex. Kunth) S. Watson, SL = *S. lasioneura* Hook., SR = *S. rotundifolia* L., ST = *S. tamnoides* L., SD = *Solanum dulcamara*, TR = *Toxicodendron radicans* (L.) Kuntze, VA = *Vitis aestivalis* Michx., VL = *V. labrusca* L., VR = *V. riparia* Michx.

et al. 2000, Schnitzer and Carson 2010). Lianas like *C. orbiculatus* have the ability to suppress regeneration of canopy trees in these gaps.

At the latter site, C*elastrus orbiculatus* was actually making its way up the lee-side dunes via root sprouts to reach the crest and grow down the lake-facing side of the dune (S. Leicht-Young, pers. obs.). Recent restoration fires in 1998 and 2007 have probably facilitated the root sprout expansion rather than gap creation processes especially since these lianas would be top killed by the fires (N. Pavlovic, unpublished data). Subsequent to some burns, *C. orbiculatus* rapidly twines into the canopy, although the mechanism for this response is unknown. Although this species can grow in the open dunes, it has a preference for more mesic and shaded habitats as indicated by the ordination and environmental results (Leicht-Young et al. 2007a, Leicht-Young et al. 2007b; Table 2). In non-forested dune habitats it appears to establish in sheltered areas of higher moisture first (i.e., in dune forests or under shrubs) before moving out into the more xeric, exposed dunes (S. Leicht-Young and N. Pavlovic, pers. obs.). The open dunes however, are also habitat for its congener, *C. scandens* which we observed in high numbers in these primary successional dune forests (Fig. 1, Table 2). The Ogden Dunes site illustrates a location where the two *Celastrus* species may interact because the dune forest and mature dune forests are adjacent to each other.

In contrast, *Celastrus scandens* was present only in successional dune forests except for one occurrence in a mature dune forest at Ogden Dunes (Table 1). In addition, *C. scandens* was the outlier species separate from all other climbers including *C. orbiculatus* (Fig. 1). Ground layer density of *C. scandens* was low compared to *C. orbiculatus*. However, numbers of stems climbing trees per transect were much higher for *C. scandens* compared to *C. orbiculatus* (Table 1). The high densties of stems climbing trees were consistent at the two successional dune forest sites, Ogden Dunes and Warren Dunes. While *C. scandens* is more of a specialist in these drier dune habitats, *C. orbiculatus* is more general in its forest habitat preferences (Leicht-Young et al. 2007b).

In this study region and throughout the eastern United States, *Celastrus orbiculatus* has become a prominent member of the landscape, especially in disturbed, second growth forests such as those succeeding from more recently abandoned old fields (Fike and Niering 1999, Mosher et al. 2009, Ladwig and Meiners 2010a, b) and in areas where windthrow has caused large portions of the overstory to be opened (N. Pavlovic, pers. obs.). Despite the higher abundance of *C. orbiculatus* in these disturbed habitats, this liana has the physiological capability to survive as seedlings even under canopies with 0.5% light transmittance such as under *Tsuga canadensis* (L.) Carrière (Leicht-Young et al. 2007a). This study confirms for the first time the expectation that *C. orbiculatus* will invade mature forests in forested landscapes.

The mature and old-growth forests of our study region as well as those of many parts of the Midwest, are essentially islands in a landscape largely dominated by agriculture and development (Levenson 1981, Brothers and Spingarn 1992). These disturbed areas on forest edges often have abundant invasive species that provide the propagules to infiltrate mature forests. Thus, the edges of these forests will often have invasive species present but they decrease further into the interior (Brothers and Spingarn 1992, Weber and Gibson 2007). However, with gaps forming in the canopies of these mature forests as trees age, die or blow down, the combination of propagule pressure with a gap in the canopy has been shown to increase the probability of invasion for some species (Eschtruth and Battles 2009). Two previous studies of invasive plants exclusively in old-growth forests in Indiana only reported the invasive lianas *Campsis radicans* (L.) Seem. ex Bureau (outside of its native range), *Euonymus fortunei* (Turcz.) Hand.-Maz. (Brothers and Spingarn 1992) and *Lonicera japonica* Thunb. (Weber and Gibson 2007). However, all of these species were concentrated < 50 m from the forest edge. *Celastrus orbiculatus* on the other hand, is a plant that is clearly capable of invading into these dark, mature forests even without a canopy opening, and remaining in the understory in a latent phase (Leicht and Silander 2006, Leicht-Young et al. 2007a). Once it has been released through an opening in the canopy or other disturbance that provides necessary light and supports, it can climb towards the canopy and eventually cover substantial portions of it (Leicht and Silander 2006, Ladwig and Meiners 2010b)

and may impact the growth of canopy trees (Ladwig and Meiners 2009).

This study illustrates that even mature forests are not immune to the infiltration of invasive lianas, specifically *Celastrus orbiculatus*, and that it is only a matter of time before invasive lianas growing in the understory will have the opportunity to ascend to the canopy after gap-phase disturbance. The invasion of *C. orbiculatus* into mature forest canopies may alter the composition and successional trajectory of these mature forests. Proactive control of young established plants by land managers will be critical in preventing damage to these important remnant habitats by invasive lianas such as *C. orbiculatus*. In other forested regions, the prospect of nonnative lianas with the ability to invade deeply shaded habitats will be an important conservation issue worldwide.

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