

# Long-term changes in liana loads and tree dynamics in a Malaysian forest

S. JOSEPH WRIGHT,<sup>1</sup> I-FANG SUN,<sup>2</sup> MARIA PICKERING,<sup>3</sup> CHRISTINE D. FLETCHER,<sup>4</sup> AND YU-YUN CHEN<sup>2,5</sup>

<sup>1</sup>*Smithsonian Tropical Research Institute, Apartado 0843–03092, Balboa, Republic of Panama*

<sup>2</sup>*Department of Natural Resources and Environmental Studies, National Donghua University, Hualien 974 Taiwan*

<sup>3</sup>*Department of Biological Sciences, Meredith College, Raleigh, North Carolina 27607 USA*

<sup>4</sup>*Forest Research Institute of Malaysia, Kepong 52109 Selangor, Malaysia*

**Abstract.** The importance of lianas through time and their effect on tree reproduction are evaluated for the first time in a Southeast Asian Dipterocarp forest. We quantified flower and seed production by lianas and trees for 13 years, assessed liana loads in the crowns of all trees larger than 30 cm in diameter at breast height (1.3 m) in 2002 and 2014, and assessed levels of reproduction for the same trees during a strong general flowering event in 2014 for the 50-ha forest dynamics plot at the Pasoh Forest Reserve, Malaysia. General flowering refers to synchronous reproduction by hundreds of plant species at irregular, multiyear intervals and only occurs in Southeast Asian Dipterocarp forests. Overall, lianas were present in 50% of tree crowns and comprised 31% of flower production and 46% of seed production. Lianas reduced growth, survival, and reproduction by their host trees. Lianas were less frequent in canopy-emergent trees, Dipterocarps comprised a disproportionately large proportion of canopy emergents, and, as a consequence, lianas were less frequent in Dipterocarps than in trees from other plant families. Lianas infested the crowns of significantly fewer trees in 2014 (47.9%) than in 2002 (52.3%); however, the decrease was restricted to trees with the lightest liana loads and sample sizes and statistical power were enormous. Lianas comprised a stable proportion of flower production and a highly variable proportion of seed production from 2002 through 2013. We conclude lianas have a huge impact on trees in this forest and were a stable component of the forest between 2002 and 2014. The emergent habit and associated ability to avoid lianas might contribute to the success of the Dipterocarpaceae.

**Key words:** *Dipterocarpaceae*; flower production; general flowering; lianas; Pasoh Forest Reserve, Malaysia; seed production; tree growth; tree survival.

## INTRODUCTION

Woody vines, or lianas, are the second most important growth form in many forests, particularly seasonal tropical forests (Schnitzer and Bongers 2002). Lianas climb host trees to reach the sunlit forest canopy and compete with their hosts for light and soil resources (Schnitzer et al. 2005). Lianas also reach between tree crowns and can bring down otherwise sound trees as their neighbors fall. Lianas affect tree dynamics and the structure of forests.

Lianas are becoming increasingly important relative to trees in Neotropical forests (Schnitzer and Bongers 2011, Schnitzer 2015). Nine studies now report increases and not one study reports a decrease in the importance of lianas in Neotropical forests (Table 1). Elsewhere the evidence is mixed. In South Carolina, the density (stems/ha) of large lianas increased dramatically in 50-yr old secondary forests between 1979 and 2001 (Allen et al. 2007), but, in Wisconsin, liana abundance was un-

changed between 1959 and 2004 (Londré and Schnitzer 2006). And, in tropical Africa, liana density decreased between 1979 and 1992 near Makakou, Gabon (Caballé and Martin 2001), between 1994 and 2007 in the Ituri Forest, Democratic Republic of the Congo (Bongers and Ewango 2015), and between 2001 and 2012 in Korup National Park, Cameroon (Thomas et al. 2015). Decreases in African tropical forests and increases in Neotropical forests raise the possibility that increasing lianas might be a regional phenomenon restricted to the Neotropics (Schnitzer and Bongers 2011). The possibility that lianas might be changing through time has not been evaluated for a single Asian forest.

The forests of Southeast Asia, the Afrotropics, and the Neotropics share warm, wet climates that favor hyperdiverse tree communities on all three continents but have evolved independently for tens of millions of years. The subfamily Dipterocarpoideae (henceforth Dipterocarps) dominates basal area in many Southeast Asian forests and is absent from the Neotropics and Africa (excepting the Seychelles). General flowering characterizes the reproductive phenology of aseasonal, Dipterocarp-dominated forests. General flowering species, including most Dipterocarps, reproduce synchro-

Manuscript received 7 November 2014; revised 3 February 2015; accepted 16 March 2015. Corresponding Editor: M. Uriarte.

<sup>5</sup> Corresponding author. E-mail: ychen@mail.ndhu.edu.tw

TABLE 1. Studies examining the importance of lianas through time.

Region, location, and response variable	Rate of change (% per yr)	Source
<b>Neotropics</b>		
Ecuador, Peru, and Bolivia (47 plots)	+3.27	Phillips et al. (2002)
Prop. stems $\geq 10$ cm DBH composed of lianas		
Barro Colorado Island, Panama		
Prop. leaf production composed of lianas	+2.61	Wright et al. (2004)
Flower production of lianas	+4.1	Wright and Calderón (2006)
Flower production of trees	+1.8	Wright and Calderón (2006)
Prop. trees with lianas	+1.84	Ingwell et al. (2010)
Stem density (no./ha) $\geq 1$ cm DBH of lianas	+2.0	Schnitzer et al. (2012)
Stem density (no./ha) $\geq 1$ cm DBH of trees	−0.6	Schnitzer et al. (2012)
Stem density (no./ha) $\geq 5$ cm DBH of lianas	+2.7	Schnitzer et al. (2012)
BDFFP, Brazil		
Stem density (no./ha) $\geq 2$ cm DBH of lianas	+1.00	Laurance et al. (2014)
La Selva, Costa Rica		
Stem density (no./ha) $\geq 1$ cm DBH of lianas	+1.76	Yorke et al. (2013)
San Emilio, Costa Rica		
Stem density (no./ha) $\geq 3$ cm DBH of lianas	+0.293	Enquist and Enquist (2011)
Stem density (no./ha) $\geq 3$ cm DBH of trees	−1.75	Enquist and Enquist (2011)
Nouragues, French Guiana		
Stem density (no./ha) $\geq 10$ cm DBH of lianas	+0.21	Chave et al. (2008)
Stem density (no./ha) $\geq 10$ cm DBH of trees	−0.59	Chave et al. (2008)
<b>Africa</b>		
IRÉT, Gabon		
Stem density (no./ha) $\geq 5$ cm DBH of lianas	−1.72	Caballé and Martin (2001)
Stem density (no./ha) $\geq 5$ cm DBH of trees	−0.37	Caballé and Martin (2001)
Ituri, Democratic Republic of Congo		
Stem density (no./ha) $\geq 2$ cm DBH of lianas	−3.84	Bongers and Ewango (2015)
Korup, Cameroon		
Stem density (no./ha) $\geq 1$ cm DBH of lianas	−1.73	Thomas et al. (2015)
<b>Asia</b>		
Pasoh, Malaysia		
Prop. trees with lianas	−0.73	this study
Prop. flower production composed of lianas	no change	this study
<b>North America</b>		
Savannah River, South Carolina, USA		
Prop. stems $\geq 4.5$ cm DBH composed of lianas	+11.4†	Allen et al. (2007)‡
Wisconsin, USA (14 forests)		
Liana abundance, lianas per tree	no change	Londré and Schnitzer (2006)

*Notes:* Temporal trends are presented separately for trees and lianas whenever possible. Insignificant temporal differences between trees and lianas are labeled no change. Schnitzer and Bongers (2011) and Schnitzer (2015) cite three additional articles for temporal change in lianas, which we exclude for the following reasons. Benítez-Malvido and Martínez-Ramos (2003) removed plants  $<1$  m tall and counted recruits six years later, which omits temporal variation associated with growth and survival. Rogers et al. (2008) pool woody vines with other life forms. Foster et al. (2008) provide incomplete information for their initial survey, which precludes an assessment of temporal change. Schnitzer and Bongers (2011) also cited an increase in the range of ivy in Germany, which we exclude because many free-standing species have also extended their ranges. “Proportion of” is abbreviated “Prop.”

† This rate of increase is suspiciously large. The secondary forests were  $>50$ -yr old when the study began. Some lianas might have first reached the large, minimum size threshold of 4.5 cm DBH during the 22-yr study.

‡ We discount a second forest disturbed by a hurricane at the beginning of the measurement period because such disturbances favor lianas.

nously at irregular, multiyear intervals (Appanah 1993, Sakai et al. 2006, Cannon et al. 2007). Dipterocarps are known to support fewer lianas than non-Dipterocarps in one Southeast Asian forest (Campbell and Newbery

1993). The impact of lianas on the reproduction of their host trees and the possibility of changing liana importance over time has never been evaluated for general flowering species.

We document the occurrence and consequences of interactions between lianas and trees at the Pasoh Research Forest, Peninsular Malaysia. Dipterocarps dominate basal area (Kochummen et al. 1990) and hundreds of tree species from at least 41 families reproduce synchronously during general flowering events (Appanah 1993). The leaves of lianas displace the leaves of their host trees on a one-to-one mass basis at Pasoh (Kira and Ogawa 1971), which suggests a large potential impact on host trees. For this reason, we focus on liana–tree interactions in which liana foliage overtops or is intermixed with the foliage of the host tree. We assessed liana–tree interactions in 2002 and 2014 and documented species-level flower and fruit production from 2001 through 2013. We answer the following questions: (1) Do lianas occur as frequently in the crowns of the Dipterocarpaceae as in the crowns of other tree families? (2) Do lianas affect the reproduction of their host trees during a strong, general flowering event? For completeness, we also ask: Do lianas affect host survival and growth? (3) Have lianas changed in importance between 2002 and 2014?

One mechanism proposed to explain the increasing importance of lianas in Neotropical forests concerns seed dispersal modes and the widespread loss of frugivores to hunters (Wright et al. 2007). More than 80% of tree species are frugivore-dispersed, while 60% of liana species are wind-dispersed in Neotropical moist forests (Gentry 1982, Muller-Landau and Hardesty 2005). For this reason, frugivore loss potentially favors lianas over trees in Neotropical moist forests. To evaluate this possibility for the Pasoh Research Forest, we determined seed dispersal modes for all species encountered in our long-term study of fruit production.

#### METHODS

The Pasoh Forest Reserve (2°58' N, 102°18' E) protects 13 000 ha of natural forest for timber production and includes the Pasoh Research Forest. The 1840-ha Research Forest includes 1240 ha protected from logging since 1974 and a central core area of 600 ha of unlogged, primary forest. A 50-ha forest dynamics plot is located in the unlogged forest. Here, all free-standing trees and shrubs  $\geq 1$  cm in diameter at breast height (DBH; 1.3 m) were mapped to the nearest 0.5 m, measured to the nearest mm, and identified to species in 1987, 1990, 1995, 2000, 2005, and 2010 following Condit (1998). The initial census included more than 320 000 individuals belonging to 814 species, 294 genera, and 78 families (Kochummen et al. 1990).

We used binoculars to assess crown position and liana load between May and September 2002 for trees  $\geq 30$  cm DBH in the 2000 census and crown position, liana load, and reproductive status between 18 July and 10 August 2014 for trees  $\geq 30$  cm DBH in the 2010 census. In 2014, we classified crown position on a five-point scale following Dawkins and Field (1978) as follows: 1, no direct light; 2, lateral light; 3, partial overhead light; 4,

more than 90% of the crown receives direct overhead light; 5, emergent crown with direct light from all directions. In 2002, we classified crown position on a three-point scale, which combined categories 1 and 2, and 4 and 5 of the five-point scale. We classified reproductive status and liana load on five-point scales following Wright et al. (2005) as follows: 0, zero activity (sterile or zero lianas); 1, up to 25% coverage; 2, 26–50% coverage; 3, 51–75% coverage; and 4, more than 75% coverage. For liana load, coverage refers to the proportion of the foliage of the host tree overtopped by or intermixed with foliage of lianas. For reproduction, coverage refers to the proportion of potential reproductive sites with flowers or fruits. Potential reproductive sites are largely limited to sun-exposed terminal branches, with the exception of cauliferous species. Two observers evaluated a subsample of trees independently in 2002 and 2014, and we used Spearman's rho for ordered levels to evaluate interobserver agreement.

We censused seed traps weekly from 13 August 2001 through 3 February 2011 and again from 17 October 2011 through 30 January 2014, following methods described in Wright and Calderón (2006). There were 247 traps for the first 53 weekly censuses and 336 thereafter. Briefly, each seed trap consisted of a square, 0.5-m<sup>2</sup>, open-topped, 1-mm mesh bag held 80 cm above the ground on a PVC frame. Sixteen traps were located in large tree-fall gaps and 320 were located in the understory at 13.5 m intervals on alternating sides of permanent trails and randomly between 4 and 10 m from the trail. We recorded the presence of flowers and counted immature fruit, mature fruit, seeds, capsules, and fruit fragments damaged by insects or vertebrates. We identified 98.4% of seeds and fruit and 97.4% of flower records to species or morphospecies. The lianas of Pasoh are poorly known, and our morphospecies are lianas observed as flowers or fruit on an unidentified liana, as well as in our traps. Flower records refer to unique species-trap-census combinations. Fruit records refer to unique species-trap-census combinations, with conspecific fruit, seeds, capsules, and fragments pooled (immature fruit excluded). We analyze both fruit records and the total number of seeds plus mature fruit captured. Finally, we determined dispersal mode for each species encountered in our seed traps on the basis of diaspore morphology. We distinguished three broad dispersal modes as follows: frugivore dispersed (zoochorous), wind-dispersed (anemochorous), and ballistically dispersed. A final category, gravity dispersed, contained two species with no apparent dispersal mechanism.

#### Analyses

*Liana loads, crown position, and the Dipterocarpaceae.*—We used a log-linear contingency analysis to evaluate associations among plant family, crown position, and liana load for 2014. Plant family contrasted all

non-Dipterocarp tree species against the 30 Dipterocarp species recorded in the 50-ha plot. Crown position pooled categories 1 and 2 because too few trees  $\geq 30$  cm DBH were in category 1. We first evaluated the saturated model, which includes the three-way interaction, and then used chi-square tests to identify and remove insignificant interactions.

*Impact of lianas on host trees.*—We used generalized linear mixed-effect models to evaluate the impact of lianas on the growth, survival, and reproduction of their host trees. Fixed effects included a continuous covariate to capture variation associated with initial tree size ( $\log(\text{DBH})$ ) and categorical measures of crown position and liana load. Random effects included intercepts for species and space. Species with five or more individuals evaluated were included, and space was arbitrarily divided into 200  $50 \times 50$  m subplots. For growth, the response variable and covariate were the logarithms of DBH in 2005 and 2000, respectively. For survival, the response variable was 10-yr survival (2000–2010), and the covariate was the logarithm of DBH in 2000. For reproduction, the response variable was reproductive status in 2014 (sterile or fertile), and the covariate was the logarithm of DBH in 2010. We chose to dichotomize reproduction to avoid potential difficulties interpreting an analysis with five categories for both the dependent and independent variables. The fixed effects of liana loads and crown position were for 2002 for growth and survival and 2014 for reproduction. Error distributions were Gaussian for growth and binomial for survival and reproduction. For the growth analysis, normal residuals (evaluated by the Shapiro-Wilks test) could only be obtained by excluding trees that grew by more than 25% or shrank by more than 10%. We believe these large diameter increments reflect measurement errors (Condit 1998).

Model selection followed Bolker et al. (2009). Significant random effects were identified for models with all fixed effects using restricted maximum likelihood and log-likelihood ratio tests. Fixed effects were evaluated for models with significant random effects using the Laplace approximation of the maximum likelihood and the Akaike's information criterion (AIC). Fixed effects with  $\Delta\text{AIC} > 10$  were retained. We chose  $\Delta\text{AIC} > 10$  to minimize Type I errors because sample sizes were very large. We re-ran the final model using restricted maximum likelihood to obtain coefficients and standard errors. To visualize the impact of lianas for tree growth, we present residuals for each level of liana load for the model obtained by removing the significant fixed effect associated with liana load from the best-fit model.

*Temporal change in lianas.*—We performed two analyses to determine whether liana loads changed between 2002 and 2014. For the first analysis, we placed the trees assessed in both years into a five-by-five contingency table corresponding to the five liana load categories in 2002 and 2014 and used the McNemar

symmetry chi-square test to evaluate the null hypothesis that liana loads were unchanged. For the second analysis, we placed all trees assessed in 2002 and all trees assessed in 2014 into a two-by-five contingency table corresponding to the two census years and the five liana load categories and used a chi-square test to evaluate the null hypothesis that liana loads were unchanged.

We performed correlation analyses to evaluate temporal change in the proportional contribution of lianas to flower and seed plus fruit production. We eliminated partial years (2001, 2011, and 2014) and evaluated correlations between year and the proportional contribution of lianas to flower records, fruit records, and seeds plus fruit captured. For completeness, we also evaluated correlations between year and the number of flower records, fruit records, and seeds plus fruit captured separately for lianas and trees. We did not expect these latter correlations to be significant given the wide variation in community-wide levels of flower and fruit production observed in general flowering forests.

We performed all analyses using R, version 2.14.0 (R Development Core Team 2011). We evaluated linear mixed-effects models using the lme4 library.

## RESULTS

In 2002, we assessed crown positions and liana loads for 3471 of 3814 trees  $\geq 30$  cm DBH in the 2000 census of the 50-ha plot. Unassessed trees were dead, missing, or not visible with binoculars. In 2014, we assessed crown position, liana loads, and reproductive status for 3364, 3323, and 3166 of 3762 trees  $\geq 30$  cm DBH in the 2010 census, respectively. The 157 trees assessed for liana loads but not for reproduction had heavy liana loads that precluded evaluation of reproduction. We will make the full data set is publicly available at DRYAD.

Two observers assessed 243 and 960 trees independently in 2002 and 2014, respectively. Spearman's rho equaled 0.779 ( $P < 10^{-6}$ ) and 0.592 ( $P < 10^{-6}$ ) for liana loads in 2002 and 2014, respectively, and 0.443 ( $P < 10^{-6}$ ) and 0.447 ( $P < 10^{-6}$ ) for crown position and reproductive status in 2014, respectively. Independent assignments were highly repeatable for liana categories and reasonably repeatable for crown and reproductive categories.

### *Liana loads, crown position, and the Dipterocarpaceae*

The three-way interaction among membership in the family Dipterocarpaceae, crown position and liana load was insignificant (deviance = 13.2,  $\text{df} = 12$ ,  $P = 0.355$ ). All three two-way interactions were highly significant. Dipterocarps tended to have lower liana loads than non-Dipterocarps (Fig. 1A; deviance = 72.3  $\text{df} = 4$ ,  $P < 10^{-10}$ ), canopy emergents tended to be Dipterocarps (Fig. 1B; deviance = 333.2,  $\text{df} = 3$ ,  $P < 10^{-10}$ ), and emergents tended to have lower liana loads than smaller trees (Fig. 1C; deviance = 220.5,  $\text{df} = 12$ ,  $P < 10^{-10}$ ).

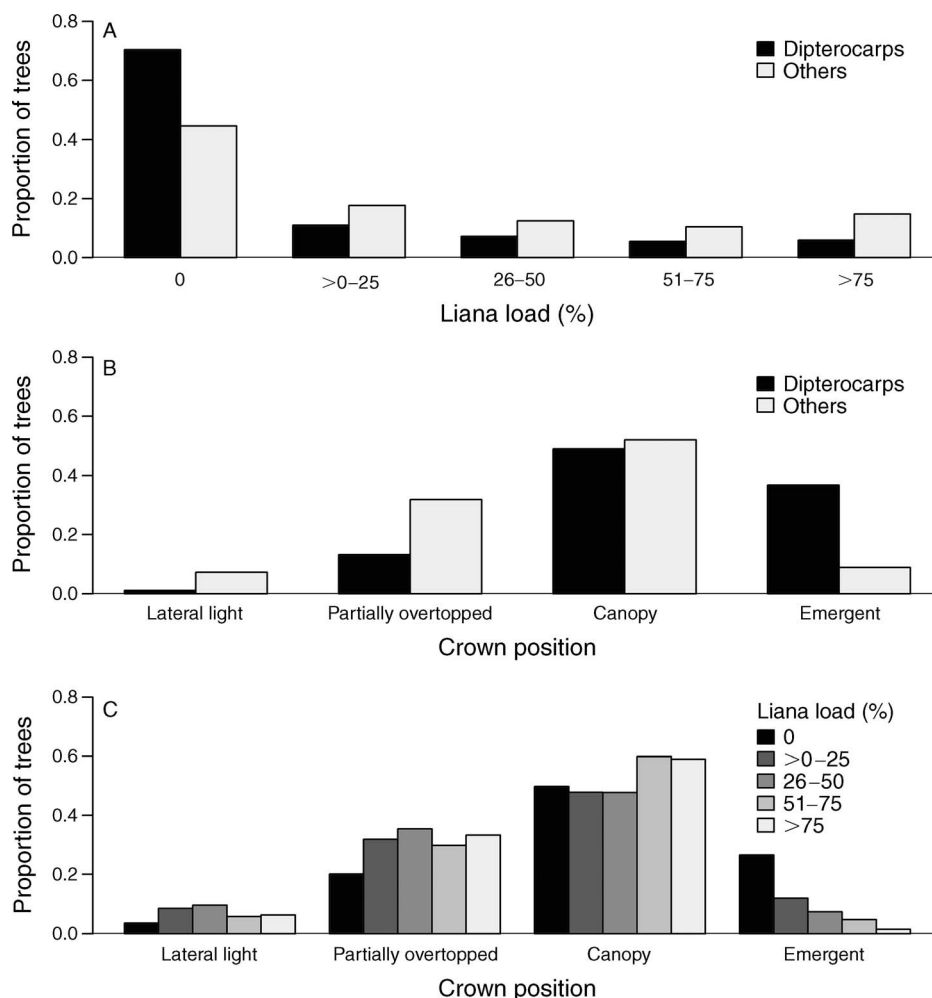


FIG. 1. Histograms illustrating significant two-way interactions between (A) liana loads and membership in the family Dipterocarpaceae, (B) crown position and the family Dipterocarpaceae, and (C) liana loads and crown position. The vertical axis refers to the proportion of individual trees  $\geq 30$  cm DBH (1.3 m). Proportions sum to 1 for each category in the inset keys. Data are from the 2014 survey of the 50-ha plot at the Pasoh Research Forest, Malaysia.

#### *Impact of lianas on host trees*

Sample sizes for the analyses of liana impact on host growth, survival, and reproduction were 2403 (149), 3043 (149), and 2706 (130) individuals (species), respectively.  $\Delta$ AIC values were 38.6, 47.2, and 46.0 for removal of the fixed-effect term for lianas from the best-fit models for growth, survival, and reproduction, respectively. Lianas reduced diameter growth, survival, and reproduction of their host trees (Fig. 2, Table 2; Appendix). Growth and reproduction declined with each successive increase in the categorical level of liana load (Fig. 2A, C). In contrast, mortality was similar for trees with less than 75% of their crowns infested with lianas (24% dead in 10 years) but much greater for trees with more than 75% of their crowns infested (42% dead; Fig. 2B).

Crown position affected tree diameter growth, with greater growth in trees exposed to more sunlight (Table

2). Crown position did not affect survival and reproduction significantly.  $\Delta$ AIC values were 29.4, 2.8, and 4.8 for removal of the fixed effect term for crown position from models for growth, survival, and reproduction, respectively.

#### *Temporal change in liana loads*

Liana loads decreased significantly from 2002 to 2014 for the 2457 trees assessed in both years (McNemar symmetry chi-square test = 36.5,  $df = 10$ ,  $P < 0.0001$ ). This is a cohort analysis, however, and the significant decrease might be related to some change associated with trees being 12 years older and larger. Possible changes include growth to large size with lower liana loads (Fig. 1C) and the high mortality rate of trees with the largest liana loads (Fig. 2B). To avoid these potential pitfalls of a cohort analysis, we also compared liana loads for all 3471 and 3325 trees assessed in 2002 or 2014, respectively. The decrease in liana loads was still



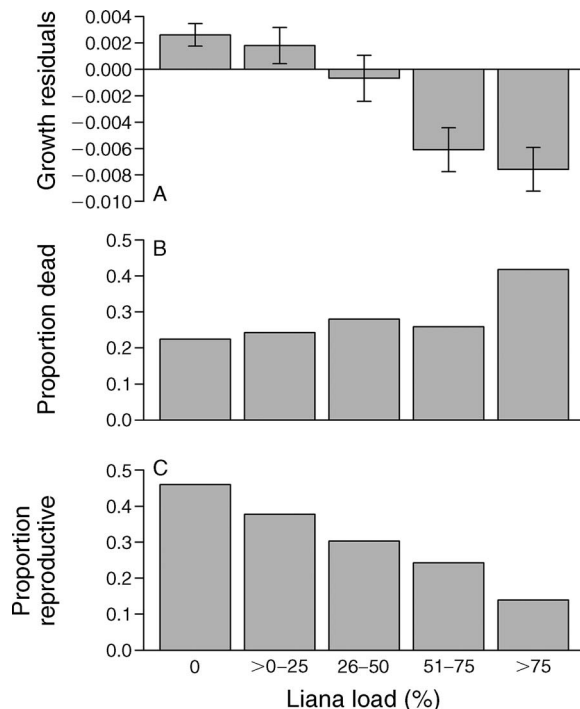


FIG. 2. Lianas effect on the (A) diameter growth, (B) survival, and (C) reproduction of their host trees. In panel (A), the histogram represents mean ( $\pm$ SE) residuals from a generalized linear mixed model obtained by removing the fixed effect of lianas from the best fit model (growth was measured in mm, then log-transformed for analysis). In panel (B), the histogram represents the proportion of trees that died between 2000 and 2010. In panel (C), the histogram represents the proportion of trees that were reproductive in July/August 2014. Liana load refers to the proportion of the foliage of the host tree that was overtopped by or intermixed with foliage of lianas. Liana loads were recorded in 2002 for (A and B) growth and survival and (C) 2014 for reproduction. All trees are  $\geq 30$  cm DBH (1.3 m).

highly significant ( $\chi^2 = 16.2$ ,  $df = 4$ ,  $P < 0.005$ ). Heavy liana loads ( $>50\%$ ) characterized similar proportions of trees in 2002 and 2014, but more trees were liana free in 2014 (Fig. 3).

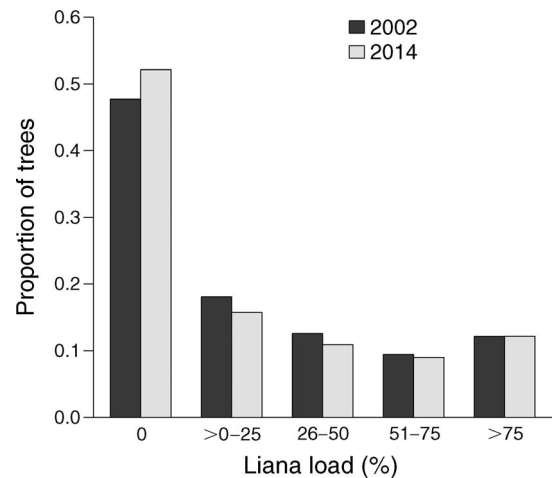


FIG. 3. Histograms of the proportion of large trees (DBH  $\geq 30$  cm) characterized by five levels of liana load in 2002 (dark gray) and 2014 (light gray).

#### Temporal change in flower and fruit production by lianas

We recorded 85 828 flower records, 36 821 fruit records, and 130 519 individual seeds plus fruit in 611 weekly censuses of 336 seed traps. Lianas comprised 32.3% of the flower records, 45.9% of the fruit records, and 49.9% of the seeds plus fruit.

Fig. 4 presents annual production for trees and lianas expressed as numbers of flower records (Fig. 4A), fruit records (Fig. 4B), and seeds plus fruit (Fig. 4C). As expected, interannual variation associated with weak general flowering events in 2002, 2005, and 2010 was large (Sun et al. 2007), and correlations between year and levels of reproduction were insignificant for lianas and trees ( $|r| < 0.465$ ,  $P > 0.15$  for the six measures of reproduction in Fig. 4). We will not return to absolute variation in reproductive output.

Fig. 5 presents the proportion of annual reproductive output comprised by lianas. This proportion was unrelated to year for flower production ( $r = 0.090$ ,  $P = 0.792$ ), but increased significantly with year for both measures of fruit production ( $r = 0.702$ ,  $P < 0.02$ , and  $r$

TABLE 2. Summary of fixed effects for the generalized linear mixed models that best explained growth, survival, and reproduction.

Fixed effect	Growth			Survival			Reproduction		
	Estimate	SE	<i>t</i>	Estimate	SE	<i>z</i>	Estimate	SE	<i>z</i>
Intercept	0.166	0.0134	12.4***	-4.33	0.933	4.64***	-8.09	1.11	-7.26***
Covariate [log(DBH)]	0.976	0.00223	438.6***	0.497	0.151	3.29***	1.15	0.180	6.41***
Liana level 2	-0.00178	0.00172	-1.0	0.00194	0.132	0.015	-0.0628	0.152	-0.414
Liana level 3	-0.00456	0.00202	-2.3*	0.232	0.147	1.58	-0.395	0.177	-2.23*
Liana level 4	-0.0101	0.00221	-4.6**	0.213	0.168	1.27	-0.798	0.196	-4.08***
Liana level 5	-0.0118	0.00202	-5.8***	1.05	0.142	7.37***	-1.47	0.238	-6.15***
Crown level 2	0.00766	0.00176	4.3**						
Crown level 3	0.0137	0.00237	5.8***						

Notes: Estimated coefficients for the categorical fixed effects of lianas and crown position are relative to trees without lianas and trees whose crowns are entirely overtopped by taller trees (receive lateral light or sunflecks only), respectively. Crown position had only insignificant effects on survival and reproduction, which are not shown. Random effects are presented in the Appendix.

\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ .

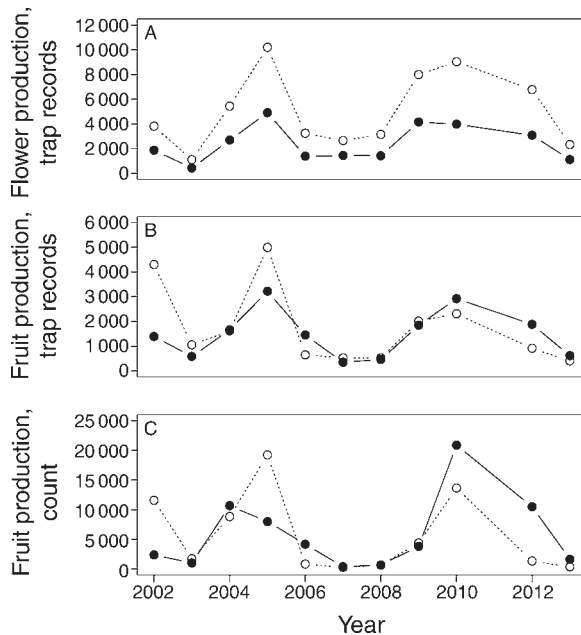


FIG. 4. The production of (A) flowers and (B and C) seeds plus fruit by lianas (solid line, solid circles) and trees (dotted line, open circles). The measure of production is (A) flower records, (B) fruit records, and (C) the total number of seeds plus fruit captured. Records refer to the summed number of species-specific presences or unique species-trap-census combinations. Levels of production are unrelated to year (all Pearson correlation coefficients are  $<0.5$  and all  $P$  values are larger than 0.15). Data are from 611 weekly censuses of 336  $0.5\text{-m}^2$  traps.

$= 0.739$ ,  $P < 0.01$  for fruit records and seeds plus fruit, respectively).

#### Seed dispersal modes

We evaluated fruit and diaspore morphology to determine dispersal mode for 104 liana and 261 tree species. Zoochory characterized 81.2% and 70.2% of the tree and liana species, respectively. Anemochory characterized 13.0% and 27.9% of the tree and liana species, respectively. The remaining species were ballistically or gravity dispersed. We evaluated 23 Dipterocarp species, 21 were anemochorous, and two were gravity dispersed.

#### DISCUSSION

Trees from the family Dipterocarpaceae have significantly lower levels of liana infestation than do non-Dipterocarps at Pasoh, Malaysia (Fig. 1A) and at Danum Valley, Sabah, Malaysia (Campbell and Newbery 1993). Campbell and Newbery (1993) hypothesize that Dipterocarps escape lianas because they shed lower branches (and presumably lianas) ontogenetically as they shift from monopodial growth as juveniles to sympodial growth as adults (Hallé and Ng 1981) and because adults have tall branch-free boles lacking trellises to support climbing lianas. We cannot evaluate the first component of this hypothesis because our data

concern adult trees  $\geq 30$  cm DBH. The results of our analysis of interactions among liana load, crown position, and plant family are consistent with the second component of the hypothesis for adult trees. The first branches of canopy emergents are above the crowns of neighboring canopy trees. Thus, all canopy emergents have relatively long, branch-free boles. At Pasoh, emergents have lower liana loads than do canopy trees (Fig. 1C), most emergents are Dipterocarps (Fig. 1B) and, as a consequence, liana loads are less severe for Dipterocarps (Fig. 1A). The insignificant three-way interaction among liana loads, canopy position, and plant family suggests that Dipterocarps enjoy no further advantage in the interaction with lianas beyond escape as canopy emergents.

Lianas reduced growth, survival, and reproduction of their host trees at Pasoh (Fig. 2). Similar negative effects on host trees have been observed elsewhere (e.g., Clark and Clark 1990, Schnitzer et al. 2005, Wright et al. 2005). The reduction in host survival is strikingly similar at Pasoh and at Barro Colorado Island, Panama. At both sites, mortality rates are similar for trees with  $<75\%$  of their foliage affected by lianas and much greater for trees with more extreme levels of liana infestation (Fig. 2B; Ingwell et al. 2010). Adult survival has a large effect on population fitness in long-lived forest trees (Franco and Silvertown 2004). More rapid growth, increased reproduction, and, in particular, greater adult survival associated with low adult liana loads could contribute to the dominance of many Southeast Asian forests by Dipterocarps if the low liana loads observed among the emergent Dipterocarps of

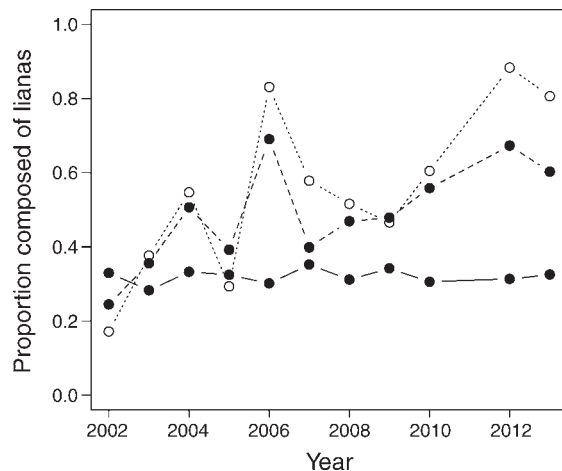


FIG. 5. The proportion of reproductive production composed of lianas. The solid line and circles represent flower production quantified by flower records, where a record refers to each unique species-trap-week combination ( $r = 0.090$ ,  $P = 0.792$ ). The dashed line and solid circles represent fruit production quantified by fruit records ( $r = 0.702$ ,  $P < 0.05$ ). The dotted line and open circles represent fruit production quantified by the total number of seeds plus fruit captured ( $r = 0.739$ ,  $P < 0.01$ ). Data are from 611 weekly censuses of 336  $0.5\text{-m}^2$  traps.

Pasoh (Fig. 1A) and Danum Valley (Campbell and Newbery 1993) are representative of Dipterocarps elsewhere.

#### *Temporal change in the importance of lianas*

Apparent results differed among our three measures of temporal change in lianas. Liana loads declined significantly between 2002 and 2014 (Fig. 3). The proportional contribution of lianas to flower production was virtually constant between 2002 and 2013 (Fig. 5), and the proportional contribution of lianas to fruit production increased significantly between 2002 and 2013 (Fig. 5).

We believe these contradictory results are readily reconciled. For liana loads, the significant decline was quantitatively small and was limited to trees with light liana loads (Fig. 3). The decline is significant only because sample sizes and statistical power are enormous (3471 and 3323 trees assessed in 2002 and 2014, respectively, including 2457 trees assessed in both years). For the proportional contribution of lianas to fruit production, the significant increase occurred amidst large interannual variation in fruit production by both lianas and trees (Fig. 4B, C). As a consequence, the proportional contribution of lianas to fruit production varied widely among years (Fig. 5). Many Pasoh species flower more frequently than they fruit (Chen 2007). For this reason, flower production is relatively stable (Fig. 4A), and we believe the proportional contribution of lianas to flower production is a better indicator of temporal trends. We conclude that lianas are relatively stable at Pasoh because liana loads and the proportional contribution of lianas to flower production changed little between 2002 and 2014 (Figs. 3 and 5).

Lianas are increasing regionally in the western Amazon (Phillips et al. 2002) and at five intensively studied Neotropical forests (Table 1). Outside the Neotropics, lianas might be increasing at one site in South Carolina, USA (Allen et al. 2007; see our footnote to Table 1), are relatively stable in Wisconsin, USA (Londré and Schnitzer 2006) and in one Southeast Asian forest (this study), and are decreasing in three African forests (Caballé and Martin 2001, Bongers and Ewango 2015, Thomas et al. 2015). Increasing liana importance appears to be a regional phenomenon restricted to the Neotropics.

Five mechanisms have been hypothesized to favor lianas in old-growth forests subjected to anthropogenic forcing, as reviewed by Schnitzer and Bongers (2011) and Schnitzer (2015). It might be possible to distinguish among these hypotheses if lianas are indeed only increasing regionally in the Neotropics. The five mechanisms involve more positive responses among lianas than among trees to rising tree turnover rates (Phillips et al. 2002), rising atmospheric CO<sub>2</sub> concentrations (Phillips et al. 2002), rising nitrogen deposition (Schnitzer 2015), declining precipitation (Swaine and Grace 2007), and frugivore removal by hunters (Wright

et al. 2007). Temporal change in tree turnover rates has only been evaluated in the Neotropics so will not be considered further. Atmospheric CO<sub>2</sub> concentrations and nitrogen deposition are increasing globally so cannot explain a regional phenomenon restricted to the Neotropics. In addition, some of the smallest regional increases in nitrogen deposition co-occur with strong increases in lianas in the western Amazon (Phillips et al. 2002, Hietz et al. 2011). Directional temporal changes in precipitation vary regionally. Precipitation is declining in central Africa (Zhou et al. 2014), but lianas are declining (not increasing) for one forest located within (Bongers and Ewango 2015) and two forests located just to the west of the region evaluated by Zhou et al. (Caballé and Martin 2001, Thomas et al. 2015). In addition, temporal changes in precipitation vary across the Neotropics (Malhi and Wright 2004) and, thus, cannot explain a regional phenomenon restricted to the Neotropics.

The final mechanism hypothesizes a causal link among lianas, frugivores, and hunters mediated by seed dispersal mode (Wright et al. 2007). The dispersal of zoochorous seeds suffers where hunters reduce frugivore abundances (Markl et al. 2012). Zoochory characterizes 70–90% of tree species throughout the tropics (Gentry 1982, Willson et al. 1989). Seed dispersal modes are more variable among regions for lianas (Gentry 1991, Gallagher and Leishman 2012). Zoochory characterizes 37% of liana species in Neotropical moist forests (Gentry 1982, Muller-Landau and Hardesty 2005); 60% of climbing genera in the Temperate Zone (Ladwig and Meiners 2015); 68% of the 20 most abundant lianas at Korup, Cameroon (dispersal mode was unknown for one species); 70.2% of the liana species at Pasoh (this study); 72% of the liana species of West African forests (Bongers et al. 2005); and 74% and 79.2% of the liana species in two central African forests (Ewango 2010, Beaune et al. 2013). In the Neotropics, the percentage of species with zoochorous seeds varies with seasonality and soil fertility, but is always substantially greater for trees than for lianas (Gentry 1982, 1991). Hunters are reducing frugivore populations throughout the Tropics (Corlett 2007, Peres and Palacios 2007, Fa and Brown 2009). Frugivore removal might favor lianas strongly in the Neotropics, because most Neotropical liana species have wind-dispersed seeds. Frugivore removal might not have this effect in the Asian and African tropics where more similar proportions of trees and lianas have zoochorous seeds.

Site-specific mechanisms must also affect the relative importance of lianas. Consider two examples. Logging, forest fragmentation, and forest edges all favor lianas (reviewed by Schnitzer and Bongers 2002). Remaining old-growth forests will receive increased liana seed input as logging, fragmentation, and edges alter local landscapes. Animals will also have site-specific effects on lianas in addition to effects mediated by seed dispersal. At Pasoh, the native wild boar (*Sus scrofa*) is hyper



abundant and selects tree saplings to build nests (Ickes et al. 2005), which should favor lianas. In southern Mesoamerica, the abundances of lianas and the native collared peccary (*Tayassu tajaca*) are inversely related, although the mechanism is unclear (Michel et al., *in press*). Some combination of local, regional, and global anthropogenic drivers affects every tropical forest today (Wright 2010). For this reason, the mechanism(s) responsible for directional changes in forest composition, structure, and dynamics will be very difficult to identify particularly when the evidence for change is limited to 15 studies with diverse results (Table 1).

## ACKNOWLEDGMENTS

Mohd. Fairuzinzam bin Ibrahim, Fauzi Mohd. B. Hassan, Ming-Yee Chew, and Chia-Ling Ne censused seed traps. We dedicate this paper to Fauzi's memory. Emma Lehrer, Yi Sun, Yen-Pin Yang, Ya-Te Chen, and Guei-Ru Lin helped with the canopy tree surveys. The National Science Foundation (DEB 0108388) and the ForestGEO program of the Smithsonian Institution provided funding. The National Dong Hwa University supported I.-F. Sun and Y.-Y. Chen.

## LITERATURE CITED

- Allen, B. P., R. R. Sharitz, and P. C. Goebel. 2007. Are lianas increasing in importance in temperate floodplain forests in the southeastern United States? *Forest Ecology and Management* 242:17–23.
- Appanah, S. 1993. Mass flowering of Dipterocarp forests in the aseasonal tropics. *Journal of Biosciences* 18:457–474.
- Beaune, D., F. Bretagnolle, L. Bollache, G. Hohmann, M. Surbeck, and B. Fruth. 2013. Seed dispersal strategies and the threat of defaunation in a Congo forest. *Biodiversity and Conservation* 22:225–238.
- Benítez-Malvido J. and M. Martínez-Ramos. 2003. Impact of forest fragmentation on understory plant species richness in Amazonia. *Conservation Biology* 17:389–400.
- Bolker, B. M., M. E. Brooks, C. J. Clark, S. W. Geange, J. R. Poulsen, M. H. H. Stevens, and J. S. S. White. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology and Evolution* 24:127–135.
- Bongers, F., and C. E. N. Ewango. 2015. Dynamics of lianas in DR Congo. Pages 23–35 in S. A. Schnitzer, F. Bongers, R. J. Burnham, and F. E. Putz, editors. *The ecology of lianas*. Wiley-Blackwell, Oxford, UK.
- Bongers, F., M. P. E. Parren, and D. Traoré. 2005. Forest climbing plants of West Africa: diversity, ecology and management. CABI Publishing, Wallingford, UK.
- Caballé, G., and A. Martin. 2001. Thirteen years of change in trees and lianas in a Gabonese rainforest. *Plant Ecology* 152:167–173.
- Campbell, E. J. F., and D. M. Newbery. 1993. Ecological relationships between lianas and trees in lowland rain-forest in Sabah, East Malaysia. *Journal of Tropical Ecology* 9:469–490.
- Cannon, C. H., L. M. Curran, A. J. Marshall, and M. Leighton. 2007. Long-term reproductive behaviour of woody plants across seven Bornean forest types in the Gunung Palung National Park (Indonesia): supranual synchrony, temporal productivity and fruiting diversity. *Ecology Letters* 10:956–969.
- Chave, J., J. Olivier, F. Bongers, P. Chatelet, P. M. Forget, P. van der Meer, N. Norden, B. Riera, and P. Charles-Dominique. 2008. Above-ground biomass and productivity in a rain forest of eastern South America. *Journal of Tropical Ecology* 24:355–366.
- Chen, Y. Y. 2007. Reproductive phenology in a lowland Dipterocarp forest and its consequences. Dissertation. University of Georgia, Athens, Georgia, USA.
- Clark, D. B., and D. A. Clark. 1990. Distribution and effects on tree growth of lianas and woody hemiepiphytes in a Costa Rican tropical wet forest. *Journal of Tropical Ecology* 6:321–331.
- Condit, R. 1998. Tropical forest census plots. Springer-Verlag and R. G. Landes Company, Berlin, Germany.
- Corlett, R. T. 2007. The impact of hunting on the mammalian fauna of tropical Asian forests. *Biotropica* 39:292–303.
- Dawkins, H. C., and D. R. B. Field. 1978. A long-term surveillance system for British woodland vegetation. Department of Forestry, Oxford University, Oxford, UK.
- Enquist, B. J., and C. A. F. Enquist. 2011. Long-term change within a Neotropical forest: assessing differential functional and floristic responses to disturbance and drought. *Global Change Biology* 17:1408–1424.
- Ewango, C. E. N. 2010. The liana assemblage of a Congolian rainforest. Diversity, structure and dynamics. Dissertation. Wageningen University, Wageningen, The Netherlands.
- Fa, J. E., and D. Brown. 2009. Impacts of hunting on mammals in African tropical moist forests: a review and synthesis. *Mammal Review* 39:231–264.
- Foster J. R., P. A. Townsend, and C. E. Zganjar. 2008. Spatial and temporal patterns of gap dominance by low-canopy lianas detected using EO-1 Hyperion and Landsat Thematic Mapper. *Remote Sensing of Environment* 112:2104–2117.
- Franco, M., and J. Silvertown. 2004. Comparative demography of plants based upon elasticities of vital rates. *Ecology* 85:531–538.
- Gallagher, R. V., and M. R. Leishman. 2012. A global analysis of trait variation and evolution in climbing plants. *Journal of Biogeography* 39:1757–1771.
- Gentry, A. H. 1982. Patterns of Neotropical plant-species diversity. Pages 1–84 in M. K. Hecht, B. Wallace, and G. T. Prance, editors. *Evolutionary biology*. Plenum Press, New York, New York, USA.
- Gentry, A. H. 1991. Breeding and dispersal systems of lianas. Pages 393–423 in F. E. Putz and H. A. Mooney, editors. *The biology of vines*. Cambridge University Press, Cambridge, UK.
- Hallé, F., and F. S. P. Ng. 1981. Crown construction in mature dipterocarp trees. *Malaysian Forester* 44:222–233.
- Hietz, P., B. L. Turner, W. Wanek, A. Richter, C. A. Nock, and S. J. Wright. 2011. Long-term change in the nitrogen cycle of tropical forests. *Science* 334:664–666.
- Ickes, K., C. J. Paciorek, and S. C. Thomas. 2005. Impacts of nest construction by native pigs (*Sus scrofa*) on lowland Malaysian rain forest saplings. *Ecology* 86:1540–1547.
- Ingwell, L. L., S. J. Wright, K. K. Becklund, S. P. Hubbell, and S. A. Schnitzer. 2010. The impact of lianas on 10 years of tree growth and mortality on Barro Colorado Island, Panama. *Journal of Ecology* 98:879–887.
- Kira, T., and H. Ogawa. 1971. Assessment of primary production in tropical and equatorial forests. Pages 309–321 in P. DuVigneaud, editor. *Productivity of forest ecosystems*. UNESCO, Paris, France.
- Kochummen, K. M., J. V. LaFrankie, and N. Manokaran. 1990. Floristic composition of Pasoh Forest Reserve, a lowland rain forest in Peninsular Malaysia. *Journal of Tropical Forest Science* 3:1–13.
- Ladwig, L. M., and S. J. Meiners. 2015. The role of lianas in temperate tree communities. Pages 188–202 in S. A. Schnitzer, F. Bongers, R. J. Burnham, F. E. Putz, editors. *The ecology of lianas*. Oxford University Press, Oxford, UK.
- Laurance, W. F., A. S. Andrade, A. Magrach, J. L. C. Camargo, J. J. Valsko, M. Campbell, P. M. Fearnside, W. Edwards, T. E. Lovejoy, and S. G. Laurance. 2014. Long-term changes in liana abundance and forest dynamics in undisturbed Amazonian forests. *Ecology* 95:1604–1611.

- Londré, R. A., and S. A. Schnitzer. 2006. The distribution of lianas and their change in abundance in temperate forests over the past 45 years. *Ecology* 87:2973–2978.
- Malhi, Y., and J. Wright. 2004. Spatial patterns and recent trends in the climate of tropical rainforest regions. *Philosophical Transactions of the Royal Society B* 359:311–329.
- Markl, J. S., M. Schleuning, P. M. Forget, P. Jordano, J. E. Lambert, A. Traveset, S. J. Wright, and K. Bohning-Gaese. 2012. Meta-analysis of the effects of human disturbance on seed dispersal by animals. *Conservation Biology* 26:1072–1081.
- Michel, N. L., T. W. Sherry, and W. P. Carson. *In press*. Do collared peccaries negatively impact understory insectivorous rainforest birds indirectly via lianas and vines? *Biotropica*.
- Muller-Landau, H. C., and B. D. Hardesty. 2005. Seed dispersal of woody plants in tropical forests: concepts, examples, and future directions. Pages 267–309 in D. F. R. P. Burslem, M. A. Pinard, and S. Hartley, editors. *Biotic interactions in the tropics*. Cambridge University Press, Cambridge, UK.
- Peres, C. A., and E. Palacios. 2007. Basin-wide effects of game harvest on vertebrate population densities in Amazonian forests: implications for animal-mediated seed dispersal. *Biotropica* 39:304–315.
- Phillips, O. L., et al. 2002. Increasing dominance of large lianas in Amazonian forests. *Nature* 418:770–774.
- R Development Core Team. 2011. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. [www.r-project.org](http://www.r-project.org)
- Rogers, D., T. Rooney, D. Olson, and D. Waller. 2008. Shifts in southern Wisconsin forest canopy and understory richness, composition, and heterogeneity. *Ecology* 89:2482–2492.
- Sakai, S., R. D. Harrison, K. Momose, K. Kuraji, H. Nagamasu, T. Yasunari, L. Chong, and T. Nakashizuka. 2006. Irregular droughts trigger mass flowering in aseasonal tropical forests in Asia. *American Journal of Botany* 93:1134–1139.
- Schnitzer, S. A. 2015. Increasing liana abundance in Neotropical forests: causes and consequences. Pages 451–464 in S. A. Schnitzer, F. Bongers, R. J. Burnham, F. E. Putz, editors. *The ecology of lianas*. Oxford University Press, Oxford, UK.
- Schnitzer, S. A., and F. Bongers. 2002. The ecology of lianas and their role in forests. *Trends in Ecology and Evolution* 17:223–230.
- Schnitzer, S. A., and F. Bongers. 2011. Increasing liana abundance and biomass in tropical forests: emerging patterns and putative mechanisms. *Ecology Letters* 14:397–406.
- Schnitzer, S. A., M. E. Kuzee, and F. Bongers. 2005. Disentangling above- and below-ground competition between lianas and trees in a tropical forest. *Journal of Ecology* 93:1115–1125.
- Schnitzer, S. A., et al. 2012. Liana abundance, diversity, and distribution on Barro Colorado Island, Panama. *PLoS ONE* 7(12):e52114.
- Sun, I. F., Y. Y. Chen, S. P. Hubbell, S. J. Wright, and N. Supardi. 2007. Seed predation rates during general flowering events of varying magnitude in a Malaysian rain forest. *Journal of Ecology* 95:818–827.
- Swaine, M. D., and J. Grace. 2007. Lianas may be favoured by low rainfall: evidence from Ghana. *Plant Ecology* 192:271–276.
- Thomas, D., R. J. Burnham, G. Chuyong, D. Kenfack, and M. N. Sainge. 2015. Liana abundance and diversity in Cameroon's Korup National Park. Pages 13–22 in S. A. Schnitzer, F. Bongers, R. J. Burnham, F. E. Putz, editors. *The ecology of lianas*. Wiley-Blackwell, Oxford, UK.
- Willson, M. F., A. K. Irvine, and N. G. Walsh. 1989. Vertebrate dispersal syndromes in some Australian and New Zealand plant communities, with geographic comparisons. *Biotropica* 21:133–147.
- Wright, S. J. 2010. The future of tropical forests. *Annals of the New York Academy of Sciences* 1195:1–27.
- Wright, S. J., and O. Calderon. 2006. Seasonal, El Niño and longer term changes in flower and seed production in a moist tropical forest. *Ecology Letters* 9:35–44.
- Wright, S. J., O. Calderon, A. Hernandez, and S. Paton. 2004. Are lianas increasing in importance in tropical forests? A 17-year record from Panama. *Ecology* 85:484–489.
- Wright, S. J., A. Hernandez, and R. Condit. 2007. The bushmeat harvest alters seedling banks by favoring lianas, large seeds, and seeds dispersed by bats, birds, and wind. *Biotropica* 39:363–371.
- Wright, S. J., M. A. Jaramillo, J. Pávon, R. Condit, S. P. Hubbell, and R. B. Foster. 2005. Reproductive size thresholds in tropical trees: variation among individuals, species and forests. *Journal of Tropical Ecology* 21:307–315.
- Yorke, S. R., S. A. Schnitzer, J. Mascaro, S. G. Letcher, and W. P. Carson. 2013. Increasing liana abundance and basal area in a tropical forest: the contribution of long-distance clonal colonization. *Biotropica* 45:317–324.
- Zhou, L., Y. Tian, R. B. Myneni, P. Ciais, S. Saatchi, Y. Y. Liu, S. Piao, H. Chen, E. F. Vermote, C. Song, and T. Hwang. 2014. Widespread decline of Congo rainforest greenness in the past decade. *Nature* 509:86–90.

## SUPPLEMENTAL MATERIAL

### Ecological Archives

The Appendix is available online: <http://dx.doi.org/10.1890/14-1985.1.sm>

### Data Availability

Data associated with this paper have been deposited in Dryad: <http://dx.doi.org/10.5061/dryad.dh439>