



TITLE:

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AUTHOR(S):

Fujimoto, Yutaro; Kanzaki, Mamoru; Meunpong, Ponthep; Wachrinrat, Chongrak; Waengsothorn, Surachit; Kitajima, Kaoru

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Legacy effects of canopy gaps on liana abundance 25 years later in a seasonal tropical evergreen forest in northeastern Thailand

Yutaro Fujimoto¹  | Mamoru Kanzaki¹ | Ponthep Meunpong² | Chongrak Wachrinrat² | Surachit Waengsothorn³ | Kaoru Kitajima¹ 

¹Graduate School of Agriculture, Kyoto University, Kyoto, Japan

²Faculty of Forestry, Kasetsart University, Bangkok, Thailand

³Sakaerat Environmental Research Station, Thailand Institute of Scientific and Technological Research, Nakhon Ratchasima, Thailand

Correspondence

Yutaro Fujimoto, Graduate School of Agriculture, Kyoto University, Kyoto, Japan.
Email: fujimoto.yutaro.24w@kyoto-u.jp

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Abstract

Lianas require host trees to reach and stay in the forest canopy, but as seedlings and juveniles, they benefit from canopy gaps created by treefalls. Here, we evaluated the relative importance of these two aspects, that is, the availability of potential hosts vs. the legacy effect of past treefall gaps, on the local abundance of liana stems in a seasonal tropical evergreen forest in the Sakaerat Biosphere Reserve in northeastern Thailand. Within a 2.5-ha plot for forest dynamics monitoring, canopy height was measured in 1993 and 2018 at 5-m intervals to distinguish areas of mature (canopy height ≥ 20 m), building (10–20 m), and gap phases (< 10 m). In 2017–2018, we surveyed all liana stems ≥ 1 cm in diameter at breast height within 50 subplots (10 m \times 10 m each) and recorded their diameter and the diameter of the host tree. Of a total of 445 liana individuals, 242 could be identified at least to the family level, while the others had clear morphological traits of climbing mechanisms. The number of liana stems was higher in areas that had been at the building/gap phase than those at the mature phase in 1993. When this 25-year-old legacy of past gap locations was considered, there was a positive association of local abundance between lianas and trees in areas at the mature phase in 2018. In conclusion, liana abundance reflected a long-term legacy of past treefall gaps more than 25 years earlier in this seasonal evergreen forest.

KEYWORDS

canopy gap dynamics, forest stand structure, liana-tree interactions, light environment, spatial distribution

1 | INTRODUCTION

The ecology of lianas (woody vines) is important in forest dynamics, especially in seasonal tropical forests, where their diversity and abundance are typically high (Gentry, 1991). In comparison with freestanding trees, lianas can grow rapidly by allocating more carbon

to stem elongation and leaf expansion than to mechanical support (Putz, 1983; Schnitzer, 2005). Once reaching the upper canopy, lianas increase shading and weight stress on their hosts, and thus, they impact forest dynamics and carbon balance of the forest stand (Medina-Vega et al., 2022; van der Heijden & Phillips, 2009). Many studies, especially those from Neotropical forests, report that liana

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abundance and their impact on forest dynamics are increasing in recent decades (Laurance et al., 2014; Phillips et al., 2002; Schnitzer et al., 2012, 2021; Schnitzer & Bongers, 2011; Wright et al., 2004). At the global scale, tropical forests with lower mean annual precipitation and longer dry seasons tend to have higher liana abundance (DeWalt et al., 2010; but see van der Heijden & Phillips, 2008).

Lianas as a group tend to have higher light demands compared to freestanding trees, although there is wide variation among liana species (Putz, 1984; Webb, 1958). Canopy gaps created by treefalls locally increase light availability, often triggering rapid liana colonization from seeds and vegetative propagation (Ledo & Schnitzer, 2014; Peñalosa, 1984; Schnitzer & Carson, 2001). Lianas that fall to the ground when their host trees fall are likely to survive, and their vegetative proliferation in the new gap results in liana tangles that reduce light availability and suppress regeneration of canopy tree seedlings near the ground (Putz, 1984). For example, Foster et al. (2008) report that canopy tree regeneration is suppressed for more than 14 years once treefall gaps become occupied by lianas in the Bolivian Amazon.

Persistence of liana individuals recruited in treefall gaps may result in a legacy effect of canopy gaps on liana distribution, which is detectable even after successional changes have led to reclosure of the canopy (Schnitzer et al., 2000; Schnitzer & Bongers, 2002). From Panama, such a legacy effect is reported from a 10-year monitoring study (Schnitzer & Carson, 2001). Another 10-year study in Panama (Schnitzer et al., 2021) reports that the local density of liana stems is about 1.5 times higher in former gap sites that have experienced canopy reclosure than compared to microsites that were continuously under closed canopy. However, how much longer such legacy effects of the past canopy gaps on the local abundance of liana stems may persist is unclear. Letcher and Chazdon (2009) found in a chrono-sequence of secondary forests in Costa Rica that abundance of liana stems with diameter at breast height (DBH) ≥ 0.5 cm decreases with forest age > 20 years. These suggest that the positive effect of forest disturbance on liana abundance may fade with time but last for about two decades.

At the same time, local abundance of lianas may be influenced by local density of potential host-tree stems, that is, support availability (Campanello et al., 2007; Nabe-Nielsen, 2001; Putz, 1984). Such positive association, however, is not always observed (Laurentino et al., 2019; Reis et al., 2020). This inconsistency among studies may reflect differences in forest stand structure, but it may also be because they do not consider the legacy effects of past treefall gaps. In some cases, treefall gaps go through successional changes via building phases to canopy closure by tall trees, but in other cases liana dominance may persist and arrest succession (Schnitzer et al., 2000, 2021).

Most studies about interactions between lianas and trees are from Neotropical forests. In contrast, our knowledge is limited as to how lianas and trees interact in SE Asian forests, which often have very different overall forest structures, including host tree allometry (e.g., taller emergent trees in SE Asian forests dominated by Dipterocarpaceae; Ashton, 2014). Here, we report field data on liana

dynamics from a seasonal evergreen forest in northeastern Thailand, where the distribution of the treefall gaps 25 years earlier had been recorded (Kanzaki et al., 2009). This forest is heavily dominated by *Hopea ferrea* (Dipterocarpaceae; Kanzaki et al., 1995). We examined how the spatial distributions of lianas were related to the spatiotemporal dynamics of the host trees or surrounding trees and tested the following two questions.

1. Is the legacy effect of canopy gaps 25 years earlier on local abundance of liana stems detectable, regardless of the current canopy condition?
2. Is there a positive association between the local stem density of lianas and trees when the legacy effect of past treefall gaps is also considered?

2 | METHODS

2.1 | Study site

This study was conducted in the Sakaerat Biosphere Reserve (82,100 ha) in Nakhon Ratchasima Province, northeastern Thailand. The mean annual precipitation is 1087 mm and the mean annual temperature is 26.3°C, with the dry season (monthly precipitation < 50 mm) from November to February (meteorological observations in 1969–2012 by Sakaerat Environmental Research Station, <https://www.tistr.or.th/sakaerat/Meteorological.htm>). The reserve contains seasonally dry deciduous forest stands and seasonally dry evergreen forest stands. In an old growth evergreen stand with no logging records in the past, a 50 m \times 50 m forest monitoring plot was established in 1993. This plot was further divided into a grid system of 10 m \times 10 m subplots, each containing four 5 m \times 5 m quadrats. Within the entire 2.5-ha plot, all tree stems with DBH ≥ 5 cm were recorded for their location, size, and subsequent survival in 1993, 1995, 2003, 2006, and 2018 (Kanzaki et al., 2009; M. Kanzaki et al., unpublished). *Hopea ferrea* (Dipterocarpaceae) was the most dominant, accounting for 47.4% of the basal area of trees ≥ 3 cm DBH, followed by *Hydnocarpus ilicifolius*, Achariaceae (5.2%) and *Lagerstroemia duperreana*, Lythraceae (4.8%; more detailed description in Kanzaki et al., 1995). Canopy height was measured at the center of every 5 m \times 5 m quadrat in 1993, and these quadrats were classified to three canopy height classes corresponding to three regeneration phases, namely mature phase (canopy height ≥ 20 m), building phase (10 m \leq canopy height < 20 m), or gap phase (canopy height < 10 m; Kanzaki et al., 2009). We repeated the canopy height survey in 2018 with the same method.

2.2 | Liana and host tree measurements

The liana survey was conducted for the first time in 2017–2018 in 50 subplots regularly spaced to subsample 20% of the entire 50 m \times 50 m plot. Following the standard protocol of Gerwing

et al. (2006) and Schnitzer et al. (2008) for liana surveys, we mapped all lianas ≥ 1 cm DBH that clearly had twining stems or climbing tools such as hooks and thorns and were rooted within the subplots, and recorded the species identity and DBH of each stem. We included freestanding liana juveniles but excluded hemi-epiphytes. For each liana stem, we determined the main host and recorded its species identity and DBH. When the original host was apparently dead, we recorded the live stem that the liana was attached as the first host. When liana stems branched above the point of DBH measurement and each branch was supported by a different host, we recorded only the host that supported the largest branch. Of 50 subplots, 23 subplots were surveyed in October 2017 and additional 27 subplots were surveyed in November 2018. Since the DBH values of a given liana stem and its host were measured on the same day, we assumed that two surveys one year apart had minimal effects on our analysis combining the data collected in 2017 and 2018.

2.3 | Statistical analysis

For statistical analyses to test differences among canopy height classes, we merged building and gap phases into one (building/gap phase) to have more balanced sample sizes. The key results were fundamentally the same when we analyzed the data with three canopy height classes (Tables S1 and S2). We used a generalized linear mixed model (GLMM, negative binomial regression) to examine the relationship of liana stem density in $5\text{m} \times 5\text{m}$ quadrats to their canopy height classes, using the canopy height classes in 1993 and 2018 as fixed effects and treating the subplot identity as a random variable. To consider the influence of tree stem density along with the legacy effect of canopy gaps 25 years earlier, we used GLMM (negative binomial regression) for only quadrats that were at the mature phase in 2018, using the canopy height classes in 1993 and tree stem density as fixed effects and treating the subplot identity as a random variable. The local density of tree stems ≥ 5 cm DBH at the quadrat level did not show consistent differences among canopy height classes either in 1993 or 2018 (Table S3 and Figure S1). We could not determine taxonomic identity for 46% of liana individuals due to lack of canopy access to obtain leaf and flower samples, but DBH distributions and the relationship between liana DBH and host DBH did not differ between identified and unidentified stems (Figure S2). All statistical tests were conducted with R 4.2.1 (R Core Team, 2021; lmerTest package for GLMM).

3 | RESULTS

3.1 | Liana community

A total of 511 liana stems ≥ 1 cm DBH belonging to 445 individuals occurred across the 50 subplots (a total of $5,000\text{m}^2$). We identified 242 individuals at least into the family level (31 species belonging to 15 families), but not the remaining 203 individuals (18

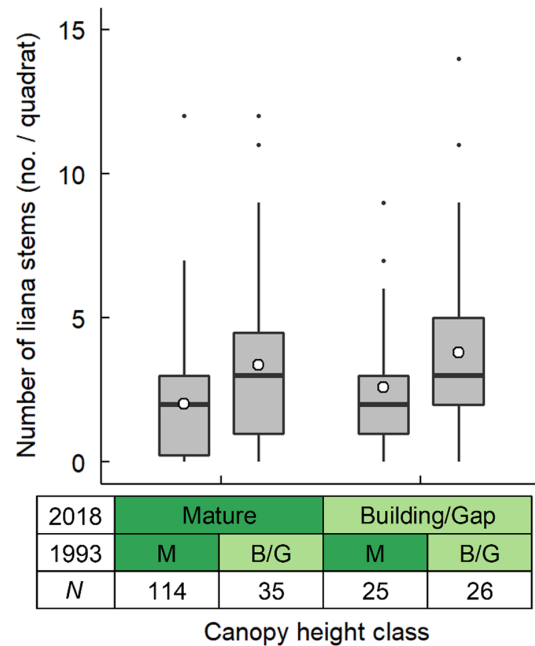


FIGURE 1 Box plot summarizing the number of liana stems in $5\text{m} \times 5\text{m}$ quadrats for combination of canopy height classes in 1993 and 2018 (Mature: canopy height ≥ 20 m, and Building/Gap: canopy height < 20 m). The number of quadrats in each combination is shown as “N”. The mean (open circle), median (horizontal line in the box), and the first and third quartiles (the top and the bottom of the box) are indicated within each box. Above and below each box, whiskers indicate 1.5 times the range of interquartile and black dots are outliers. See Table 1 for the statistical differences of liana stem density explained by canopy height classes in 1993 and 2018.

individuals belonging to 10 morphospecies, and 185 individuals with no identification). These data on the liana community are reported as supporting information (Table S4). The most abundant family was Convolvulaceae with 65 individuals, followed by Ancistrocladaceae (50 individuals) and Fabaceae (34 individuals). We did not find any root climbers, which use adventitious roots to attach and can climb large-diameter host trees. The DBH was < 5 cm for $> 80\%$ of the stems, while the largest stem had DBH of 18.5 cm. For lianas with DBH ≥ 5 cm, the basal area was $4,089\text{cm}^2$, which was equivalent to 2.10% of the basal area of trees with DBH ≥ 5 cm. The size of liana stems was larger on larger host trees (Type II regression, $\log_{10} y = -0.26 + 0.63\log_{10} x$, $N = 451$, $R^2 = .33$, $p < .001$), with the scatter plot showing that small-diameter lianas were rare on trees with DBH > 10 cm (Figure S3).

3.2 | Impacts of past canopy gaps on liana abundance

Figure 1 summarizes the liana stem density in 2018 for each of the canopy height class combinations (2 classes in 1993 \times 2 classes in 2018), along with the sample size for each combination. Of the 139 quadrats that had been at the mature phase (canopy height ≥ 20 m) in 1993, 25 quadrats were at the building ($10\text{m} \leq$ canopy height < 20 m)

or gap (canopy height < 10m) phase in 2018, while 114 quadrats were again at the mature phase in 2018. Of the 61 quadrats that had been at the building/gap phase in 1993, 35 quadrats were classified to the mature phase in 2018, while 26 quadrats were classified to the building/gap phase. The quadrats that had been at the building/gap phase in 1993 had higher liana stem density, compared to those at the mature phase in 1993 ($e^{0.45} = 1.6$ times higher; Table 1). In contrast, canopy height classes in 2018 showed no significant association with liana stem density (Table 1).

3.3 | Relationship between local densities of liana and tree stems

Liana stem density in 2018 increased with tree stem density, both for quadrats that had been at the mature phase in 1993 and for those at the building/gap phase in 1993 (Table 2, Figure 2). The quadrats at the building/gap phase in 1993 showed stronger positive correlation of tree stem density with liana stem density than those at the mature phase in 1993 ($e^{0.45} = 1.6$ times higher; Table 2, Figure 2).

4 | DISCUSSION

4.1 | Legacy effects of canopy gap locations on liana abundance

We detected the predicted legacy effect, that is, liana abundance should reflect locations of past canopy gaps even after 25 years. The duration of this legacy effect could last even longer because a location in the building phase in 1993 had been a canopy gap even further back in the past. A similar legacy effect of 10 years is demonstrated by previous studies in Panama (Schnitzer & Carson, 2001; Schnitzer et al., 2021). Our study included liana stems with DBH ≥ 1 cm. For this size class, whether a location is currently a treefall gap or not did not affect liana abundance. Perhaps liana seedlings

TABLE 1 Result of a GLMM analysis to examine local stem density of lianas, as a function of canopy height class in 1993, canopy height class in 2018, and subplot identity (random effect).

Canopy height class contrast	Coefficient	Standard error	Z	p
(Intercept)	0.62	0.11	5.67	<.001
1993 Building/ Gap vs. Mature	0.45	0.15	2.89	.004
2018 Building/ Gap vs. Mature	0.12	0.15	0.82	.412

Note: Negative binomial distribution was assumed for the liana stem density (= number of stems per 5 m \times 5 m quadrat). Three canopy height classes in 1993 and in 2018 are coalesced to two: mature phase and building/gap phase.

recruited in gaps would require several years to grow up to reach DBH ≥ 1 cm. More detailed information on canopy gap dynamics is desirable in order to understand how long it might take liana seedlings to persist and grow during the building phase. Nevertheless, the result of our study strongly supports the idea that the spatial distribution of canopy gaps continues to explain local abundance of lianas over multiple decades, long after the site shows successional transition to the mature phase.

4.2 | Positive effects of local densities of tree stems on liana abundance

Beyond the seedling stage, lianas require host stems to reach and persist in the forest canopy. Our study found that this effect, that is, a positive correlation between local stem density of lianas and trees, could be detectable when we took into account whether a microsite was in the building/gap phase 25 years earlier or not. We have no information about factors that make the variation in the tree stem density among microsites, which could reflect many ecological factors including colonization and competition dynamics among trees. Our study enumerated tree stems with DBH ≥ 5 cm as potential hosts, whereas previous studies that examined the potential correlation of liana abundance with tree stem density used trees with DBH ≥ 10 cm (Campanello et al., 2007; Laurentino et al., 2019; Reis et al., 2020). Thus, we ran similar analyses for tree stems with DBH < 10 cm versus DBH ≥ 10 cm at the quadrat scale. Doing so, we found that liana stem density was positively correlated with the density of small tree stems but not with the density of large tree stems (Table S5). Similar effects of host stem size are reported by Nabe-Nielsen (2001). Thus, the availability of small tree stems, rather than that of large tree stems, would contribute to liana abundance.

Overall tree density (and other stand characteristics) of the forest may also influence whether a positive correlation exists between liana abundance and stem density of large trees. In a semi-deciduous subtropical forest, Campanello et al. (2007) found a positive correlation between liana abundance and density of tree stems ≥ 10 cm DBH (293 stems/ha). In contrast, neither our study nor Nabe-Nielsen (2001)'s found such a strong correlation in forests with much higher density of tree stems ≥ 10 cm DBH (498 and 700 stems/ha, respectively).

5 | CONCLUSION

In this seasonal tropical evergreen forest, the locations of past canopy gaps 25 years earlier, rather than those of current gaps, explained the spatial distribution of established liana stems. For areas currently under a closed canopy, by simultaneously considering the legacy effect of past gap locations in areas, local abundance of liana stems showed positive correlation with tree stem density. These results suggest that the legacy effects of treefall gaps on liana abundance remain over multiple decades. To test these phenomena more

	Coefficient	Standard error	Z	p
(Intercept)	0.32	0.17	1.92	.055
Tree stem density	0.10	0.04	2.37	.018
1993 Building/Gap vs. Mature	0.45	0.18	2.50	.012

TABLE 2 Result of a GLMM analysis (negative binomial regression) of local stem density of lianas in areas at the mature phase in 2018, as a function of tree stem density, canopy height class in 1993, subplot identity (random effect).

Note: For both lianas and trees, stem density is the number of stems per 5 m × 5 m quadrat. Three canopy height classes in 1993 are coalesced to two: mature phase and building/gap phase.

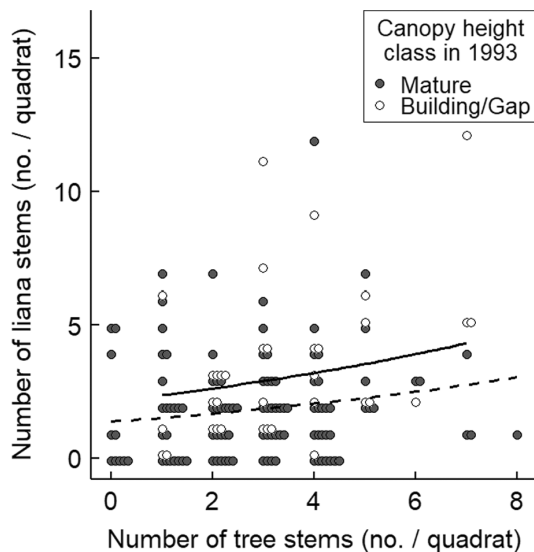


FIGURE 2 Liana stem density plotted against tree stem density in areas at the mature phase in 2018, distinguishing those that had been at the mature phase (closed circles) and the building/gap phase (open circles) in 1993. A dashed curve and a solid curve are the predictions by negative binomial regression for the mature phase and the building/gap phase, respectively. Because many points are overlapping completely, they were jittered horizontally within each 1993 canopy-phase category, and vertically between the canopy-phase categories. See Table 2 for the statistical tests of the effects of tree stem density and canopy height class in 1993 of liana stem density in 2018.

directly, a longitudinal study will be necessary to follow recruitment of liana juveniles with over multiple decades. Data of canopy gap dynamics which have multiple and shorter-interval measurements will help us examine the temporal fluctuation of the legacy effects.

AUTHOR CONTRIBUTION

YF, MK, and KK conceived and designed the study. YF conducted fieldwork and analyzed the data. PM, CW, and SW gave logistic support and provided on-site advice. YF wrote the manuscript, and all authors edited it.

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CONFLICT OF INTEREST STATEMENT

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.8sf7m0ct6> (Fujimoto et al., 2023).

ORCID

Yutaro Fujimoto [ID](https://orcid.org/0000-0001-5050-8310) <https://orcid.org/0000-0001-5050-8310>

Kaoru Kitajima [ID](https://orcid.org/0000-0001-6822-8536) <https://orcid.org/0000-0001-6822-8536>

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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