

# Insects and light interact to mediate vine colonization of fast growing *Microberlinia bisulcata* tree seedlings in gaps of an African rain forest

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## Abstract

Vines thrive in lowland tropical forests, yet the biotic factors underlying their colonization of host tree seedlings and saplings remain surprisingly understudied. Insect herbivores presumably could influence this process, especially where disturbance has opened the canopy (i.e., gaps)—temporary areas of higher primary productivity favoring the recruitment of vines and trees and invertebrates in forests—but their impact on vine colonization has never been experimentally tested. Using data from an insect herbivore exclusion (mesh-netting cages) experiment conducted in an African rain forest (Korup, Cameroon), I logistically modeled the probability of vines colonizing seedlings of three co-dominant species (*Microberlinia bisulcata* vs. *Tetraberlinia bifoliolata* and *T. korupensis*) in paired shaded understory and sunny gap locations (41 blocks across 80 ha, starting  $n = 664$  seedlings) in a 1–2-yr period (2008–2009). Vine colonization occurred almost exclusively in gaps, occurring on 16% of seedlings there. Excluding herbivores in gaps doubled colonization of the light-demanding and faster growing *M. bisulcata* but had negligible effects on the two shade-tolerant, slower growing and less palatable *Tetraberlinia* species, which together were twice as susceptible to vines under natural forest gap conditions (controls). When protected from herbivores in gaps, more light to individual seedlings strongly increased vine colonization of *M. bisulcata* whereas its well-lit control individuals supported significantly fewer vines. These results suggest vines preferably colonize taller seedlings, and because light-demanding tree species grow faster in height with more light, they are more prone to being colonized in gaps; however, insect herbivores can mediate this process by stunting fast growing individuals so that colonization rates becomes more similar between co-occurring slow and fast growing tree species. Further influencing this process might be associational resistance or susceptibility to herbivores linked to host species' leaf traits conferring shade-tolerant ability as seedlings or saplings. A richer understanding of how vines differentially influence forest regeneration and species composition may come from investigating vine–tree–herbivore interactions across light gradients, ideally via long-term studies and intercontinental comparisons.

Abstract in French is available with online material.

## KEYWORDS

forest ecology, gap-phase regeneration, herbivory, plant–insect interactions, light-demanding tree species, treefall gaps, tropical forest, vines

## 1 | INTRODUCTION

Climbing plants (vines) attain their greatest biomass, abundance, and diversity in lowland tropical forests, where they figure prominently in the structure, composition, and dynamics of these species-rich communities (Gentry & Dodson, 1987; Richards, 1996; Schnitzer & Bongers, 2002). Nevertheless, biogeographically, vine abundance varied almost 10-fold among 30 pantropical forest sites in relation to climate, with the highest vine diversity (Fisher's alpha) currently found in the central African rain forest of Korup National Park (DeWalt et al., 2015). In using neighboring plants for structural support, vines hinder the growth of their host trees (Putz 1984; Schnitzer & Carson, 2010; reviewed by Marshall et al., 2017), which, by altering recruitment rates in to the canopy, could influence the composition of vegetation recovering from disturbance (Barry, Schnitzer, van Breugel, & Hall, 2015) and host-population dynamics, especially of faster growing, light-demanding tree species whose vine loads can greatly decrease their per capita survival rates (Visser, Schnitzer, et al., 2018a). But despite early calls (Clark & Clark, 1990 [p. 329]), we still know little of the factors influencing young vines' attachment to very young trees (hereafter "vine colonization"). This interaction should be studied because not only are tree seedlings abundant, they are also highly vulnerable to mortality yet strongly limited in growth by attenuated light resources (Richards, 1996). Both factors may be exacerbated by having to support vines whose leaves would interfere with host plant capture of already scarce light near the forest floor; this would not only reduce growth but also could push seedlings of some species below their light-compensation points (Perez-Salicrup, 2001; Toledo-Aceves & Swaine, 2008a, 2008b). In short, vines may function as a biotic stress factor in the key seedling-to-sapling life stage transition in forests.

For most vines, their abundance and diversity in tropical forests is enhanced by disturbances that open the canopy (Richards, 1996; Schnitzer & Bongers, 2002), whether from logging or natural tree deaths and large branch-falls (Putz 1984; Babweteera, Plumptre, & Obua, 2000; Marshal et al., 2017; Schnitzer & Carson, 2001). It is in such treefall or canopy gaps—long recognized as a prominent feature of tropical forests influencing their turnover and species distributions (Denslow, 1987)—that vines often aggregate and proliferate (Dalling et al., 2012; Piironen, Nyeko, & Roininen, 2013), presumably benefiting from not only more light for germination and growth (Richards, 1996), but also more suitable growing support trees to climb onto than available in surrounding shaded forest (Putz 1984). A long history of removal experiments show that vines negatively affect multiple dimensions of tree regeneration, including hosts' access to water and light, growth and reproduction, and survival (reviewed by Estrada-Villegas & Schnitzer, 2018), but this impact may depend on the local light environment as well as the shade tolerance and

species identity of hosts (Perez-Salicrup, 2001; Schnitzer & Carson, 2010; Toledo-Aceves & Swaine, 2008a, 2008b). From a young vine's perspective, locating a suitable support—one that increases its probability of survival or its growth rate—is arguably critical for its recruitment (Gianoli, 2015), so colonizing taller, vigorously growing tree seedlings and saplings in gaps should be favored, because these hosts would offer more stable support and access to more light resources than slower growing ones. Conspicuously missing, however, from this burgeoning research on vine–tree interactions is the involvement of herbivores, especially invertebrates.

A hypothesized role for herbivores in the interaction between regenerating vines and young trees in gaps is tenable for several reasons. Firstly, the greater light in gap habitats stimulates plant growth (Denslow, 1987), and this sustained production of vegetation can strongly structure invertebrate communities (e.g., Perry, Wallin, Wenzel, & Herms, 2018), especially when serving as high-quality food (young stem and leaf tissues) that support higher insect herbivore densities and rates of folivory—hereon, "herbivore pressure"—than in the understory (Richards & Coley, 2007, 2008). Secondly, leaf herbivory can differentially suppress and limit the stature of potential host tree species (in height or leaf area), especially if they lack sufficient resistance, or fail to compensate for eaten tissues, or cannot escape discovery by density dependent natural enemies (Pearson, Burslem, Goeriz, & Dalling, 2003; Marquis, 2005; Massey, Massey, Press, & Hartley, 2006; Norghauer, Malcolm, & Zimmerman, 2008; Norghauer & Newbery, 2014; Lemoine, Burkepille, & Parker, 2017). If vines can distinguish among and grow toward dark, shaded areas cast by very small stems (<1 cm) of taller seedlings with more leaves, not unlike the skototropism demonstrated for root climbers of buttressed tropical trees (Strong & Ray, 1975) and other hosts (Gianoli, 2015), then herbivory could reduce host susceptibility to vine colonization in gaps. Thirdly, although vines can compete with their hosts for light and belowground resources (Schnitzer, Kuzee, & Bongers, 2005; Toledo-Aceves & Swaine, 2008a; Toledo-Aceves & Swaine, 2008b; Alvarez-Cansino, Schnitzer, Reid, & Powers, 2015), there is evidence from temperate systems of associational effects benefiting the fitness of the vine (Gonzalez-Tueber & Gianoli, 2008) or host plant (Sasal & Suarez, 2011). Fourthly, co-occurring vine and tree species likely share similar life-history trade-offs soon after establishment (Gilbert, Wright, Muller-Landau, Kitajima, & Hernández, 2006) and that plant species identity and associated functional traits strongly influence susceptibility to herbivory is now well supported (Endara & Coley, 2011). The fact, moreover, that globally tropical vines generally have lower leaf mass per area (LMA), lower foliar defenses (phenolics), and higher nitrogen and phosphorus per leaf mass than trees (reviewed by Wyka, Oleksyn, Karolewski, & Schnitzer, 2013) probably makes them particularly palatable to insects in gaps, which also might influence their ability to find and colonize host

trees. Lastly, the high quantity of light (hereon, “light availability”) reaching the forest floor in gaps is not uniform within and among them (Denslow, 1987). Even small spatial differences in light may introduce further variation in plant growth rates and antiherbivore defenses (Dudt & Shure, 1994). This may affect not only host stature and vine foraging behavior reliant on such associated cues (Gianoli, 2015; Strong & Ray, 1975) but vines’ own exposure to herbivory as well (Aide & Zimmerman, 1990).

Another reason to study current plant–animal species interactions is to better predict implications of climate change. Dale et al. (2001) warned that the frequency, intensity, and duration of forest disturbances would likely be altered by climatic changes, driving shifts in the dynamics of forest ecosystems and their future composition. There is evidence that such projected increases in drought events are already hastening tree mortality (Allen et al., 2010). This, in combination with conditions favoring severe storms (hurricanes, windstorms; Dale et al., 2001), should generate more canopy-disturbed areas, including treefall gap formations; but since they tolerate drought better than trees, both factors are predicted to augment the abundance of vines (Schnitzer & Bongers, 2011). Hence, interactions between vines, their hosts, and insects that eat them may strengthen over time, becoming increasingly crucial during gap-phase tree regeneration for structuring the community composition of tropical forests.

After reviewing the literature, I could not find any field studies that have attempted to experimentally quantify how herbivores influence the colonization of tree seedlings by vines. Marquis (2005) also noted this absence, “No studies are available that test the impacts of herbivores on vine colonization of their support hosts” (p. 336). Since then, a recent check (March 2019) did not list any such experimental vine–tree–herbivore studies in the data base of <http://www.lianaecologyproject.com>. Given the ubiquity of vines, insects, and seedlings in tropical forests, their possible three-way interaction deserves some investigation by ecologists and foresters alike. Here, I used data available from a large field experiment that excluded insects from seedlings of three canopy tree species in a central African rain forest, analyzed at the genus level (two shade-tolerant congeners vs. a long-lived, light-demanding species), to test three predictions: (a) Vine colonization increases with light availability to tree seedling hosts; (b) Tree species with contrasting maximal growth rates (slow vs. fast) differ in their probability of being colonized by vines in light-rich patches of forest (i.e., canopy gaps); and (c) By equalizing host species’ stature (height and leaf area), insect herbivore pressure on tree seedlings interferes with the vine colonization process in these gaps.

## 2 | METHODS

### 2.1 | Field herbivore exclusion experiment

The data came from primary lowland rain forest on nutrient-poor soil, in Korup National Park, Cameroon, in the 82.5-hr permanent “P-plot” established in 1991 (Newbery, Songwe, & Chuyong, 1998, 2013).

Briefly, the experiment had a fully crossed factorial design—canopy cover  $\times$  herbivory treatments—tested on three ectomycorrhizal, masting tree species: one fast growing (*Microberlinia bisulcata* A. Chev) and two slow growing (*Tetraberlinia bifoliolata* Harms [Haumann], *Tetraberlinia korupensis* Weiringa) of contrasting shade tolerance in the Fabaceae subfamily Caesalpinioideae (Newbery, Chuyong, Zimmermann, & Praz, 2006). A total of  $n = 664$  newly established seedlings (replicates, 13.5 to 32.3 cm tall) were physically protected from insects (caged treatment) or accessible to them (control) in shaded understory and sunny gap locations (= 41 blocks). Starting sample sizes and seedling heights are given in Table S1, with more details found in Norghauer and Newbery (2013). A cage had sides of mesh netting with 1-mm  $\times$  4-mm holes and its initial dimensions ( $W \times L \times H$ , all in cm) were c. 40  $\times$  40  $\times$  50, while the control consisted of only a mesh rooftop (50  $\times$  50) with open sides, likewise supported by four bamboo posts. Leaf litter on the control and cage structures was removed regularly during the experiment’s duration (every 5–7 days, returned under rooftops of control and into the cages). To accommodate the growing seedlings in gaps, cages there were enlarged 1–3 times, as needed, to one or more dimensions: 50  $\times$  50  $\times$  75 or 100, 75  $\times$  75  $\times$  100 or 150, or 100  $\times$  100  $\times$  150 or 200; each time, its nearest control of the same species was similarly enlarged (i.e., given the same rooftop area of mesh; Norghauer & Newbery, 2014). The mesh worked well at deterring herbivory from medium-sized insects: generally, throughout the experiment the caged seedlings had median values of 0%–5% for leaf area eaten (refer to Table 3, Fig. 3,4 in Norghauer & Newbery, 2013). Still, the experiment had several unavoidable limitations: namely, mammals were also excluded from cages; apart from the vines that germinated in cages, the entry or exit of other vines was likely impeded by the walled mesh netting—tendrils would have pass through the 4-mm<sup>2</sup> holes—whereas they could do so more easily under the control rooftop; and lastly, the bamboo frame of controls and cages may have drawn vines toward them.

### 2.2 | Light measurements

The amount of light reaching each seedling was directly quantified halfway through the experiment, in mid-November 2008, under overcast conditions (Norghauer & Newbery, 2013). To do this, at 1 m above each seedling (or higher for some larger individuals) a quantum photon sensor (model SKP215; Skye Instruments) was placed and leveled to record the incident photosynthetic photon flux density (PPFD); at the same time, PPFD was recorded by a second sensor (same model type) positioned above the forest canopy (at ca. 0.5 km from the P-plot). Both sets of instantaneous measurements were made over a 1-week period (15–21 November, 2008). This rapid approach to determine light availability, developed by Messier and Puttonen (1995), was used because in other forests such diffuse light readings, when expressed as percentage of above-canopy PPFD, are strongly correlated with mean daily percent PPFD values in the understory (Comeau, Gendron, & Letchford, 1998; Machado & Reich, 1999).

### 2.3 | Vine data recorded

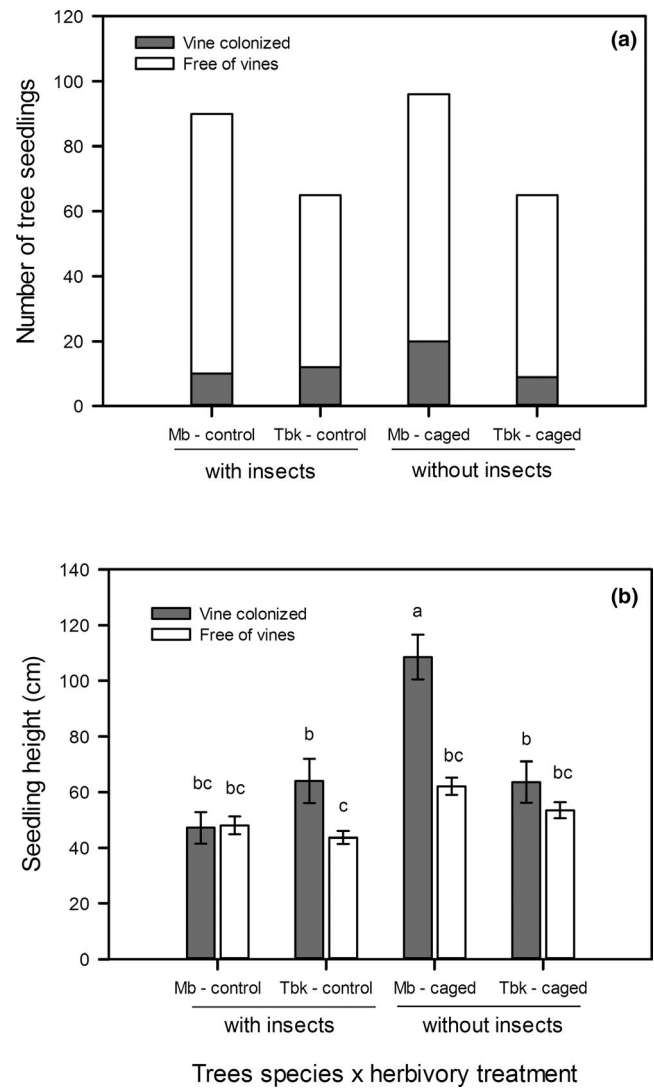
The herbivore exclusion experiment had been installed over a 1-month period (mid-December 2007 to mid-January 2008), which represented the *first census* when starting plant sizes were measured; after ca. 22 months, the mesh cages and rooftops were removed from all tree seedlings (refer to Figure 1 in Norghauer & Newbery, 2013). Vine data for experimental seedlings in gaps was obtained from the *third and fourth censuses only*, as detailed below. At the start of the experiment, all seedlings (Table S1) were free of vines.

In the second census (mid-November 2008), this initial sample of 664 experimental seedlings was increased to 706 by adding “replacements”, primarily to offset sample size reductions of seedlings lethally felled by rodents (Norghauer, Röder, & Glauser, 2016): for *M. bisulcata*, 32 controls and 3 caged in gaps, and 2 controls in the understory; for *T. bifoliolata*, 3 controls in gaps; and for *T. korupensis*, 2 controls (gap and understory each).

In the third census (mid-March 2009), each surviving seedling was checked and scored for a vine climbing it (twined on the main stem or attached via tendrils = a vine colonization event); if present, the vine(s) was clipped back—this was also done in the prior census—to maintain the same growing conditions of control and caged seedlings (apart from their light and herbivore exposure). This vine colonization of a seedling was observed just once in the understory but 33 times in the gaps during this census. So, in the next (fourth) census (October 2009), vine occurrence was recorded on surviving seedlings *in canopy gaps only*.

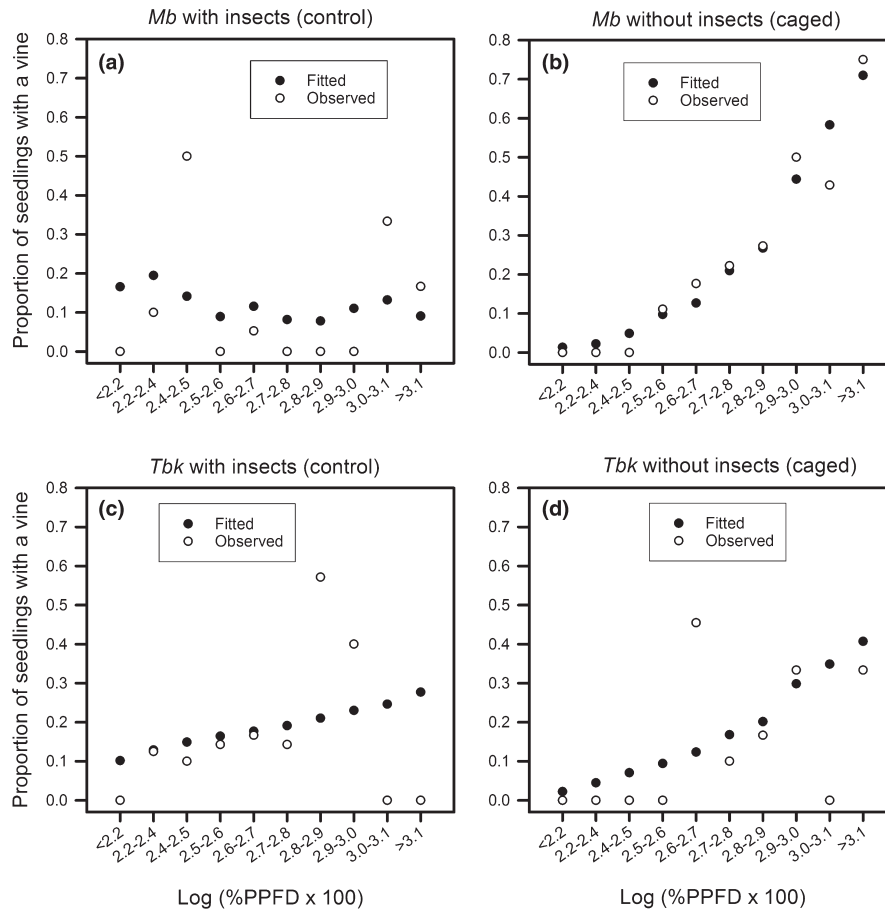
To prevent temporal pseudo-replication, as well as possible cases of re-sprouting vines, seedling responses were pooled over the latter two censuses (i.e., third + fourth). Thus, a given seedling received an overall “vine colonization event” score of “1” based on whether it had hosted a vine at either time while still alive in 2009. Otherwise, a seedling was scored as “0”. Occasionally, two vines (three cases in March 2009, all *M. bisulcata*), or even three vines (one case in March 2009, with *T. korupensis*) were found on the same seedling. Similarly, in October 2009, 5 of the 31 vine-colonized seedlings at this time had two vines on them (three cases with *M. bisulcata*; plus one each for *T. bifoliolata* and *T. korupensis*). To simplify the analyses, all these cases were scored as a single vine colonization event. Vines were not taxonomically identified; hence, they possibly included herbaceous in addition to any woody vine species.

From the March 2009 census, data were missing for one *M. bisulcata* seedling, a control. From the October 2009 census, 10 other seedlings (3 *M. bisulcata*, 2 *T. bifoliolata*, and 5 *T. korupensis*) also lacked data. These 11 seedlings were removed from the pooled data set before it was analyzed. Because insect herbivores substantially reduced the height and leaf numbers of faster growing, less resistant *M. bisulcata* seedlings in gaps, whereas the corresponding growth rates of the more shade-tolerant *Tetraberlinia* species were negligibly affected after almost 2 yr



**FIGURE 1** (a) Tallies of overall vine colonization events of tree seedlings protected from (caged) and exposed to insect herbivores (control) in rain forest gaps at korup, cameroon, and (b) their corresponding mean ( $\pm$  SE) heights of surviving seedlings in November 2009. Mb: *Microberlinia bisulcata*, Tbk: *Tetraberlinia bifoliolata* and *T. korupensis*. Seedling height was  $\log_{10}$ -transformed in a linear mixed model (LMM, Table S5): the 2nd order interaction term of host species group  $\times$  herbivory treatment  $\times$  vine colonization was significant ( $F_{1, 238.4} = 7.79, p = .006$ ). Different letters indicate statistically different means, based on planned LSD tests (5% alpha level). The mean %PPFD ( $\pm$ SE) of the four groups of seedlings, from left to right, was  $5.39 \pm 0.40, 5.59 \pm 0.45, 5.59 \pm 0.35,$  and  $4.91 \pm 0.35$ . (%PPFD is the percentage of photosynthetic photon flux density transmitted through the forest canopy reaching a seedling.) In (b), the samples size per bar, going from left to right: 9, 50, 12, 48, 20, 73, 9, and 56 seedlings. The goodness of fit for this LMM, following Nakagawa and Schielzeth (2013), had a conditional  $R^2 = 0.566$

(refer to Figure 2d, h in Norghauer & Newbery, 2013), the latter two species were grouped for the current analysis. Hereon, I shall simply refer to *M. bisulcata* as “Mb”, and the grouped *T. bifoliolata* and *T. korupensis* as “Tbk”.



**FIGURE 2** Observed and fitted proportions of tree seedlings colonized by a vine in rain forest gaps at Korup (Cameroon) as a function of light resource availability (x-axis), when exposed to insect herbivores (a, c) or protected from them by mesh-netting cages (b, d) for the two species identity groups (*Mb*: *Microberlinia bisulcata*, *Tbk*: *Tetraberlinia bifoliolata* and *T. korupensis* grouped). Observed proportions (y-axis) for each light interval are shown. Curvature in the data of (a) was accommodated by a quadratic term for light availability in the GLMM (Table S4); however, in (c), adding a quadratic term did not significantly improve the fitted model. “%PPFD”: percentage of photosynthetic photon flux density transmitted through the forest canopy reaching a seedling. Sample sizes (total  $n = 315$ ) per light interval (left to right): (a) 5, 10, 12, 6, 19, 14, 11, 3, 3, and 6; (b) 7, 5, 12, 9, 17, 18, 11, 6, 7, and 4; (c) 1, 8, 10, 7, 6, 14, 7, 5, 2, and 5; (d) 3, 4, 11, 13, 11, 10, 6, 3, 1, and 3. The goodness of fit of each GLMM, following Nakagawa and Schielzeth (2013), had conditional  $R^2$  values of 0.335 and 0.256 for *Mb* and *Tbk*, respectively

## 2.4 | Evaluating vine colonization in gaps, with and without herbivores

Individual probability of vine colonization of the monitored seedlings, *in gaps* only, was modeled by logistic regression in a GLMM (generalized linear mixed model). This used the logit link function, an estimated dispersion parameter, and the Schall fitting method, with the fixed effects and variance components estimated by REML (restricted maximum likelihood), which sequentially reduces the weighted [or generalized] sums of squares (akin to a Type I SS strategy). The gap location of seedlings (“block”) was an important random term, as vine abundance varies strongly in space (Putz 1984; Dalling et al., 2012). The first fixed term was light availability, expressed as a continuous explanatory variable: the percent transmittance of PPFD (%PPFD) through the canopy incident above each seedling. This variable was transformed and entered as  $\log_{10}(\%PPFD \times 100)$ , which normalized its distribution (Figure S3), and also centered (i.e., zero-weighted

mean). The herbivory treatment (caged vs. control) was the next fixed term, followed by its interaction with light availability.

Because of too-small sample sizes for robust logistic regression, the GLMM had to be fitted separately for *Mb* and *Tbk* using their ungrouped binary data (Agresti, 2007)—each seedling had a single binary outcome for vine colonization over the observation period (Figure S3)—in GenStat v16.2 (VSN International Ltd. 2013). Importantly, for all fixed terms, Wald-type  $F$  statistics were obtained for inference whose denominator (residual) degrees of freedom (d.df) were calculated using the method of Kenward and Roger (1997). This default correction in Genstat (Payne, 2015) helped to better control the Type 1 error rate in the GLMM; it is the same Kenward–Roger approximation algorithm used for linear mixed models (LMMs) but applied to the LMM on the transformed (link) scale at the last step of the underlying iterative algorithm.

Goodness-of-fit tests based on Pearson ( $\chi^2$ ) and deviance ( $G^2$ ) statistics are not applicable to ungrouped binary data (p. 147 in Agresti, 2007). Instead, the average estimated probability of vine



colonization was obtained for 10 equal intervals of light availability, by summing the fitted individual probabilities and dividing by the number of seedlings in a given interval (pp. 103–4 in Agresti, 2007). These were then visually compared with the observed sample proportions of vine colonization. Additionally, conditional  $R^2$  values are provided for the GLMMs (and for the LMMs described below), as described in Nakagawa and Schielzeth (2013).

## 2.5 | Seedlings under herbivore pressure in gaps

To explain the GLMM results, an attempt was made to link susceptibility to folivory and vine colonization. To directly gauge the activity of insect herbivores, only unprotected seedlings in gaps (i.e., control group) were investigated further (since the caged treatment prevented insect attacks). Specifically, the proportion of extant leaves on a seedling with signs of insect chewing was examined, which I had recorded on all live experimental tree seedlings in October 2009 (full details on this measurement is described in Norghauer & Newbery, 2013). This included all but one control seedling with a vine colonization event. To determine how this incidence of leaf herbivory differed between a seedling's identity (*Mb* vs. *Tbk*) and whether or not it experienced vine colonization (1 vs. 0 score = yes vs. no), a linear mixed model (LMM) was used: light availability ( $\log_{10} [\%PPFD \times 100]$ ) was entered first, with gap as the blocking (random) term.

## 2.6 | Corroborating host tree stature importance for vine colonization in gaps

In an ad-hoc explanatory analysis, a three-way crossed factorial LMM tested whether vine-colonized seedlings that were taller—that is, seedling height was the response variable—than those lacking a vine (yes vs. no) depended on host species identity (*Mb* vs. *Tbk*) and exposure to insects (caged vs. control; i.e., a significant 2nd order interaction). Inclusion of host tree height as a covariate in the earlier GLMM was not justified because it is confounded with light availability and the herbivory treatment (it was known a priori that insects suppressed *Mb*'s growth in height and leaf numbers in gaps; see Norghauer & Newbery 2013). Using height as a proxy for plant stature is justified given the strong correlations between final heights, leaf numbers, and basal stem diameters of the three tree species (nine Pearson  $r$ -values = 0.73–0.92, all  $P$ -values < 0.001). Both this LMM and the one described before, for leaf herbivory, were fitted well (had normal residuals and homogeneity of variance).

# 3 | RESULTS

## 3.1 | Vines in the understory versus gaps

In the gap habitat 33 and 31, tree seedlings had at least one vine on them in March and October 2009, respectively. By contrast, in

the forest understory just one case was recorded out of 257 live seedlings surveyed in March 2009. The following results thus apply to the gap sample only.

## 3.2 | Overall vine colonization frequencies in gaps

When the data from gaps in both censuses were tallied and combined, a total of 51 out of 315 scored seedlings were vine-colonized (as 13 seedlings hosted vines in both censuses). Remarkably, the overall proportion of seedlings—that is, irrespective of the herbivory treatment—hosting a vine was identical between the two tree species groups, at 0.16 (30/185 for *Mb* and 21/130 for *Tbk*; Figure 1a). Ignoring continuous light availability, an association between herbivory and vine colonization of *Mb* was plausible ( $2 \times 2$  contingency table test,  $\chi^2 = 3.25$ ,  $p = .072$ ) but clearly not for *Tbk* ( $\chi^2 = 0.51$ ,  $p = .475$ ; Figure 1a). However, relatively more of the latter species (22.6%) had vines than did the former (12.7%) under normal gap conditions (i.e., when exposed to insects), while this pattern was reversed, albeit slightly less pronounced, when seedlings were protected from herbivore pressure (*Mb*: 26.3% and *Tbk*: 16.1%; Figure 1a).

## 3.3 | Vine colonization with higher light in gaps

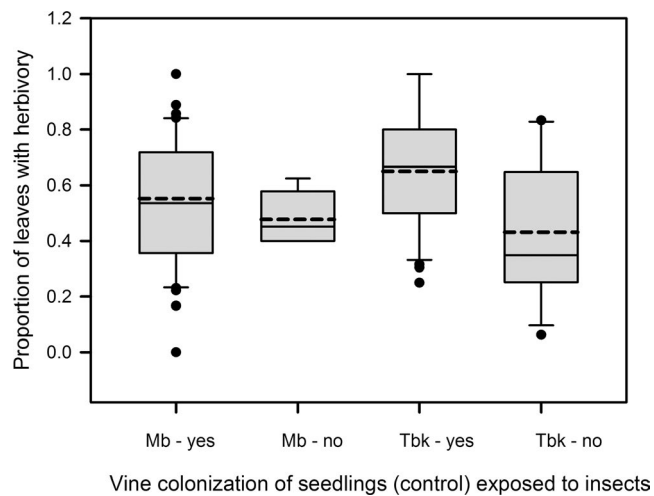
For *Mb* seedlings, light availability influenced vine colonization differently whether they were accessible to insects or not (GLMM,  $PPFD \times$  treatment interaction, Wald-type  $F$  statistic $_{1, 167.3} = 11.22$ ,  $p = .001$ ; Table S4). When herbivores had access to seedlings, as they would naturally, vine colonization was generally low across light levels, with some bimodality indicated (at  $\log \%PPFD = \sim 2.4$  and  $\geq 3.1$ ; Figure 2a); however, when protected from herbivores the better-illuminated seedlings increasingly became more susceptible to vines (Figure 2b). Vine colonization of control seedlings apparently peaked at two levels of light availability, whose fit was improved by adding a quadratic light term to the GLMM (AIC reduced by 9.35; Table S4) as initially suggested by their binary data distributions (Figure S3). Some gap locations had greater vine colonization of *Mb* seedlings than did others (the block term's variance component was 18% larger than its standard error), but this spatial effect was negligible for *Tbk*.

For the *Tbk* seedlings, the light environment only had a slightly positive effect on their colonization by vines ( $PPFD$  term, Wald-type  $F_{1,126.0} = 3.40$ ,  $p = .064$ ; Table S4), while exposure to insect herbivores clearly did not change their susceptibility to it ( $p = .683$  and  $p = .283$  for treatment and interaction terms, respectively). Unlike for *Mb*, the apparent peak in colonization at higher light availability ( $\log \%PPFD = \sim 2.8$ – $3.0$ ; Figure 2c) in the *Tbk* control seedlings could not be accommodated by a quadratic term (AIC increased from 404.62 to 437.56, model not shown). Evidently, the ability of the tested ecological factors (light availability, insect herbivores) to jointly predict vine colonization events was more reliable for *Mb* (its GLMM's goodness of fit was more acceptable than *Tbk*'s). While good predictive power was obtained for the caged *Mb* seedlings (Figure 2b), in the other cases

(Figure 2a,c,d), the fit was poor at several light intervals. Importantly, in the absence of insect herbivores, of those seedlings receiving the most light in gaps 60%–80% of *Mb* were found colonized by a vine (Figure 2b), slightly more than twice that of *Tbk* (Figure 2d).

### 3.4 | Linking folivory to vine colonization in gaps

The unprotected (control) seedlings colonized by a vine had a lower proportion of their leaves damaged by insects (adjusted mean = 0.60) than counterparts free of vines (= 0.48; LMM, vine colonization main term, Wald-type  $F_{1,109.2} = 8.51$ ,  $p = .004$ ). This difference did not depend on their species identity (vine  $\times$  species interaction term,  $p = .211$ ; Figure 3), after first accounting for effects of light availability (light term, Wald-type  $F_{1,114.0} = 1.85$ ,  $p = .177$ ) and the tree species (a priori known) differences in susceptibility to herbivory (species term, Wald-type  $F_{1,104.4} = 4.68$ ,  $p = .033$ ). In this LMM, when a plant's height was substituted for the light it received in a gap—including both predictors in a single model violated its assumptions, since light had a strong positive effect on height (Norghauer & Newbery, 2013, 2014)—the taller control seedlings generally had experienced a lower incidence of insect herbivory (LMM, seedling height covariate, Wald-type  $F_{1,114.0} = 7.39$ ,  $p = .008$ ), as did the vine-colonized seedlings



**FIGURE 3** Box plots showing the incidence of insect herbivory on leaves of unprotected (i.e., control group) tree seedlings with and without vines, in rain forest gaps at Korup (Cameroon). Data are shown for two species identity groups (*Mb*: *Microberlinia bisulcata*, *Tbk*: *Tetraberlinia bifoliolata* and *T. korupensis* grouped). Group sample sizes, from left to right, were  $n = 50, 9, 48,$  and 12 individual seedlings, for which corresponding raw (unadjusted) means ( $\pm$  SE) were  $0.55 \pm 0.033, 0.48 \pm 0.031, 0.65 \pm 0.031,$  and  $0.43 \pm 0.073$ . These were analyzed in a linear mixed model (LMM) able to accommodate the unbalanced sample sizes (in which the means were first adjusted for light availability [as a centered covariate] to individual seedlings). The goodness of fit for that LMM, following Nakagawa and Schielzeth (2013), had a conditional  $R^2 = 0.304$

(Wald-type  $F_{1,108.8} = 6.20$ ,  $p = .014$ ), irrespective of species identity (the interaction remained insignificant,  $p = .320$ ).

### 3.5 | Host stature when vine colonized in gaps

As Figure 1b shows, the herbivore-exposed seedlings of *Mb* were similar in height whether vine-colonized or not, but when released from herbivore pressure in gaps the caged seedlings of this fast growing species that hosted a vine were almost twice as tall as those not colonized. Notably, this pattern was reversed for *Tbk*, in that its control seedlings colonized by a vine were significantly greater in height than those found vine-free, whereas when caged this size-difference effect weakened (LMM, three-way interaction term shown in Figure 1b; Table S5).

## 4 | DISCUSSION

We need more field studies that manipulate plant exposure to insects to determine their influence upon vine colonization of seedlings and saplings in forests. The experimental results here suggest insects could differentially alter vine colonization of dominant tree species with contrasting life histories. This mediating effect, presumably from herbivory to seedlings or vines, or both, further depended on microsite light availability for the dominant, long-lived grove-forming tree *M. bisulcata*, a large fast growing and light-demanding species that has been studied at Korup National Park since 1991 (Newbery et al., 1998, 2013).

The identical overall colonization between host species groups in gaps (16.1%) across  $\sim 80$  ha of Korup forest would suggest these vines, as a group, behaved as generalist structural parasites (Putz 1984; Babweteera et al., 2000; recently Visser, Schnitzer, et al., 2018a). Nevertheless, rates of vine colonization likely change with tree ontogeny; for example, trees of  $\geq 20$  cm stem diameter in Panama had woody vine infestations that varied strongly among species and with their shade tolerance (Visser, Muller-Landau, et al., 2018b). By contrast, in the understory at Korup, the experiment's newly established *M. bisulcata* and *Tetraberlinia* seedlings barely grew in height (Norghauer & Newbery, 2013), thus limiting their availability as suitable support hosts (Putz 1984). However, owing to their shade tolerance, over a longer time frame the better survival of *T. bifoliolata* and *T. korupensis* seedlings (Newbery et al., 2006) creates a combined sapling bank that greatly exceeds that of *M. bisulcata* (Newbery et al., 1998). This represents a stable supply of potential hosts for vine species able to tolerate shaded conditions once the gaps closed up.

Insects suppressed vine colonization of *M. bisulcata*, especially of its well-illuminated hosts (Figure 2a,b), but not so for *Tbk*, whose seedlings were nonetheless more prone to vines when exposed to these herbivores (Figure 1a). Two explanatory mechanisms related to species differences in host size and leaf traits are plausible. First, by keeping *M. bisulcata* seedlings small in height but not *Tetraberlinia* spp. (Figure 1b), insect herbivores reduced the likelihood of vines encountering hosts in gaps by chance alone,

given their strong co-occurrence there (e.g., Blick & Burns, 2011). But it is not at all inconceivable that vines may have searched for a larger-sized host plant near them, by growing away from the light, and toward the tallest seedlings casting the most shade through a form of skototropism (Strong & Ray, 1975), given the very contrasting light-dependent patterns of Figure 2a,b, and the fact that, overall, relatively more *Tetraberlinia* controls were colonized than smaller-sized *M. bisulcata* counterparts (Figure 1a). As argued recently by Gianoli (2015), a preference for taller hosts may confer a greater fitness currency to vines, in the parlance of optimal foraging theory, especially if they are capable of cue-oriented growth (e.g., skototropism) among neighboring plants to find favorable supports.

Second, it may be that vines failed to colonize well-lit *M. bisulcata* (in Figure 2a) because they too were heavily eaten by insects in gaps—as predicted by the plant vigor hypothesis (Price, 1991; e.g., Hough-Goldtsein & LaCoss, 2012)—or due to associational susceptibility (Gianoli, 2015) with this host tree species and its thin, palatable leaves (Norghauer & Newbery, 2014). Conversely, in addition to host size, vines might also have benefited from associational resistance with the more herbivore-resistant (less palatable) *Tetraberlinia bifoliolata* and *T. korupensis* leaves (Norghauer, Glauser, & Newbery, 2014). For example, in a temperate South American forest, the proportion of leaf area damaged in *Vicia nigricans* on one shrub species was double that on its other host (Sasal & Suarez, 2011). It is less clear whether or not vines may confer associational resistance to juvenile host trees, as suggested by Piironen et al. (2013), who reported the leaf area eaten (%) of the pioneer *Neoboutonia macrocalyx* was lower on its seedlings with fewer vines on them in gaps of post-logged conifer plantations in Kibale National Park (Uganda). No such evidence was found at Korup, where tree seedlings generally incurred more frequent bouts of herbivory when hosting a vine in canopy gaps (Figure 3), pointing instead to associational susceptibility. Such associational effects for herbivory between co-occurring plant species in patchy resource-rich habitats deserve more field study (Hambäck, Inouye, Andersson, & Underwood, 2014) and may prove crucial for predicting vine–tree interactions in tropical forest communities.

A third factor possibly relevant to vine colonization is leaf trait morphology of host plants. In re-analyzing the two *Tetraberlinia* species in separate GLMMs (Table S6), light availability strongly promoted vine colonization of *T. bifoliolata* (light term,  $p = .004$ ) which has a leaf consisting of two large, lobed leaflets (bifoliate). However, for *T. korupensis*, whose leaves are morphologically very similar to *M. bisulcata* (simply pinnate, with many opposite leaflets) but chemically better defended, exposure to insects only interacted to some extent with host's seedling light environment (PPFD  $\times$  treatment interaction,  $p = .160$ ). Although this post-hoc investigation had low statistical power ( $n < 100$  per GLMM, further justifying the *Tbk* grouping before), it points to leaf morphological differences among species perhaps being important for influencing vine–insect–tree interactions in canopy-disturbed areas. Plants with pinnate compound leaves, whose leaflets are easily shed (from biotic or abiotic

damage), may have a lower leaf area index (LAI) than those with thicker, non-pinnate leaves, making the latter species more liable to be colonized if vines gravitated toward larger-sized host seedlings in gaps using LAI as a primary search cue.

This study has several caveats, whose consideration illustrates the logistical difficulty involved in conducting a “clean experiment” in a tropical rain forest. First, hosts in the control treatment, with its mesh rooftop and open sides, could have been accessible to more vines if these foraged more than  $\sim 0.5$  m across the ground and came from dispersed seeds  $> 1 \text{ mm} \times 4 \text{ mm}$  in size (= mesh opening) that landed nearby. Yet, by the same token, a vine established near a control seedling could move further away from it and colonize a different host, whereas in a caged treatment its mesh sides limited both aspects of vine behavior. Second, by enlarging a cage, relatively more germinating or established vines could have been inadvertently “trapped” inside it with the host seedling. Third, both herbivory treatments were supported by bamboo posts, which being bare for the control seedlings may have lured vines away from them, while those affixed with mesh side walls could have provided scaffolding for vines to climb inside the cages. The net effects of these experimental artifacts on the results are unknown. Vegetation cover around the seedlings was systematically assessed in November 2009 and found to be similar at two strata between cages and controls in gaps (Norghauer & Newbery, 2013). Another caveat is that the mesh netting also excluded potential mammalian herbivores; at Korup they apparently neither grazed nor browsed the studied tree seedlings, but rodents can lethally sever their stems near the base, especially those of *M. bisulcata* (Norghauer et al., 2016). Hopefully, highlighting these caveats may better prepare ecologists intending to experimentally investigate vine colonization of young trees. Alternatively, one could try to chemically exclude insects from host seedlings, but the efficacy of this is questionable in gaps open directly to rain, especially in very wet lowland forests like Korup, and it may have other unintended consequences too.

Compared with *M. bisulcata*, relatively higher vine colonization on the *Tetraberlinia* spp. under normal forest conditions (i.e., with exposure to insects = control) may lead to recurring higher liana loads on these shade-tolerant, slower growing trees as they ascend to the canopy and mature. Hence, these findings appear consistent with the reportedly stronger direct impacts of vines on shade-tolerant tree species (e.g., Schnitzer & Carson, 2010). Nonetheless, *M. bisulcata* seedlings were at risk of colonization even at low light in gaps; over time, a survivorship bias toward those being vine-free may occur if vine loading reduces survival rates of faster growing species (Visser, Schnitzer, et al., 2018a), especially following canopy gap closure. But whether or not this vine interference can also reduce *M. bisulcata*'s population-wide sapling and adult recruitment rates is unknown, it depending on the proportion of stems colonized and host tolerance to vine infestations (Visser, Muller-Landau, et al., 2018b). If it does, this may contribute cryptically to the currently poor regeneration of *M. bisulcata* groves at Korup (Newbery et al., 2006, 1998). However, should the better-illuminated *M. bisulcata* juveniles be able to tolerate interference from vines or soon shed them



through ontogeny—particularly via its remarkably fast growth in 10–50-cm stem diameter size classes (Newbery et al., 2013)—then it is plausible this species recruitment may benefit from conditions that also favor vine recruitment. Conversely, vine colonization likely has little immediate impact on the persistence of *Tetraberlinia* seedlings and saplings, since shade-tolerant species can also better tolerate hosting vines (Visser, Muller-Landau, et al., 2018b) after gap closure. Yet, ontogenic shifts in host tolerance to vine infestation should not be discounted either: for example, among bole- and adult-sized trees (>20 cm stem diameter), more of *T. bifoliolata*, and *T. korupensis* to a lesser extent, are found vine-laden than *M. bisulcata* (Norghauer, pers. observations), and this biotic stress may contribute to the higher *Tetraberlinia* spp. mortality rates at Korup (Newbery et al., 2013). Woody vines are thought to compete directly with juvenile trees for belowground resources (Schnitzer et al. 2005; Toledo-Aceves & Swaine, 2008b), especially for water during dry periods in seasonal forests (Alvarez-Cansino et al., 2015; Schnitzer & Bongers, 2011). It is tempting to speculate that vine colonization and interference with shade-tolerant competitors of *M. bisulcata*, such as the two *Tetraberlinia* species (and perhaps others), would strengthen during large-scale regional droughts. These climatic events, as argued by Newbery et al. (2013), are necessary for *M. bisulcata* grove maintenance at Korup, and they might also reduce forest-wide insect herbivore abundance and pressure, further favoring *M. bisulcata*'s regeneration.

Almost all the vines observed on seedlings/saplings had wound themselves on main stem (twining) or latched laterally using tendrils. No attempt was made to quantify either climbing habit, nor were the vines taxonomically identified, so it is unknown if any were perhaps herbaceous. Currently, it is also unknown which insect taxa feed on vines in gaps at Korup. Future studies that manipulate exposure to herbivores, whether of invertebrates or vertebrates, should consider recording the habits of vines on young trees using very large samples ( $n > 200$ ) of multiple host species along the fast–slow growth spectrum. To my knowledge, a systematic in situ community-level study of herbivory of both vines and their host trees has yet to be done.

To conclude, the results demonstrated how herbivores could interact with canopy disturbances to differentially shape vine colonization events on tree hosts across space, which could broaden our understanding of forest regeneration dynamics. Vines prefer to colonize taller hosts, to more quickly climb or be carried upward, but insects interact with light to mediate this process in gaps, by stunting the vertical growth of faster growing individuals of more palatable light-demanding species. This causes vine colonization rates at higher light levels to become more similar between slow and fast growing tree species. Since both vines and gaps are fundamental features of tropical forests, these findings from Korup may apply to other co-existing tree species on the fast–slow growth rate spectrum associated with shade tolerance as juveniles. In particular, it would be pertinent to know how changes in soil fertility and seasonality influence vine colonization and to conduct long-term studies of its impact on tree population dynamics, while the relative importance of mycorrhizal associations of co-occurring vine and tree

species seems ripe for study. Investigations of vine–tree–herbivore interactions may also be timely for understanding vines' behavior (Gianoli, 2015), and their ongoing abundance and biomass increases in tropical America but not Africa (Schnitzer & Bongers, 2011). For these reasons, well-replicated intercontinental experiments may prove particularly insightful.

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## DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.sf7m0cg1p> (Norghauer, 2019).

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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