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Lianas reduce community-level canopy tree reproduction in a Panamanian forest

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Abstract

1. Lianas are a key component of tropical forests, where they compete intensely with trees, reducing tree recruitment, growth and survival. One of the most important potential outcomes of liana competition is the reduction of tree reproduction; however, no previous study has experimentally determined the effects of lianas on tree reproduction beyond a single tree species.
2. We used a large-scale liana removal experiment to quantify the effect of lianas on community-level canopy and understorey tree and palm reproduction. In 2011, we removed lianas from eight 6,400-m^2 plots (eight plots served as controls) and surveyed understorey tree reproduction in 2012, canopy tree and palm reproduction in 2013, and a second census of all plants in 2016.
3. We found that lianas significantly reduced canopy tree community flowering and fruiting after liana removal. Two years after liana removal, the number of canopy trees with fruits was 173% higher, fruiting individuals had 50% more of their canopy covered by fruits and the number of tree species with fruits was 169% higher than in control plots where lianas were present. Five years after liana removal, the number of canopy trees with fruits was 150% higher, fruiting individuals had 31% more of their canopy covered by fruits and the number of tree species with fruits was 109% higher than in unmanipulated control plots.
4. Liana removal had only a slight positive effect on palms and on understorey tree flower and fruit production, even though understorey light levels had increased 20% following liana cutting.
5. *Synthesis*. Our findings provide the first experimental demonstration that competition from lianas significantly reduces community-level canopy tree reproduction. Reduced reproduction increases canopy tree seed and dispersal limitations, and may interfere with deterministic mechanisms thought to maintain tropical canopy tree species diversity, as well as reduce food availability to many animal species. Because lianas are increasing in abundance in many neotropical forests, the effects of lianas on tree reproduction will likely increase, and if the effects of lianas on tree reproduction vary with tree species identity, lianas ultimately could have a destabilizing effect on both tree and animal population dynamics.

KEYWORDS
community ecology, competition, determinants of plant community diversity and structure, dispersal limitation, liana cutting, plant–plant interactions, tropical forests

1 | INTRODUCTION

Reproduction is a fundamental process structuring plant populations and communities. The cumulative fecundity of a plant population will dictate how that population changes over time, and thus will ultimately determine the relative abundance of that species in the community. Population growth for many plant species is limited by their ability to produce and disperse seeds (Dalling & John, 2008; Stevens, Bunker, Schnitzer, & Carson, 2004). Furthermore, the ability of plants to produce copious amounts of seeds and to disperse them broadly is a critical component of plant coexistence (Dalling & John, 2008; Hubbell, 2001; Peng, Zhou, and Zang 2012), and also provides a critical food source to higher trophic levels (frugivores and granivores). While there are many factors that can influence the reproductive output of plant populations, such as pest pressure, disease or seed predation, interspecific competition may play a strong role in reducing reproduction, with the dominant competitors growing and reproducing more than subordinate ones (e.g. Tilman, 1982).

In tropical forests, a common form of competition is between lianas and trees (e.g. Ledo et al., 2016; Martinez-Izquierdo, Garcia-Leon, Powers, & Schnitzer, 2016; Schnitzer, Dalling, & Carson, 2000; Schnitzer, Kuzee, & Bongers, 2005; Schnitzer, van der Heijden, Mascaro, & Carson, 2014; Toledo-Aceves, 2015). Lianas are woody vines that are present in high density and diversity in lowland tropical forests, where they use the architecture of trees to ascend to the forest canopy (Schnitzer & Bongers, 2002). Once in the canopy, lianas can form layers of foliage over that of their host trees, thereby reducing the amount of light available to canopy trees (Avalos & Mulkey, 1999; Rodriguez-Ronderos, Bohrer, Sanchez-Azofeifa, Powers, & Schnitzer, 2016). Lianas may also compete for below-ground resources, which has been confirmed in various manipulative studies (Alvarez-Cansino, Schnitzer, Reid, & Powers, 2015; Dillenburg, Whigham, Teramura, & Forseth, 1993; Toledo-Aceves, 2015). For example, in a west African forest, Schnitzer et al. (2005) reported that tree saplings grew five times faster without competition from lianas, and that the majority of this competition appeared to be for below-ground resources.

Competition from lianas may reduce reproduction for many tropical trees (e.g. Fonseca, Vidal, & Maes Dos Santos, 2009; Stevens, 1987). For example, Kainer, Wadt, and Staudhammer (2014) found that the reproductive output of Brazil nut trees 10 years after removing lianas was 77% higher than that of conspecific trees that hosted lianas during the same period. Wright et al. (2005) reported that the presence of lianas was negatively correlated with reproduction in multiple canopy tree species. Lianas may also reduce the reproduction of understorey plants. Understorey plants are thought to increase reproduction in response to light availability (e.g. Levey, 1988) and, by reducing light, lianas may limit the ability of understorey plants to reproduce. Therefore, lianas may significantly reduce canopy and understorey plant reproduction, increasing tree seed and dispersal limitations (Dalling & John, 2008; Stevens et al., 2004; Wright et al., 2005). By contrast, palms are thought to suffer little from lianas, either by avoiding liana infestation (Putz, 1984) or by favouring wetter soils and microsites that are avoided by many liana species (Dalling et al., 2012; Schnitzer, 2005).

Previous experimental studies on the effect of lianas on tree reproduction have typically focused on only single tree species—usually one of economic importance. For example, Kainer, Wadt, Gomes-Silva, and Capanu (2006) and Kainer et al. (2014) quantified the effects of lianas on the Brazil nut tree (*Bertholletia excelsa*), which produces an edible seed that is sold globally. Fonseca et al. (2009) examined the effect of liana infestation on the reproduction of *Chrysophyllum lucentifolium*, a valuable timber tree that is used widely for construction and furniture. Other studies have examined the correlation between the presence of lianas in canopy trees and their reproductive output (Wright et al., 2005). To date, however, no study has experimentally evaluated the effect of lianas on canopy tree reproduction at the community level. Furthermore, no studies have evaluated the effects of lianas on palm and understorey plant reproduction. Here we used a large-scale liana removal experiment to evaluate the effects of lianas on canopy and understorey tree reproduction, as well as palm reproduction in a lowland tropical forest in the Republic of Panama. We tested the general hypothesis that lianas reduce woody plant and palm reproduction in both the canopy and the understorey, and therefore, the removal of lianas will increase reproduction of these plants. This is the first experimental study to evaluate the role of lianas on community-wide plant reproduction.

2 | MATERIALS AND METHODS

In 2008, we established 16 long-term 80 × 80 m experimental plots in an ~60-year-old secondary forest on Gigante Peninsula, a protected mainland forest that is part of the Barro Colorado Natural Monument (BCNM 09°10′N, 79°51′W) in central Panama. Mean annual rainfall at Gigante Peninsula is 2,600 mm, with a dry season from January until May (Leigh, 1999; Schnitzer & Carson, 2010). We permanently tagged, spatially mapped, measured the diameter and identified to species all trees and lianas ≥1 cm diameter within the 60 × 60 m centre area, and all trees ≥20 cm diameter and lianas ≥5 cm diameter in the entire 80 × 80 m area (Alvarez-Cansino et al., 2015; Martinez-Izquierdo et al., 2016; Reid, Schnitzer, & Powers, 2015; Rodriguez-Ronderos et al., 2016; van der Heijden, Powers, & Schnitzer, 2015). In

April 2011, we randomly selected eight plots to receive a liana cutting treatment, while the remaining eight plots served as controls. We cut all lianas growing in the plot, including lianas that originated outside of the 10-m plot border. Lianas were cut at the base and were not removed from the trees to avoid damaging the tree canopy. Resprouting lianas were cut every 3 months (follows Schnitzer & Carson, 2010; Schnitzer et al., 2014), and control and liana removal plots were visited at the same frequency to avoid unanticipated visitation effects (e.g. Cahill, Castelli, & Casper, 2001; Schnitzer, Reich, Bergner, & Carson, 2002).

2.1 | Field measurements for understorey and canopy plant reproduction

We quantified understorey plant (tree and shrub) reproduction in three randomly selected 20 × 20 m quadrants within each of the 16 plots. In each quadrant, we counted the number of flowers and fruits and recorded the species identity of every understorey flowering plant (≥1 cm diameter, <10 m tall). We surveyed the reproductive status of understorey plants roughly every 5 weeks for a total of seven censuses from February 2012 until September 2012.

In 2013, we surveyed canopy trees each month from January until July (six censuses total). In each of the 16 plots, we randomly selected 36 target canopy trees (576 total). We estimated the number of flowers and fruits from the ground using a 5-point scale, where 0 = no flowers or fruits, 1 = 1–25% of the canopy had flowers or fruits, 2 = 26–50% of the canopy had flowers or fruit, 3 = 51–75% of the canopy had flowers or fruits and 4 = more than 75% of the canopy had flowers or fruits (follows Ingwell, Wright, Becklund, Hubbell, & Schnitzer, 2010; Schnitzer & Carson, 2010; Wright et al., 2005). We also selected up to six palms that were located in the canopy or subcanopy in each plot. Some plots had fewer than six palms and one control plot had no palms; in those plots, we surveyed all palms that were present (85 palms total). For each palm, we quantified the number of flower and fruit clusters, which are typically displayed in bunches hanging below the palm foliage. The vast majority of tree reproduction in central Panama typically occur between December and July (Wright et al., 2005), and thus our censuses captured the peak flowering period.

In 2016, 5 years after the initial liana cutting, we repeated the canopy and understorey censuses each month from January until July using identical methods to confirm that the results from the first censuses were not an ephemeral artefact of the liana manipulation. If one of the original canopy trees had died between census periods, we replaced it with the nearest canopy tree in the same plot.

2.2 | Data analyses

To capture the total amount of plant community reproduction per plot and to account for differences in reproductive timing among species, we summed the total amount of plant reproduction in the understorey (the number of flowers and fruits, separately) and total amount of tree reproduction in the canopy (the proportion of the tree crown covered by flowers and fruits, separately) over the sampling periods. Plants that had flowers or fruits that spanned multiple census periods were counted only once, and the largest monthly estimate of reproduction for that individual was used. We used a generalized linear mixed model (glmer) to compare reproductive output in the liana removal and control plots for each census period (and the treatment by year interaction) in terms of: (1) the number of individuals with flowers and fruits; (2) the number of species with flowers and fruits; and (3) the mean proportion of the canopy covered (for canopy trees), the mean number of flowers and fruits (for understorey plants) or the mean number of flower and fruit clusters (for palms). Flowers and fruits were analysed separately. We included the plot number as a random term in the model to account for the two measurement periods. We used a Shapiro test to confirm that the model residuals did not deviate significantly from a normal distribution. All analyses were conducted using R statistical computing software (R Development Core Team, 2015).

3 | RESULTS

3.1 | Canopy trees

Of the 576 total canopy trees in the study, 393 individuals comprising 65 species in 57 genera and 34 families were reproductive in the first census (Table S1). The mean number of canopy trees (per plot) with flowers and fruits was significantly higher in the liana removal plots than in the control plots (flowers: 67% higher in 2013 and 109% higher in 2016: $z = 2.85$, $p = .004$; fruits: 173% higher in 2013 and 150% higher in 2016: $z = 4.79$, $p < .0001$; Figure 1a). The mean number of canopy tree species with flowers and fruits was also higher in the liana removal plots compared to the control plots (flowers: 82% higher in 2013 and 63% higher in 2016: $z = 2.82$, $p = .005$; fruits: 169% in 2013 and 109% higher in 2016: $z = 4.31$, $p < .0001$; Figure 1b). For each reproductive individual, the mean estimate of the quantity of flowers and fruits that covered the canopy was significantly higher in the liana removal than in the control plots (flowers: 48% higher in 2013 and 13% higher in 2016: $z = 2.82$, $p = .005$; fruits: 50% higher in 2013 and 31% higher in 2016: $z = 2.55$, $p = .01$; Figure 1c). Furthermore, the number of canopy trees (and species) with flowers and fruits was consistently higher in the liana removal than in the control plots at nearly every sampling period. There was not a significant effect of year or a year by treatment interaction for any of the comparisons. Consequently, when lianas were removed, far more canopy tree individuals and species produced flowers and fruits, each reproductive individual had more flowers and fruits, and these effects were extremely strong both 2 and 5 years after cutting lianas.

3.2 | Palms

We surveyed a total of 85 palms in 2013 and 2016, which consisted of three species in the Arecaceae family: *Astrocaryum standleyanum*, *Oenocarpus mapora* and *Socratea exorrhiza*. *Oenocarpus mapura* and *S. exorrhiza* are tall subcanopy palms, and *Astrocaryum stanlyanum* is a canopy palm. The vast majority (67) of the 74 reproductive palms in our

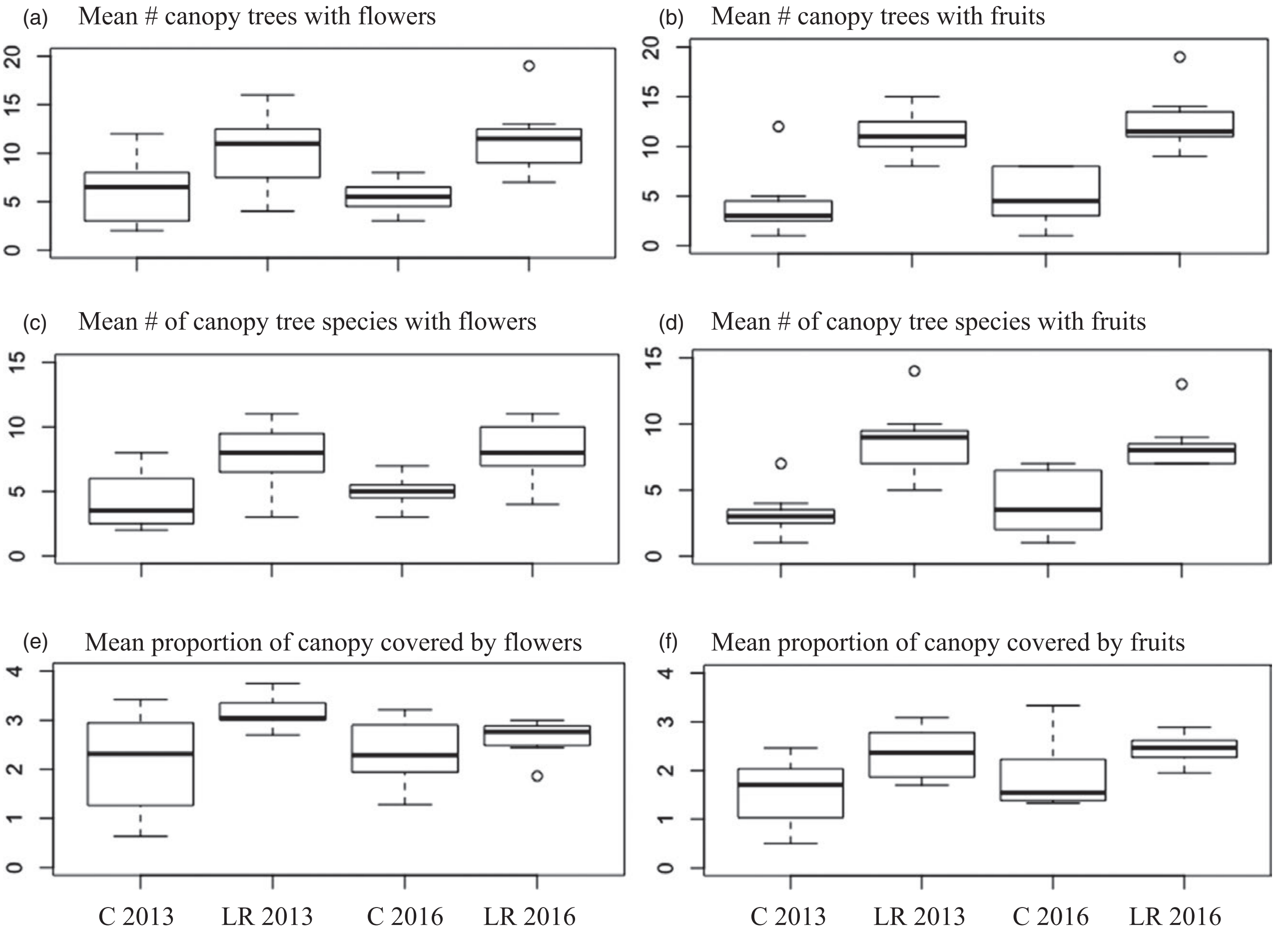

FIGURE 1 Removing lianas significantly increased: the mean number of canopy trees with flowers (a) and fruits (b); the mean number of canopy tree species with flowers (c) and fruits (d), as well as the mean proportion of the crown covered by flowers (e) and fruits (f) for each reproductive canopy tree compared to control plots on Gigante Peninsula in the Republic of Panama. Control plots are labelled 'C' and liana removal plots are labelled 'LR' and the canopy tree reproduction censuses were conducted in 2013 and 2016, 2 and 5 years following liana cutting. Data are based on a survey of 576 canopy trees in 16 plots; eight liana removal plots and eight non-manipulated controls (36 trees per plot)

plots in 2013 were *O. mapura*, with only seven *A. stanlyanum* and one *S. exorrhiza*. The number of reproductive palms was identical among the treatments in 2013 (37 individuals each) and nearly identical in 2016 (31 in the liana removal plots and 30 in the control plots). In 2013, the mean number of palm flower clusters per plot did not differ among the treatments (liana removal: 1.5 ± 0.5 *SE*, control: 1.9 ± 0.8 *SE*). By 2016, however, the mean number of flower clusters was nearly 50% higher in the liana removal plots (removal: 5.123 ± 0.60 *SE*, control: 2.63 ± 1.79 *SE*; $z = 1.74$, $p = .08$; Figure 2). The mean number of palm fruit clusters in 2013 was 50% higher in the liana removal than in the control treatment (liana removal: 13.5 ± 2.44, control: 9.0 ± 1.5; Figure 2). By 2016, however, the number of fruit clusters was very low in both treatments (liana removal: 1.5 ± 0.5, control: 1.9 ± 0.8), and overall the number of fruit clusters did not differ among treatments ($z = 0.72$, $p = .47$). There was a significant effect of year on palm fruit production, indicating much stronger fruit production in 2013 ($z = 2.59$, $p = .009$). There was not a significant year by treatment interaction for any of the comparisons, and restricting our analysis to *O. mapura* (excluding *S. exorrhiza* and *A. stanlyanum*) did not change our findings.

3.3 | Understorey plants

We recorded a total of 617 reproductive understorey plants, which included 56 species belonging to 45 genera and 23 families in the first census (Table S2). The mean number of understorey plants with flowers and fruits was greater in the removal plots in both censuses (individuals with flowers in 2012 and 2016: 30% and 109%, respectively; individuals with fruits in 2012 and 2016: 162% and 101%, respectively; Figure 3a). These differences were statistically significant for fruits ($z = 2.24$, $p = .025$), but not for flowers ($t = 0.65$, $p = .52$). The mean number of understorey plant species with flowers and fruits did not differ significantly between treatments (flowers: $z = 1.44$, $p = .15$; fruits: $z = 0.67$, $p = .50$; Figure 3b), nor did the mean number of flowers and fruits per reproductive individual (flowers: $t = 1.29$, $p = .20$; fruits: $t = 1.11$, $p = .26$; Figure 3c). There was not a significant year by treatment interaction for any of the comparisons, and the two census periods differed significantly only for the number of individuals with fruits ($t = 4.61$, $p < .0001$) and mean number of fruits per individuals ($t = 2.30$, $p = .02$).

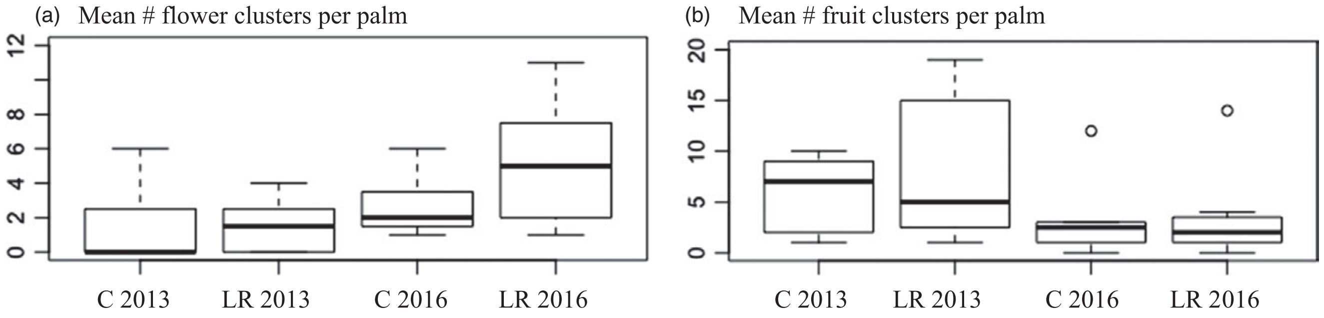

FIGURE 2 The mean number of flower clusters (a) and fruit clusters in palms trees in liana removal and control plots on Gigante Peninsula in the Republic of Panama. Control plots are labelled 'C' and liana removal plots are labelled 'LR' and the palm reproduction censuses were conducted in 2012 and 2016, 1 and 5 years following liana cutting. Data are based on a survey of 85 palms in 16 plots; eight liana removal plots and eight non-manipulated controls

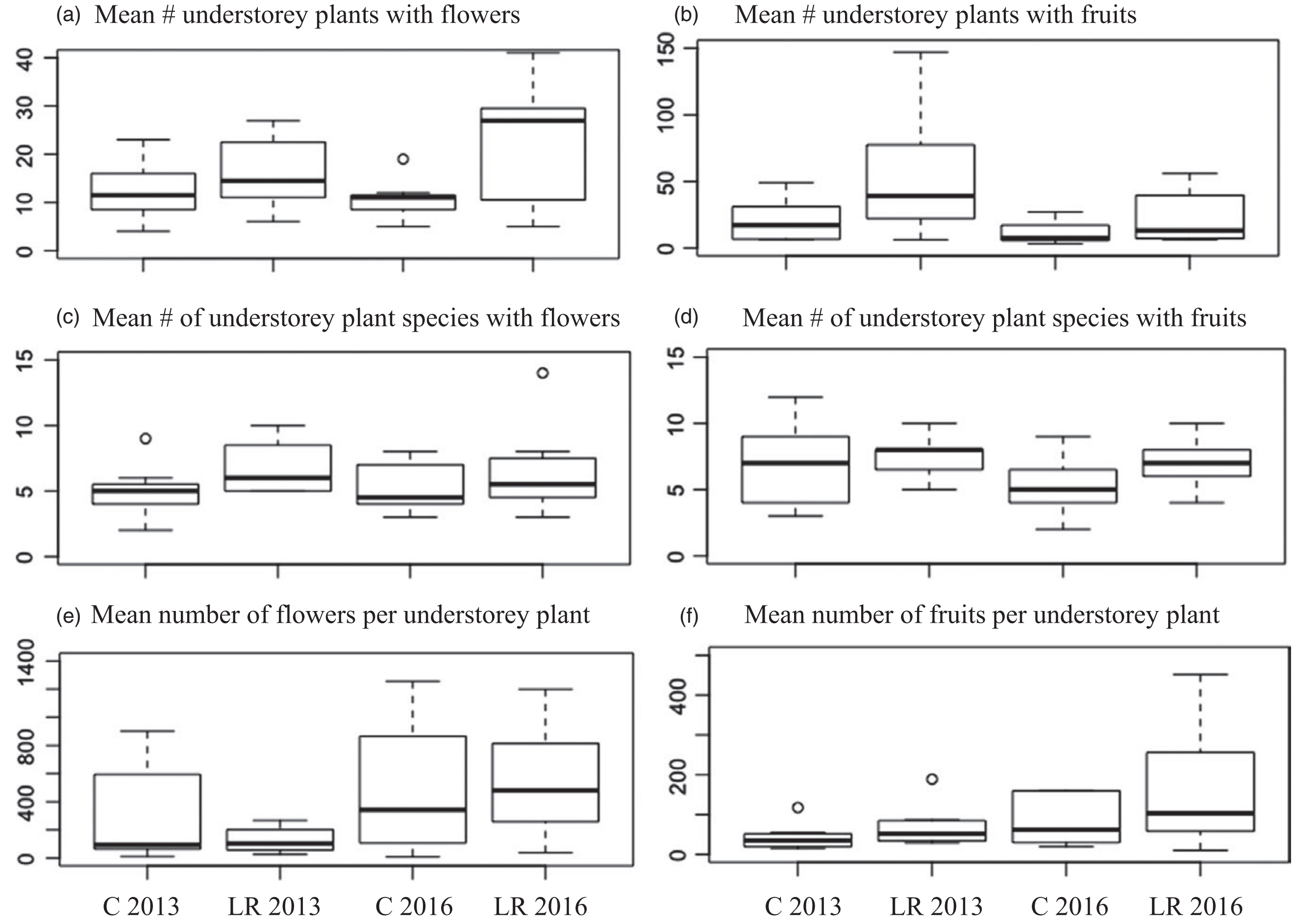

FIGURE 3 The mean number of understorey plants with flowers (a) and fruits (b); the mean number of understorey plant species with flowers (c) and fruits (d), as well as the mean number of flowers (e) and fruits (f) for each reproductive understorey plant in liana removal and control plots on Gigante Peninsula in the Republic of Panama. Control plots are labelled 'C' and liana removal plots are labelled 'LR' and the canopy tree reproduction censuses were conducted in 2012 and 2016, 1 and 5 years following liana cutting. Data are based on a survey of 617 understorey plants in 16 plots; eight liana removal plots and eight non-manipulated controls

4 | DISCUSSION

Competition from lianas caused a significant reduction in canopy tree community-level reproduction, which has important implications for the maintenance of species diversity in tropical forests. Reduced flowering and fruiting limits seed production and thus seed dispersal, which may limit deterministic processes hypothesized to maintain species diversity, such as niche diversification. For example, experimental studies in tropical forests and grasslands have shown that the addition of seeds results in greater plant recruitment and species diversity (Clark, Poulsen, Levey, & Osenberg, 2007; Stevens et al., 2004), which facilitates niche diversification (Paine & Harms, 2009). If community-level seed production and dispersal are limited, then a sufficient number of propagules may fail to reach enough regeneration sites for competition and niche diversification to maintain diversity (Brokaw & Busing, 2000; Dalling & John, 2008). Under this latter scenario, the ability to establish early can become more important than 'competitive ability' per se (sensu Tilman, 1982), resulting in competitive interactions that appear to be weak or neutral (sensu Hubbell, 2001). Indeed, studies that have failed to find strong deterministic signals in plant distribution patterns in response to environmental variation have suggested that the inability of seeds to disperse across the landscape may have prevented deterministic factors from operating (e.g. Brokaw & Busing, 2000; Hubbell et al., 1999).

Previous studies in tropical forests have attributed seed and dispersal limitations to the inability of species to produce enough seeds, or to pre-dispersal or post-dispersal seed predation (e.g. Dalling & John, 2008; Hubbell et al., 1999), rather than competition among canopy plants. In our study, competition from lianas substantially reduced canopy tree reproduction, which could increase forest-level dispersal limitation. Two years following liana removal, the number of canopy trees with fruits was ~170% higher in the liana removal plots than in the control plots (where lianas were present), and fruiting trees had 50% more of their canopy covered by fruits in liana removal plots than did trees in control plots. The effects of liana removal were still strong after 5 years, with the number of canopy trees with fruits 150% higher in the liana removal plots than in the control plots, and fruiting trees had 30% more of their canopy covered by fruits in liana removal plots than did trees in control plots. These observed increases in fruiting are consistent with the more than doubling of fruit production (in terms of biomass) that we found (via littertraps) in the liana removal plots compared to the sum of liana and tree fruit production in the control plots (van der Heijden et al., 2015; figure 2c, supplemental materials). Thus, competition from lianas severely reduces canopy tree reproduction, which contributes to seed and dispersal limitation in tropical forest trees and may limit the efficacy of niche diversification.

Even when canopy tree seeds arrive at suitable regeneration sites (e.g. treefall gaps), lianas may smother their regeneration and recruitment for decades (Schnitzer et al., 2000; Tymen et al., 2016). Liana density and diversity are particularly high in treefall gaps (Dalling et al., 2012; Ledo & Schnitzer, 2014; Schnitzer & Carson, 2001), which are foci of vigorous tree recruitment and regeneration in tropical forests. In an 8-year liana removal experiment in the Gigante Peninsula forest in Panama, the competitive and mechanical effects of lianas significantly reduced tree recruitment, growth, biomass accumulation and species diversity in treefall gaps (Schnitzer & Carson, 2010; Schnitzer et al., 2014). Lianas also reduce tree seedling growth and survival in the forest understorey. For example, working in the same experimental plots as this current study, Martinez-Izquierdo et al. (2016) examined the effects of liana removal on the seedlings of 14 partially and fully shade-tolerant tree species and found that seedling growth and survival for all tree species were significantly lower when lianas were present. Therefore, lianas appear to reduce tree regeneration by first reducing seed production and increasing seed and dispersal limitations, and then by reducing seedling regeneration in treefall gaps and in the forest understorey.

If the negative effect of lianas on tree reproduction varies with species identity, then lianas may alter tree community composition. For example, lianas may have a stronger negative effect on the population demography of fast-growing pioneer trees than on slow-growing shade-tolerant trees (Visser et al., in press). If so, the trend of increasing liana abundance in neotropical forests (Schnitzer, 2015; Schnitzer & Bongers, 2011) may favour shade-tolerant tree population growth rates by decreasing their reproductive output (and thus fecundity) less than for shade-intolerant trees. However, whether lianas have differential effects on trees based on tree species identity is currently unresolved. Recent studies on the effects of lianas on non-pioneer tree seedlings, saplings and adults indicate that lianas have a strong negative effect on tree growth, sap-flow and mortality, regardless of species identity. For example, working in a subset of the Gigante liana removal plots, Alvarez-Cansino et al. (2015) reported that lianas reduced sap velocity and growth of canopy trees, and that all seven species examined responded in a similar manner. Likewise, Martinez-Izquierdo et al. (2016) reported that liana removal increased the growth and survival of seedlings of all 14 tree species planted in the eight liana removal plots compared to those planted in the eight control plots. By contrast, in a separate study in Panama, Wright, Tobin, Mangan, and Schnitzer (2015) reported that one of three species of tree seedlings examined responded differently to liana removal, a finding consistent with other small-scale liana removal studies on tree seedlings (e.g. Pérez Salicrup, 2001; Toledo-Aceves & Swaine, 2008).

None of the previous studies experimentally tested the effects of lianas on community tree reproduction, which may be a key metric of the impact of lianas on trees at the population and community levels. Determining the negative effects of lianas on the demography of multiple tree populations ultimately will be the most important way to measure the effect of lianas on tree populations over time, which is critical to determine whether lianas alter tree community composition (e.g. Visser et al., in press). In our study, we focused on the community-level effect of lianas because the high diversity of the plant community (65 tree species in 31 families of canopy trees and 56 species in 23 families of understorey plants) resulted in too few species with sufficient replication among plots to evaluate whether the effect of lianas varied with tree species identity. Nonetheless, if the negative effects of lianas on canopy tree reproduction vary with tree species identity (Pérez Salicrup, 2001; Toledo-Aceves & Swaine, 2008; Wright et al., 2015), and reproduction influences population demography (Visser et al., in press), then lianas will likely alter canopy tree demography and thus community composition.

The reduction in tree reproduction by lianas also likely reduces the resource base for the many forest animals that depend on forest fruits. Tree species in neotropical forests have a much greater proportion of animal-dispersed fruits compared to the liana species that inhabit them, whereas neotropical liana species tend to be dominated by wind-dispersed species (Croat, 1978). As lianas reduce tree reproduction, forest-level reproductive output will shift towards being dominated by wind-dispersed fruits, which are smaller and relatively nutrient-poor compared to animal-dispersed fruits. Indeed, the amount of fruit biomass of trees in the liana removal plots was more than double that of the sum of fruit biomass produced by liana and trees in the control plots (van der Heijden et al., 2015). Thus, lianas reduce forest-level fruit production because they themselves do not compensate for the reduction that they cause in tree reproductive output, and that will ultimately reduce resource availability for forest animals.

The lack of a strong increase in understorey plant reproduction was a surprise as liana removal resulted in a large (20%) increase in light in the first year of the study, and light remained higher in the understorey until 4 years after cutting lianas (Rodriguez-Ronderos et al., 2016). Four years following liana cutting, however, trees had completely compensated for the loss of lianas, and plant area index had increased to pre-manipulation levels (Rodriguez-Ronderos et al., 2016). We had expected that understorey plants would reproduce in response to increased light in the first census, as understorey species can respond rapidly to increases in light with elevated reproduction (Levey, 1988). Instead, we found a muted response of understorey plants to liana removal. For instance, the number of individuals and species with flowers and fruits, as well as the mean number of flowers and fruits per individual were all slightly higher in the liana removal plots (Figure 3), but only the mean number of understorey plants fruits was significantly higher. This significant effect was particularly evident in the first sampling period, but was absent 5 years following liana removal. Thus, it appears that lianas have a far stronger effect on canopy trees than on understorey plants.

The slight but positive response of palms to liana removal was unexpected because palms are thought to avoid liana infestation (e.g. Putz, 1984), and thus most studies have ignored the effects of lianas on palms. However, the mean number of palm fruit clusters was 50% higher 2 years after liana removal and the mean number of palm flower clusters was nearly 50% higher 5 years after liana removal. The differences among the treatments were only marginally significant, possibly due to low sample sizes or a relatively weak negative effect of lianas on palms. The apparent increase in palm reproduction may have been due to higher light availability in the understorey (Rodriguez-Ronderos et al., 2016) or competition for below-ground resources (e.g. Schnitzer et al., 2005). The dominant palm in our study was *O. mapura*, which is a subcanopy species that would likely benefit from increased light (Croat, 1978). Therefore, even if liana infestation rates on palms are low, lianas may still reduce palm reproductive output through shading or competition for below-ground resources.

Lianas commonly infest more than 75% of the canopy trees in lowland tropical forests (Ingwell et al., 2010; Toledo-Aceves, 2015), and thus lianas likely reduce community-level canopy tree reproduction and increase seed and dispersal limitation in most lowland tropical forests. Lianas will likely have a much larger effect on canopy tree reproduction and animal communities where they are most abundant, such as in highly seasonal forests (DeWalt et al., 2015; Schnitzer, 2005) and in secondary forests (Barry, Schnitzer, van Bruegal, & Hall, 2015; DeWalt, Schnitzer, & Denslow, 2000). The reported increase in liana abundance relative to trees in a wide range of neotropical forest types (e.g. Phillips et al., 2002; Schnitzer, 2015; Schnitzer & Bongers, 2011) may further increase tree seed and dispersal limitations across the neotropics, and if the effects of lianas vary with tree species identity, lianas may have a destabilizing effect on tree population dynamics, as well as on the animal populations that rely on both wind-dispersed and fleshy fruits.

In summary, while lianas had a small effect on palm and understorey plant reproduction, they had a substantial negative effect on canopy tree reproduction. Lianas substantially reduced the number of canopy trees and species that reproduced, and for the individuals that had flowers and fruits, lianas limited their reproductive output. The ability of lianas to substantially reduce community-level canopy tree reproduction may influence plant and animal community composition, as well as the mechanisms that maintain tree diversity in tropical forests, and these effects may increase with increasing liana abundance.

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AUTHORS’ CONTRIBUTIONS

M.M.G.L., S.A.S. and L.M.I. designed the study on the effects of lianas on tree and palm reproduction; M.M.G.L., S.A.S., L.M.I. and F.N.A.M. collected the data; M.M.G.L. and S.A.S. analysed the data and wrote the initial manuscript; S.A.S. and J.S.P. conceived the liana removal study; all authors contributed to editing the manuscript.

DATA ACCESSIBILITY

Canopy, understorey and palm data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.m2471 (García León, Martínez Izquierdo, Mello, Powers, & Schnitzer, 2017).

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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