Chapter 29

ECOLOGICAL EFFECTS
OF LIANAS IN
FRAGMENTED
FORESTS

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OVERVIEW

Understanding how biodiversity persists in the small fragments of forest that remain in many tropical regions is a vital priority. If lianas flourish in fragmented forests, as is expected, then they might have a wide array of ecological effects, including those on biodiversity. In this chapter, we review available studies on liana communities and liana–tree interactions in fragmented tropical forests. Although much remains unknown, it is apparent that lianas often increase dramatically in abundance in fragmented forests, especially those with large amounts of forest edge or recurring canopy disturbance. Where lianas are particularly abundant, they reduce tree survival, growth, fecundity, and regeneration. Abundant lianas also alter tree-community composition and reduce forest carbon storage, though the magnitude of these effects is variable and not fully understood. Finally, liana proliferation at the expense of trees affects rain forest fauna that are dependent on resources provided by trees such as fruits, nectar, foliage, and tree cavities, as well as fauna that capitalize on liana resources. If lianas benefit markedly in the future from rising atmospheric CO₂ levels or other global change phenomena, then they will become even more dominant in fragmented forests.

INTRODUCTION: TROPICAL FOREST FRAGMENTATION

Whether by happenstance or design, deforestation rarely removes all pre-existing vegetation in a given area (Laurance & Bierregaard 1997), but leaves isolated fragments of the original vegetation surrounded by new habitat types (Wilcove et al. 1986). This process of habitat fragmentation leads to the modification of a variety of biological and physical processes within the fragmented forests that can be deleterious to the constituent species and their ecological interactions (e.g., see reviews by Fahrig 2003; Fischer & Lindenmayer 2007; Laurance et al. 2011). However, remnant forest fragments now represent a large proportion of the remaining tropical forested area (Achard et al. 2002; Broadbent et al. 2008) and despite their degradation, they provide an important biodiversity repository for many landscapes including the preservation of many rare and endangered species and threatened ecosystems (e.g., Guindon 1996; Tabanez & Viana 2000; Arroyo-Rodriguez & Mandujano 2006; Muthuramkumar et al. 2006; Arroyo-Rodriguez et al. 2009). The importance of remnant tropical forest fragments for biodiversity conservation increases with continued worldwide tropical forest loss (Achard et al. 2002; Broadbent et al. 2008).

Maximization of the conservation values of forest fragments requires that they are not only retained, but are managed effectively, which necessitates an understanding of their ecology. One potentially important, yet minimally examined component of fragmented tropical forests is the liana community: how lianas respond to forest fragmentation and the antagonistic interaction that they have with their tree hosts (Fig. 29.1, Jacobs 1976; Schnitzer & Bongers 2002; Toledo-Aceves, Chapter 12 in this volume).

Fig. 29.1 Lianas proliferating along an abrupt forest edge in Gabon, central Africa. (Source: Photo by William Laurance. Reproduced with permission.)
ECOLOGICAL EFFECTS OF LIANA DIVERSITY

Lianas generally comprise 20–25% of the woody species diversity in undisturbed tropical forest (Putz 1984b; Gentry 1991; Appanah et al. 1992) but can be as high as 35% of the species in some forests, such as the one on Barro Colorado Island, Panama (Schnitzer et al., Chapter 7 in this volume). During the loss of forest concurrent with the initial fragmentation process, local extirpation of many sparsely distributed species of trees and lianas can occur, resulting in decreased landscape-scale species diversity (Laurance et al. 1999; Zhu et al. 2004). After the initial forest loss, however, liana diversity is usually proportionally greater in forest fragments (relative to trees) than in comparable undisturbed forest, with this enhanced diversity linked to increased forest edge area and elevated disturbance levels (Laurance 1997; Oliveira et al. 1997; Laurance et al. 2001; Schnitzer & Bongers 2002; Zhu et al. 2004).

Although an increase in local liana diversity compared to trees within forest fragments is the more common trend, two major factors can potentially depress liana diversity in fragments. First, fragmentation results in a number of potential impacts on populations and communities, such as genetic drift, isolation of breeding populations, propagule-dispersal limitation, and pollination limitation through local extirpation of obligatory dispersers or pollinators, which may decrease the diversity of both trees and lianas within forest fragments (e.g., Aizen & Feinsinger 1994; Young et al. 1996; Benítez-Malvido & Martínez-Ramos 2003). Second, a collapse in the availability of structural hosts (available trees) within heavily disturbed forest fragments can also reduce liana diversity (Muthuramkumar et al. 2006; Arroyo-Rodríguez & Toledo-Aceves 2009; Addo-Fordjou et al. 2012). This host loss can occur through both continued anthropogenic disturbances within fragments (e.g., repeated logging; Muthuramkumar et al. 2006; Arroyo-Rodríguez & Toledo-Aceves 2009) or through cascades of impacts initiated by forest loss and fragmentation (e.g., enhanced tree mortality (Laurance et al. 1998a; Laurance et al. 2000; Laurance et al. 2006a), such as edge effects, that alter forest microclimate and increase wind damage (Kapos 1989; Williams-Linera 1990; Laurance & Curran 2008).

FOREST FRAGMENTATION EFFECTS ON LIANA ABUNDANCE

Fragmentation of once-continuous primary forests results in a considerable increase in landscape-wide liana abundance and rates of tree infestation (Laurance 1997; Oliveira e. al. 1997; Viana et al. 1997; Laurance et al. 2001; Benítez-Malvido & Martínez-Ramos 2003). There are three main reasons for the increase in liana abundance. First, the area of forest edge greatly increases within fragmented forest landscapes (Laurance & Yensen 1991) and forest edges are preferential liana habitat (Figs. 29.2, 29.3. Laurance 1997; Laurance et al. 2001; Oliveira et al. 1997; Londré & Schnitzer 2006). Second, elevated rates of large tree mortality, turnover and treefall-gap creation (Laurance et al. 1997; Laurance et al. 1998a; Laurance et al. 2000; Hill & Curran 2003; Laurance et al. 2006a) occur in many forest fragments, which again enhance the amount of available disturbed and well-lit habitat preferred by lianas (Schnitzer & Bongers 2002, 2011). Finally, initial forest loss and fragmentation may lead to a greater area of forest regeneration (“younger” forest).

Fig. 29.2 Lianas tend to increase near the abrupt, artificial boundaries of forest fragments. Shown is the number of liana stems (≥2 cm diameter) within 1-hectare plots as a function of distance of plots from the nearest forest edge, in the rain forests of the central Amazon (results from a Spearman rank correlation).
LIANA IMPACT UPON FRAGMENTED VEGETATION COMMUNITIES

Any increase in liana abundance may be highly detrimental to the tree community of a fragmented forest due to the enhanced structural stress and increased resource competition experienced by trees infested with lianas (Fig. 29.1; Putz 1984b; Stevens 1987; Schnitzer & Bongers 2002; Schnitzer et al. 2005; Toledo-Aceves, Chapter 12 in this volume). Liana infestation may even contribute to the death of individual trees (Putz 1984b; Clark & Clark 1990; Schnitzer & Bongers 2002; Ingwell et al. 2010; van der Heijden et al., Chapter 13 in this volume). Consequently, a fragment-wide decline or extirpation of vulnerable tree species may occur, changing the composition and diversity of the tree community (Laurance et al. 1997; Laurance et al. 2001; Laurance et al. 2006b; van der Heijden et al., Chapter 13 in this volume). This problem is particularly pertinent for "vulnerable" tree species whose morphology leads to a high probability of liana infestation (Putz 1980, 1984a; Hegarty 1991; Talley et al. 1996; Schnitzer & Bongers 2002) and for tree species that are isolated from other meta-populations or otherwise restricted in their potential for recruitment (Young et al. 1996). Lianas may also hasten the decline of tree species diversity within forest fragments via their differential impact on different successional guilds of trees. Traits that serve as liana "defence," such as fast growth, large leaves, and few branches, occur more often in pioneer or secondary succession species than in large mature-phase (shade-tolerant) tree species (Putz 1980, 1984a; Clark & Clark 1990; Schnitzer & Bongers 2002). Consequently, mature-phase tree species host lianas more frequently (Clark & Clark 1990; Laurance et al. 2001; Schnitzer & Bongers 2002; Schnitzer & Carson 2010), and increased liana abundance within forest fragments may contribute to their decline or loss (Phillips & Gentry 1994; Laurance et al. 2000; Laurance et al. 2001; Laurance et al. 2006a). The loss of mature-phase tree species may be exacerbated through a synergism with the enhanced wind shear and altered microclimates that forest fragments experience (Kapos 1989; Williams-Linera 1990; Laurance & Curran 2008), accelerating the alteration of the tree community composition (Laurance et al. 1998a; Laurance et al. 2006a).

A third mechanism by which lianas may alter the tree composition of a forest fragment is via their impact upon the succession process itself. Lianas can alter the succession pathway and eventual vegetation type, or arrest succession within treefall gaps (Schnitzer et al. 2000; Schnitzer & Carson 2001, 2010; Schnitzer & Bongers 2002, 2005; Toledo-Aceves & Swaine 2008; Letcher, Chapter 10 in this volume; Toledo-Aceves, Chapter 12 in this volume). Additionally, lianas may promote treefall-gap formation by elevating tree mortality (Putz 1984b; Clark & Clark 1990; Schnitzer & Bongers 2002; Schnitzer, Chapter 30 in this volume) and collateral damage during a treefall event (Appanah & Putz 1984; Putz 1984b). Accordingly, an increased liana abundance may alter the succession of the tree community and the formation of a canopy gap, promoting the loss of mature-phase tree species in fragments (Oliveira et al. 1997; Viana et al. 1997).
FOREST BIOMASS

In addition to altering the composition of the tree community, lianas can also suppress tree biomass in fragments (Laurance et al. 1997; Nascimento & Laurance 2004; van der Heijden et al., Chapter 13 in this volume). When lianas are abundant, they can kill or reduce growth in trees and thereby reduce the ability of fragmented forests to sequester and store carbon (Fig. 29.4; Laurance et al. 1997; Laurance et al. 1998b; Laurance et al. 2001; Phillips et al. 2002; Nascimento & Laurance 2004). Any increase in liana biomass is relatively negligible and does not offset the loss of tree biomass, because lianas generally comprise less than one-tenth of the aboveground biomass even in disturbed forests (Hegarty & Caballé 1991; DeWalt et al. 2000; Gerving & Farias 2000). Given that tropical forests store ~44% (or 228 billion tons of carbon, Baccini et al. 2012) of the globe’s terrestrial vegetation-derived carbon (Dixon et al. 1994; Phillips et al. 1998; Malhi & Grace 2000), liana effects on fragmented forest biomass could have nontrivial impacts on the global carbon cycle (van der Heijden et al., Chapter 13 in this volume).

FUTURE LIANA INCREASE WITHIN FRAGMENTED FORESTS

Lianas seem likely to increase in abundance in fragmented forests for three reasons. First, future climatic predictions suggest tropical storms will become more frequent and increase in intensity (Emanuel 2005; Elsner et al. 2008) and trees in fragmented forests are known to display an increased vulnerability to wind damage (Laurance & Curran 2008). Therefore, in the future, forest fragments are likely to experience elevated tree turnover rates, greater vegetation disturbance, and substantial changes in forest microclimates (Webb 1958; Turton & Siegenthaler 2004; Laurance & Curran 2008), all of which could favor lianas (Putz 1984b; Schnitzer & Bongers 2002).

Second, lianas achieve their peak abundance in tropical forests with a pronounced dry season (Gentry 1991; Schnitzer 2005; DeWalt et al. 2010; DeWalt et al., Chapter 11 in this volume) and rainfall in many tropical regions is projected to increase in seasonality (Malhi & Wright 2004). A transition from wetter to more seasona. forest types would favor an increase in liana abundance (see also Schnitzer & Bongers 2011; Schnitzer, Chapter 30 in this volume). This process might be magnified in fragmented forests because forest edges are often prone to desiccation (Kapos 1989; Williams-Line et al. 1990).

Finally, liana growth rates may increase proportionately more than tree growth rates in response to rising atmospheric CO$_2$ levels (Granados & Korner 2002; Phillips et al. 2002; Schnitzer & Bongers 2011). If so, there could be a shift in the competitive interactions between trees and lianas in fragmented forests even more in favor of lianas (Tabazan & Viana 2000; Dalling et al. 2012). However, the extent of any potential increase in liana growth might be somewhat ameliorated if increased air temperatures limit the duration of transpiration periods (Betts et al. 1997).

**Fig. 29.4** Lianas are negatively correlated with the aboveground biomass of live trees in Amazonian forests (results from a Pearson correlation; adapted from Laurance et al. 2001). This negative relationship can arise both because lianas reduce tree survivorship and growth and because external disturbances, such as windstorms, can fell or damage trees and thereby create disturbed conditions favored by lianas. (Source: Adapted from Laurance et al. 2001. Reproduced with permission of Ecological Society of America.)
CONCLUSION

Fragmented forests are ubiquitous in tropical landscapes and are occasionally the last surviving remnants of rare habitats and species for which conservation is an urgent priority. Given the potent role that lianas can play in some fragmented forests, and are likely to play in the future, understanding how lianas affect forest ecology and ecological interactions is a key priority. In some circumstances, control and management of lianas might be necessary if lianas are having major deleterious impacts on rare ecosystems or species.

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REFERENCES


