Chapter 1

THE PAST, PRESENT, AND POTENTIAL FUTURE OF LIANA ECOLOGY

Stefan A. Schnitzer,[1,2] *Francis E. Putz,*[3]
Frans Bongers,[4] *and Kristina Kroening*[1]

[1]University of Wisconsin-Milwaukee, Milwaukee, WI, USA
[2]Smithsonian Tropical Research Institute, Balboa, Republic of Panama
[3]University of Florida, Gainesville, FL, USA
[4]Wageningen University and Research Centre, Wageningen, The Netherlands

Ecology of Lianas, First Edition. Edited by Stefan A. Schnitzer, Frans Bongers, Robyn J. Burnham, and Francis E. Putz.

Companion Website: www.wiley.com/go/schnitzer/lianas

OVERVIEW

Over the past decade there has been increasing recognition of the substantial contribution of lianas to tropical and temperate forest dynamics, diversity, management, and ecosystem function. The increased interest in the ecology of lianas has apparently led to a significant increase in the number of publications focused on liana ecology. We quantified the change in this publication rate using the comprehensive and searchable database of liana publications found at: www.LianaEcologyProject.com. We compared liana publication trends to the background rate of general ecology publications from 1900–2005 using the 72 journals in JSTOR. We found a 22-fold jump in liana ecology publications over the past three decades, whereas the increase in all general ecology publications was approximately a twofold increase over a similar period.

The rapid rise in the liana publication rate reflects the increasing recognition of the importance of lianas in tropical forest dynamics, diversity, and regeneration. One of the major findings to emerge from these new studies is that lianas reduce tree recruitment, growth, reproduction, and survival, effects that, in turn, reduce tree diversity. Furthermore, the effects of lianas can cascade across trophic levels and alter fundamental ecosystem processes. A second major finding is that liana abundance, biomass, and productivity have increased substantially in neotropical forests. There are now 12 studies documenting striking increases in lianas relative to trees over the past 30 years – a phenomenon that has serious implications for the future of tropical forests.

The increasing importance of lianas as a key component of tropical forests calls for a deeper understanding of liana ecology and life-history, as well as the myriad roles lianas play in tropical forest dynamics and functioning. Increases in liana density and biomass may impose important changes on tropical forests, particularly on tree growth and survival, as well as on ecosystem properties. Increasing liana abundance also raises new challenges for forest managers, resulting in the need for thoughtful liana management plans for tropical forest timber tree production. In terms of basic research, lianas provide an excellent alternative to trees for the study of ecological theory, and thus the entire field of ecology (as well as the study of lianas) will benefit when the study of lianas moves beyond the realm of applied ecology and a tropical curiosity, and becomes part of the body of mainstream ecological research.

INTRODUCTION

Lianas are a conspicuous component of many forests, particularly in the tropics, and their importance has been noted in the literature since Darwin's (1865) publication, "On the movements and habits of climbing plants." Darwin and others recognized the unique ability of lianas to use tree stems as trellises to climb to the forest canopy. Once in the canopy, lianas produce large numbers of leaves that cover those of their host-trees, thus competing for light (Putz 1983; Gerwing & Farias 2000). Lianas also compete intensely with trees for belowground resources – primarily water and nutrients (e.g., Dillenburg et al. 1993, Schnitzer et al. 2005; Toledo-Aceves, Chapter 12 in this volume). Thus, lianas limit tree growth, fecundity, and survival (Putz 1984; Wright et al. 2005; Ingwell et al. 2010; Schnitzer & Carson 2010; Ladwig & Meiners, Chapter 15 in this volume; van der Heijden et al., Chapter 13 in this volume). Lianas also can be aggressive invaders, and both native and exotic lianas are among the world's most noxious weeds (e.g., Horvitz & Koop 2004; Forseth & Innis 2004; Leicht-Young & Pavlovic, Chapter 28 in this volume). Additionally, lianas have long been exploited by humans as food (e.g., passion fruits, gourds, legumes), construction material (ropes), stimulants (e.g., guarana from *Paullinia cupana*), medicines (e.g., curare from *Strychnos toxifera* and *Chondrodendron tomentosum*), and for the production of alcoholic beverages such as wine and cognac from grapes (*Vitis spp.*) and beer from hops (*Humulus lupulus*).

In the ecological literature, lianas were largely ignored historically while studies of trees abounded (Schnitzer & Bongers 2002). More recently, lianas have been recognized as important and integral components of forests, particularly in the tropics (e.g., Isnard & Silk 2009; Paul & Yavitt 2010; Schnitzer & Bongers 2011; van der Heijden et al. 2013; Wyka et al. 2013), and the renewed scientific interest in lianas is reflected in a rapidly rising publication rate. However, since the number of publications in all areas of ecology is increasing, it is difficult to evaluate whether the rate of liana-related publications is actually rising faster than the background rate of the entire spectrum of ecology publications.

We evaluated whether the spate of new publications on liana ecology reflects growing interest in this particular growth-form, or whether the increase is an artifact of the general escalation in ecological publishing, by comparing the rate of peer-reviewed, liana-specific publications over the past century to that of general ecology publications. We compiled a comprehensive list of over 650 liana publications from 1865 until 2009 using extensive literature searches, which is available in the comprehensive and searchable liana database at the *Liana Ecology Project* website: www.LianaEcologyProject.com. We classified liana publications as being either focused primarily on liana ecology or publications that included lianas but in which lianas were not the main emphasis of the study. Since both metrics yielded similar results, we used only the former in our analyses. We excluded herbaceous vines, rattans and other climbing palms, as well as non-ecology/environmental publications in our analyses, even though these publications, as well as publications after 2009, are included in the www.LianaEcologyProject.com database. For a metric of all ecology publications, we examined the 72 journals in JSTOR from 1900 until 2005 and searched for all publications with the term "Ecology" in the title, abstract, or keywords.

EXPONENTIALLY INCREASING LIANA PUBLICATION RATE

Liana publication rate was extremely low until the 1980s, after which it began a rapid rise (Fig. 1.1A). The highest number of publication was in 2009, the last complete year of our literature survey, during which 44 liana-specific articles were published, along with 12 additional publications that included lianas, but in which lianas were not the focus of the study (56 total publications in 2009). The rate of increase in liana publications was much greater than for all ecological publications, whose rate also increased over the past century, with the steepest annual increase beginning in the early 1960s, followed by a steady linear increase thereafter (Fig. 1.1B). For example, the number of liana publications increased 22-fold between 1980 and 2009 (Fig. 1.1C), compared to the twofold increase in the number of all ecology publications over a similar period (Fig. 1.1D).

IMPORTANCE OF LIANAS IN TROPICAL FORESTS

The rapid relative increase in the liana publication rate indicates a growing recognition of the importance of lianas in forests, particularly in the tropics. Lianas add considerably to the diversity of tropical forests, often more than would be predicted based on their stem density. For example, in a survey of all lianas $\geq$1 cm diameter on Barro Colorado Island, Panama, lianas composed 35% of the woody species and 25% of the woody stem density (e.g., Schnitzer et al. 2012; Schnitzer et al., Chapter 7 in this volume). Lianas can compete intensely with other growth forms, such as trees (Fig. 1.2), and both large-scale observational and experimental studies have shown that lianas reduce tree regeneration, diversity, growth, and biomass in numerous tropical forests (Grauel & Putz 2004; Peña-Claros et al. 2008; van der Heijden et al. 2008; Ingwell et al. 2010; Schnitzer & Carson 2010; Tobin et al. 2012; Schnitzer et al. 2014). Lianas reduce tree fecundity (e.g., Wright et al. 2005; Kainer et al. 2006, 2014) and the density and richness of trees recruiting into treefall gaps (Schnitzer et al. 2000; Schnitzer & Carson 2010). Lianas increase tree mortality; trees heavily infested by lianas (e.g., Fig. 1.2) have twice the probability of death than trees with fewer lianas in their crowns (Ingwell et al. 2010).

Lianas also appear to have a much greater competitive effect on trees than would be predicted by their biomass. Tobin et al. (2012) removed similar amounts of liana or tree biomass from target trees and found that the target trees consistently responded immediately to liana cutting, but the target trees did not respond to tree cutting. Furthermore, lianas may have the capacity to alter tree community composition by competing particularly intensely with some tree species (Schnitzer & Bongers 2002). For example, lianas reduce recruitment and growth of shade-tolerant trees, while some pioneer trees are largely unaffected (e.g., van der Heijden et al. 2008, van der Heijden et al., Chapter 13 in this volume; Schnitzer & Carson 2010).

At the ecosystem level, lianas reduce rates of carbon uptake by trees, which typically store more than 90% of aboveground forest carbon (van der Heijden & Phillips 2009; Durán & Gianoli 2013; Schnitzer et al. 2014). These losses are not offset by increases in liana biomass; lianas store only a fraction of the carbon that they displace due to their thin stems and low wood volumes relative to the trees with which they compete. For

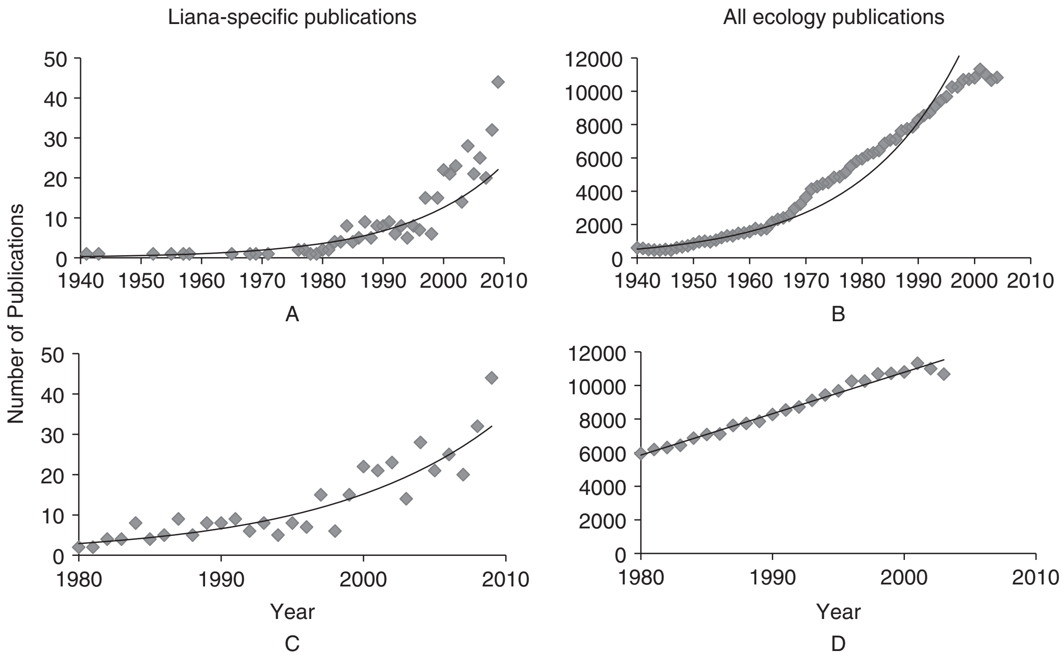

Fig. 1.1 The annual number of publications focused on liana ecology from 1940 until 2009 (A) versus the number of general ecological topics from 1940 until 2005 (B). The number of liana publications was estimated using extensive literature searches. The number of general ecological publications was calculated by searching the 72 journals in JSTOR for all publications with the term "Ecology" in which the title, abstract, or keywords were included. Data were collected from 1865–2009 for lianas and from 1900–2005 for general ecological publications, but graphing data starting in 1940 was sufficient to accurately portray the patterns. The different panels per column use the same data, but focus on different time periods. Exponential and linear curves, where appropriate, were fitted to the data. Liana publication rate increased exponentially since 1980 (C), whereas the rate of all ecology publications has increased linearly over this time period (D).

example, in a liana-removal study in central Panama, Schnitzer et al. (2014) reported that lianas reduced tree biomass accumulation in gaps by nearly 300% over an 8-year period, but lianas themselves compensated for only 24% of the biomass uptake that they displaced in trees (see also van der Heijden et al. 2013; van der Heijden et al., Chapter 13 in this volume). In the Peruvian Amazon, lianas appeared to reduce tree annual biomass increment by around 10%; however, that liana annual increment compensated only around 29% for what was displaced in trees (van der Heijden & Phillips 2009). In addition, the increase in tree mortality due to lianas (Ingwell et al. 2010) reduces overall forest carbon storage even further, and forest areas with high liana densities can have far lower biomass than forest areas with low liana densities (e.g., Chave et al. 2001; Durán & Gianoli 2013). Furthermore, lianas are increasing in abundance in many neotropical forests (Schnitzer & Bongers 2011; Schnitzer, Chapter 30 in this volume), and thus, the effects of lianas on trees at all life-history stages (recruitment, growth, reproduction, and mortality), as well as the influence of lianas on tropical forest ecosystem processes, are likely to increase (Schnitzer et al. 2011; van der Heijden et al., Chapter 13 in this volume).

LIANA MANAGEMENT: FORESTRY AND WILDLIFE IMPACTS

The increase in liana abundance will motivate forest managers to more actively manage lianas in timber-producing forests. The deleterious impacts of lianas on trees, plus the observation that when a liana-infested tree falls or is felled, it often pulls down its neighbors, have led to the often-made but

Fig. 1.2 Lianas blanketing trees on Barro Colorado Island, Panama. (Source: C. Ziegler. Reproduced with permission.) *See plate section for color representation of this figure*.

seldom-followed recommendation that lianas be cut prior to selective logging. Pre-felling liana cutting, if done at least 6 months in advance of the harvest to allow cut liana stems time to decompose and weaken, can considerably reduce felling damage to neighboring trees (e.g., Appanah & Putz 1984; Garrido-Perez et al. 2008). Furthermore, cutting lianas that entangle the target trees' canopy prior to logging will reduce post-logging liana infestations of logging gaps (Alvira et al. 2004; Schnitzer et al. 2004), where lianas can arrest tree regeneration and density, as well as reduce tree survival and ultimately tree diversity (Schnitzer et al. 2000; Schnitzer & Carson 2010; Schnitzer et al. 2014). Selective liana cutting can also benefit future timber trees by reducing their susceptibility to logging damage as well as acclimatizing them to post-logging increases in light intensities and temperatures, which will stimulate their growth and increase their survival.

In terms of overall forest biodiversity, retaining lianas should be a priority because lianas substantially increase plant diversity (e.g., Gianoli 2004; Schnitzer et al. 2012) as well as providing an important resource for many forest animals (Putz et al. 2001). Lianas produce leaves, flowers, and fruits that may be critical for the survival of many animal species, especially during the dry season when lianas grow more and produce more leaves and fruits than trees (e.g., Putz & Windsor 1987; Schnitzer 2005; Dunn et al. 2012; Arroyo-Rodríguez, Chapter 27 in this volume). By connecting tree canopies, liana stems also provide critical inter-crown pathways for non-volant arboreal animals (e.g., ants, sloths, rodents, monkeys; Montgomery & Sunquist 1978; Dunn et al. 2012; Yanoviak, Chapter 24 in this volume; Fig. 1.3). Liana tangles in the understory provide structure, forage, and predator escape for birds and small mammals (e.g., Putz et al. 2001; Kilgore et al. 2010; Michel et al., Chapter 25 in this volume; Lambert & Halsey, Chapter 26 in this volume), and bind the forest canopy together, thus potentially reducing treefalls when liana connectivity is high (Garrido-Pérez et al. 2008). Consequently, selectively cutting lianas from timber trees, rather than cutting all lianas, is an appropriate compromise between sustaining timber production and maintaining biodiversity in forests managed for timber.

Fig. 1.3 Three-toed sloth in central Panama using a liana to ascend to the forest canopy. (Source: Photo credit: S.A. Schnitzer. Reproduced with permission.) *See plate section for color representation of this figure.*

NEW FRONTIERS IN LIANA ECOLOGY

The accelerating pace of liana research reflects increasing recognition that lianas are an ecologically important component of tropical forests. Lianas can be used to test basic ecological theory on the factors controlling plant species distribution, the maintenance of species diversity, plant competition, and large-scale structural change in tropical forests. Until recently, however, trees were used almost exclusively to test major ecological theories that pertain to tropical forests, whereas lianas were largely ignored. Lianas differ from trees in their anatomy, physiology, and leaf characteristics (Angylossy et al., Chapter 19 in this volume; Asner & Martin, Chapter 21 in this volume; Santiago et al., Chapter 20 in this volume), and thus if the theories to explain the distribution and diversity maintenance of plant species are to be accepted as general, these theories must be tested beyond solely using trees.

Recent evidence suggests that the mechanisms that control tree and liana distribution and diversity maintenance differ substantially. For example, among forests, liana density and biomass increase with decreasing mean annual precipitation and increasing seasonality – a pattern that differs strikingly from trees (Schnitzer 2005; DeWalt et al. 2010; DeWalt et al., Chapter 11 in this volume). Within a given forest, there is now strong evidence that disturbance and treefall gap formation maintain liana diversity (Schnitzer & Carson 2001; Ledo & Schnitzer 2014; Schnitzer et al., Chapter 7 in this volume), with little evidence for edaphic specialization and negative density dependence as causative mechanisms (Dalling et al. 2012; Ledo & Schnitzer 2014). In contrast, the putative mechanisms responsible for the maintenance of tree species diversity and distribution are edaphic specialization and negative density dependence (e.g., John et al. 2007; Mangan et al. 2010); whereas disturbance appears to have little influence on tree distribution or diversity (Hubbell et al. 1999; Schnitzer & Carson 2001; Bongers et al. 2009). Therefore, the mechanisms responsible for distribution of species and the maintenance of diversity appear to differ between lianas and trees (Ledo & Schnitzer 2014). Determining the mechanisms that control liana distribution and diversity maintenance and investigating how these mechanisms differ from other growth forms, such as trees, will lead to insights into how and when these varied mechanisms operate, thus contributing to a more comprehensive understanding of the maintenance of plant species diversity and the factors that control plant species distribution.

The causes and consequences of increasing liana abundance and biomass will likely become an active area of future study. Determining the factors responsible for liana increases, as well as the effects of increased lianas on forest dynamics, diversity, and ecosystem function are critical to our understanding of tropical forest ecology. Increasing levels of drought, temperature, disturbance, nitrogen deposition, and CO_2 have all been proposed as potential causes of increasing liana abundance (Schnitzer & Bongers 2011; Schnitzer et al. 2011; Schnitzer, Chapter 30 in this volume). To fully understand the drivers of increasing liana abundance, however, these factors need to be tested both separately and in combination along major environmental gradients (Schnitzer et al., Chapter 7 in this volume).

Another important line of research is determining the relative strengths of aboveground and belowground competition between lianas and trees, and how these effects vary with changes in resource availability (Toledo-Aceves, Chapter 12 in this volume). As with other plant growth forms, there is less research on liana roots than on their shoots. Given that large structural roots are not required to support liana stems, a larger proportion of their investments belowground should be available for root elongation, leading to aggressive water and nutrient foraging. To the extent that this so-far-untested prediction is true, it might explain why lianas appear to be such effective competitors with trees for belowground resources (e.g., Dillenburg et al. 1993; Schnitzer et al. 2005; Toledo-Aceves & Swaine 2008; Toledo-Aceves, Chapter 12 in this volume).

A deeper understanding of liana life-history strategies and how these strategies enable lianas to compete successfully with trees may reveal the causes of increasing liana abundance and biomass, and the ways in which these increases will alter future tropical forest dynamics. Furthermore, a balanced assessment of both the positive and negative ecological effects of lianas on community and ecosystem processes, as well as their contribution to biodiversity within and across trophic levels, is necessary to assess how increasing lianas will affect future forests. Considering the importance of these issues to tropical forest ecology, therefore, we predict that the steep climb in liana ecology publications will continue.

ACKNOWLEDGMENTS

Financial support for this chapter and the *Liana Ecology Project* website was provided by National Science Foundation grants DEB-0613666, DEB-0845071, and DEB-1019436, UWM Research Growth Initiative, and UWM Office for Undergraduate Research.

REFERENCES

Alvira, D., Putz, F.E. & Fredericksen, T.S. (2004) Liana loads and post-logging liana densities after liana cutting in a lowland forest in Bolivia. *Forest Ecology and Management*, **190**, 73–86.

Appanah, S. & Putz, F.E. (1984) Climber abundance in virgin dipterocarp forest and the effect of pre-felling climber cutting on logging damage. *Malaysian Forester*, **47**, 335–342.

Benítez-Malvido, J. & Martínez-Ramos, M. (2003) Impact of forest fragmentation on understory plant species richness in Amazonia. *Conservation Biology*, **17**, 389–400.

Bongers, F., Poorter, L., Hawthorne, W.D. & Sheil, D. (2009) The intermediate disturbance hypothesis applies to tropical forests, but disturbance contributes little to tree diversity. *Ecology Letters*, **12**, 1–8.

Chave, J., Riéra, B. & Dubois, M.A. (2001) Estimation of biomass in a neotropical forest of French Guiana: spatial and temporal variability. *Journal of Tropical Ecology*, **17**, 79–96.

Dalling, J.W., Schnitzer, S.A., Baldeck, C. et al. (2012) Resource-based habitat associations in a neotropical liana community. *Journal of Ecology*, **100**, 1174–1182.

Darwin, C.R. (1865) On the movements and habits of climbing plants. *Journal of the Linnean Society of London (Botany)*, **9**, 1–118.

DeWalt, S.J., Schnitzer, S.A., Chave, J. et al. (2010) Annual rainfall and seasonality predict pan-tropical patterns of liana density and basal area. *Biotropica*, **42**, 309–317.

Dillenburg, L.R., Whigham, D.F., Teramura, A.H. & Forseth, I.N. (1993) Effects of below- and aboveground competition from the vines *Lonicera japonica* and *Parthenocissus quinquefolia* on the growth of the tree host *Liquidambar styraciflua*. *Oecologia*, **93**, 48–54.

Dunn, J.C., Asensio, N., Arroyo-Rodríguez, V. et al. (2012) The ranging costs of a fallback food: liana consumption supplements diet but increases foraging effort in howler monkeys. *Biotropica*, **44**, 704–714.

Durán, S.M. & Gianoli, E. (2013) Carbon stocks in tropical forests decrease with liana density. *Biology Letters*, **9**, 20130301.

Forseth, I.N. & Innis, A.F. (2004) Kudzu (*Pueraria montana*): history, physiology, and ecology combine to make a major ecosystem threat. *Critical Reviews in Plant Science*, **23**, 401–413.

Garrido-Pérez, E.I., Dupuy, J.M., Durán-García, R. et al. (2008) Structural effects of lianas and Hurricane Wilma on trees in Yucatan Peninsula, Mexico. *Journal of Tropical Ecology*, **24**, 559–562.

Gerwing, J.J. & Farias, D.L. (2000) Integrating liana abundance and forest stature into an estimate of total aboveground biomass for an eastern Amazonian forest. *Journal of Tropical Ecology*, **16**, 327–335.

Gianoli, E. (2004) Evolution of a climbing habit promotes diversification in flowering plants. *Proceedings of the Royal Society B*, **271**, 2011–2015.

Grauel, W.T. & Putz, F.E. (2004) Effects of lianas on growth and regeneration of *Prioria copaifera* in Darien, Panama. *Forest Ecology and Management*, **190**, 99–108.

Horvitz, C.C. & Koop, A. (2004) Removal of nonnative vines and post-hurricane recruitment in tropical hardwood forests of Florida. *Biotropica*, **33**, 268–281.

Hubbell, S.P., Foster, R.B., O'Brien, S.T. et al. (1999) Light-gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. *Science*, **22**, 554–557.

Ingwell, L.L., Wright, S.J., Becklund, K.K. et al. (2010) The impact of lianas on 10 years of tree growth and mortality on Barro Colorado Island, Panama. *Journal of Ecology*, **98**, 879–887.

Isnard, S. & Silk, W.K. (2009) Moving with climbing plants from Charles Darwin's time into the 21st Century. *American Journal of Botany*, **96**, 1205–1221.

John, R., Dalling, J.W., Harms, K.E. et al. (2007) Soil nutrients influence spatial distributions of tropical tree species. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 864–869.

Kainer, K.A., Wadt, L.H.O., Gomes-Sliva, D.A.P. & Capanu, M. (2006) Liana loads and their association with *Bertholletia* *excelsa* fruit and nut production, diameter growth and crown attributes. *Journal of Tropical Ecology*, **22**, 147–154.

Kainer, K.A., Wadt, L.H.O. & Staudhammer, C.L. (2014) Testing a silvicultural recommendation: Brazil nut responses 10 years after liana cutting. *Journal of Applied Ecology*. doi: 10.1111/1365-2664.12231

Kilgore, A., Lambers, T.D. & Adler, G.H. (2010) Lianas influence fruit and seed use by rodents in a tropical forest. *Tropical Ecology*, **51**, 265–271.

Ledo, A. & Schnitzer, S.A. (2014) Disturbance, not negative density dependence or habitat specialization maintains liana diversity in a tropical forest. *Ecology*, in press.

Mangan, S.A., Schnitzer, S.A., Herre, E.A. et al. (2010) Negative plant-soil feedback predicts relative species abundance in a tropical forest. *Nature*, **466**, 752–756.

Montgomery, G.G. & Sunquist, M.E. (1978) Habitat selection and use by two-toed and three-toed sloths, in *The Ecology of Arboreal Foliovores* (ed G.G. Montgomery), Smithsonian Institution Press, Washington, DC, pp. 329–359.

Paul, G.S. & Yavitt, J.B. (2010) Tropical vine growth and the effects on forest succession: a review of the ecology and management of tropical climbing plants. *The Botanical Review*, **77**, 11–30.

Peña-Claros, M., Fredericksen, T.S., Alarco, A. et al. (2008) Beyond reduced-impact logging: silvicultural treatments to increase growth rates of tropical trees. *Forest Ecology and Management*, **256**, 1458–1467.

Putz, F.E. (1983) Liana biomass and leaf area of a tierra firme forest in the Rio Negro Basin, Venezuela. *Biotropica*, **15**, 185–189.

Putz, F.E. (1984) The natural history of lianas on Barro Colorado Island, Panama. *Ecology*, **65**, 1713–1724.

Putz, F.E., Sirot, L.K. & Pinard, M.A. (2001) Tropical forest management and wildlife: silvicultural effects on forest structure, fruit production, and locomotion of non-volant arboreal animals, in *The Cutting Edge: Conserving Wildlife in Managed Tropical Forests* (eds R. Fimbel, A. Grajal & J. Robinson), Columbia University Press, New York.

Putz, F.E. & Windsor, D.M. (1987) Liana phenology on Barro Colorado Island, Panama. *Biotropica*, **19**, 334–341.

Schnitzer, S.A. (2005) A mechanistic explanation for global pattern of liana abundance and distribution. *American Naturalist*, **166**, 262–276.

Schnitzer, S.A. & Bongers, F. (2002) The ecology of lianas and their role in forests. *Trends in Ecology and Evolution*, **17**, 223–230.

Schnitzer, S.A. & Bongers, F. (2011) Increasing liana abundance and biomass in tropical forests: emerging patterns and putative mechanisms. *Ecology Letters*, **14**, 397–406.

Schnitzer, S.A., Bongers, F. & Wright, S.J. (2011) Community and ecosystem ramifications of increasing lianas in neotropical forests. *Plant Signaling & Behavior*, **6**, 598–600.

Schnitzer, S.A. & Carson, W.P. (2001) Treefall gaps and the maintenance of species diversity in a tropical forest. *Ecology*, **82**, 913–919.

Schnitzer, S.A. & Carson, W.P. (2010) Lianas suppress tree regeneration and diversity in treefall gaps. *Ecology Letters*, **13**, 849–857.

Schnitzer, S.A., Dalling, J.W. & Carson, W.P. (2000) The impact of lianas on tree regeneration in tropical forest canopy gaps: Evidence for an alternative pathway of gap-phase regeneration. *Journal of Ecology*, **88**, 655–666.

Schnitzer, S.A., Kuzee, M.E. & Bongers, F. (2005) Disentangling above-and below-ground competition between lianas and trees in a tropical forest. *Journal of Ecology*, **93**, 1115–1125.

Schnitzer, S.A., Mangan, S.A., Dalling, J.W., et al. (2012) Liana abundance, diversity, and distribution on Barro Colorado Island, Panama. *PLoS One* 7(12): e52114. doi:10.1371/journal.pone.0052114.

Schnitzer, S.A., Parren, M.P.E. & Bongers, F. (2004) Recruitment of lianas into logging gaps and the effects of pre-harvest liana cutting. *Forest Ecology and Management*, **190**, 87–98.

Schnitzer, S.A., van der Heijden, G.M.F., Mascaro, J., Carson, W.P. (2014) Lianas reduce biomass accumulation in a tropical forest. *Ecology*, in press.

Tobin, M.F., Wright, A.J., Mangan, S.A., & Schnitzer, S.A. (2012) Lianas have a greater competitive effect than trees of similar biomass on tropical canopy trees. *Ecosphere*, **3**, Article 20: 1-11. 10.1890/ES11-00322.1

Toledo-Aceves, T. & Swaine, M.D. (2008) Above- and below-ground competition between the liana *Acacia kamerunensis* and tree seedlings in contrasting light environments. *Plant Ecology*, **196**, 233–244.

van der Heijden, G.M.F., Healey, J.R. & Phillips, O.L. (2008) Infestation of trees by lianas in a tropical forest in Amazonian Peru. *Journal of Vegetation Science*, **19**, 747–756.

van der Heijden, G.M.F. & Phillips, O.L. (2009) Liana infestation impacts tree growth in a lowland tropical moist forest. *Biogeosciences*, **6**, 2217–2226.

van der Heijden, G.M.F., Schnitzer, S.A., Powers, J.S. & Phillips, O.L. (2013) Liana impacts on carbon cycling, storage and sequestration in tropical forests. *Biotropica*, **45**, 682–692.

Wright, S.J., Jaramillo, M.A., Pavon, J. et al. (2005) Reproductive size thresholds in tropical trees: variation among individuals, species and forests. *Journal of Tropical Ecology*, **21**, 307–315.

Wyka, T.P., Oleksyn, J., Karolewsk, P., & Schnitzer, S.A. (2013) Phenotypic correlates of the lianescent growth form: a review. *Annals of Botany*, **112**, 1667–1681.