The evolution of host specificity in liana-tree interactions

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ABSTRACT

Lianas, woody climbing plants, comprise up to 40% of woody individuals and species in tropical forest. While early studies of liana-host interactions were made by Charles Darwin, the co-evolutionary relationships of lianas and their hosts remains poorly understood. This review synthesizes information from functional anatomy and morphology, ecology, floristics, and the fossil record of woody plants to explore the evolution of interactions between lianas and their hosts. Elwyn Hegarty (1991) suggested that lianas and trees do not engage in species-specific relationships; this review supports this hypothesis and suggests that liana-tree interactions evolved in a diffuse, generalist fashion. Trees served as selective filters, enhancing the effectiveness of anomalous stem anatomy and anchoring mechanisms in lianas, but it is highly unlikely that lianas played much of any role in the maintenance of adaptations in trees to avoid and shed them. This is consistent with the existence of generalist liana-tree interactions in extant forests. In addition, the record of colonization of the terrestrial environment by woody plants suggests that liana-host interactions were always generalized and that any trend to establish species-specific engagement or co-evolution was interrupted by extinctions of lianas and trees. Liana diversity is lower in tropical dry forests, but liana abundance is higher there, suggesting that global change-related intensification of the dry season in many tropical forests may lead many liana species to extinction, and to the proliferation of surviving species.

RESUMEN

Las lianas son plantas trepadoras leñosas que comprenden hasta un 40% de los individuos y especies leñosas en las selvas tropicales. Pese a que los primeros estudios de las relaciones liana-hospedero fueron realizados por Charles Darwin, aún se conoce poco sobre las relaciones co-evolutivas entre las lianas y los árboles. Esta revisión sintetiza las informaciones provenientes de la anatomía y morfología funcionales, la ecología, la florística y el registro fósil de las plantas leñosas a fin de explicar la evolución de las interacciones entre las lianas y sus hospederos. En 1991 Elwyn Hegarty propuso que las lianas y los árboles no establecían relaciones especie-especie; nuestra revisión apoya esta hipótesis e indica que las interacciones liana-hospedero evolucionaron de modo generalista. Los árboles fueron factores de selección que mejoraron la efectividad de la anatomía anómala del tallo en las lianas así como los mecanismos de anclaje de éstas. Sin embargo, es muy improbable que las lianas jugasen algún rol en el mantenimiento de adaptaciones de los árboles para evitar que las lianas los trepen o deshacese de ellas. Esto es consistente con la existencia de interacciones generalistas entre las lianas y los árboles en las selvas actuales. Más aún, la historia de la colonización del ambiente terrestre por las plantas leñosas indica que las interacciones liana-hospedero fueron siempre generalistas y que cualquier tendencia al surgimiento de relaciones especie-especie o co-evolución fue interrumpida por la extinción de las lianas y los árboles. La diversidad de las lianas es menor en los bosques tropicales secos, pero es precisamente allí donde la abundancia de las lianas es mayor. Esto indica que la intensificación de las sequías en relación con el cambio global en muchas selvas tropicales debe conducir a la extinción de muchas especies de lianas, así como a la proliferación de las especies que sobreviven.

PALABRAS CLAVES; KEY WORDS

Anatomía anómala del tallo, co-evolución, diversidad de lianas, diversidad de árboles, estrategias de anclaje, mecanismos de anclaje; Anomalous stem-anatomy, anchoring strategies, climbing mechanisms, co-evolution, liana diversity, tree diversity, evolution.
INTRODUCTION

Lianas (climbing woody vines, Fig. 1) comprise up to 40% of the woody individuals and species in tropical forests (Gentry 1991, Schnitzer & Bongers 2002). Charles Darwin (1867) took a special interest in climbers, culminating in a book on the mechanisms of climbing. However, almost 150 years after Darwin’s work on lianas, the evolution of lianas and their influence on tree evolution remains poorly understood. In contrast, many studies were published in the 19th and 20th centuries on the anatomy, anchoring mechanisms, and biomechanics of a wide variety of liana species (e.g. Darwin 1867, Schenk 1892, Carlquist 1991, Putz & Holbrook 1991, Isnard & Silk 2009). Ecological studies were published on the effects of lianas on trees, although such studies rarely targeted the role of particular liana species (reviewed in Schnitzer & Bongers 2002). Lianas have been surveyed in forests of different types, with one study comprising an intercontinental biogeographic overview (Gentry 1991). Only at the beginning of the 21st century were reports of fossil lianas in the paleontological literature collated into a single document (Burnham 2009). Here we apply these various results to an evolutionary reconstruction focused on the relationship between lianas and their host trees.

The importance of lianas

Lianas proliferate in disturbed sites that are widespread in the tropics: forest gaps, edges, and secondary forests (DeWalt et al. 2000, Schnitzer et al. 2000, Caballé & Martin 2001, Laurance et al. 2001). Indeed, selective logging, deforestation, and field abandonment, with subsequent regeneration of forests are all related to the proliferation of lianas (Schnitzer & Bongers 2002, Garrido-Pérez & Gerold 2009). Moreover, increasing atmospheric CO₂ may accelerate gap dynamics by faster growth of lianas and subsequent toppling of trees, further increasing the abundance of lianas with respect to trees (Phillips & Gentry 1994, Phillips et al. 2002, Wright et al. 2004, Schnitzer & Bongers 2011). Once lianas colonize a gap, they can retard tree closure in the gap (Schnitzer et al. 2000). Global change may also favour lianas by enhancing the intensity of hurricanes (Emanuel 1987, 2003): hurricanes form gaps that are intensively colonized by lianas (Schnitzer et al. 2000). This suggests that a better understanding of the relationships between lianas and trees will contribute to a better understanding of the dynamics in tropical forests.

Liana-tree coevolution?

The flexible stems of lianas allow them to grow without support only up to about 1.5 meters in height (Putz 1984a, Caballé 1998). In order to reach the canopy, lianas must climb on trees; otherwise they must continue to grow very slowly in the low light of the understory (Putz 1984a). Thus, many lianas evolved specialized stem-borne anchoring organs (Fig. 2-4). However, trees that host too many lianas will grow more slowly, be susceptible to breaking during strong winds, and reproduce less than trees hosting fewer lianas (Stevens 1987, Wright et al. 2005, Kainer et al. 2006, Garrido-Pérez et al. 2008, Garrido-Pérez & Gerold 2009). It has been suggested that trees have adaptations to avoid liana attachments (e.g., large compound leaves), and adaptations for shedding lianas (e.g., abscission of liana-infested branches; Putz 1984b, Rich et al. 1987). If true, this suggests liana-tree co-evolution. However, in 1991 Elwyn Hegarty proposed that this is not
the case, based on morphological evidence and ecological arguments (Hegarty 1991). She suggested that the rapid height growth of tree trunks allows for emergence above the existing tree canopy. Such emergent trees would leave lianas in the lower levels of the forest. Hegarty argued that these hypotheses are very difficult to test; in fact other explanations are more plausible. For example, rapid growth is a characteristic of pioneer trees and is proposed as an adaptation to occupy open spaces (Martínez-Ramos 1994), while compound leaves dissect the boundary layer of photosynthetic organs and thus avoid overheating (Nobel 2005). Here, we suggest that trees have influenced the evolution of the climbing growth form more than climbers influenced the evolution of trees.

This review asks the question: Is the relationship between trees and lianas species-specific and can tight co-evolution between specific trees and specific lianas have been maintained over millions of years? We address the question by expanding on the arguments of Hegarty (1991). We propose that lianas interact with trees in a generalist way, that selection favors this generalist interaction, and that this is consistent with the functional morphology and anatomy of trees and lianas, as well as ecology, floristics, and the fossil record. While, co-evolutionary relationships are more likely to evolve when lineages are in consistent association with one another over large areas or long time periods (Thorpe et al. 2011), the fossil record suggests that such associations were repeatedly interrupted.

**Anatomical and morphological adaptations**

**Trees as selective agents in liana evolution**

Evidence from the morphology and anatomy of woody plants suggest that trees have been a major selective agent in the evolution of lianas. Lianas have wide xylem vessels and narrow stems; the stems of many lianas are flexible near their base and relatively stiff toward their distal branches (Carlquist 1991, Rowe et al. 2004). This makes the vascular tissues of lianas prone to collapse when experiencing torsion, bending, tension, and compression produced by winds, which induce both movement and tree and branch falls (Carlquist 1991, Acevedo-Rodríguez 2003). The stem anatomy of many lianas is so different from other vascular plants that the entire class of anatomical features is called “anomalous growth” and “cambial variants” (Carlquist 1991).

Anatomical studies accumulating since the 19th century suggest that cambium variants are adaptations effective under the biomechanical challenges that trees exert on lianas. Literature reviews detail the following critical adaptive characteristics (Carlquist 1991, Fisher & Ewers 1991). (1) Xylem-vessel dimorphism, with narrow xylem vessels next to wide vessels, allowing stems to be more rigid and resistant than without narrow vessels. (2) Vascular tissues segregated or semi-segregated from one another by abundant parenchyma. In this “cable-like” arrangement, the collapse of some vascular elements does not interrupt sap flow because the intact elements remain active. (3) Healing of injured tissues by adjacent parenchyma. (4) Xylem rays capable of yielding to torsion without collapse of the xylem vessels. (5) Inter-axial phloem embedded in secondary xylem which avoids deformation of the sieve elements (Pace et al. 2009). (6) Presence of an elastic body that is capable of recovering the original structure after bending (Putz & Holbrook 1991, Rowe et al. 2005). In addition to the clear advantage of inclusion of regenerative cells (parenchyma) within the stem body, these xylem attributes appear to be selectively...
advantageous in the face of mechanical damage caused by the movement and fall of trees throughout the evolution of the various lineages of lianas (Fig. 5-7), but not by specific tree species. This suggests that such adaptations do not result from a species-specific co-evolution of lianas and trees.

Lianas are also modified to colonize trees via their anchoring and climbing mechanisms. The shape and functioning of tendrils, tendril-like spines, hooks, “sandpaper-like” bark due to trichomes, and circumnutation of the tree trunks by apical meristems of lianas are features whose main function is to anchor onto the host trees (Fig. 2-4). Tendrils effectively attach as lateral organs to the narrower branches of large trees, as well as the narrow trunks of young trees. Hooks and spines of climbers fasten best to fine tree branches and foliage (Bauer et al. 2011), while bark trichomes of lianas increase liana-host stem friction. Importantly, the circumnutation of trees by lianas results from sophisticated thigmotropism, which twists lianas around their host trees resulting in a very tight anchor and the lowest risk of anchorage failure (Darwin 1867, Isnard & Silk 2009). Because a liana is best served by ascending the closest suitable host to its rooting position, the upright and sturdy architecture of trees in general – rather than only a few tree species – maintains the effectiveness of the anchoring and climbing strategies of lianas.

**Do trees have adaptations against lianas?**

It has been proposed that liana-tree co-evolution was so intense that it was energetically worthwhile for certain tree species to maintain modifications that enhance avoiding or shedding lianas. Some of the most frequently proposed strategies are: smooth or exfoliating barks, compound leaves, rapid growth, and abscissing liana-infested branches (or leaves of palms) (Putz 1984b, Rich et al. 1987, see review in Hegarty 1991).

Functional plant morphology and liana-induced tree damage suggest that the previously-mentioned characteristics are not only effective as liana avoidance strategies (Hegarty 1991). For example, liana-induced abcission zones on tree branches and trunks broken by overweight lianas are not common among trees (Fig. 8). Compound leaves have been proposed to reduce the boundary layer of plants, thereby facilitating air flow around leaves to avoid overheating (Nobel 2005). Therefore, the role of compound leaves as liana shedders may be at least shared by the role they play in energy balance and water relations. Similarly, rapid growth is typical of pioneer trees in high light environments, and this life history strategy enables pioneer trees to colonize open spaces (Martínez-Ramos 1994). The advantages of these characteristics in reducing liana infestation on trees may be an added selective advantage, realized after the adaptation was in effect in areas of high liana density (see also Hegarty 1991). This entire line of reasoning is consistent with evidence from community ecology, which suggests that lianas do not engage with trees in a species-specific fashion (Pérez-Salicrup et al. 2001, Pérez-Salicrup & De Meijere 2005, Malizia & Grau 2006).

**Liana communities vs. tree communities: generalist interactions**

If lianas could locate specific tree species “preferentially”, some tree species would bear a higher liana load and the spatial distribution of lianas would be biased towards such tree species. For example, trees species that commonly bear low branches should facilitate both climbing and
distal canopy access by lianas. A similar distribution would occur if liana success was greater when growing on tree taxa that were less able to shed lianas. Conversely, if no taxonomically specialized liana-tree associations exist, then the distribution of lianas on trees would follow a random pattern with respect to the taxonomic identity of trees. The latter was found by several liana-tree community studies (Pérez-Salicrup et al. 2001, Pérez-Salicrup & De Meijere 2005, Malizia & Grau 2006) implying that lianas and trees relate to each other in a generalist pattern, rather than a specialized or preferential pattern.

Tropical forests have very high tree species richness. In spite of the populations of some tree species being spatially aggregated (Condit 1998), the distance between trees of the same species normally is not short enough for a single liana individual to consistently grow on neighbouring conspecific trees. Moreover, the liana life-form is species–rich and phylogenetically diverse, both locally and globally across the tropics (Gentry 1991, Garrido-Pérez & Gerold 2009). Given the high liana diversity, tree species are unlikely to interact consistently with the same liana species.

The more diverse a forest, the higher should be its potential to include generalist liana-tree interactions. A. H. Gentry accumulated data on species richness of lianas and trees in tropical forests worldwide (Gentry 1991, Phillips & Miller 2002). He surveyed trees and lianas 2.5 cm diameter at breast height (dbh) on more than 200 plots of 0.1ha. From these data, we selected 44 strictly tropical sites; for example some plots located in Nicaragua and Mexico were classified by Gentry as “subtropical” based on vegetation type, and were thus excluded. We included only plots located ≤ 855m above sea level, thereby excluding premontane and montane forests. This assumes that the mortality of lianas and trees are differentially affected by altitudinal changes, probably because of temperature fluctuations. We excluded plots located in flooded areas (Gentry 1991; see also Phillips & Miller 2002), on the assumption that species of lianas and trees suffer differential mortality in inundated areas. Further, we excluded plots located in hurricane- or typhoon-prone areas, like Mexico and the Philippines where tree-fall gaps might be more common (Schnitzer et al. 2000, Garrido-Pérez et al. 2008). This avoided potential over-estimations of the diversity of lianas. We excluded plots from islands (e.g., Cuba, Providencia, Madagascar), assuming that island diversities would be under-represented because of differential colonization from the mainland (McArthur & Wilson 2003). Most of Gentry’s plots are located in the Neotropics, so only seven of the 44 plots used for this study are located in Africa.

The moist tropical forest plots had an average of 130 species of trees and shrubs (s.d.=44; n=28) and an average of 36 liana species (s.d.=12, n=28 Table 1). The tropical dry forests averaged 52 species of trees and shrubs (s.d.=15) and 23 species of lianas (±13, n= 16, Table 1). At the upper extreme of tree-and shrub diversity with respect to liana diversity were plots from the Chocó of Colombia, where the annual rainfall reaches 9000mm and there is no dry season (Clinebell et al. 1995, Phillips & Miller 2002): there, the number of tree and shrub species was 219 with only 25 liana species, so 10% of the woody plant species are lianas (Table 1). At the lower extreme were the African dry forests plots averaging 63 tree and shrub species, with 38 liana species representing 38% of the woody plant species (Table 1).
Table 1. Average number (± 1 standard deviation) of tree and shrub species for 44 plots 0.1 hectare located in mainland tropical, non-flooded lowland forests (after Gentry 1991 and Phillips & Miller 2002).

<table>
<thead>
<tr>
<th>Habitat (annual rainfall in mm)</th>
<th>Region (sensu Gentry 1991)</th>
<th>Number of tree-species (±SD)</th>
<th>Number of liana-species (±SD)</th>
<th>% lianas (100%=number of woody plant-species)</th>
<th>Number of plots (n)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Humid-to-very humid (2000-9000)</td>
<td>Amazonia</td>
<td>132 (±40)</td>
<td>37 (±11)</td>
<td>21 (±4)</td>
<td>18</td>
</tr>
<tr>
<td></td>
<td>Trans-andean</td>
<td>104 (±13)</td>
<td>23 (±10)</td>
<td>18 (±5)</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td>Chocó</td>
<td>219 (±10)</td>
<td>25 (±3)</td>
<td>10 (±0.6)</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>Africa</td>
<td>106 (±40)</td>
<td>44 (±3)</td>
<td>30 (±9)</td>
<td>3</td>
</tr>
<tr>
<td>Dry (500-1855)</td>
<td>Neotropical dry</td>
<td>47 (±12)</td>
<td>15 (±6)</td>
<td>24 (±8)</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td>Trans-andean</td>
<td>56 (±8)</td>
<td>32 (±15)</td>
<td>36 (±14)</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>Africa</td>
<td>63 (±10)</td>
<td>38 (±8)</td>
<td>38 (±5)</td>
<td>4</td>
</tr>
<tr>
<td>Combined humid-to-very humid</td>
<td></td>
<td>130 (±44)</td>
<td>36 (±12)</td>
<td>21 (±6)</td>
<td>28</td>
</tr>
<tr>
<td>Combined dry</td>
<td></td>
<td>52 (±15)</td>
<td>23 (±13)</td>
<td>29 (±10)</td>
<td>16</td>
</tr>
</tbody>
</table>

With some simplifications, these data suggest that liana-tree relationships should be generalistic. If we assume that each species of liana, shrub, and tree is represented by just one individual, that all individuals are randomly distributed, and that the liana-host, host-host, and liana-liana distances are similar. Further, assume that all individuals of lianas and trees are the same age, share the same lifespan, and the same birth and mortality rates. If all these simplifications are accepted, then the average probability (P) of a given liana species to associate with a particular tree species during one generation is given by the equation \( P = 1/S_A \), where \( S_A \) = number of tree species. Compared to the Chocó, \( P \) may be high for four African dry forests: \( P = 1/63 = 0.02 \) (or 2.0%) vs. \( P = 1/219 = 0.005 \) (0.5%) for the Chocó. However, in order for co-evolution to occur, the same liana must associate with the same tree species throughout successive generations. Thus, for the second generation in the African dry forests, the probability of the same liana species to climb the same tree species as in the previous generation is \( P^2 = 0.02^2 = 0.0004 \); for the third generation it will be \( P^3 = 0.02^3 = 0.000008 \) and so on. This suggests that, even for the tropical dry forests surveyed by Gentry (1991), the possibility of a given liana species co-evolving with a particular tree species is extremely low.

In contrast, it is much more likely that a liana will climb a tree, or even another liana, independent of its species identity. Thus, under all conditions described above (especially one individual per species), it is possible to assume that the total number of tree species plus the total number of liana species represents the total number of woody plants on which a given liana can climb.

This evidence from Gentry’s census data suggest that the probabilities of species-specific liana-tree interactions are extremely low and decrease through time while generalist interactions better explain the long-term presence of lianas in tropical forests. This is supported by a series of...
studies that demonstrate that lianas and trees are not engaging in species-specific associations (Pérez-Salicrup et al. 2001, Pérez-Salicrup & De Meijere 2005, Malizia & Grau 2006). This argument also implies that if tropical forests over time were species rich, like today’s forests, then liana-tree interactions in ancient forests were also generalized.

Caveats to the above calculations include the simplifications made, but also involve the fact of rampant clonal reproduction of lianas. A single liana species may in fact climb the same tree individual many times because of clonal reproduction of a single liana individual, thus creating a slight skew toward species-specific values in forests where genetically distinct individuals are not identified.

The explanations above do not exclude the possibility that certain lineages of lianas and trees could associate with each other in some specialized relationships. For example, in low diversity forests, like the Cativo forests (*Prioria copaifera* Griseb., Fabaceae) in Darién, Panama or temperate zone forests there may be a higher probability for species-specific interactions (Grauel & Putz 2004, Ladwig & Meiners 2010). Compared to tropical forests in *terra firme* forest, cativo forests are in flooded areas and temperate forests are limited by large annual temperature and rainfall fluctuations. This suggests that past climate changes, as well as meandering of rivers, may have reduced the diversity of lianas and trees, enhancing the likelihood of co-evolution.

**The fossil record, lianas and the first liana-tree interactions**

**Interruption of co-evolutionary trends**

The colonization of land by vascular plants started approximately 410 million years ago (Mya) when some plants successfully survived out of a purely aquatic environment (Bateman et al. 1998). During colonization of areas not previously inhabited by other organisms, plants underwent adaptive radiations, manifested in high taxonomic diversity throughout the fossil record (Stewart & Rothwell 1993). Plants capable of extended growth in height were ultimately favored because they captured more of the available sunlight. Tree height added complexity to the terrestrial landscape: the vertical trunks and horizontal branches of trees expanding the available area for other plants. As a consequence, lianas colonized these early trees, and ultimately grew laterally among trees to extend their photosynthetic area. Evidence of early fossil vines seems to demonstrate relatively simple attachment organs, but quite rapidly the types of attachment morphologies expand to rival those present among climbers today (Burnham 2009). Evidence certainly suggests that lianas were capable of crossing from tree to tree in the Carboniferous, and no clear evidence of any species-specific relationships can be detected, at present. Moreover, the fossil record suggests that any species-specific interactions were interrupted by extinction, because the fossil record shows the alternation of explosive adaptive radiations with mass extinctions (McElwain & Punyasena 2007, Burnham 2009).

The fossil record shows three periods of vigorous proliferation and adaptive radiation of climbing plants alternating with long periods where there was lower diversity in climbing plants (Burnham 2009). The first adaptive radiation of climbing plants occurred in the Palaeozoic, specifically during the Pennsylvanian (about 318 Mya, Burnham 2009); roughly 100 million years after the colonization of land by vascular plants (Bateman et al. 1998). At least 488 fossil records of
climbing plants are documented representing ferns (Filicales) and seed ferns (Pteridosperms) of diverse lineages. However, toward the end of the following period –the Permian– there are as few as 16 records of climbing plants (Burnham 2009). The Mesozoic record is poor (including the Jurassic), and while some of the record is due to poorly known sedimentological sequences, even the taxonomic diversity of the known sequences is species poor in climbing plants. Only during the late Cretaceous (~70 Mya) do we see increased number of climbers, this time among the angiosperms and ferns. By the Eocene (56 Mya), another increase in diversity shows an increase to at least 250 records of climbers (and certainly more once this record is thoroughly recorded). Another apparent increase in diversity is evident during the Miocene (23 Mya), with at least 120 species of climbing plants (Burnham 2009). All these data are far more reliably drawn from macrofossil evidence and the detail in the late Cenozoic was not included in the study by Burnham. Presumably the rich pollen record could be used for the Quaternary record, with assumptions that modern genera of lianas are also vines in the fossil record (e.g., Vitis, Dioscorea, most Menispermaceae). During both the Cenozoic radiations (Eocene and Miocene), angiosperms and ferns represented the bulk of the climber record, representing 91 and 90% of the recorded species, respectively (Burnham 2009).

The evolution of the climbing habit occurred rapidly, and was repeated many times among several different plant lineages. A slow and gradual record from a single progenitor would have produced a fossil record of steadily increasing numbers of climbing plant species through time. On the contrary, the pattern of liana records (Burnham 2009), as well as the fossil record of angiosperms (McElwain & Punyasena 2007) is consistent with bursts of evolutionary innovation followed by slower increases in diversity (Gould & Eldredge 1993). For lianas, these periods of accumulation were interrupted by extinction, opening an ecological niche that was ultimately refilled by species of different lineages (angiosperms), with the consistent presence of ferns throughout the record (Burnham 2009). The fossil record suggests that any co-evolutionary trend between species of trees and lianas was repeatedly interrupted. This helps to explain why current communities of woody plants are composed of lianas and trees engaged in generalist relationships more than species-specific relationships (Pérez-Salicrup et al. 2001, Pérez-Salicrup & De Meijere 2005, Malizia & Grau 2006).

Palaeo-floristic diversity and generalist liana-tree interactions

While lianas have been through periods of high and low diversity during their evolution, trees attained a breadth of diversity even prior to the proliferation of lianas climbing on them (Stewart & Rothwell 1993, Bateman et al. 1998). The proliferation of extant angiosperm lianas (more than 90 families of extant angiosperm include substantial clades of lianas) coincides with a strong adaptive radiation of angiosperms in general (McElwain & Punyasena 2007). We propose that once liana life forms had evolved, they were faced with a relatively diverse tree community, including seed plants as well as tree-sized lepidodendrid lycopods. Lianas also diversified, creating forested communities of species-rich lianas and trees. This strongly reduced the chances of consistent liana-tree species-specific engagements. Even if such specialist interactions occurred, they were reset by extinctions that levelled the playing field for new liana and tree lineages.
CONCLUSIONS AND PERSPECTIVES

Evidence from ecology, morphology, and paleobotany suggest that liana-tree interactions take a generalist form, rather than being species-specific. We propose based on these lines of evidence that the variety of tree forms were less influenced by lianas, than are lianas in their interactions with trees. It has been difficult to marshall evidence demonstrating that trees have specific morphological and anatomical adaptations that are only effective in shedding lianas (Hegarty 1991). In contrast, the anchoring strategies and stem anatomical characteristics of lianas are clear adaptations favoring their growth on upright trees. Their morphological characteristics that resist and repair injuries caused by the movement and fall of trees is testament to their continued survival when their hosts collapse.

Climate has also played a major role in liana evolution, abundance, and diversity. While liana species richness is lower in tropical dry forests than tropical rainforests (Table 1; Gentry 1991), their abundance (density) is higher in dry forests than in rainforests (Schnitzer 2005, Schnitzer & Bongers 2011). Intensification of dry seasons as a result of global change may produce extinction of rainforest liana species, while tropical dry forests lianas increase in abundance (Wright et al. 2004). Comparison of liana density and species composition is desperately needed throughout the tropics where more species stand in danger of extinction from radically altered climatic regimes. Knowing the geographic and climatic range of all liana species is beyond our immediate grasp, but we recommend this as a first attempt to understand which species are already at their climatic limits, or beyond.

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Fig. 1. The liana *Davilla sp* (Dilleniaceae) at Parque Nacional Soberania, Republic of Panama. Fig. 2. Tendrils of *Passiflora pergrandis* Holm-Niels & Lawesson (Passifloraceae). Fig. 3. When contacting a host, the spines of *Dalbergia glabra* (Mill.) Standl. (Fabaceae) coil like tendrils. Fig. 4. *Petrea sp*. (Verbenaceae): a liana used ornamentally on the Maya Zone of Northern Quintana Roo, Mexico. Notice the circumnutant stem that coil around trees and other lianas. Figs. 5-7. Stem anomalies (cambium variants) in stems of (5) *Davilla sp*. (Dilleniaceae), (6) *Arrabidaea sp*. (Bignoniaceae) and (7) *Serjania sp*. (Sapindaceae) specimens coming from Bagala and San Carlos, Chiriqui, Republic of Panama. Notice that the injury suffered by lianas in (5) and (6) did not affect all vascular segments because they were segregated by abundant parenchyma. Fig. 8. Liana-induced tree fall after a hurricane in the Maya Zone of Northern Quintana Roo, Mexico. Notice the absence of abscission zone where the trunk broke.