The ecology of lianas and their role in forests

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Recent studies have demonstrated the increasingly important role of lianas (woody vines) in forest regeneration, species diversity and ecosystem-level processes, particularly in the tropics. Mechanisms responsible for the maintenance of liana species diversity could yield new insights into the maintenance of overall species diversity. Lianas contribute to forest regeneration and competition, not only by competing directly with trees, but also by differentially affecting tree species and thus changing how trees compete among themselves. In addition, they contribute considerably to ecosystem-level processes, such as whole-forest transpiration and carbon sequestration. As the rate of tropical forest disturbance increases, they are likely to increase in relative abundance throughout the tropics and the importance of lianas to many aspects of forest dynamics will grow.

Lianas (woody vines) are an abundant and diverse group of plants in forests throughout the world, particularly in the tropics (Box 1). Historically, the prevalence and presumed importance of lianas in forest dynamics made them a focus of interest to biologists and natural historians [1,2]. More recently, lianas were found to play a vital role in many aspects of forest dynamics, including suppressing tree regeneration, increasing tree mortality, providing a valuable food source for animals and physically linking trees together, thereby providing canopy-to-canopy access for arboreal animals [3,4]. Our current understanding of the ecology of lianas and their role in forest dynamics, however, has lagged well behind that of most other vascular plant groups [4,5]. The relative paucity of studies is probably a result of the difficulty in studying a group of plants that exhibit seemingly erratic growth patterns and rampant vegetative reproduction [leading to the problem of distinguishing ramets (vegetatively produced plants) from genets (sexually produced plants)], and taxonomic uncertainties, including difficulty with field identification [6]. Because relatively little is known about lianas and their ecology, many researchers might have assumed that lianas play a limited role in forest dynamics and hence most contemporary community-level forest studies have excluded them.

In the past few years, with the recognition that lianas are important players in many areas of forest ecology, there has been an explosion in liana-related research. Here, we review and synthesize recent advances in our understanding of the ecology of lianas and their role in several aspects of forest dynamics. We examine the contribution of lianas to the overall abundance and species diversity of plants in tropical forests, the maintenance of liana species diversity by both small- and large-scale disturbances, the mechanisms by which lianas structure tropical forest diversity and regeneration, and the significant contribution they make to whole-forest transpiration and carbon sequestration.

Liana abundance and diversity

Although lianas are common in many temperate forests (e.g. *Vitis*, *Parthenocissus* and *Toxicodendron* spp.), their contribution to forest abundance, diversity and structure is most substantial in tropical forests (Box 2). Lianas typically constitute ~25% of the woody stem density (abundance) and species diversity (species richness) in many tropical forests [7,8]. The mean abundance, diversity and taxonomic composition of lianas in lowland tropical moist and wet forests are similar among tropical regions, although liana abundance is higher in Africa (Table 1). Liana abundance and diversity, however, can be quite variable among individual sites [7–10]. For example, in liana-poor forests, such as in Semengoh, Sarawak, lianas can comprise <10% of the overall woody species diversity [8]. Conversely, in forests such as those on the rim of the Amazon basin, liana diversity can be as high as 44% of the woody species, averaging 51 liana species ha^{-1} [10].

Liana abundance varies with several key abiotic factors, including total rainfall, seasonality of rainfall, soil fertility and disturbance. Gentry [7] reported that, in the neotropics, liana abundance increased with the seasonality of rainfall. The mechanism responsible for this pattern, however, is currently unknown. Studies conducted throughout the neotropics and in Asia (Sarawak) suggest that liana abundance tends to increase with soil fertility [11–13], but this relationship is weak. For example, in central Amazon, soil richness significantly predicted liana abundance in the forest interior, but not near the forest edge, whereas forest disturbance and tree biomass significantly predicted liana abundance throughout the forest [13]. In a Mexican forest, however, soil richness did not appear to determine liana abundance [9]. In an analysis of 32 moist, wet and pluvial neotropical forests, Gentry [7] reported high variation in liana abundance among forest and soil types, resulting in no strong trend in liana abundance with soil fertility. Although highly variable, liana abundance was as much as four times higher in some nutrient-rich sites than in some nutrient-poor, sandy ones, causing Gentry [7] to conclude 'there is a very slight tendency for greater liana density on richer soils'.

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Box 1. The liana strategy

Lianas are a polyphyletic group of woody plants all sharing a common growth strategy that centers on ascending to the canopy using the architecture of other plants. Unlike trees, lianas have relatively little structural support, so they can allocate more resources to reproduction, canopy development, and stem and root elongation [a,b]. Thus, they typically have a very high canopy:stem ratio, which results in a higher proportion of photosynthetic biomass than is present in most woody plants. Lianas differ from other structural parasites (epiphytes and hemiepiphytes) in that they remain rooted to the ground throughout their lives [c].

Lianas have a variety of adaptations for attaching themselves to their host and climb towards the forest canopy. These adaptations include stem twining, clasping tendrils arising from stem, leaf and branch modifications, thorns and spines that attach the liana to its host, downward-pointing adhesive hairs, and adhesive, adventitious roots [d,e]. Although most of these climbing types can be found in any tropical forest [f,g], some are better than others at colonizing different successional stages of a forest [e]. For example, in an analysis using only small (<1.5 cm diameter) climbing lianas, DeWalt *et al.* [e] found that the relative abundance of tendril climbers decreased and stem twiners increased with forest age (Fig. I). Tendril climbers were more abundant in young forests probably because of the availability of suitable-sized trellises (small host trees), whereas the relative proportion of stem twiners, which do not depend on small trellises, increased with forest age. Thus, the relative proportion of lianas with different climbing mechanisms might be directly influenced by the successional stage or disturbance regime of the forest.

Fig. I. Adaptation of liana climbing strategies to the successional stage of forest regeneration. Stem twiners (closed circles) increased in relative abundance ($P<0.05$, $r^2=0.43$, $n=10$) with forest age, whereas tendril-climbers (open circles) show the opposite response ($P<0.05$, $r^2=0.40$, $n=10$) [e]. There was no significant relationship between branch climbers and forest age (closed triangles). Each point represents each climbing type from one forest. Reproduced, with permission, from [e].

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Disturbance and the maintenance of liana species diversity

Determining the mechanisms that maintain the species diversity of disparate plant growth forms (e.g. trees, lianas, shrubs, herbs and epiphytes) is essential to our understanding of the maintenance of local species diversity [14,15]. For forests, small-scale disturbances, such as treefall gaps, have long been hypothesized to maintain species diversity [16]. Although such gaps might be a general mechanism to maintain overall plant diversity, in nearly all tests of the gap hypothesis only trees have been examined, whereas the contribution of lianas has been largely ignored [14,15]. Interestingly, there is little compelling evidence that tree species diversity is maintained by gaps [17] and, based on this lack of evidence, several recent studies have concluded that gaps do not maintain overall species diversity in forests [18]. However, new studies demonstrate that liana species diversity is maintained by gaps [15,19] and that lianas can radically alter gap-phase regeneration (Box 3). For example, liana species richness was significantly higher in gaps than in nongap sites on Barro Colorado Island, Panama [15]
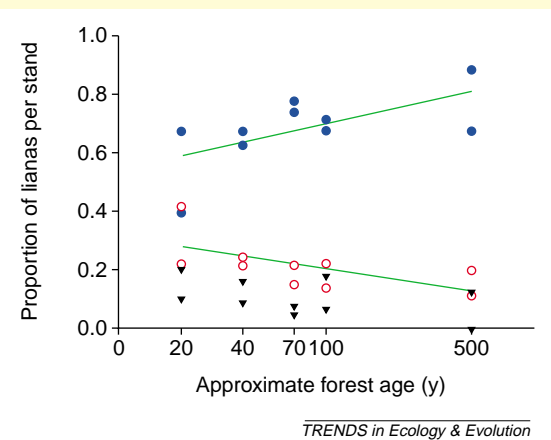
(Fig. 1), suggesting that gaps maintain liana species diversity. Because lianas, combined with pioneer trees, constitute a large proportion of the woody species diversity in many tropical forests (e.g. 43% in an old-growth forest, Barro Colorado Island, Panama [14]), including lianas has provided strong support for the hypothesis that treefall gaps do maintain much of the vascular plant species diversity in tropical forests.

The small-scale disturbance of treefall gaps might not be the only type of disturbance that is important for maintaining liana diversity. Liana diversity also increases considerably following larger scale forest disturbance from natural forces, such as hurricanes, as well as from anthropogenic forces, such as clear cutting and selective logging. For example, in a chronosequence of tropical forests in central Panama, liana abundance and diversity were significantly greater in young secondary forests (20–40 years old) than in older forests (70+ years old) [20]. In this study, the authors measured diversity using Fisher's α, an index that yields a measure of diversity independent of density, demonstrating that, even without the confounding effects of liana density, liana diversity increases after stand-clearing disturbance. Forest

Box 2. Lianas and the latitudinal gradient

The abundance of lianas in tropical forests has often been cited as the single largest physiognomic difference between temperate and tropical forests [a]. As with most plants and animals, liana species diversity increases with decreasing latitude [b], but liana abundance and diversity increase proportionally with decreasing latitude at a much faster rate than in other major growth forms (e.g. trees, shrubs and herbs; with notable exceptions, such as epiphytic plants). For example, when taken as a proportion of the total flora, liana species richness increases fivefold from temperate to lowland tropical forests (Table I). In comparison, the proportional increase in tree diversity is less than twofold, and shrub diversity increases by only one half (Table I). When examined as the proportion of woody species (trees, lianas and shrubs), liana richness increases from 10% of the temperate woody species to 25% of the tropical woody species [b]. Liana diversity, however, decreases with increasing altitude in the tropics [c]. Thus, along latitudinal and altitudinal gradients, liana abundance and diversity appear to peak in the relatively warm, lowland tropics.

Table I. Percentage of woody species of total flora in three habitat types[a]

Region	Lianas (%)	Trees (%)	Shrubs (%)
Prairie (1 site)	1	5	3
Temperate forest (7 sites)	2	12	6
Continental tropics (7 sites)	10	21	9

[a]Woody species includes lianas, trees and shrubs but not herbs, vines, hemiepiphytes and epiphytes. Data from [b] and references therein.

One explanation is that most lianas cannot tolerate the freezing temperatures of high altitudes and northern temperate climates. The extremely long and wide vessel elements that enable lianas to conduct water and nutrients over very long lengths, coupled with their relatively narrow, uninsulated stems, could make them particularly susceptible to freezing, causing irreversible vascular damage [d]. Nevertheless, there are some exceptions. One example is wild grape *Vitis* spp., which survives prolonged freezing temperatures by completely draining its vessel elements before the onset of Northern Hemisphere winter temperatures [e]. This has allowed *Vitis* to proliferate throughout many temperate forests, particularly those that are highly disturbed [f]. Although lianas can be an important factor in temperate forest dynamics [g], they are predominantly a tropical phenomenon.

The origin of the high diversity of lianas throughout tropical forests is probably a result of the repeated independent evolution of the climbing habit. Nearly 60% of all dicotyledenous plant orders have at least one representative climber [h]. This repeated but independent evolution could explain why lianas have so many different yet homologous adaptations, such as an adaptation for climbing (Box 1). Although they have a wide range of pollination syndromes, seed sizes and seed dispersal mechanisms, overall, the relative abundance of these characteristics differs from that of other plant groups. For example, lianas tend to have fairly small, wind-dispersed seeds compared with trees or shrubs [i,j]. The animals that pollinate them also tend to differ from that of other plant groups, with large bees and beetles disproportionately well represented [i]. Although more detailed studies on the pollination biology of lianas are needed, the variation in liana taxa, species diversity, climbing strategy, seed size and dispersal mechanisms suggests that there are many ways to be a liana and that being one is a prosperous way in which to make a living.

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fragmentation also increases liana diversity. In central Amazon, liana abundance and diversity (Fisher's α) were significantly higher within 100 m of forest edges than in forest interiors [13]. In a subtropical forest in southern Florida, liana species richness significantly increased following large-scale hurricane damage, with nonindigenous invasive species comprising 34% of the increased liana diversity [21].

Table 1. Mean abundance and species richness of lianas in four tropical regions[a]

Continent/Region (number of forests sampled)	Mean abundance (± standard deviation)	Mean species richness (± standard deviation)
Africa (7)	111.0 (± 35.8)	39.1 (± 7.1)
Asia (11)	66.0 (± 35.1)	36.2 (± 17.0)
South America (27)	61.6 (± 22.2)	33.7 (± 10.9)
Central America and Mexico (5)	59.6 (± 11.4)	28.2 (± 5.5)

[a]Data based on 0.1-ha area in lowland moist and wet forest sites (<500 m altitude, >1600 mm precipitation y⁻¹) in which all lianas >2.5 cm diameter at breast height were included. Data from [7] and [8]. More data are needed before we can accurately generalize about such areas; however, see [7] for a comprehensive survey of liana density and diversity in forests around the world.

How does disturbance maintain liana diversity?

Disturbance might maintain local liana diversity by at least two different mechanisms, neither of which is mutually exclusive. First, lianas with different competitive abilities might partition the abundant and heterogeneous resources that result from a disturbance, providing a mechanism that directly maintains liana diversity [22]. Although there is no direct experimental evidence for this hypothesis, several studies have found that liana diversity is maintained independently of density [13,15,20], suggesting that a mechanism such as resource partitioning among liana species is possible. A second mechanism might be that lianas require the high light levels of a treefall gap or larger scale disturbance for colonization and survival, similar to the regeneration requirements of high-light-demanding tree species. Several studies have suggested that lianas could be classified as early successional or gap-dependent pioneer species [20,23,24]. Conversely, other studies have demonstrated a wide range of

Box 3. The rise and fall of lianas in treefall gaps

Small-scale disturbances, such as treefall gaps, are key processes in forest dynamics and regeneration [a]. Gap-phase regeneration theory suggests that gaps are rapidly colonized by trees and redevelop a high closed canopy soon thereafter [b]. A large proportion of gaps (possibly >20%) [c], however, does not rapidly redevelop such a canopy in this simple, but commonly accepted way. Instead, these gaps follow an alternative successional pathway, whereby they are dominated by lianas and can remain in a low-canopy state for over 13 years [c,d]. Lianas can colonize gaps very early, growing rapidly in the increased light, and smothering slow-growing shade-tolerant trees as a result. When there are no suitable-sized saplings to act as trellises in a gap, the growing lianas can form a tangle of vegetation, which further blocks and delays conventional gap-phase regeneration of trees by preempting light, imposing mechanical interference and possibly causing intense belowground competition.

Some forests can become composed primarily of lianas [e,f], especially after logging [g]. In most forests, however, trees eventually escape from the liana tangle. As trees, particularly pioneer species [c,h], escape from the edge of the tangle, they reduce the light level in the gap, and the lianas might grow less vigorously, which can result in more trees breaking through the liana tangle, consequently ending the domination of lianas in the gap. The legacy of a liana-dominated gap, an impenetrable tangle of liana stems, often persists in the intact forest for many years after the completion of gap-phase regeneration.

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shade tolerance in lianas [12,25–27]. For example, Putz [27] classified only three of the 65 liana species that he examined on Barro Colorado Island, Panama, as strictly early successional or gap-phase species.

Although there is contrasting evidence for the regeneration requirements of lianas as a group, there

Fig 1. Maintenance of local liana species abundance and diversity by treefall gaps. Liana abundance (density) and diversity (species richness) were significantly greater in gap sites (green bars) compared with same sized nongap sites (open bars) in an old-growth forest on Barro Colorado Island, Panama (Fisher's exact test; *P*=0.01, *n*=17 and *P*<0.001, *n*=17 for liana abundance and species richness, respectively) [15]. Error bars represent one standard error. Rarefaction analysis (not shown here) revealed that liana species richness was also significantly greater in gaps on a per capita basis (*P*<0.05); thus, the significant increase in richness was not merely an artifact of increased density. Modified, with permission, from [15].
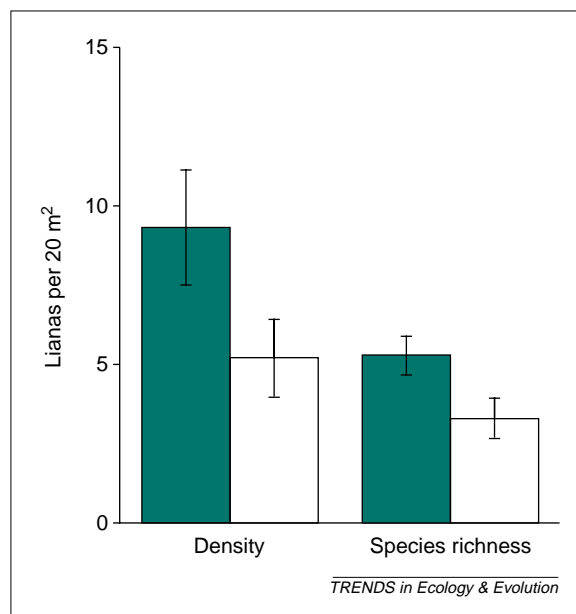

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are several potential explanations for these disparate results. One fairly speculative explanation is that lianas share attributes of both high-light-demanding and shade-tolerant species. Specifically, lianas might require the high light levels provided by treefall gaps for establishment, but, once established, they can persist in the forest understorey after the canopy is closed. Indeed, this type of regeneration strategy has been documented for some tree species [28]. A more plausible explanation is that lianas establish immediately following a disturbance and grow rapidly thereafter. The ability to grow rapidly in the high light levels resulting from a disturbance could allow even relatively shade-tolerant liana species to grow at a rate similar to that of pioneer species [12].

The ability to establish following a disturbance might be particularly important for lianas, because they have four ways to colonize, whereas most other vascular plants have only two. Most vascular plants can colonize via both seed and advance regeneration (the seedlings and saplings that were present in the understorey before the disturbance). Unlike most other vascular plants, however, lianas can also colonize immediately after a disturbance as adults. Putz [27] found that ~90% of the adult lianas that are dragged into a gap with a treefall survive the event. Lianas are particularly adept at surviving treefalls because of their anomalous stem anatomy, which reduces stem breakage and accelerates the repair of damaged vascular tissue [29]. They can also colonize disturbed sites, such as treefall gaps, by growing laterally into, and subsequently rooting in, gaps from areas adjacent to the gap [30]. Many tree species can also colonize a gap as adults via resprouting [31]; however, lianas can actually increase in relative abundance in a gap by vigorously producing many independently rooting stems, thereby greatly increasing their chances of survival. Although the exact regeneration requirements of lianas as a group can be as varied as the liana taxa themselves, liana diversity appears to be maintained primarily by disturbance, possibly by resource partitioning, but more likely because lianas can arrive in high numbers, reproduce vegetatively and grow rapidly for long periods.

Untangling the negative effects of lianas on trees

The interactions between lianas and trees have been of great interest to ecologists and foresters because of the detrimental effect that lianas have on their tree hosts [32,33] (Box 4). Many studies have demonstrated that, even in relatively low abundance, lianas decrease the growth, fecundity and even survivorship of trees in intact, closed-canopy forest, treefall gaps and managed forests [27,34–36]. Very few of these studies, however, were designed to test explicitly the mechanisms by which lianas affect trees. Recently, several key experiments have been undertaken to disentangle these mechanisms by comparing the relative contributions of above- and belowground competition between lianas and trees [33,37–41].

Box 4. To cut or not to cut: the question of liana control in managed forests

The detrimental effect of lianas on trees is a widely recognized problem for tree regeneration in managed and heavily logged forests [a]. Lianas are particularly abundant in such forests, where they reduce tree growth rates, increase the number of trees that are killed and damaged during timber harvest, and cause trees to bend, distorting their trunk and thus reducing their value as timber [b,c]. Indeed, logged forests can have nearly twice the density of lianas than do primary, nonlogged forests. For example, Campbell and Newbery [d] reported that only 30% of the trees (>20 cm in diameter) in a post-logging forest were vine free, whereas 59% of the trees (>10 cm in diameter) remained vine free in a nonlogged, primary forest. Consequently, many foresters and forest ecologists recommend the active management of lianas via periodic and pre-harvest liana cutting [a,c]. Periodic liana cutting can greatly reduce the number of lianas in the crowns of trees [e] and preharvest liana cutting can reduce the amount of collateral tree damage by up to 50% and reduce postharvest canopy gap sizes.

The efficiency of preharvest liana cutting, however, is still hotly debated. It is expensive and time consuming, and its overall effectiveness is still not fully resolved [b,f]. Recently, several studies have quantified the effectiveness of liana cutting for forest management [c,e,f] and some concluded that blanket liana cutting was not effective [f].

A compromise endorsed by nearly all of these studies is one of selective liana cutting; that is, lianas are removed only from the trees that have a high density of lianas in their crown. This solution can reduce the expense of liana cutting whilst maintaining a high degree of liana control [c,f]. In addition, many studies warn against wholesale liana cutting in managed forests because lianas provide essential food and much needed canopy structure to many forest animals [g]. Overall, liana cutting still appears to be the most ecologically sound and cost-effective strategy for forest management, but only when done selectively, on a tree-by-tree basis. Further research is needed to quantify the approximate level at which the density or biomass of lianas in a tree becomes problematic for forest management.

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Historically, most studies on liana–tree interactions have assumed that aboveground competition is the predominant effect of lianas on trees [25,35]. Such competition can be quite apparent, especially in disturbed forests (Fig. 2). However, belowground competition plays a much greater role in liana versus tree competition than has been previously suspected [37–40]. For example, in a series of controlled experiments in the northeastern USA, Dillenburg and collaborators tested the relative strengths of above- and belowground competition among the liana species *Lonicera japonica* and *Parthenocissus quinquefolia*, and the tree *Liquidambar styraciflua*. They found that belowground competition, particularly for soil nitrogen, rather than aboveground competition for light, was responsible for the drastically reduced rates of tree growth. Competition for soil water was not a factor in these studies, possibly because water was never a limiting factor at the study site.

Competition between lianas and trees for soil water, however, could be intense in forests that experience seasonally low rainfall. For example, during the dry season in a lowland Bolivian forest, the pre-dawn water potential of the host tree *Senna multijuga* became significantly less negative within one day after encroaching lianas were cut from the tree [40], suggesting strong competition for water between lianas and trees during the dry season. Interestingly, the same authors failed to find the same result in a companion study on another focal tree species, the mahogany *Swietenia macrophylla* [41].

Do lianas affect tree species differentially?

The disparate results of Pérez-Salicrup and collaborators suggest that lianas affect tree species differently and thus could alter the tree community by changing the relative competitive ability of tree species. Indeed, there is evidence to support this assertion [13,15,27,33,36,42,43]. Lianas appear to harm slow-growing, shade-tolerant tree species, whilst not affecting, or even indirectly promoting pioneer tree species [13,27,42] (Fig. 3). Putz [43] described several key characteristics, such as a flexible trunk, large leaves and rapid growth rate, which allowed trees, such as palms and pioneers, to shed or avoid lianas. For example, in a lowland tropical forest in Costa Rica, lianas were found in only one out of 142 adult pioneer trees, whereas the canopy of most of the shade-tolerant trees (50–97% of trees >70 cm in diameter) hosted lianas [36]. Schnitzer *et al.* [42] argued that lianas indirectly promote pioneer trees in gaps by reducing the competition from shade-tolerant trees via smothering and prolonging the life of a gap and thus extending the opportunity for pioneers to colonize (Box 3). Pioneer trees can emerge from liana-suppressed gaps into the open, high-light zone of the gap up to 20 years after gap formation [27,42]. Lianas can also indirectly promote pioneer tree abundance by creating more and larger gaps through increasing tree mortality and pulling down neighboring trees in a treefall [44]. Because lianas affect tree species differentially, the abundance of lianas in any given forest probably plays an integral role in tree species competition and colonization, and thus in the overall composition of the tree community. Further studies, however, are necessary to quantify the extent of the ability of lianas to structure tree communities in tropical forests.
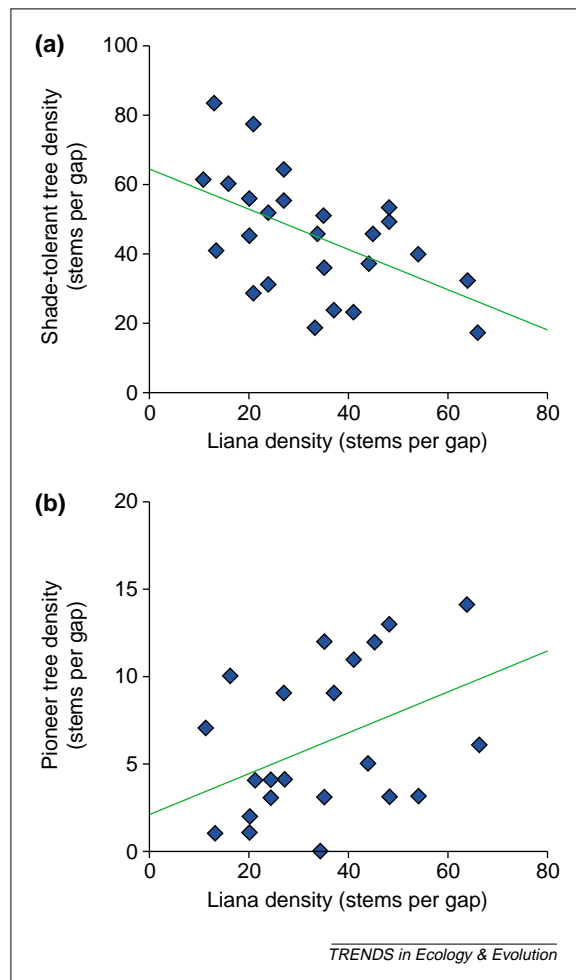
Lianas and ecosystem-level processes

Lianas have a major impact in tropical forests at the ecosystem level, particularly for processes such as whole-forest transpiration and carbon sequestration [45–47]. With their high canopy:stem ratio, extremely long and wide vessel elements, and very deep root systems, lianas are thought to have high sap flow and transpiration rates compared with trees [48,49]. Recently, Andrade *et al.* challenged this paradigm, showing that the rate of sap flow was no greater in lianas than it was in trees of an old-growth

Fig. 2. An adult tree covered by lianas, mostly *Entada monostachia*, in a disturbed area in a semi-deciduous season forest in western Costa Rica. Lianas can become very abundant in disturbed forests and the trees pay a heavy toll. Most studies assume that aboveground competition is the predominant effect that lianas have on trees [25,35]; however, recent studies have demonstrated that belowground competition is also intense [37–40]. Photograph taken by S. Schnitzer.

Panamanian forest (J.L. Andrade *et al.*, unpublished). However, lianas did have a high transpiration rate and they continued to transpire throughout the dry season, tapping water deeper in the soil profile as the dry season progressed. Most of the large trees at this site, however, extracted available water only from relatively shallow sources throughout the dry season

(J.L. Andrade *et al.*, unpublished, [46]). In addition, lianas constituted ~25% of the woody plants in this forest and nearly all lianas remained evergreen, whereas many of the trees were deciduous during the dry season [50]. By contrast, transpiration in lianas was significantly lower in the dry season than in the wet season in a secondary forest in eastern Amazonia, whereas transpiration in trees remained the same throughout the year [49]. Overall, these results suggest that lianas contribute a large proportion to the transpiration of tropical forests, particularly during the dry season, but that dry season transpiration might depend on the site and liana species being considered.

Lianas also play a prominent role in forest-wide carbon sequestration. Heavy liana infestations following disturbance inhibit tree regeneration [13,42,44], which reduces the amount of carbon that is sequestered in plant biomass [45,51]. For example, in the many areas of a forest in French Guiana where liana abundance was extremely high, mean aboveground dry biomass (AGBM) of trees was ~33% lower than the mean tree AGBM of the entire forest [51]. The loss in tree biomass, however, was not offset by the increase of liana biomass. Because of their relatively slender stems and low wood density, lianas sequester far less carbon than do trees [45,52,53]. For example, between ten and 17 years following forest fragmentation in central Amazon, total AGBM of trees decreased by 36.1 Mg ha^{-1} within 100 m of the edge of a fragmented forest, whereas liana AGBM increased by only 0.46 Mg ha^{-1}, even though liana abundance greatly increased [13,45].

The exact contribution of lianas to the total biomass in tropical forests is currently unresolved. One problem for estimating liana biomass is the paucity of the allometry data that are needed to calculate liana biomass from stem basal area. Existing data are based on only a few individuals (<20) and species (<17) in unreplicated forests [47,54]. Unsurprisingly, the estimates of liana biomass based on these limited allometry data can be radically different, even in forests where liana abundance is similar. For example, in a Venezuelan forest, Putz [54] estimated that lianas constituted 4.5% (15.7 ton ha^{-1}) of the AGBM. Conversely, in an eastern Brazilian forest, Gerwing and Farias [47] developed their own allometric model and estimated that the proportion of liana AGBM was more than three times higher than that of Putz [54] (14%, 43 ton ha^{-1}) and that this proportion reached up to 30% in low-stature, disturbed areas of the forest. The abundance of lianas in these two forests, however, was quite similar, with 35 and 43 lianas 0.1 ha^{-1} in the Venezuelan and Brazilian forest, respectively.

Regardless of the exact contribution of lianas to the aboveground biomass of forests, they play a large role in the forest carbon budget. Furthermore, the contribution of lianas to forest carbon sequestration is likely to change over time as their abundance increases with increasing forest productivity, climate change and natural and anthropogenic disturbance [13,45,55].

Fig. 3. Effect of lianas on surrounding vegetation. Lianas harm shade-tolerant tree species (a) whilst indirectly promoting pioneer trees (b) in treefall gaps in an old-growth forest on Barro Colorado Island, Panama [42]. Shade-tolerant trees are negatively correlated with liana density (P=0.01, r^2=0.28, n=25), whereas pioneer trees are positively correlated with liana density (P=0.04, r^2=0.18, n=24). These findings suggest that, when abundant, lianas alter competition among these species in gaps, possibly by reducing the competitive ability of shade-tolerant trees. Each point represents one gap. Modified, with permission, from [42].

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Before we can make educated predictions on the future role of lianas in the global carbon budget, however, more data are needed on liana allometric relationships, the relative abundance of liana and tree biomass in both disturbed and naturally functioning, intact forests, and how these relative abundances are changing over time.

Prospects

In the tropics, lianas play an integral role in forest regeneration, the maintenance of species diversity and whole-forest level ecosystem processes. Recent evidence has begun to elucidate how liana diversity is maintained, the exact mechanisms by which lianas impact trees, and the growing role of lianas in ecosystem processes. However, many important questions remain. Specifically, what are the exact mechanisms by which disturbance maintains liana species diversity? What proportion of lianas is truly shade-intolerant, shade-intolerant solely during their colonization phase, or shade-tolerant throughout their entire lifetime? What are the exact mechanisms by which lianas colonize and subsequently arrest regeneration following disturbance; specifically, what proportion of lianas recruit into the disturbed area from the canopy, from the intact forest via advanced regeneration, and from seeds? Also, what is the role of belowground competition in arresting canopy regeneration? Do lianas have extensive and deep root systems that severely limit water and nutrient uptake in other plants? We now know that lianas play a role in whole-forest transpiration and carbon budget, but their specific role is currently unresolved.

Overall, it is becoming clear that lianas are important players in many aspects of forest dynamics, far more important than was realized a decade ago. The fact that forests are becoming increasingly disturbed worldwide will increase the relative importance of lianas in many aspects of forest dynamics. We need long-term data from both field and greenhouse studies on the ecology, behavior, anatomy and physiology of many liana species to be able to answer the questions raised above.

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Inbreeding effects in wild populations

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Whether inbreeding affects the demography and persistence of natural populations has been questioned. However, new pedigree data from field populations and molecular and analytical tools for tracing patterns of relationship and inbreeding have now enhanced our ability to detect inbreeding depression within and among wild populations. This work reveals that levels of inbreeding depression vary across taxa, populations and environments, but are usually substantial enough to affect both individual and population performance. Data from bird and mammal populations suggest that inbreeding depression often significantly affects birth weight, survival, reproduction and resistance to disease, predation and environmental stress. Plant studies, based mostly on comparing populations that differ in size or levels of genetic variation, also reveal significant inbreeding effects on seed set, germination, survival and resistance to stress. Data from butterflies, birds and plants demonstrate that populations with reduced genetic diversity often experience reduced growth and increased extinction rates. Crosses between such populations often result in heterosis. Such a genetic rescue effect might reflect the masking of fixed deleterious mutations. Thus, it might be necessary to retain gene flow among increasingly fragmented habitat patches to sustain populations that are sensitive to inbreeding.

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Small and isolated populations are inherently more vulnerable to external environmental perturbations and chance fluctuations in local survival and fecundity [termed 'ENVIRONMENTAL STOCHASTICITY' and 'DEMOGRAPHIC STOCHASTICITY', respectively (see Glossary)]. Are they also threatened by inbreeding and the loss of genetic diversity? With data on the effects of inbreeding in wild populations scarce, some zoologists questioned its importance (or even its existence) in natural populations [1–3]. Recent evidence, however, now suggests that both inbreeding and inbreeding depression are more pervasive than previously realized. In addition, some studies point to inbreeding as an important threat that can directly affect population persistence, making it a key concern for conservation biologists. Here, we review this recent work, including studies of both plant and animal populations that exploit a range of traditional and molecular genetic techniques. Although we emphasize the empirical results, we also present the background theory needed to evaluate critically these approaches and place the results into context.

What genetic threats exist?

If populations remain small and isolated for many generations, they face two genetic threats. As alleles are randomly fixed or lost from the population by drift, levels of quantitative genetic variation necessary for adaptive evolution erode [4]. Simultaneously, deleterious mutations will tend to accumulate, because selection is less effective in small populations [5]. This could eventually lead to a 'mutational meltdown' for populations with an effective size (N_e) of <100. Both processes tend to be gradual, however, and thus do not threaten populations in the short term. By contrast, inbreeding can act swiftly. By restricting opportunities for mating, small populations foster inbreeding via mating among relatives. Simultaneously, small populations tend to fix an appreciable fraction of the GENETIC LOAD by drift, resulting in among-population inbreeding. Both forms of inbreeding increase the frequency of individuals that are homozygous for alleles identical by descent (Box 1). Such inbreeding results in the reduction in fitness that we term inbreeding depression. Although any of these genetic mechanisms could threaten population persistence, inbreeding poses the most immediate risk.

When should we expect inbreeding depression?

In spite of its prevalence, some researchers question whether inbreeding depression is important in wild populations, invoking two main arguments. First, if the many inbreeding avoidance mechanisms evident