

Lianas as structural parasites: A re-evaluation

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Lianas are a principal physiognomic component of tropical and subtropical forests and are typically considered to be parasites of trees. In contrast, the substantial contribution of lianas to rainforest leaf litter production (up to 40%) suggests that they play important roles in nutrient cycles and may benefit their host trees. Lianas contribute disproportionately to total forest litter production at least partially because lianas invest relatively little in support structures and proportionately much more to leaf production when compared with trees. In contrast to tree leaves, liana leaves are higher in nutrient concentrations, relatively short-lived, and decompose more rapidly. In addition, the special life form of lianas allows them to grow vertically and horizontally in the forest and relocate nutrients, mainly towards their host trees, through the production of leaf litter. Consequently, lianas may contribute substantially to the high rainforest productivity, and the roles they play in liana/tree associations and rainforest dynamics needs to be re-evaluated.

Liana, compensatory effect, nutrient dynamics, leaf litter, rainforest

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Lianas are woody vines that climb other plants to ascend forest canopies [1]. The non-self-supporting life form of lianas has been considered as an evolutionary adaptation driven by competition for light and allows lianas to invest more in transportation and photosynthetic organs, principally leaves [2]. Lianas occur in almost all forest types but are more abundant in tropical forests [1]. The number of species and the abundance of lianas decrease with an increase in latitude and show a sharp drop near the Tropic of Cancer where the climate changes northwards from tropical to temperate. The low occurrence of lianas in temperate regions has been ascribed to frequent low winter temperatures that may cause freezing-induced embolisms in lianas' long vessel systems and lead to unrecoverable damage [3]. As a principal physiognomic component of tropical and subtropical rainforests, lianas comprise around 25% of the diversity of woody plants in these ecosystems [1,4,5]. Their abundance and diversity increase along a low to high rainfall gradient, and peak in tropical rainforest sites near the

Equator, such as the Amazonian lowland rainforest, co-occurring with the highest tree species diversity [1,6]. Additional factors, including soil type, seasonality of rainfall and disturbance, have been proposed as being important in determining local liana distribution [6–8]. The high liana abundance in seasonal rainforests reflects their ability to maintain growth during dry seasons by accessing ground water via deep roots and efficient vascular conducting systems [6]. This ability to obtain water during dry periods allows lianas to take advantage of the high solar radiation environment associated with dry seasons. Thus, lianas grow much faster than trees during the dry season in seasonal rainforests [6].

Lianas play important roles in forest dynamics. They add substantially to baseline levels of plant diversity in forests and maintain tree diversity through their role in gap dynamics [9]. A high liana load in tree canopies may cause high tree-fall rates, thus maintaining rainforests in a perpetual disclimax and thereby potentially maintaining diversity by reducing dominance levels among tree species [10]. Many studies have found that lianas increase in both abundance

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and diversity following natural and anthropogenic disturbance [8,11,12]. Consequently, they play an important role in regulating forest regeneration processes [12]. The increase in the abundance of lianas reflects their ability to regenerate vegetatively and grow both vertically and horizontally in response to changes in the light environment. Thus, as rainforest fragmentation increases across the tropics, an increase in the dominance of lianas in rainforests is expected [8,11]. Indeed, this effect may be enhanced through a positive feedback loop driven by increases in atmospheric carbon dioxide [13,14]. Finally, lianas, perhaps through their lower levels of chemical foliar defenses, are the preferred hosts of many herbivores, particularly insects, and liana occurrence in forests may substantially increase animal diversity through food-web effects in canopies and leaf litter [15,16].

Lianas have long been considered as parasites of trees [11,17]. This hypothesis is based on the proposition that they have detrimental effects on the growth and reproduction of their host trees by causing physical damage and by competing for limited resources such as water, nutrients and light [6,18,19]. Lianas may also significantly delay rainforest regeneration during the gap phase by competing with trees, especially those of shade-tolerant species [20]. The majority of studies on lianas, especially those conducted in a silvicultural context, have only focused on negative effects on their host trees [21]. However, many liana-bearing trees are actually large canopy trees that live for many years and readily grow and produce seeds [22]. Presently, there are still no explanations for how liana-bearing trees are able to maintain their growth in highly competitive rainforest while incurring negative impacts from lianas. Although the importance of lianas in forests has been widely accepted [23], the possibility that trees might benefit from the presence of lianas has been overlooked. By reviewing published research, we demonstrate that lianas may play important roles in nutrient dynamics by producing a large amount of nutritious and easily decomposed leaf litter and can benefit their host trees via nutrient transportation.

1 Characteristics of liana leaves

Lianas produce a larger quantity of leaves than trees, and their leaves are structurally and nutritionally different from those of trees (Table 1). These differences have profound

impacts on the litter decomposition process in rainforests. Liana leaves have significantly lower mass per unit leaf area (LMA) than tree leaves, because of the faster growth and different resource allocation strategies of lianas [24–26]. Furthermore, liana leaves have a much higher nitrogen concentration than those of their host trees (Table 1). Although most studies compared only green leaves, we expect that leaf litter follows the same pattern because the nutrient content of green and senesced leaves are highly correlated [27]. Low LMA and high leaf nitrogen concentration have been suggested to be economical trade-offs [28] and may generate faster rates of litter decomposition than leaves with high LMAs and low nitrogen concentrations. Moreover, leaves with low LMA and high nitrogen contents, such as those of lianas, tend to have a shorter life span than those of many trees [29–31], thereby maintaining a rapid nutrient cycling system.

Liana leaves also have a high concentration of phosphorus [31–33], a major plant growth element generally limited in many rainforests [34]. A recent study has shown that lianas have a lower phosphorus resorption rate from senescing leaves than do trees [32], which may be caused by the high nitrogen content [30] and the short lifespan of liana leaves. Thus, we expect that the leaf litter of lianas is higher in phosphorus concentration than that of trees. Given the pervasive phosphorus deficiency in many rainforests, lianas potentially play an important role in phosphorus recycling in rainforests by producing leaf litter with a high concentration of this element [25,32,35]. Moreover, phosphorus availability also has been considered to be an important factor regulating microbial decomposition processes in rainforests [36–38]. Leaf litter with a high phosphorus concentration may potentially promote microbial processes and thus make more of the element available to plants through microbial phosphorus immobilization [36]. That is, phosphorus is taken up by microbes and then slowly released back into the system as they die, thereby preventing rapid loss of phosphorus.

The microenvironment created by liana leaf litter could promote the decomposition of associated tree leaf litter, thus providing an efficient nutrient recycling system. Plants and soils nutrients interact in a manner such that correlations between them may be caused by nutrient limitations to plant growth or by plant effects on soils [39,40]. The unresolved association of lianas with richer soils [1,4], especially those

Table 1 Comparison of leaf nutrient contents of lianas and trees

Forest type	Liana			Tree			Reference
	N (mg g ⁻¹)	P (mg g ⁻¹)	LMA (g m ⁻²)	N (mg g ⁻¹)	P (mg g ⁻¹)	LMA (g m ⁻²)	
Mountain rainforest	15.3	0.7	94.9	11.7	0.4	170.5	[25]
Lowland rainforest	24.1	–	68.2	18.4	–	97.9	[24]
Tropical mountain rainforest	24.6	1.24	101	22.8	1.21	115	[32]
Tropical seasonal rainforest	28.79	1.58	49.1	22.22	1.12	63.2	[31]

with high phosphorus concentrations [8,41], may be because of the high nutrient content of liana leaf litter and its high rate of decomposition, and not the inherent nutrient-rich soil *per se*.

2 Leaf litter production by lianas

Leaf litter production is an important part of forest nutrient cycling [42,43], and liana litter production is distinct from those of trees owing to their different life strategies [44]. Lianas seldom exceed 5% of total forest biomass [5]. However, their level of leaf production is relatively much higher than that of trees, contributing up to 36% of total above-ground leaf biomass (Table 2) and as much as 40% of total leaf area in tropical rainforests [5,45]. Compared with trees with the same diameter at breast height, lianas produce much more leaf dry mass because, unlike trees, they do not invest heavily in mechanical support organs (stems, branches and buttresses). Accordingly, a larger proportion of their resources can be directed to the production of leaves [44,46], and up to 16%–40% of all leaf litter within rainforests is derived from lianas (Table 2). Thus, liana leaves have a disproportionate importance in any consideration of nutrient dynamics, especially those in the nutrient-poor rainforests [14,47,48]. Moreover, the proportion of liana leaves in forest leaf litter production increased from 10.1% in 1986 to 17.1% in 2002 in tropical

rainforest in Barro Colorado Island, Republic of Panama. This dramatic increase has been proposed to be because of increasing atmospheric levels of carbon dioxide [14] and may have important applications in rainforest management.

3 Lianas as nutrient transporters

Lianas are able to grow horizontally from the places where they are rooted until they reach a suitable vertical structure (e.g., a trellis tree or an existing liana), which they can use to gain access to the canopy and light [11,50]. Some lianas are reported to grow horizontally as far as 100 m before beginning to grow vertically to gain access to the tree canopy [50]. Furthermore, lianas are capable of rooting at multiple places and may root multiple times at different places during their life cycle [11,51]. This makes them more flexible in accessing resources than trees that are normally rooted at only one place during their life time. As a result, lianas may relocate nutrients in the form of nutrient-rich and easily-decomposed leaf litter. Apart from this horizontal transport of nutrients, lianas usually have a deep root system that allows them to access nutrients and water beyond the reach of trees [6,18]. Consequently, liana-supporting trees may receive a better supply of nutrients than liana-free trees through regular input of liana leaf litter around their rhizosphere (Figure 1).

Table 2 Annual leaf litter production (t hm^{-2}) of trees and lianas in tropical and subtropical forests^{a)}

Study area	Forest type	Tree	Liana	Reference
Gabon	Tropical seasonal rainforest	3.85 (62%)	2.34 (38%)	[47]
BCI [*]	Tropical seasonal rainforest	5.91–7.80 (83%–87%)	0.87–1.59 (13%–17%)	[14]
Brisbane, Australia	Subtropical rainforest	4.74 (76%)	1.47 (24%)	[49]
Coromandel coast, India	Tropical dry evergreen forest	6.9 (71%)	2.8 (29%)	[48]
Coromandel coast, India	Tropical dry evergreen forest	5.6 (62%)	3.4 (38%)	[48]

a) *, Data are ranges of annual leaf litter production over 17 years in a tropical seasonal rainforest on Barro Colorado Island, Panama. Data in parentheses are the proportions of all leaf litter.

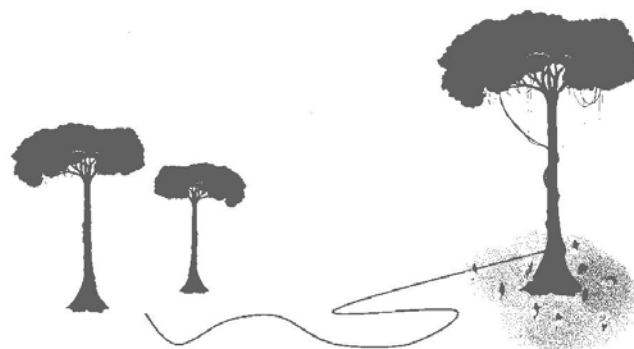


Figure 1 Illustration of a compensatory liana and host-tree relationship in which lianas provide nutrients through large amounts of nutrient-rich and easily-decomposed leaf litter to compensate for the negative effect of using trees as support.

4 Liana and gap dynamics

In rainforests, tree-fall gaps play a central role in tree dynamics [52]. The formation of many tree-fall gaps involves subsequent vigorous growth of lianas, which may enlarge the opening by 'locking-down' neighboring trees and thus causing more damage to the canopy [11,12]. Under these circumstances, a majority of fallen lianas can survive the tree-fall, and many lianas may grow into the gap horizontally from nearby intact forest [11,12,50]. Although the high abundance of lianas in tree-fall gaps may delay redevelopment of the forest canopy by competing directly with trees [9,20], the presence of lianas in the forest gaps may promote local nutrient cycling and thus contribute to the regeneration during gap dynamics.

Tree-fall gaps provide a high-light environment for both lianas that survive the tree-fall and lianas in the adjacent undisturbed forest, leading to a temporary increase in the number of lianas in the forest gaps [4,12]. The increase in assemblages of small trees near forest gaps may facilitate access of lianas to the tree canopy [4]. The high number of lianas in tree-fall gaps may also act as nutrient transporters contributing to redevelopment of the forest canopy. Many lianas that have their crown in forest gaps are actually rooted in the nearby forest interiors. High abundance of lianas in tree-fall gaps may lead to a high input of nutrient-rich leaf litter, which may partly explain the increase in soil nutrient levels, particularly phosphorus, within gaps [34]. A similar phenomenon also has been observed in Amazonian rainforests, where the distribution of lianas was significantly correlated with phosphorus concentration [8].

5 Lianas and rainforest

Lianas are integral elements of rainforest which, together with trees, form the rainforest canopies that foster the most diverse terrestrial ecosystem on earth. Many trees, especially large trees, bear lianas. For example, Putz [4] found that half of the trees with DBH > 20 cm were host to at least one liana in a Malaysian rainforest. Despite the wide recognition of their receiving negative effects from lianas, host trees may also benefit from the input of liana leaf litter and associated ecological processes. This extra source may play an important role in balancing the growth of liana-bearing trees and liana-free trees, the latter depending mainly on local supplies of nutrients. The benefits host trees receive, however, may not compensate for the negative effects once the trees are climbed by excessive lianas over time. In addition, lianas may also produce roots close to the host trees and compete with them both below and above ground. Under these circumstances, trees may experience reduced growth and fecundity or even higher mortality rates [11,17,18].

Rainforests are the most productive terrestrial ecosystems on Earth even though most tropical soils are among the

poorest in terms of their nutrient content [53]. The productivity of rainforest generally is limited by nutrients such as nitrogen [54] and phosphorus [43]; therefore an efficient nutrient cycling system is crucial for tropical rainforests to maintain the high productivity [35]. Gentry [44] noticed that the litter to wood production ratio was higher in tropical rainforests than in temperate forests and attributed the difference to the presence of abundant lianas producing a large amount of leaf litter in rainforest.

An increasing number of studies have reported the high production of liana leaf litter in different rainforests (Table 2). As discussed above, lianas contribute not only nutrient-rich and easily-decomposed leaf litter, but are also able to relocate nutrients within the rainforest. We hypothesize that lianas are key elements in maintaining the productivity in highly dynamics rainforests. Thus, a comprehensive re-evaluation of the interaction of lianas and trees is needed.

6 Future research

It is becoming clear that lianas may play important roles in the maintenance of rainforest diversity through their interactions with trees and other life forms [5,10]. Apart from a few reports on the positive impacts of lianas on rainforests as physical and nutritional resources for animals [15,55], most research has focused on the negative impacts of lianas on trees and the rainforest as a whole [8,17,18]. Although the role of lianas in nutrient cycling, as discussed in this paper, can be very important in maintaining the high productivity of rainforests, it has received little attention. Lack of understanding of the roles that lianas play in rainforest dynamics may lead to inappropriate practices in rainforest conservation and management. The liana-tree association proposed here provides new insights for further study of lianas and contributes to a better understanding of the maintenance of high biodiversity and of the coexistence of species in rainforest.

Many aspects of the proposed new liana-tree association need to be tested by further investigation and long-term studies. We suggest the following questions as focal points for future studies.

(i) What are the rates and amounts of nutrient transport from lianas to their host trees? The answer to this question is central to formulate the compensatory liana-tree relationship. Isotope techniques can be used to monitor nutrient flow from lianas to trees and verify their function in relocating nutrients in forests.

(ii) What is the contribution of liana leaf litter to litter decomposition in different kinds of forests? The disproportionate leaf litter production of lianas may contribute significantly to nutrient cycling in forests, not only through rapid decomposition of liana leaf litter *per se*, but also by an elevated decomposition rate for the whole forest, as liana leaf litter may also have an additive effect and promote the

decomposition of leaf litter from other plants.

(iii) Are there changes in rooting locations of lianas and host trees across latitude, altitude, and rainfall gradients and during forest regeneration after disturbance? By rooting at different positions, lianas and hosts are able to minimize below-ground competition for nutrients and water. The distance between the rooting positions of lianas and hosts, however, may be affected by environmental factors, such as temperature and water availability, that regulate the transportation efficiency of lianas. We expect this distance will become shorter from low to high latitudes and altitudes and will also shift during forest regeneration through disturbances.

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- 1 Gentry A. The distribution and evolution of climbing plants. In: Putz F, Mooney H, eds. *The Biology of Vines*. Cambridge: Cambridge University Press, 1991. 3–49
- 2 Putz F E, Holbrook N M. Biomechanical studies of vines. In: Putz F, Mooney H, eds. *The Biology of Vines*. Cambridge: Cambridge University Press, 1991. 73–97
- 3 Ewers F W, Fisher J B, Chiu S T. A survey of vessel dimensions in stems of tropical lianas and other growth forms. *Oecologia*, 1990, 84: 544–552
- 4 Putz F E, Chai P. Ecological studies of lianas in Lambir National park, Sarawak, Malaysia. *J Ecol*, 1987, 75: 523–531
- 5 Schnitzer S A, Bongers F. The ecology of lianas and their role in forests. *Trends Ecol Evol*, 2002, 17: 223–230
- 6 Schnitzer S A. A mechanistic explanation for global patterns of liana abundance and distribution. *Am Nat*, 2005, 166: 262–276
- 7 DeWalt S, Ickes K, Nilus R, et al. Liana habitat associations and community structure in a Bornean lowland tropical forest. *Plant Ecol*, 2006, 186: 203–216
- 8 Laurance W F, Perez-Salicrup P, Delamonica P, et al. Rain forest fragmentation and the structure of Amazonian liana communities. *Ecology*, 2001, 82: 105–116
- 9 Schnitzer S A, Carson W P. Treefall gaps and the maintenance of species diversity in a tropical forest. *Ecology*, 2001, 82: 913–919
- 10 Strong D R. Epiphyte loads, tree falls, and perennial forest disruption: A mechanism for maintaining higher tree species richness in the tropics without animals. *J Biogeogr*, 1977, 4: 5–21
- 11 Putz F E. The natural history of lianas on Barro Colorado Island, Panama. *Ecology*, 1984, 65: 1713–1724
- 12 Schnitzer S A, Dalling L, Carson W, et al. The impact of lianas on tree regeneration in tropical forest canopy gaps: Evidence for an alternative pathway of gap-phase regeneration. *J Ecol*, 2000, 88: 655–666
- 13 Phillips O L, Martinez R V, Arroyo L, et al. Increasing dominance of large lianas in Amazonian forests. *Nature*, 2002, 418: 770–774
- 14 Wright S J, Calderon O, Hernandez A, et al. Are lianas increasing in importance in tropical forests? A 17-year record from Panama. *Ecology*, 2004, 85: 484–489
- 15 Aide T, Zimmerman J. Patterns of insect herbivory, growth, and survivorship in juveniles of a Neotropical liana. *Ecology*, 1990, 71: 1412–1421
- 16 Odegaard F. The relative importance of trees versus lianas as hosts for phytophagous beetles (Coleoptera) in tropical forests. *J Biogeogr*, 2000, 27: 283–296
- 17 Stevens G. Lianas as structural parasites: The *Bursera simaruba* example. *Ecology*, 1987, 68: 77–81
- 18 Schnitzer S, Kuzee M, Bongers F. Disentangling above- and below-ground competition between lianas and trees in a tropical forest. *J Ecol*, 2005, 93: 1115–1125
- 19 Wright S J, Jaramillo M A, Pávon J, et al. Reproductive size thresholds in tropical trees: Variation among individuals, species and forests. *J Trop Ecol*, 2005, 21: 307–315
- 20 Schnitzer S A, Parren M P E, Bongers F. Recruitment of lianas into logging gaps and the effects of pre-harvest climber cutting in a lowland forest in Cameroon. *Forest Ecol Manag*, 2004, 190: 87–98
- 21 Schnitzer S A, Carson W P. Lianas suppress tree regeneration and diversity in treefall gaps. *Ecol Lett*, 2010, 13: 849–857
- 22 Perez-Salicrup D R, de Meljere W. Number of lianas per tree and number of trees climbed by lianas at Los Tuxtlas, Mexico. *Biotropica*, 2005, 37: 153–156
- 23 Isnard S, Silk W K. Moving with climbing plants from Charles Darwin's time into the 21st century. *Am J Bot*, 2009, 96: 1205
- 24 Kazda M, Salzer J. Leaves of lianas and self-supporting plants differ in mass per unit area and in nitrogen content. *Plant Biol*, 2000, 2: 268–271
- 25 Salzer J, Matezki S, Kazda M. Nutritional differences and leaf acclimation of climbing plants and the associated vegetation in different types of an Andean montane rainforest. *Oecologia*, 2006, 147: 417–425
- 26 Schimper A F W. *Plant-Geography Upon A Physiological Basis*. Oxford: Clarendon Press, 1903
- 27 Kobe R K, Lepczyk C A, Iyer M. Resorption efficiency decreases with increasing green leaf nutrients in a global data set. *Ecology*, 2005, 86: 2780–2792
- 28 Wright I, Reich P, Cornelissen J, et al. Modulation of leaf economic traits and trait relationships by climate. *Global Ecol Biogeogr*, 2005, 14: 411–421
- 29 Hegarty E. Leaf life-span and leafing phenology of lianes and associated trees during a rainforest succession. *J Ecol*, 1990, 78: 300–312
- 30 Reich P B, Walters M B, Ellsworth D S. Leaf life-span in relation to leaf, plant, and stand characteristics among diverse ecosystems. *Ecol Monogr*, 1992, 62: 365–392
- 31 Zhu S D, Cao K F. Contrasting cost-benefit strategy between lianas and trees in a tropical seasonal rain forest in southwestern China. *Oecologia*, 2010, 163: 591–599
- 32 Cai Z, Bongers F. Contrasting nitrogen and phosphorus resorption efficiencies in trees and lianas from a tropical montane rain forest in Xishuangbanna, south-west China. *J Trop Ecol*, 2007, 23: 115–118
- 33 Lambert J, Arnazon J, Iyer M. Leaf-litter and changing nutrient levels in a seasonally dry tropical hardwood forest, Belize, C.A. *Plant Soil*, 1980, 55: 429–443
- 34 Vitousek P M, Denslow J S. Nitrogen and phosphorus availability in treefall gaps of a lowland tropical rainforest. *J Ecol*, 1986, 74: 1167–1178
- 35 Vitousek P M. Litterfall, nutrient cycling, and nutrient limitation in tropical forests. *Ecology*, 1984, 65: 285–298
- 36 Cleveland C C, Townsend A R, Schmidt S K. Phosphorus limitation of microbial processes in moist tropical forests: evidence from short-term laboratory incubations and field studies. *Ecosystems*, 2002, 5: 680–691
- 37 Kaspari M, Garcia M N, Harms K E, et al. Multiple nutrients limit litterfall and decomposition in a tropical forest. *Ecol Lett*, 2008, 11: 35–43
- 38 McGlynn T P, Salinas D J, Dunn R R, et al. Phosphorus limits tropical rain forest litter fauna. *Biotropica*, 2007, 39: 50–53
- 39 Finzi A C, van Breemen C, Canham C D, et al. Canopy tree-soil interactions within temperate forests: Species effects on soil carbon and nitrogen. *Ecol Appl*, 2008, 18: 440–446
- 40 Sollins P. Factors influencing species composition in tropical lowland rain forest: does soil matter? *Ecology*, 1998, 79: 23–30
- 41 van der Heijden G M F, Phillips O L. What controls liana success in Neotropical forests? *Global Ecol Biogeogr*, 2008, 17: 372–383

- 42 Vitousek P M, Sanford Jr R L. Nutrient cycling in moist tropical forest. *Ann Rev Ecol Evol S*, 1986, 17: 137–167
- 43 Vitousek P M, Porder S, Houlton B Z, et al. Terrestrial phosphorus limitation: Mechanisms, implications, and nitrogen phosphorus interactions. *Ecol Appl*, 2010, 20: 5–15
- 44 Gentry A. Lianas and the “paradox” of contrasting latitudinal gradients in wood and litter production. *Trop Ecol*, 1983, 24: 63–67
- 45 Hladik A. Importance des lianes dans la production foliaire de la forêt équatoriale du Nord-Est du Gabon. *C R Acad Sc*, 1974, 278: 2527–2530
- 46 Putz F E. Liana biomass and leaf area of a “Tierra Firme” Forest in the Rio Negro Basin, Venezuela. *Biotropica*, 1983, 15: 185–189
- 47 Hladik A. Phenology of leaf production in rain forest of Gabon: Distribution and composition of food for folivores. In: Montgomery G G, ed. *The Ecology of Arboreal Folivores*. Washington: Smithsonian Institution Press, 1978. 51–71
- 48 Pragasam L, Parthasarathy N. Litter production in tropical dry evergreen forests of south India in relation to season, plant life-forms and physiognomic groups. *Curr Sci India*, 2005, 88: 1255
- 49 Hegarty E. Leaf litter production by lianes and trees in a sub-tropical Australian rain forest. *J Trop Ecol*, 1991, 7: 201–214
- 50 Penalosa J. Basal branching and vegetative spread in two tropical rain forest lianas. *Biotropica*, 1984, 16: 1–9
- 51 Caballe G. Ramet proliferation by longitudinal splitting in the Gabonese rain forest liana *Dalhousiea africana* S. Moore (Papilionaceae). *Biotropica*, 1994, 26: 266–275
- 52 Brokaw N, Busing R T. Niche versus chance and tree diversity in forest gaps. *Trends Ecol Evol*, 2000, 15: 183–188
- 53 Huston M A, Wolverton S. The global distribution of net primary production: Resolving the paradox. *Ecol Monogr*, 2009, 79: 343–377
- 54 LeBauer D S, Treseder K K. Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed. *Ecology*, 2008, 89: 371–379
- 55 Emmons L H, Gentry A H. Tropical forest structure and the distribution of gliding and prehensile-tailed vertebrates. *Am Nat*, 1983, 121: 513

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