



Can lianas assist in rainforest restoration?

Authors: Campbell, Mason J. , Edwards, Will, Odell, Erica, Mohandass, Dharmalingam, and Laurance, William F.

Source: Tropical Conservation Science, 8(1) : 257-273

Published By: SAGE Publishing

URL: <https://doi.org/10.1177/194008291500800119>

Opinion Article

Can lianas assist in rainforest restoration?

Mason J. Campbell^{1*}, Will Edwards¹, Erica Odell², Dharmalingam Mohandass³ and William F. Laurance¹

¹Centre for Tropical Environmental and Sustainability Science (TESS) and College of Marine and Environmental Sciences, James Cook University, Cairns, Queensland, 4878, Australia

²Faculty of Environmental Sciences, Griffith University, Nathan, Queensland, 4111, Australia

³Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden (XTBG), Chinese Academy of Sciences (CAS), Menglun Town, Yunnan - 666 303. P.R. China

*Corresponding author. Email: mason.campbell@my.jcu.edu.au

Abstract

Can the strategic incorporation of lianas (woody vines) into rainforest restoration plantings enhance biodiversity-conservation outcomes? Lianas are an integral component of primary tropical rainforests yet are often omitted from rainforest restoration plantings as they may damage trees and compete with them for resources. However, there is increasing evidence that many ecological and physiognomic characteristics of lianas may be of some value to restoration plantings, at least in certain contexts. We propose strategies for experimentally incorporating lianas into rainforest-restoration plantings to explore whether they can expedite rainforest establishment and enhance biodiversity-conservation outcomes.

Key words: Afforestation, Reforestation, Regeneration, Revegetation, Vines

Resumen

¿Puede la incorporación estratégica de lianas a plantaciones que buscan restaurar la vegetación de las selvas húmedas, mejorar los resultados para la conservación y la biodiversidad? Las lianas son un componente integral de las selvas húmedas tropicales, sin embargo, son omitidas frecuentemente en plantaciones que buscan restaurar bosques, ya que estas pueden dañar los árboles y competir con ellos por recursos. No obstante, evidencia creciente indica que muchas características ecológicas y físicas de las lianas pueden tener cierto valor para las plantaciones de restauración, por lo menos en algunos contextos. Nosotros proponemos estrategias para la incorporación experimental de lianas a las plantaciones de restauración, con el fin de explorar si las lianas pueden acelerar el establecimiento de la vegetación, mejorando así los resultados para la conservación y la biodiversidad.

Palabras clave: Aforestación, lianas, reforestación, regeneración, revegetación

Received: 7 August 2013; Accepted 13 August 2014; Published: 23 March 2015

Copyright: © Mason J. Campbell, Will Edwards, Erica Odell, Dharmalingam Mohandass and William F. Laurance. This is an open access paper. We use the Creative Commons Attribution 4.0 license <http://creativecommons.org/licenses/by/3.0/us/>. The license permits any user to download, print out, extract, archive, and distribute the article, so long as appropriate credit is given to the authors and source of the work. The license ensures that the published article will be as widely available as possible and that your article can be included in any scientific archive. Open Access authors retain the copyrights of their papers. Open access is a property of individual works, not necessarily journals or publishers.

Cite this paper as: Campbell, M. J., Edwards, W., Odell, E., Mohandass, D. and Laurance, W. F. 2015. *Can lianas assist in rainforest restoration?* *Tropical Conservation Science* Vol.8 (1): 257-273. Available online: www.tropicalconservationscience.org

Introduction

Lianas limit seedling recruitment, damage saplings, compete with trees for limited resources and increase tree mortality [1-5], resulting in their deliberate exclusion from rainforest-restoration efforts. However, as knowledge of liana ecology increases [e.g. 6, 7, 8], it is becoming apparent that they often play an integral role in supporting local biodiversity and overall forest functioning. Consequently, it is possible that many of their ecological and physiognomic characteristics could be strategically exploited to enhance and accelerate rainforest-restoration processes. Here we propose questions to be answered by the experimental incorporation of strategic liana plantings into rainforest restoration efforts (Table 1) in the hope that these will be trialled and their value to restoration practitioners determined. Additionally, we suggest why we think these liana-planting strategies could potentially expedite rainforest establishment and improve biodiversity-conservation outcomes.

Table 1. Potential topics for experimental examination using strategic liana plantings in rainforest restoration plots

1.	Does planting lianas on the edge of rainforest restoration plots result in the rapid obtainment of a preferential forest interior micro-climate leading to a decrease in shade-intolerant weed species incursions?
2.	Does the planting of a liana and tree species mix expedite closed-canopy attainment and limit shade-intolerant weed abundance?
3.	Does incorporating lianas into deciduous-rainforest restoration plantings assist in minimizing weed incursions?
4.	Does the addition of lianas to restoration plantings increase nutrient turnover and soil biota diversity?
5.	Does planting lianas in locations with exposed soil surfaces aid in soil erosion mitigation and limit localized shade-intolerant weed germination?
6.	Does planting lianas on deciduous rainforest restoration plot edges result in a decrease in low-intensity fire incursions?
7.	Does planting lianas on restoration plot edges lessen wind damage in early successional stages?
8.	Does planting lianas at restoration sites containing a heavy undesirable tree species load decrease tree vigour, abundance and recruitment?
9.	Could linear plantings of lianas within restoration corridors aid faunal dispersal?
10.	Could faunal movement within restoration plantings be guided by densely-planting thorny lianas or rattans?
11.	Does incorporating lianas into restoration plantings support enhanced mammalian and insect diversity through the provision of additional food resources?
12.	Could including lianas within restoration plantings lessen herbivorous insect damage to planted trees?
13.	Does the addition of liana species with conspicuous fruits and flowers to restoration site plantings aid in the passive introduction of tree species and novel genetic material?
14.	Can the practical impediments to liana incorporation in restoration plantings be overcome?

Weed management, soil management and soil fauna support

- 1. Does planting lianas on the edge of rainforest restoration plots result in the rapid obtainment of a preferential forest interior micro-climate leading to a decrease in shade-intolerant weed species incursions?**

Comprising on average only 4-5% of the total biomass of a lowland moist rainforest [9, 10], lianas produce up to 40% of all leaves in the forest [10-13]. Hence, leaf-litter production from lianas in tropical forests is much greater than would be expected from their biomass contribution alone [14]. Additionally, lianas

produce leaves rapidly in comparison to most canopy-forming trees because their leaves typically have a low leaf-mass-to-area ratio (LMA) and a short lifespan [15-18]. The prodigious and rapid leaf output of lianas might be beneficial to the restoration process, and could be used to limit the incursion of shade-intolerant weeds into semi-established restoration plots. To test this idea, lianas would need to be planted on the forest edge to vegetatively 'seal' it [19-21], thereby creating a dark forest-interior, unsuitable for shade-intolerant weed colonization [21, 22]. Planting lianas along restoration-plot margins in conjunction with bushy tree or shrub species (to act as climbing trellises), might allow for faster and more complete 'sealing' of forest edges than would occur by using tree species alone [17, 23, 24]. If so, this edge sealing would be an important contribution to restoration efforts as weeds are "probably the most important obstacle to ecological restoration... and may completely stop ... or deflect succession" in restoration plots [22].

In support of this edge-planting strategy, lianas are known to be more abundant on primary and remnant forest edges than in their interiors [25-29]. Therefore, dense planting of lianas on restoration-plot edges may simply hasten edge sealing due to this underlying successional process [21, 30, 31]. As an added benefit, restoration plots that have been sealed by lianas may also suffer less from detrimental forest edge effects, such as increased light penetration and desiccation [32, 33]. However, if this planting strategy were undertaken, it is likely that the trees on the edge of the restoration plots would also suffer proportionally more deleterious impacts due to increased liana infestations, as occurs "naturally" for trees on the edge of primary and remnant forests [25]. This may be a trade-off regeneration practitioners would need to accept if they were to include lianas in restoration edge-plantings. Regardless, an experimental examination of the value of planting lianas on restoration plot edges would enable comparison of the costs and benefits of this planting strategy.

2. Does the planting of a liana and tree species mix expedite closed-canopy attainment and limit shade-intolerant weed abundance?

Planting lianas among juvenile trees in an existing restoration plot would allow one to assess their value for use as a means of reducing the time required until forest canopy-closure. A key goal for rainforest restoration is minimising the time to establish a closed-canopy because this helps to eliminate shade-intolerant weed species, thereby decreasing weed-management costs [34]. Additionally, restoration sites with a closed canopy may provide suitable conditions for the passive recruitment of shade-tolerant, forest-interior tree species [31], thereby increasing the biodiversity value of the site. Canopy establishment within rainforest-restoration sites using pioneer tree species alone often takes many years [22]. Lianas, due to their rapid growth rates [17, 23, 24], may significantly accelerate canopy closure as they can potentially cover large areas of forest canopy within short periods, as they have previously been found to do following a disturbance [35, 36]. An experiment to determine whether planting lianas within semi-established restoration plots accelerates canopy-closure, and at what cost to the resident trees this occurs, would provide restoration practitioners with the empirical data with which to assess the ecological value of lianas in this role. Additionally, experimentally evaluating lianas as a means of rapid canopy closure, would allow for the determination of the economic costs versus benefits associated with the differing planting strategies of either a dense tree seedling planting without lianas or a less dense tree spacing with them.

Admittedly, integrating liana and tree planting for faster canopy establishment would likely result in a lowered forest canopy height [30, 31]. Additionally, the greater abundance of lianas within plantings could potentially increase tree damage and reduce tree growth rates and fecundity [1-4]. As the restored forest approached maturity, however, liana abundance would likely decline due to natural successional

processes [37-39]. Moreover, if the desired outcome of the restoration process was to obtain a closed-canopy in the shortest possible time, a decrease in tree health may be a lesser concern. For example, rapid canopy closure at the expense of tree health may be the priority when creating a faunal movement corridor to link isolated remnant forest blocks [40]. Such a corridor might require rapid closed-canopy establishment at the expense of tree health to facilitate the earliest possible useage by animals, since the local extinction of animal species in isolated forest fragments can occur relatively quickly [41].

3. Does incorporating lianas into deciduous-rainforest restoration plantings assist in minimizing weed incursions?

Incorporating lianas into deciduous-rainforest restoration plantings could potentially assist in minimizing weed incursions. Within seasonal rainforests, many canopy tree species are deciduous or dormant during periods of water stress [42]. When canopy trees shed leaves an increased penetration of light into the forest provides the ground-layer vegetation with an enhanced level of photosynthetically active radiation (PAR) [43, 44]. In addition, canopy trees are often “dormant” during periods of deciduousness and as such provide decreased competition for soil resources such as water and nutrients [45, 46]. As a consequence, deciduous forests often experience considerable weed incursions particularly during periods of water stress [47]. Lianas often retain their canopy [however see 12] and remain photosynthetically active during periods of water stress at locations where forest trees are deciduous [24]. They can remain evergreen and photosynthetically active due to their proportionately large root investment when compared to trees [17, 24, 48] and efficient vascular system, both of which enhances their ability to access and use ground water [24, 49]. Thus, lianas could potentially be used to minimize weed incursions at deciduous forest restoration sites, especially during periods of water stress, through limiting the availability of PAR and competing for limited soil resources [46, 50].

4. Does the addition of lianas to restoration plantings increase nutrient turnover and soil biota diversity?

The limited availability of soil nutrients, particularly plant-available nitrogen, commonly impedes restoration efforts [51, 52]. Nutrient limitation is often a result of slow mineralisation because of a lack of soil biota [53]. Soil organisms are imperative to ecosystem functioning and contribute significantly to nutrient cycling, decomposition, mineralisation, and maintenance of soil structure [54-56]. Soil organisms are often lacking in restoration sites as a consequence of previous site-management practices [56, 57]. The inclusion of lianas into restoration plantings could rapidly augment soil organic matter through fast leaf production and turnover [10-13, 15-18] which may in turn increase the abundance of soil fauna. As a consequence, improved soil health and nutrient mineralisation rates would result. If lianas were found to provide any improvement to soil health and nutrient mineralisation rates this function may be particularly beneficial for restoration sites located on nutrient limited soils.

Can lianas support beneficial soil arthropods in restoration plantings? Liana leaves differ from leaves of other plants in a variety of ways [17]. In general, liana leaves have lower leaf mass per unit area (LMA) and higher nutrient concentrations compared to leaves from trees and shrubs [14, 56, 58]. As a result, leaves from lianas may decompose faster [however see 59] and produce more nutritious organic matter for soil organisms [14]. This feature has been suggested to create a source of nutrients around the base of host trees [14], and may also provide some insight as to why lianas are often linked with nutrient-rich soils [11, 60, 61]. Encouraging the return of beneficial soil arthropods through decomposing liana leaf litter in restoration plantings could additionally, potentially promote the decomposition of associated tree litter.

5. Does planting lianas in locations with exposed soil surfaces aid in soil erosion mitigation and limit localized shade-intolerant weed germination?

Lianas could potentially assist in decreasing soil erosion at restoration sites through the increased addition of leaves to the soil surface. In the tropics, bare soils are often prone to erosion [62] and nutrient leaching due to heavy rainfall [e.g. 63]. The rapid addition of leaves to the soil surface of restoration sites by lianas could potentially act as a mechanism of “natural mulching”, limiting the impact of raindrops and decreasing soil erosion [64–66]. Additionally, any augmentation of vegetative material to the soil surface by lianas could potentially slow the overland flow of surface water during rainfall events and promote water infiltration into the soil [65, 66]. As a potential additional benefit, liana leaves on the soil surface may decrease the amount of bare soil available for weed species to colonize [67].

Site protection and management

6. Does planting lianas on deciduous rainforest restoration plot edges result in a decrease in low-intensity fire incursions?

Experimentally planting lianas within restoration plots would permit the determination of their value for improving several site protection and management issues, such as the minimization of low-intensity fire incursions. The ability of lianas to maintain an evergreen canopy during periods of water-stress [24, 49] as well as their production of new leaves along fire-vulnerable forest edges [68] may make combustion of these forests less likely [51, 69]. There are two reasons for this. First, an evergreen canopy may retain higher sub-canopy humidity levels through the trapping of transpired moisture [51, 69]. Second, the new leaves lianas produce along fire-vulnerable forest edges [68] are less flammable than older leaves due to their higher moisture contents [70]. One possible negative aspect of planting lianas on forest edges to limit fire incursions is that, as mentioned previously, lianas produce proportionately more leaf-litter than trees [10–13], which could potentially increase the fuel load of a restoration site. Consequently, experimentally determining whether lianas do indeed limit low-intensity fire incursions into restoration plots may be of significant value, particularly as fire is a major and increasing cause of forest damage in many tropical forest regions [68, 69, 71, 72].

7. Does planting lianas on restoration plot edges lessen wind damage in early successional stages?

Determining the value of lianas as a means of reducing wind damage to restoration plantings is another site protection issue worthy of experimental exploration. Restoration sites are often forest fragments and as such suffer significantly more wind damage than do non-fragmented forests [73]. Lianas may help minimise some wind impacts as they are known to bind trees together, protecting them against wind damage [29], and this in turn reduces wind-induced gap formation in young forest stands [74]. However, lianas have also been found to enhance wind induced-tree falls in older forest stands and increase tree mortality by pulling down adjacent trees when a treefall does occur [29, 74, 75]. Consequently, experimental studies of lianas in restoration plots should determine both the overall value of lianas as a means of reducing wind damage to forests and the temporal management requirements to reduce negative effects i.e. when, and if, management is required to remove them as the forest ages.

8. Does planting lianas at restoration sites containing a heavy undesirable tree species load decrease tree vigour, abundance and recruitment?

Lianas could potentially be a useful restoration site management tool for decreasing woody-weed abundance and vigour prior to tree planting. Lianas compete strongly with trees for limited soil and light resources, increase tree mortality and decrease both tree establishment success and fecundity [1–5, 76]. Consequently, dense plantings of lianas at restoration sites containing an undesirable tree species composition may be a relatively inexpensive and efficient ancillary method of decreasing undesirable tree

species abundances. This practice could reduce management costs prior to site clearing and planting. Granted, the cost and labour requirements of planting lianas may be quite high and the lianas in turn may require removal themselves prior to site preparation. However, if a non-clonal liana species was used and the locations of the plantings were recorded (Table 2), liana removal could potentially be cheaper and less arduous than the management of the uncontrolled undesirable tree species.

Table 2. Cautionary notes on the experimental planting of lianas during rainforest restoration

1.	Lianas should be planted away from desirable trees to prevent underground competition
2.	Lianas should be planted near desired trees only after the trees are established and structurally capable of supporting the weight of lianas
3.	Preferentially use liana species that predominantly reproduce sexually to prevent excessive site colonization through the clonal pathway
4.	Preferentially avoid using liana species that climb by main stem twinning as they may girdle and damage desirable trees. Other liana climbing types that may be substituted for main stem twiners include those that climb by tendrils, hooks/spines or adventitious roots
5.	Preferentially use liana species that are indigenous to the local region as many exotic species of lianas are serious rainforest weeds. Additionally, indigenous liana species are likely to better handle localized climate, topographical and altitudinal conditions
6.	If lianas are to be removed once a fully functioning tree species canopy is established, then their location must be carefully recorded for future re-location. Additionally, single stemmed (non-clonal) species should be selected for efficient future removal (cutting)
7.	Lianas can damage small trees and suppress natural succession if they are planted too early in the revegetation process or left on site without management

Faunal conservation and lianas in restoration plots

9. Could linear plantings of lianas within restoration corridors aid faunal dispersal?

Facilitating the safe movement of endangered faunal species across fragmented landscapes is often a major reason for initiating rainforest restoration efforts [40, 77]. Consequently, restoration sites often exist as corridors between larger blocks of rainforest; created to aid animal movement [e.g. 40, 77, 78]. Experimental, strategic planting of lianas within restoration corridors could be done to determine whether they enhance faunal dispersal capabilities, as lianas are well known to function as both aerial pathways (i.e. natural rope bridges) and nesting sites for a diverse array of animal species (Fig. 1) [11, 79-82]. Furthermore, experimentation could determine whether lianas allow animals to traverse corridors while remaining in the canopy [83], thereby lessening the risk of ground predation by both wild and domestic predators [84, 85].

10. Could faunal movement within restoration plantings be guided by densely-planting thorny lianas or rattans?

Restoration practitioners often wish to focus animal movements; for example, by directing them towards strategically placed road culverts, or away from dangers such as nearby roads. This is frequently achieved via the erection of expensive artificial barriers such as fences [86]. Dense stands of liana or rattan species that possess prodigious thorns or spines often form an almost impenetrable “wall” of vegetation that limits both large-animal and human movement (M. Campbell, pers. obs.). Thorny lianas are often especially prevalent in areas of past disturbance such as treefall gaps (Fig. 1) [7, 87]. Consequently, strategic linear “wall” plantings of thorny liana or rattan species in areas of high disturbance such as the

forest edges of restoration sites [19, 21, 33, 88, 89], could be trialled as a short-term, cost-effective and natural alternative to artificial barrier erection.



Fig. 1. Upper photo left: The flowers of the Burny Bean (*Mucuna gigantea*) liana host aphids which in turn are farmed for their “honey dew” by Green Ants (*Oecophylla smaragdina*); photo credit: Mason Campbell. Upper right photo: A Green Ring Tail Possum (*Pseudochirops archeri*) uses a liana to traverse the rainforest canopy; photo credit: Mason Campbell. Bottom-left photo top: A recent treefall clearing is fully colonized by the rattan known as Yellow Layer Cane (*Calamus moti*) preventing large animal and human movement; photo credit: Mason Campbell. Bottom-right photo: The fearsome spines on the canes of the Yellow Layer Cane (*Calamus moti*); photo credit: Mason Campbell.

Lianas as a food source and a distraction for herbivores

11. Does incorporating lianas into restoration plantings support enhanced mammalian and insect diversity through the provision of additional food resources?

Lianas produce leaves that are less chemically and/or structurally protected than those of many tree species [15, 17, 18]. As a result, lianas often provide an important component of the overall food intake of mammalian folivores (leaf eaters), particularly under localized conditions where tree diversity is reduced (i.e. degraded forest fragments) [79, 82, 90-92]. Restoration plots are often tree-species poor due to time and resource constraints [22]. Consequently, the experimental addition of liana species to restoration plantings could determine whether their presence results in an increase in the abundance and rate of site usage of mammalian folivores.

Lianas also play an important role in the structuring and maintenance of local arthropod diversity. Many phytophagous beetles and Lepidopterans are intimately linked to lianas and depend solely on their availability for survival [93-95]. Lianas aid insect diversity by creating a variety of complex and suitable habitats (Fig. 1) [96, 97] and are at least as important a food source for herbivorous insects as canopy trees [94]. This importance may be due to the fact that, as mentioned above, liana leaves in general contain less foliar biochemical defences than tree leaves [15]. Additionally, in general, lianas direct greater concentrations of nitrogen and phosphorus to their leaves than trees [14, 18, 58, 98] both of which are important for supporting many energetic and cellular processes in insects [99, 100]. Liana leaves are thus more nutritious and pose a considerably lower threat to insects than tree leaves. Additionally, lianas turnover leaves faster than trees [15-18] and young leaves are generally attacked by insects more often than are older leaves, presumably because of their higher palatability and digestibility [101, 102]. It is likely these features are of great importance to maintaining insect herbivore assemblages, particularly during the dry season when new leaves and other food sources may be scarce. Consequently, experimentally including lianas within restoration plantings may be used to determine whether they are of assistance in enhancing localized arthropod diversity and conservation.

12. Could including lianas within restoration plantings lessen herbivorous insect damage to planted trees?

Herbivory can often be problematic during the early stages of regeneration, especially for young trees. Intensively grazed individuals may suffer reduced developmental rates [103] and a lowered capacity to compensate for other environmental stressors [104-106]. Lianas could potentially decrease insect herbivory of trees within restoration sites by acting as a “distraction” to herbivorous insects. Again, this might be expected as a function of liana leaves representing a high quality and quantity food source (as described above). For instance, Foaham [107] found that insect herbivory on trees was greatest in forests where lianas had been removed, suggesting liana presence within restoration plots could potentially aid in mitigating insect herbivory of trees. Furthermore, there are potential flow-on benefits. For example, if lianas were found to lessen insectivorous herbivore pressure on trees, restoration practitioners could potentially decrease insecticide usage, possibly resulting in less accidental negative impacts on important non-targeted insect species such as predatory insects and beneficial soil arthropods.

Lianas as an attraction for seed dispersers

13. Does the addition of liana species with conspicuous fruits and flowers to restoration site plantings aid in the passive introduction of tree species and novel genetic material?

Many restoration sites are established using a framework-species approach because of the cost-efficient nature of this method [108]. This restoration technique aims to incorporate a few highly fecund and often conspicuous, flower- or fruit-producing tree species within plantings to attract seed dispersers [usually

frugivorous birds or bats]; with the aim of increasing the likelihood of further passive introductions of tree species [through droppings] and genetic material to the site [22, 108, 109]. Many liana species are both prolific flower and fruit producers [110-112], providing copious food resources that attract both pollinators and frugivores [79, 93, 113-116]. For instance, Boulter et al. [111] found liana flowers to be, on average, more colourful than those of the resident tree species in the rainforest of Australia's Wet Tropics bioregion. Similarly, Ansell et al. [116] found logged Bornean rainforests with a high abundance of lianas contained higher bird species richness, in particular obligate frugivores, than forests with a low liana abundance. Furthermore, lianas may have the potential to enhance the sustained attraction of seed dispersers to forests as Wright and Calderon [110] found in their long-term study (17 years) of the Barro Colorado Island forest where lianas have exhibited a significantly greater increase in both flower and fruit production over time than the resident tree species. Consequently, the experimental inclusion of lianas into restoration plantings could enable the determination of their value for attracting pollinators and frugivorous seed dispersers to restoration sites as a means of facilitating passive tree species and genetic diversity introductions in both the immediate and long-term.

14. Can the practical impediments to liana incorporation in restoration plantings be overcome?

As well as determining the ecological value of lianas to rainforest restoration, resolving the practical and economic constraints of liana usage would need to occur prior to their regular incorporation into restoration plantings. For instance, it is likely that lianas would not be easy to maintain in a plant nursery setting because their growth habit would require regular cutting back and structural support prior to planting out. However, this restriction may not be overly onerous as climbing plants are widely used in the horticultural trade [112] and as such initial practical advice may be sought there and subsequently built upon.

In addition to the maintenance of lianas within nurseries, ascertaining the appropriate time to plant them during restoration trials would be vital if the strategy is to be successful. In particular, lianas require a tree trunk or foliage (trellis) of a suitable diameter to climb [29] and in certain cases these may not be available until planted trees are several years old. Conversely, if lianas were introduced at the initial tree planting stage their vigorous growth may overwhelm and smother tree seedlings as they do in forest treefall gaps [2, 5, 7]. Consequently, trials of liana plantings during different restoration successional phases and in conjunction with different trellis partners (e.g. shrubs, trees and fallen logs) would likely allow strategy conferring maximum efficiency and effectiveness to be determined.

As well as determining the correct temporal usage of lianas in restoration plantings, understanding their effective spatial usage could be an initial practical and economic consideration. For example, determining how many lianas should be incorporated into a planting and how this changes depending upon the required outcome or goal (as per sub-headings above) would enable increased efficiency in their ecological and economic usage. Additionally, determining how planting density interacts with the scale of the restoration effort, is vital foundation knowledge especially when determining the economic viability of the practice.

Discussion

Since the reinvigoration of liana ecological research in the 1970s, evidence of the negative impacts of lianas on rainforest trees have been accumulating [1-5]. It is now abundantly clear that lianas damage saplings, compete with trees for limited resources, prevent tree recruitment in canopy gaps and increase tree mortality [e.g. 1-5]. However, this strong flow of empirical evidence may be masking the fact that

liana species (and the ecological strategies they employ) are often nearly as diverse as the tree species with which they compete [e.g. 7, 11, 117]. Thus, complete exclusion of all liana species from restoration plantings in response to the potential threat that individual species or climbing guilds display ignores the now equally abundant fact that some lianas, under certain conditions, can support considerable biodiversity [79, 82, 90-95, 113-116], assist in regulating forest microclimate [17, 118, 119] and are invaluable in forest wide processes such as nutrient turnover through enhanced and rapid leaf litter production [10-14, 17, 23, 24].

In addition to supporting biodiversity and aiding ecological and geochemical processes, the fact that many liana species are themselves rare [11, 25, 120, 121] and threatened with localized extinction due to anthropological threats, may alone, justify their inclusion in biodiversity restoration plantings. For instance, numerous studies of geographically distinct rainforests have found that lianas make up a considerable proportion of the local woody plant diversity [e.g. 7, 11, 117] of which rare liana species often comprise a substantial fraction [11, 25, 120, 121]. As such, it is highly likely that they are threatened by the same deleterious effects of deforestation and forest degradation (e.g. fragmentation) as rare tree species [122-124]. Consequently, excluding all liana species from restoration efforts, and in particular rare liana species, may result in the loss of considerable localized liana diversity with likely flow-on effects to reliant faunal species.

Selectively utilizing the morphological features and ecological functions of liana species by strategically incorporating (Table 1, 2 and 3) them within rainforest restoration efforts may have the potential to considerably enhance restoration efficiency and biodiversity conservation outcomes. However, the magnitude of any benefit can only be determined through the outcomes of experimental plantings. It is clear that including lianas in restoration efforts will be costly in terms of funds, time and labour. Moreover, if done incorrectly (Table 2), excessive on-site liana abundance could occur [125, 126]. Yet, the current practice of complete liana exclusion from restoration sites followed by eventual self-recruitment is equally fraught with costs. For instance, allowing for liana species self-recruitment is likely to result in a resident liana community composition that is non-representative of the landscape-wide species composition [25, 28, 122, 123] as it is determined by dispersal capabilities and site locality [123, 124]. Intrinsically, a local liana community that represents a small subset of the landscape-wide community is likely to support lower levels of biodiversity, especially in forests where a high degree of mutualism exists [127]. Additionally, allowing self-recruitment may result in a high abundance of lianas occurring in non-preferred areas of restoration plots increasing overall management costs. Conversely, deliberate planting of lianas allows for the spatial location and liana community composition to be determined, at least to a reasonable extent, *A priori* and thus species and their relative distributions can be tailored to match management goals.

Until the benefits and costs of strategic liana usage in restoration efforts are experimentally quantified we can only guess at their potential value for restoration practitioners and ultimately restored forests. As such, we propose that selected lianas (Table 3) be experimentally and strategically incorporated into rainforest restoration plantings (Tables 1 and 2) to assess whether they can enhance biodiversity conservation and expedite rainforest restoration efforts. As primary rainforests throughout the world continue to be deforested and degraded [128-130], maximising the efficiency and effectiveness of rainforest restoration techniques is becoming increasingly essential for the long-term sustainability of this ecosystem and its constituent biota.

Table 3. Desirable liana traits for restoration experimentation

Desirable trait	Potential benefits for experimental exploration*
1. High leaf production and turnover	-Enhance forest edge sealing and shade-intolerant weed species exclusion (1) -Increase nutrient turnover and soil biota diversity (4) -Lessen soil erosion (5)
2. Rapid growth rate	-Enhance forest edge sealing, forest canopy closure and shade-intolerant weed species exclusion (1, 2)
3. High nutrient content in leaves	-Increase nutrient turnover and soil biota diversity (4) -Support faunal site usage and abundance (11) -Lessen herbivorous insect damage to planted trees (12)
4. Evergreen canopy with regular new leaf production	-Decrease weed abundance in deciduous rainforests (3) -Decrease low-intensity fire incursions (6) -Lessen soil erosion (5)
5. Good inter-tree linkage capabilities	-Limit wind damage to young forests (7) -Enhance faunal dispersion capabilities and lessen their predation by ground dwelling predators (9)
6. High competitive resource capture rate and negative impacts on trees#	-Decrease undesirable tree: vigour, abundance and recruitment (8)
7. Heavily armed stems and leaves with a capability to grow in dense stands	-Guide animal movement (10)
8. Palatable foliage with low levels of structural and chemical defence	-Enhanced mammalian and insect diversity through food provision (11) -Lessen herbivorous insect damage to planted trees through distraction (12)
9. Species possessing animal dispersed, conspicuous fruits and flowers with high nectar and other "attractant" properties	-Attract seed dispersers and pollinators to aid in the passive introduction of tree species and novel genetic material (13)

Note this trait is desirable solely for restoration sites containing a heavy undesirable tree species load and is not compatible with the other proposed usages of lianas in restoration plantings

*Numbers in brackets represent the experimental topic for investigation as per Table 1

Acknowledgements

This research was supported by an Australian Research Council Discovery Grant awarded to William F. Laurance. The authors would like to thank Ana Palma for her assistance and three anonymous reviewers for their constructive comments.

References

- [1] Ingwell, L.L., Wright, S. J., Becklund, K. K., Hubbell, S. P. and Schnitzer, S. A. 2010. The impact of lianas on 10 years of tree growth and mortality on Barro Colorado Island, Panama. *Journal of Ecology* 98:879-887.
- [2] Schnitzer, S.A. and Carson, W.P. 2010. Lianas suppress tree regeneration and diversity in treefall gaps. *Ecology Letters* 13:849-857.
- [3] Schnitzer, S.A., Kuzee, M.E. and Bongers, F. 2005. Disentangling above- and below-ground competition between lianas and trees in a tropical forest. *Journal of Ecology* 93:1115-1125.
- [4] Stevens, G.C. 1987. Lianas as structural parasites: the *Bursera simaruba* example. *Ecology* 68: 77-81.
- [5] Schnitzer, S.A., van der Heijden, G.M.F., Mascaro, J. and Carson, W.P. 2014. Lianas in gaps reduce carbon accumulation in a tropical forest. *Ecology* 95:3008-3017.

- [6] Putz, F.E. and Mooney, H. A. Eds. 1991. *The biology of vines*. Cambridge: Cambridge University Press.
- [7] Schnitzer, S. A. and Bongers, F. 2002. The ecology of lianas and their role in forests. *Trends in Ecology & Evolution* 17:223-230.
- [8] Schnitzer, S.A. and Bongers, F. 2011. Increasing liana abundance and biomass in tropical forests: emerging patterns and putative mechanisms. *Ecology Letters* 14:397-406.
- [9] DeWalt, S.J. and Chave, J. 2004. Structure and biomass of four lowland Neotropical forests. *Biotropica* 36:7-19.
- [10] Putz, F.E. 1983. Liana biomass and leaf area of a "Tierra Firme" forest in the Rio Negro Basin, Venezuela. *Biotropica* 15:185-189.
- [11] Gentry, A.H. 1991. The distribution and evolution of climbing plants. In: *The biology of vines*. Putz, F.E. and Mooney, H.A. (Eds.), pp.3-49. Cambridge University Press, Cambridge.
- [12] Hegarty, E.E. 1991. Leaf litter production by lianes and trees in a sub-tropical Australian rain forest. *Journal of Tropical Ecology* 7:201-214.
- [13] Hladik, A. 1974. Importance des lianes dans la production foliaire de la forêt équatoriale du nord-est du Gabon. *Comptes rendus hebdomadaires des séances de l'Académie des sciences. D, Sciences naturelles* 278:2527-2530.
- [14] Tang, Y., Kitching, R. and Cao, M. 2012. Lianas as structural parasites: A re-evaluation. *Chinese Science Bulletin* 57:307-312.
- [15] Asner, G.P. and Martin, R.E. 2012. Contrasting leaf chemical traits in tropical lianas and trees: implications for future forest composition. *Ecology Letters* 15:1001-1007.
- [16] Cai, Z.Q., Schnitzer, S.A. and Bongers, F. 2009. Seasonal differences in leaf-level physiology give lianas a competitive advantage over trees in a tropical seasonal forest. *Oecologia* 161:25-33.
- [17] Wyka, T.P., Oleksyn, J., Karolewski, P. and Schnitzer, S.A. 2013. Phenotypic correlates of the lianescent growth form: a review. *Annals of Botany* 112:1667-1681.
- [18] Zhu, S.D. and Cao, K.F. 2010. Contrasting cost-benefit strategy between lianas and trees in a tropical seasonal rain forest in southwestern China. *Oecologia* 163:591-599.
- [19] Harper, K.A., Macdonald, S.E., Burton, P.J., Chen, J., Brososke, K.D., Saunders, S.C., Euskirchen, E.S., Roberts, D., Jaiteh, M.S. and Esseen, P-A. 2005. Edge influence on forest structure and composition in fragmented landscapes. *Conservation Biology* 19:768-782.
- [20] Strayer, D.L., Power, M. E., Fagan, W. F., Pickett, S. T. A. and Belnap, J. 2003. A classification of ecological boundaries. *Bioscience* 53:723-729.
- [21] Williams-Linera, G. 1990. Vegetation structure and environmental conditions of forest edges in Panama. *Journal of Ecology* 78:356-373.
- [22] Goosem, S. and Tucker, N. I. J. 2013. *Repairing the rainforest (second edition)*. Wet Tropics Management Authority and Biotropica Australia Pty Ltd, Cairns.
- [23] Paul, G.S. and Yavitt, J.B. 2011. Tropical vine growth and the effects on forest succession: a review of the ecology and management of tropical climbing plants. *The Botanical Review* 77:11-30.
- [24] Schnitzer, S.A. 2005. A mechanistic explanation for global patterns of liana abundance and distribution. *American Naturalist* 166:262-276.
- [25] Laurance, W.F., Perez-Salicrup, D., Delamonica, P., Fearnside, P.M., D'Angelo, S., Jerozolinski, A., Pohl, L. and Lovejoy, T.E. 2001. Rain forest fragmentation and the structure of Amazonian liana communities. *Ecology* 82:105-116.
- [26] Magrach, A., Rodríguez-Pérez, J., Campbell, M. and Laurance, W.F. 2014. Edge effects shape the spatial distribution of lianas and epiphytic ferns in Australian tropical rain forest fragments. *Applied Vegetation Science* 17:754-764.

- [27] Mohandass, D., Hughes, A.C., Campbell, M. and Davidar, P. 2014. Effects of patch size on liana diversity and distributions in the tropical montane evergreen forests of the Nilgiri Mountains, southern India. *Journal of Tropical Ecology* 30:579-590.
- [28] Zhu, H., Xu, Z.F., Wang, H. and Li, B. G. 2004. Tropical rain forest fragmentation and its ecological and species diversity changes in southern Yunnan. *Biodiversity and Conservation* 13:1355-1372.
- [29] Putz, F.E. 1984. The natural history of lianas on Barro-Colorado island, Panama *Ecology* 65:1713-1724.
- [30] Oliveira, A.T., deMello, J. M. and Scolforo, J. R. S. 1997. Effects of past disturbance and edges on tree community structure and dynamics within a fragment of tropical semideciduous forest in south-eastern Brazil over a five-year period (1987-1992). *Plant Ecology* 131:45-66.
- [31] Chazdon, R.L. 2014. *Second growth: The promise of tropical forest regeneration in an age of deforestation*. University of Chicago Press, Chicago.
- [32] Laurance, W.F., Delamonica, P., Laurance, S. G., Vasconcelos, H.L. and Lovejoy, T. E. 2000. Conservation: Rainforest fragmentation kills big trees. *Nature* 404:836-836.
- [33] Laurance, W.F., Lovejoy, T.E., Vasconcelos, H.L., Bruna, E.M., Didham, R.K., Stouffer, P.C., Gascon, C., Bierregaard, R.O., Laurance, S.G. and Sampaio, E. 2002. Ecosystem decay of Amazonian forest fragments: A 22-year investigation. *Conservation Biology* 16:605-618.
- [34] Wagner, S., Fischer, H. and Huth, F. 2011. Canopy effects on vegetation caused by harvesting and regeneration treatments. *European Journal of Forest Research* 130:17-40.
- [35] Webb, L.J. 1958. Cyclones as an ecological factor in tropical lowland rainforest, north Queensland. *Australian Journal of Botany* 6:220-230.
- [36] Catterall, C.P., McKenna, S., Kanowski, J. and Piper, S.D. 2008. Do cyclones and forest fragmentation have synergistic effects? A before–after study of rainforest vegetation structure at multiple sites. *Austral Ecology* 33:471-484.
- [37] DeWalt, S.J., Schnitzer, S.A., and Denslow, J.S. 2000. Density and diversity of lianas along a chronosequence in a central Panamanian lowland forest. *Journal of Tropical Ecology* 16:1-19.
- [38] Letcher, S.G. and Chazdon, R.L. 2009. Lianas and self-supporting plants during tropical forest succession. *Forest Ecology and Management* 257:2150-2156.
- [39] Letcher, S.G. and Chazdon, R.L. 2009. Rapid recovery of biomass, species richness, and species composition in a forest chronosequence in northeastern Costa Rica. *Biotropica* 41:608-617.
- [40] Lamb, D., Parrotta, J., Keenan, R. and Tucker, N. I. J. 1997. Rejoining habitat remnants: Restoring degraded rainforest lands. In: *Tropical forest remnants: ecology, management and conservation of fragmented communities*. Laurance, W.F. and Bierregaard Jr, R.O. (Eds.) pp.366-385. The University of Chicago Press, Chicago.
- [41] Gibson, L., Lynam, A.J., Bradshaw, C.J.A., He, F., Bickford, D.P., Woodruff, D.S., Bumrungsri, S. and Laurance, W.F. 2013. Near-complete extinction of native small mammal fauna 25 years after forest fragmentation. *Science* 341:1508-1510.
- [42] Givnish, T.J. 2002. Adaptive significance of evergreen vs. deciduous leaves: solving the triple paradox. *Silva Fennica* 36:703-743.
- [43] Lee, D.W. 1989. Canopy dynamics and light climates in a tropical moist deciduous forest in India. *Journal of Tropical Ecology* 5:65-79.
- [44] Lerda, M., Holbrook, N.M., Mooney, H., Rich, P. and Whitbeck, J. 1992. Seasonal patterns of acid fluctuations and resource storage in the arborescent cactus *Opuntia excelsa* in relation to light availability and size. *Oecologia* 92:166-171.
- [45] Souza, F.M., Gandolfi, S. and Rodrigues, R.R. 2014. Deciduousness influences the understory community in a semideciduous tropical forest. *Biotropica* 46:512-515.
- [46] Álvarez-Cansino, L., Schnitzer, S.A., Reid, J.P. and Powers, J.S. 2014. Liana competition with tropical trees varies seasonally but not with tree species identity. *Ecology* Pre-print.

- [47] Latch, P. 2006. *Recovery Plan for Mabi Forest 2007-2011*. Queensland Parks and Wildlife Service, Brisbane.
- [48] Restom, T.G., and Nepstad, D.C. 2004. Seedling growth dynamics of a deeply rooting liana in a secondary forest in eastern Amazonia. *Forest Ecology and Management* 190:109-118.
- [49] Chen, Y.-J., Cao, K.-F., Schnitzer, S. A., Fan, Z.-X., Zhang, J.-L. and Bongers, F. 2015. Water-use advantage for lianas over trees in tropical seasonal forests. *New Phytologist* 205:128-136.
- [50] Wright, A., Tobin, M., Mangan, S., and Schnitzer, S.A.. 2014. Unique competitive effects of lianas and trees in a tropical forest understory. *Oecologia* 177:561-569.
- [51] Uhl, C., Kauffman, J.B. and Cummings, D.L. 1988. Fire in the Venezuelan Amazon 2: Environmental conditions necessary for forest fires in the evergreen rainforest of Venezuela. *Oikos* 53:176-184.
- [52] Holl, K.D. 1999. Factors limiting tropical rain forest regeneration in abandoned pasture: Seed rain, seed germination, microclimate, and soil. *Biotropica* 31:229-242.
- [53] Persson, T. 1989. Role of soil animals in C and N mineralisation. *Plant Soil* 115:241-245.
- [54] Lavelle, P., Decaëns, T., Aubert, M., Barot, S., Blouin, M., Bureau, F., Margerie, P., Mora, P. and Rossi, J.-P. 2006. Soil invertebrates and ecosystem services. *European Journal of Soil Biology* 42:S3-S15.
- [55] Lee, K. and Foster, R. 1991. Soil fauna and soil structure. *Soil Research* 29:745-775.
- [56] Wagg, C., Bender, S.F., Widmer, F. and van der Heijden, M. G. A. 2014. Soil biodiversity and soil community composition determine ecosystem multifunctionality. *Proceedings of the National Academy of Sciences* 111:5266-5270.
- [57] Oddsdóttir, E.S., Svavarsdóttir, K. and Halldorsson, G. 2008. The influence of land reclamation and afforestation on soil arthropods in Iceland. *Icelandic Agricultural Sciences* 21:3-13.
- [58] Reich, P.B., Walters, M.B., and Ellsworth, D.S. 1992. Leaf life-span in relation to leaf, plant, and stand characteristics among diverse ecosystems. *Ecological Monographs* 62:365-392.
- [59] Santiago, L.S. 2010. Can growth form classification predict litter nutrient dynamics and decomposition rates in lowland wet forest? *Biotropica* 42:72-79.
- [60] Vitousek, P.M. and Denslow, J.S. 1986. Nitrogen and phosphorus availability in treefall gaps of a lowland tropical rainforest. *Journal of Ecology* 74:1167-1178.
- [61] Putz, F.E. and Chai, P. 1987. Ecological studies of lianas in Lambir national park, Sarawak, Malaysia. *Journal of Ecology* 75:523-531.
- [62] El-Swaify, S.A., Dangler, E.W. and Armstrong, C.L. 1982. *Soil erosion by water in the tropics*. College of Tropical Agriculture and Human Resources, University of Hawaii, Honolulu, Hawaii.
- [63] Cahn, M.D., Bouldin, D.R., Cravo, M.S. and Bowen, W.T. 1993. Cation and nitrate leaching in an oxisol of the Brazilian Amazon. *Agronomy Journal* 85:334-340.
- [64] Geddes, N. and Dunkerley, D. 1999. The influence of organic litter on the erosive effects of raindrops and of gravity drops released from desert shrubs. *Catena* 36:303-313.
- [65] Hartanto, H., Prabhu, R., Widayat, A.S.E. and Asdak, C. 2003. Factors affecting runoff and soil erosion: plot-level soil loss monitoring for assessing sustainability of forest management. *Forest Ecology and Management* 180:361-374.
- [66] Sayer, E.J. 2006. Using experimental manipulation to assess the roles of leaf litter in the functioning of forest ecosystems. *Biological reviews* 81:1-31.
- [67] Chalker-Scott, L. 2007. Impact of mulches on landscape plants and the environment-a review. *Journal of Environmental Horticulture* 25:239-249.
- [68] Cochrane, M.A. and Laurance, W.F. 2002. Fire as a large-scale edge effect in Amazonian forests. *Journal of Tropical Ecology* 18:311-325.
- [69] Cochrane, M.A. 2003. Fire science for rainforests. *Nature* 421:913-919.
- [70] Kauffman, J.B., Uhl, C., and Cummings, D.L. 1988. Fire in the Venezuelan Amazon 1: Fuel biomass and fire chemistry in the evergreen rainforest of Venezuela. *Oikos* 53:167-175.

- [71] Balch J.K., Nepstad, D.C., Curran, L.M., Brando, P.M., Portela, O., Guilherme, P., Reuning-Scherer, J.D. and de Carvalho, O. 2011. Size, species, and fire behavior predict tree and liana mortality from experimental burns in the Brazilian Amazon. *Forest Ecology and Management* 261:68-77.
- [72] Cochrane, M.A. and Laurance, W.F. 2008. Synergisms among fire, land use, and climate change in the Amazon. *Ambio* 37:522-527.
- [73] Laurance, W.F. and Curran, T.J. 2008. Impacts of wind disturbance on fragmented tropical forests: A review and synthesis. *Austral Ecology* 33:399-408.
- [74] Garrido-Pérez, E.I., Dupuy, J.M., Durán-García, R., Ucan-May, M., Schnitzer, S.A. and Gerold, G. 2008. Effects of lianas and Hurricane Wilma on tree damage in the Yucatan Peninsula, Mexico. *Journal of Tropical Ecology* 24:559-562.
- [75] Appanah, S. and Putz, F.E. 1984. Climber abundance in virgin dipterocarp forest and the effect of pre-felling climber cutting on logging damage. *Malaysian Forester* 47:335-342.
- [76] Kainer, K.A., Wadt, L.H.O., Gomes-Silva, D. A. P. and Capanu, M. 2006. Liana loads and their association with *Bertholletia excelsa* fruit and nut production, diameter growth and crown attributes. *Journal of Tropical Ecology* 22:147-154.
- [77] Tucker, N.I.J. 2000. Linkage restoration: Interpreting fragmentation theory for the design of a rainforest linkage in the humid Wet Tropics of north-eastern Queensland. *Ecological Management & Restoration* 1:35-41.
- [78] Rosenberg, D.K., Noon, B.R. and Meslow, E.C. 1997. Biological corridors: Form, function, and efficacy. *BioScience* 47:677-687.
- [79] Asensio, N., Cristobal-Azkarate, J., Dias, P. A. D. , Vea, J.J. and Rodriguez-Luna, E. 2007. Foraging habits of *Alouatta palliata mexicana* in three forest fragments. *Folia Primatologica* 78:141-153.
- [80] Rendigs, A., Radespiel, U., Wrogemann, D. and Zimmermann, E. 2003. Relationship between microhabitat structure and distribution of Mouse Lemurs (*Microcebus* spp.) in northwestern Madagascar. *International Journal of Primatology* 24:47-64.
- [81] Yanoviak, S. P., and Schnitzer, S. A. 2013. Functional roles of lianas for forest canopy animals. In: *Tree tops at risk*. Lowman, M., Devy, S. and Ganesh, T. (Eds.), pp. 209-214. Springer Verlag, New York.
- [82] Arroyo-Rodríguez, V., Asensio, N., Dunn, J.C., Cristóbal-Azkarate, J., and Gonzalez-Zamora, A., 2015. Use of lianas by primates: more than a food source. In: *Ecology of lianas*. Schnitzer, S.A., Bongers, F., Burnham, R. and Putz, F.E. (Eds.), pp.407-426. Wiley-Blackwell Publishing, Oxford.
- [83] Goosem, M. 2012. Mitigating the impacts of rainforest roads in Queensland's Wet Tropics: Effective or are further evaluations and new mitigation strategies required? *Ecological Management & Restoration* 13:254-258.
- [84] Newell, G.R. 1999. Australia's tree-kangaroos: current issues in their conservation. *Biological Conservation* 87:1-12.
- [85] Andrén, H. 1995. Effects of landscape composition on predation rates at habitat edges. In: *Mosaic Landscapes and Ecological Processes*. Hansson, L., Fahrig, L. and Merriam, G. (Eds.), pp. 225-255. Springer, Netherlands.
- [86] Taylor, B.D. and Goldingay, R.L. 2003. Cutting the carnage: wildlife usage of road culverts in north-eastern New South Wales. *Wildlife Research* 30:529-537.
- [87] Schnitzer, S.A., Dalling, J.W. and Carson, W.P. 2000. The impact of lianas on tree regeneration in tropical forest canopy gaps: evidence for an alternative pathway of gap-phase regeneration. *Journal of Ecology* 88:655-666.
- [88] Laurance, W.F. and Yensen, E. 1991. Predicting the impacts of edge effects in fragmented habitats. *Biological Conservation* 55:77-92.
- [89] Murcia, C. 1995. Edge effects in fragmented forests: implications for conservation. *Trends in Ecology and Evolution* 10:58-62.

- [90] Lambert, T.D., Malcolm, J.R. and Zimmerman, B.L. 2006. Amazonian small mammal abundances in relation to habitat structure and resource abundance. *Journal of Mammalogy* 87:766-776.
- [91] Wong, S.N.P., Saj, T.L. and Sicotte, P. 2006. Comparison of habitat quality and diet of *Colobus vellerosus* in forest fragments in Ghana. *Primates* 47:365-373.
- [92] Dunn, J.C., Asensio, N., Arroyo-Rodríguez, V., Schnitzer, S. and Cristóbal-Azkarate, J. 2012. The ranging costs of a fallback food: Liana consumption supplements diet but increases foraging effort in howler monkeys. *Biotropica* 44:705-714.
- [93] Benson, W.W. 1978. Resource partitioning in passion vine butterflies. *Evolution* 32:493-518.
- [94] Ødegaard, F. 2000. The relative importance of trees versus lianas as hosts for phytophagous beetles (Coleoptera) in tropical forests. *Journal of Biogeography* 27:283-296.
- [95] Orr, A. and R. Kitching, R. 2010. *Butterflies of Australia*. Jacana Books, Crows Nest, New South Wales.
- [96] Erwin, T.L. 1983. Tropical forest canopies: The last biotic frontier. *Bulletin of the Ecological Society of America* 29:14-20.
- [97] Stork, N., Adis, J. and Didham, R. 1997. *Canopy arthropods*. Chapman and Hall, London, UK.
- [98] Cai, Z. and Bongers, F. 2007. Contrasting nitrogen and phosphorus resorption efficiencies in trees and lianas from a tropical montane rain forest in Xishuangbanna, South-West China. *Journal of Tropical Ecology* 23:115-118.
- [99] Bobbink, R. and Hicks, W.K. 2014. Factors affecting nitrogen deposition impacts on biodiversity: An overview. In: *Nitrogen Deposition, Critical Loads and Biodiversity*. Sutton, M.A., Mason, K.E., Sheppard, L.J., Sverdrup, H., Haeuber, R. and Hicks, W.K. (Eds.), pp. 127-138. Springer, Netherlands.
- [100] Throop, H.L. and Lerdau, M.T. 2004. Effects of nitrogen deposition on insect herbivory: Implications for community and ecosystem processes. *Ecosystems* 7:109-133.
- [101] Coley, P. 1998. Possible effects of climate change on plant/herbivore interactions in moist tropical forests. *Climatic Change* 39:455-472.
- [102] Reichle, D.E., Goldstein, R.A., Hook, Jr., R.I.V. and Dodson, G.J. 1973. Analysis of insect consumption in a forest canopy. *Ecology* 54:1076-1084.
- [103] Bergvall, U.A., Rautio, P., Kesti, K., Tuomi, J. and Olof, L. 2006. Associational effects of plant defences in relation to within- and between-patch food choice by a mammalian herbivore: Neighbour contrast susceptibility and defence. *Oecologia* 147:253-260.
- [104] Stone, C. and Bacon, P. E. 1994. Relationships among moisture stress, insect herbivory, foliar cineole content and the growth of River Red Gum *Eucalyptus camaldulensis*. *Journal of Applied Ecology* 31:604-612.
- [105] Louthan, A.M., Doak, D.F., Goheen, J.R., Palmer, T.M. and Pringle, R.M. 2013. Climatic stress mediates the impacts of herbivory on plant population structure and components of individual fitness. *Journal of Ecology* 101:1074-1083.
- [106] Willis, A., Ash, J. and Groves, R. 1995. The effects of herbivory by a mite, *Aculus hyperici*, and nutrient deficiency on growth in *Hypericum* species. *Australian Journal of Botany* 43:305-316.
- [107] Foaham, B. 2002. *Insect pest incidence on timber tree species in natural forest in south Cameroon*. Tropenbos-Cameroon Programme, Kribi, Cameroon.
- [108] Goosem, S.P. and Tucker, N.I.J. 1995. *Repairing the rainforest: theory and practice of rainforest re-establishment in North Queensland's wet tropics*. Wet Tropics Management Authority, Cairns, Queensland.
- [109] Sritongchuay, T., Gale, G.A., Stewart, A., Kerdkaew, T. and Bumrungsri, S. 2014. Seed rain in abandoned clearings in a lowland evergreen rain forest in southern Thailand. *Tropical Conservation Science* 7:572-585.
- [110] Wright, S.J. and Calderón, O. 2006. Seasonal, El Niño and longer term changes in flower and seed production in a moist tropical forest. *Ecology Letters* 9:35-44.

- [111] Boulter, S.L., Kitching, R.L., Gross, C.L., Goodall, K.L. and Howlett, B.G. 2008. Floral morphology, phenology and pollination in the Wet Tropics. In: *Living in a Dynamic Tropical Forest Landscape*. Turton, S.L. and Stork, N.E. (Eds.), pp.224-239. Blackwell Publishing, Oxford.
- [112] Menninger, E.A. 1970. *Flowering vines of the world: an encyclopedia of climbing plants*. Hearthside Press, New York.
- [113] Kilgore, A., Lambert, T. D. and Adler, G.H. 2010. Lianas influence fruit and seed use by rodents in a tropical forest. *Tropical Ecology* 51:265-271.
- [114] Snow, D.W. 1981. Tropical frugivorous birds and their food plants: A world survey. *Biotropica* 13:1-14.
- [115] Hodgkison, R., Sharon, T.B., Zubaid, A. and Kunz, T. H. 2003. Fruit bats (Chiroptera: Pteropodidae) as seed dispersers and pollinators in a lowland Malaysian rain forest. *Biotropica* 35:491-502.
- [116] Ansell, F.A., Edwards, D.P. and Hamer, K.C. 2011. Rehabilitation of logged rain forests: Avifaunal composition, habitat structure, and implications for biodiversity-friendly REDD+. *Biotropica* 43:504-511.
- [117] Perez-Salicrup, D. R., Sork, V.L. and Putz, F.E. 2001. Lianas and trees in a liana forest of Amazonian Bolivia. *Biotropica* 33:34-47.
- [118] Kochummen, K. and Ng., F.S.P. 1977. Natural plant succession after farming in Kepong. *Malaysian Forester* 40:61-78.
- [119] Campanello, P. I., Genoveva Gatti, M., Ares, A., Montti, L. and Goldstein, G. 2007. Tree regeneration and microclimate in a liana and bamboo-dominated semi-deciduous Atlantic Forest. *Forest Ecology and Management* 252:108-117.
- [120] Parthasarathy, N., Muthuranikumar, S. and Reddy, M.S. 2004. Patterns of liana diversity in tropical evergreen forests of peninsular India. *Forest Ecology and Management* 190:15-31.
- [121] Santos, K. D., Kinoshita, L.S. and Rezende, A.A. 2009. Species composition of climbers in seasonal semideciduous forest fragments of Southeastern Brazil. *Biota Neotropica* 9:175-188.
- [122] Laurance, W. F., Gascon, C. and Rankin-de Merona, J.M. 1999. Predicting effects of habitat destruction on plant communities: a test of a model using Amazonian trees. *Ecological Applications* 9:548-554.
- [123] Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics* 34:487-515.
- [124] Lienert, J. 2004. Habitat fragmentation effects on fitness of plant populations – a review. *Journal for Nature Conservation* 12:53-72.
- [125] Yorke, S. R., Schnitzer, S.A., Mascaro, J., Letcher, S.G. and Carson, W.P. 2013. Increasing liana abundance and basal area in a tropical forest: The contribution of long-distance clonal colonization. *Biotropica* 45:317-324.
- [126] Ledo, A., and Schnitzer, S.A. 2014. Disturbance and clonal reproduction determine liana distribution and maintain liana diversity in a tropical forest. *Ecology* 95:2169-2178.
- [127] Magrach, A., Laurance, W.F., Larrinaga, A.R. and Santamaria, L. 2014. Meta-analysis of the effects of forest fragmentation on interspecific interactions. *Conservation Biology* 28:1342-1348.
- [128] Hansen, M.C., Potapov, P. V., Moore, R., Hancher, M., Turubanova, S.A., Tyukavina, A., Thau, D., Stehman, S.V., Goetz, S.J., Loveland, T.R., Kommareddy, A., Egorov, A., Chini, L., Justice, C.O. and Townshend, J.R.G. 2013. High-resolution global maps of 21st-century forest cover change. *Science* 342:850-853.
- [129] Asner, G.P., Rudel, T. K., Aide, T. M., Defries, R. and Emerson, R. 2009. A contemporary assessment of change in humid tropical forests. *Conservation Biology* 23:1386-1395.
- [130] Dirzo, R. and Raven, P. 2003. Global state of biodiversity and loss. *Annual Review of Environment and Resources* 28:137-167.