

Logging effects on liana diversity and abundance in Central Guyana

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Tropenbos-Guyana Reports
2003-1

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LOGGING EFFECTS ON LIANA DIVERSITY AND ABUNDANCE IN CENTRAL GUYANA

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Tropenbos International
Wageningen, the Netherlands
March 2003

Tropenbos-Guyana Reports: 2003-1

The Tropenbos-Guyana Reports series presents results of current research activities and projects in the Tropenbos-Guyana Programme.

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The Tropenbos-Guyana Programme is a partnership between Tropenbos International, Utrecht University, Guyana Forestry Commission, University of Guyana and National Agricultural Research Institute.

This project is implemented by the Nationaal Herbarium Nederland (Utrecht University branch) for the Tropenbos-Guyana Programme. It is financially supported by the European Commission under contract B7-6201/98-13/FOR “Conservation and sustainable use of botanical diversity in Guyana” to Tropenbos International. The views expressed in this publication do not necessarily reflect the views of the European Commission.

Front matter: *Connarus perrottetii* (DC.) Planch. (top left and bottom right) and *Potamogonos microcalyx* (G.F.W. Mey.) Sandw. (top right and bottom left), pictures by Renske Ek, Roderick Zagt



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EXECUTIVE SUMMARY: LIANAS AND LOGGING

Forests represent a renewable resource of wood and other products and services, covering a very large proportion of the Earth's land surface. Hundreds of millions of people derive income and goods from forests. However, over large areas, forests are replaced by other land uses and little of the remaining area is managed in a way that conserves their integrity and capacity to continue producing those products and services.

Over the past decades, awareness has gradually grown of the plight of forests and the potentially devastating effects of their demise on human well-being. Many initiatives have arisen to understand the causes and consequences of forest decline and to devise ways to improve their management for the benefit of people that depend on them.

RATIONALE AND OBJECTIVE OF THE STUDY

One of the main ambitions of sustainable forest management is to reconcile logging with the high biodiversity value of tropical rain forests. It is generally accepted that at least two-thirds of the world's terrestrial species is found in forests, and over 50% in tropical rain forests. In most modern forestry legislation and all existing systems for the certification of "good" forest management there are requirements for the safeguarding of forest biodiversity. This ambition must be interpreted against the background of the history of logging of tropical rain forest, which is one of over-exploitation and massive loss of biodiversity. The impacts of sustainable forest management on biodiversity are imperfectly known. A recent review of logging impacts on biodiversity (defined in a very broad sense) concluded that "the answer to the question 'Is logging compatible with biodiversity protection?' can only be a very unsatisfactory 'It depends'" (Putz et al. 2000).

This study is an attempt to quantify the impact of logging on one component of biodiversity *s.l.*, viz. species richness of lianas and woody climbers. The overall objective of the study is to develop locally relevant parameters of sustainability of sustainable forest management in Guyana. The specific objective is to assess changes in species composition and biodiversity in relation to logging damage after the first cut in primary forest, over short to medium time scales. In addition, the study identifies potential indicators and assesses their usefulness as a tool to predicting biodiversity trends in logged versus conserved forest. This exercise is conducted using the liana community of a commercial forest type in Central Guyana as a case study.

Species or species groups are often proposed as suitable indicators describing some aspect of the condition of the forest ecosystem, such as biodiversity or measures of ecosystem "health". This is based on the assumption that there is a strong relation between the ecological behaviour of one species (group) and that of other species groups or of ecosystem characteristics.

Lianas were selected as a suitable candidate group to study changes in the forest ecosystem as the result of logging. They form a conspicuous component of tropical rain forest ecosystems and are widely believed to be favoured by disturbance, a finding that is based on their increased abundance in gaps, large-scale disturbances, and forest edges. They rapidly colonise disturbed sites, including logged forests (Putz et al. 1984), which suggests that they would be suitable as sensitive indicators for logging-related disturbance. It is expected that the abundance and species composition of liana vegetations will be related to the degree of disturbance of a forest, and as such, lianas could be used as a "warning system" for unacceptable modifications of the original forest habitat.

RESEARCH QUESTIONS

In this study, the value of lianas as indicators is assessed for several criteria, which are linked to the degree of modification of the original forest habitat: forest disturbance and biodiversity.

Four main questions were addressed

- What is liana abundance and composition of undisturbed forests?
- What is the impact on liana abundance and composition of different intensities of logging (reduced impact logging)?
- How do liana abundance and composition of logged forests develop as the time since logging progresses?
- Are lianas suitable indicators of forest disturbance or biodiversity?

Data on the composition and abundance of liana communities were collected by enumerating liana individuals in sample plots of 1 ha, which were located in either undisturbed forests or in forests that had been disturbed by logging. The first question was researched by describing plots in undisturbed forest, the second by comparing liana communities before and after logging in an experiment whereby logging intensity was varied and the third question by comparing plots of different age since logging. The results of the first three questions are the basis for determining the value of lianas as indicators for assessing disturbance and diversity.

The study area was located in Central Guyana, near Mabura Hill in the Demerara Timbers Ltd. Concession. Within this area, several clusters of plots were located in four sites, of which Pibiri was the most important one.

LIANA ABUNDANCE AND COMPOSITION OF UNDISTURBED FOREST

A total of 23 plots of one hectare in undisturbed Greenheart-bearing Mixed Forest were available to describe intact liana communities. Three of these were measured repeatedly. Intact liana communities in the study region were somewhat less diverse than tree communities in the same area and also less diverse than liana communities elsewhere in the tropics. Nevertheless, a total of 146 liana taxa were described from these plots. Most individuals are small while fewer than 20 large lianas with a diameter over 10 cm were present in each hectare. Species composition varied from place to place, to such an extent, that in each one hectare plot just 45% of all species was present. The larger the distance between plots, the larger the difference in species composition, even though the general forest type was the same. Remarkably, liana communities in this area were characterised by dominance of a single species, *Connarus perrottetii*, which accounted for 45% of all individuals.

LOGGING INTENSITY IMPACTS ON LIANA COMMUNITIES

Liana communities were compared before and four years after logging in 12 one ha plots in Pibiri, representing four treatments: four levels of harvesting intensity: 0, 4, 8 and 16 trees removed per hectare, using reduced impact logging techniques. Each treatment was replicated three times.

Logging alters the structure of the forest and therefore the growth conditions for plants. In particular, the cutting of trees creates canopy gaps, allowing light to penetrate to the forest floor. The manoeuvring of large skidders on skidtrails disturbs the soil, thereby uprooting existing vegetation, baring the subsoil and bringing concealed seeds to the surface. The combination of skidtrails and canopy gaps ("skidded gaps") represents the largest change.

Logging had a large impact on the composition of liana communities, but how large depended on the logging intensity and the species concerned. Nineteen species, of 102 present before logging, disappeared from the plots after logging. All species lost were rare, and it is likely that chance effects played a large role in determining which species disappeared rather than their sensitivity to logging. Thirty-five species appeared after logging, so the net effect of logging was an increase in the number of species present.

The most obvious effect of logging on liana communities was an increase in overall liana abundance. However, this increase was only found in the most heavily logged plots, while in plots with light or moderate logging intensity no increase in abundance was noted.

Species diversity, whether expressed as the number of species present or Fisher's α , increased with logging intensity. Two factors contributed to this increase. In the first place, increased stem density in the most heavily logged plots increases the probability that a species is present (the density effect). In the second place, logging creates habitats that are rare or not present in undisturbed forest: gaps, and more in particular, skidded gaps. Several species are specialists of high light environments or are stimulated by the soil disturbance caused by skidders. Hence, many species that are rare or absent in undisturbed forest find suitable growth conditions in gaps or skidded gaps.

These trends are also found on the smaller scale of habitats. Forest patches that are untouched by logging activities have the lowest diversity, while gaps have the highest. Skidded gaps have intermediate diversity, but because of the complete removal of pre-existing vegetation and the different growth conditions on bare and compacted soil of skidtrails, their species composition is least similar to the undisturbed forest.

Comparing the responses of individual species, it was evident that certain species responded much stronger to the opportunities offered by increased gap area and soil disturbance than others. Of 59 common species, sixteen showed relatively strong and consistent positive responses to logging and logging-related habitats, while only three showed negative responses. Twenty-two species can be considered indifferent to logging and logging intensity, while the remaining eighteen species showed variable or inconsistent responses. Other species were not abundant enough to draw conclusions. A small number of species, exemplified by the common species passion flower (*Passiflora glandulosa*) and fire rope (*Pinzonia coriacea*), were strongly associated with skidded gaps. Another set was more strongly associated with gaps. Together these species demonstrate pioneer-like ecological behaviour.

In spite of the changes caused by logging, pre-existing spatial patterns of species composition remain relatively strong, even in the small geographic area of Pibiri. Logged plots were still very similar in species composition to nearby unlogged plots, while similarity with plots logged at the same intensity decreased with increased distance.

SUCCESSIONAL DEVELOPMENT OF LIANA COMMUNITIES AFTER LOGGING

After logging, a succession takes place during which sites opened by logging regain vegetation cover and biomass. Gradually, sun-loving species that colonise the open patches give way to species that can grow in the forest understorey. In principle, it is expected that liana communities will gradually grow back into an "undisturbed" state closely resembling pre-harvest species composition and abundance. To study this process, liana communities were compared among 18 plots that differed in age since they were logged. Plot age varied from 0-16 years. All plots were heavily logged, comparable to the heaviest treatment of the logging intensity study. As is usual in these so-called "chronosequence studies", species composition of liana communities of the plots varied with other environmental and site parameters and with logging method along with plot age. This problem was partly overcome by comparing logged plots at each site with nearby unlogged controls.

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There was a very clear development of liana abundance over the 16 years covered by the chronosequence. Liana abundance increased over the first 6-7 years after logging before declining and reaching near-natural levels by 16 years after logging. Still, there were differences between undisturbed control plots and 16-year-old communities, as the latter were relatively rich in large-stemmed lianas (dbh > 5 cm) and poor in small individuals. This is the result of a wave of lianas that recruits just after logging and increases in mean size as the community ages. In plots of increasing age, this wave is noted by maxima in abundance at ever increasing size classes, although the number of lianas in the wave is gradually depleted through mortality.

The increase in liana abundance over the first 6-7 years after logging was matched by an increase in species richness and diversity, just as this was the case in the logging intensity study. After that time, a gradual decline in diversity occurred, but this was not as clear as for abundance and it appeared that even 16 years after logging diversity was still well above the level of undisturbed control plots. Species with a strong gap and skidded-gap preference, which proliferate immediately after logging, are rare after 16 years. Yet, post-logging liana communities still have a different composition from control plots, and heavily disturbed habitats within those plots are still different from interior forest habitats by 16 years after logging.

Trends in species composition related to the age of the forest since logging were obscured by geographic patterns of species occurrence in this dataset. Just 20% of the species were common to all sites, while 35% were confined to one site only. However, this problem was avoided if not species but ecological species groups were compared.

LIANAS: ARE THEY USEFUL INDICATORS?

Liana were expected to be useful as indicators for assessing the amount of damage inflicted to forests by logging. The results show that, in particular, species belonging to the ecological group of pioneers showed predictable and consistent preferences for heavily disturbed habitats. These species share a preference for gaps and skidded gaps, proliferate after logging and gradually disappear as the regenerating vegetation ages. Their abundance is well correlated with skidtrail area in relatively young plots, a measure of logging damage. After *c.* 8 years the effects of logging damage and recovery of the liana vegetation start to interact, leading to a decline of pioneer abundance regardless of logging damage.

The value of pioneer abundance as an indicator is probably universal but requires validation. The species composition of the pioneer group varies from site to site and must be established prior to applying the indicator.

This indicator would only be of practical value in conditions where direct measurement of skidtrail area proves to be difficult, or in conditions where a direct estimate of the consequence of unacceptably high skidtrail area is required, for instance when norms need to be defined for logging damage. The norms associated with this indicator are not universal but would vary with location and species composition of the pioneer species group. They must be established prior to applying the indicator.

There is little evidence in this study that lianas will contribute useful indicators for biodiversity or liana biodiversity. No lianas for found in this study that have indicative value for the condition (abundance, species diversity) of intact liana communities of undisturbed old growth forest, mainly because few lianas appear to be strongly negatively affected by logging.

There was little evidence that pre-harvest liana cutting was responsible for the reduced abundance of large lianas (> 5 cm dbh) that was observed in the first few years after logging. Liana cutting was restricted to individuals growing in trees earmarked for harvesting and not carried out as a blanket treatment.

1 INTRODUCTION

1.1 OBJECTIVE OF THE STUDY

Timber is a major high-value commodity that is produced from forests throughout the tropics, for both local use and international trade. Several countries derive substantial income from the international trade in timber. Timber is one of few economically viable products that can be harvested from tropical forests without converting them – even though examples to the contrary abound. However, even though the technical requirements of sustainable forest management have largely been worked out, timber extraction, for many different reasons, rarely takes place in a way that maintains or enhances other forest values.

A growing international concern about tropical forests and recognition of the role that forest management for timber could play in maintaining tropical rain forests, has stimulated the development of forest certification systems, such as the international FSC and ISO schemes, the Indonesian LEI and Malaysian MTCC scheme. These systems are set up to provide independent third party verification that forest management is conducted in accordance with a set of economic, social and environmental criteria that are broadly supported by local, national and international interests. Certification allows customers to distinguish timber that has been produced in sustainably managed forests from timber from unsustainable sources and thus exert influence over the way forests are managed.

The assessment of “sustainability” of forest management is not straightforward. Not only is the concept of sustainability subject to continuous evolution, but local variations in legislation, social and economic environment and ecological conditions hamper a simple and easy measurement and interpretation of the impacts of forest management. The main certification schemes are based on a generic, internationally invariant system of principles and criteria that summarise the current international consensus of what is “sustainable forest management”. To be just and effective locally, these principles and criteria need to be interpreted in locally relevant indicators and norms by which forest management is judged.

One of the main ambitions of sustainable forest management, that needs to be addressed in forest certification systems, is to reconcile logging with the high biodiversity value of tropical rain forests. This ambition must be interpreted against the background of the history of logging of tropical rain forest, which is one of over-exploitation and massive loss of biodiversity (Putz *et al.* 2000). The impacts of sustainable forest management on biodiversity are imperfectly known. A recent review of logging impacts on biodiversity (defined in a very broad sense) concluded that “the answer to the question ‘Is logging compatible with biodiversity protection?’ can only be a very unsatisfactory ‘It depends’” (Putz *et al.* 2000). The studies quoted that addressed the impact of logging on species composition of plants show a wide array of responses, from increasing species diversity to dominance by invasive species.

This study is an attempt to quantify the impact of logging on one component of biodiversity *s.l.*, viz. species richness. The overall objective of the study is to develop locally relevant parameters of sustainability of sustainable forest management in Guyana. The specific objective is to assess changes in species composition and biodiversity in relation to logging damage after the first cut in primary forest, over short to medium time scales. In addition, the study will identify potential indicators and assess their usefulness as a tool to predicting biodiversity trends in logged versus conserved forest. This exercise will be conducted using the liana community of a commercial forest type in Central Guyana as a case.

Ultimately, the results of the study should

1. Contribute to increased understanding of short to medium-term changes in liana abundance and biodiversity in logged forests in Guyana
2. Provide information that, in the framework of forest certification, allows stakeholders to define adequate indicators for biodiversity-related criteria in certification systems,

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and certifiers and forest managers to use lianas to discriminate acceptable from unacceptable liana density.

One of the tenets of this study is that lianas form a suitable group to assess changes in disturbance parameters of the forest (see section 1.3.5).

Therefore, in addition to the objectives stated above, the study should also

3. Contribute to increased understanding of the relation between logging-related damage and short and medium-term changes in liana biodiversity in logged forests in Guyana
4. Provide information that, in the framework of forest certification, allows stakeholders to define adequate indicators for logging-damage related criteria in certification systems, and certifiers and forest managers to use lianas to discriminate acceptable from unacceptable liana density.

Finally, a high abundance of certain groups of lianas is detrimental for safety, for a speedy regeneration of logging gaps and for reducing logging damage. Therefore, it is relevant to assess liana abundance in its own right (see 1.3.4, p. 8). The study should also

5. Provide information that, in the framework of forest certification, allows stakeholders to define adequate indicators for density of certain groups of lianas in certification systems, and certifiers and forest managers to use lianas to discriminate acceptable from unacceptable liana density.

1.2 CONTEXT OF THE STUDY

This study is conducted in the framework of the Tropenbos-Guyana Programme (TGP). TGP aims to develop guidelines for conservation and sustainable exploitation of the forests of Guyana for timber and other forest products and services. To this end, it carries out biophysical and socio-economic baseline studies, studies to provide parameters for sustainability and research to establish the cost of achieving sustainability. The current project is within the group of projects to provide parameters for sustainability. In these projects, the impacts of logging on a number of components of the forest ecosystem are quantified and evaluated. The overall objective of this group of studies is to contribute practical indicators of sustainability to processes of standard setting in Guyana and internationally. Biodiversity is the subject of several of these projects, viz. botanical biodiversity (Ek 1997, this study), tree diversity (van der Hout 1999, Arets in prep.; van Ulft in prep.) and herbivorous insect biodiversity (Basset 2001, Charles 1998).

1.3 BIOLOGICAL INDICATORS

1.3.1 Definition

In a certification standard, an indicator is defined as a qualitative or quantitative parameter that can be assessed in relation to a criterion (Lammerts van Buren & Blom 1997). A criterion is a state or aspect of the forest ecosystem that must be in place in order to conform to sustainable management. An example of a criterion that is relevant in the context of this report is: “the liana composition of logged forest resembles that of the original forest”. Indicators that can be used to evaluate this criterion are, for example, “liana species richness” or “liana diversity as expressed by Fisher’s α ”. An indicator must be associated with a norm or threshold value in order to enable the assessment of the criterion. In many standards of sustainable forest management, indicators are more loosely formulated as prescriptions of the required state of a forest (*e.g.*, FSC 2000)

Three types of indicators are commonly distinguished (Lammerts van Buren & Blom 1997): input, process and outcome (performance) indicators. Unlike input and process indicators, outcome indicators directly refer to desired outcomes of sustainable forest management. For this reason they are potentially very powerful in assessing criteria. Few good biological output indicators are currently defined in certification standards, as the ecological insight in most

natural processes is too limited for the identification of simple yet robust, sensitive and widely applicable indicators and their associated norms.

1.3.2 Use of species as indicators

Species or species groups are frequently proposed as suitable indicators describing some aspect of the condition of the forest ecosystem, such as biodiversity or measures of ecosystem “health” (e.g. as a theme within the NWO priority programme on disturbed ecosystems, www.nwo.nl). This is based on the assumption of a strong correlation between the ecological behaviour of one species (group) and that of other species groups or of ecosystem characteristics. The value of using indicator species for assessing tropical forests is disputed. Generally, little is known about the requirements of indicator species; there is uncertainty about the validity of extrapolation of indicative power from one area to another area with potentially different species communities and about the relation between indicator species abundance and biodiversity of all other taxa. Reliably measuring changes in abundance of the indicator species itself is often a problem. Comparison of patterns of change in a number of animal groups over a gradient of habitat disturbance in African forest led Lawton *et al.* (1998) to conclude that “attempts to assess the impacts of tropical forest modification and clearance using changes in the species richness of one or a limited number of indicator taxa to predict changes in richness of other taxa may be highly misleading.” This was the reason why the indicator species concept was abolished when developing criteria and indicators for biodiversity in the CIFOR framework (Stork *et al.* 1997, CIFOR C&I team 1999).

1.3.3 Requirements for indicator species

Ecological indicators (including indicator species) should satisfy at least the following criteria:

- There should be a direct and measurable relation between the indicator and the underlying variable of interest;
- The species should be sensitive in presence or abundance to changes in the variable of interest;
- Easy methods should be available to reliably measure presence and abundance of the species
- Identification of the indicator species should be straightforward
- The ecological behaviour of the indicator species (group) should be predictable and constant over a considerable spatial and temporal scale
- The relationship between indicator value (species abundance) and the value of the response variable (level of damage) should be unambiguous, reciprocal and preferably linear, *i.e.*, a high level of damage should always be associated with a high abundance of the indicator species, but, conversely, a high abundance of the indicator species should always be associated with a high level of logging damage.

Preferably, an indicator provides an integrative measure or summary over space and time of the state of the relevant criterion. “Keystone” species (Terborgh 1986) are often suggested to be suitable indicator species with a high integrative value as their abundance in a community will influence the abundance of many other members in that community.

1.3.4 Criteria addressed in this study

In this study the criteria or response parameters of interest are biodiversity (taken as liana biodiversity), logging damage and the abundance of lianas that present a problem for forestry. The precise formulation of suitable criteria is not addressed here.

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Logging damage

Many aspects of the health and functioning of managed forest ecosystems are heavily dependent on the amount of damage inflicted by logging, *e.g.* growth and survival of trees (Sist & Nguyen-Thé 2002), forest structure, accessibility of the forest, composition of animal and plant populations etc. (Putz *et al.* 2000). Therefore, the reliable assessment of logging damage is a critical element of any certification system.

Logging affects liana communities in two different ways: direct and indirect. Direct logging damage occurs when falling trees and machinery physically kill or damage lianas, or when lianas are cut prior to logging to avoid problems during the cutting of trees.

Indirectly, logging leaves a mosaic of habitat types, which differ in the type and severity of damage inflicted by the harvesting operations. Variation in extent and severity of damage to the canopy (creating gaps) and to the soil (principally on skid trails) determines the conditions for germination, establishment, growth and survival of plants including lianas. The composition of the liana community will therefore be determined by the damage patterns created during logging. In forest-interiors (no damage) the composition will be very similar to the pre-harvest species composition, while on skid trails leading through gaps (complete removal of the canopy and of the topsoil) an entirely new community will emerge that will contain many early successional species.

One of the challenges presented by logging is the large spatial variation in damage patterns: locally many trees are cut and/or damaged, whereas elsewhere in the same forest damage may be very limited. For this reason it is difficult to quickly obtain a reliable measure of logging damage at the scale of hectares or more. If logging damage is closely associated with the growth conditions of certain species, then the occurrence of such species may serve as an indicator of (certain aspects of) logging damage.

It is quite likely that soon after logging direct assessment of logging damage is the preferred alternative to applying indirect measures, such as the occurrence of indicator species. However, once secondary vegetation has developed into dense thickets, direct assessment might be hampered by poor visibility and indirect indicators may provide suitable means of damage assessments. In addition, the abundance of unwanted species may still be a useful parameter even if the opportunity exists to measure logging damage in a direct way. After all, the objective of sustainable forest management is to limit the actual occurrence of negative consequences of inappropriate logging, regardless whether planned targets of logging damage are met or not. The information obtained can be fed back into the management system in order to adjust and refine operational procedures.

Biodiversity

The use of liana species as indicators for biodiversity (at the community level) might present a larger problem. Even though many species or species groups are known to respond to logging by shifts in abundance, correlations between trends in species richness of different groups are often low (Lawton *et al.* 1998). This will not be attempted in this report. The remaining issue is whether any liana taxon can be used as an indicator of diversity within the liana guild. While in most cases it will be possible to demonstrate clear causal relationships between logging and changes of abundance and distribution of individual species, these relations are less clear for the rather intangible concepts of diversity or even species richness.

Detrimental effects of lianas

In spite of their obvious ecological value in tropical rain forests, lianas as a group enjoy a bad reputation with foresters. On the positive side, lianas are species rich components of forest communities and their fruits and leaves are important components of primate diets. Morrelato and Leitão-Filho (1996) showed phenological patterns of climbers that were complementary to those of trees, suggesting that lianas could span periods of lower tree flower and fruit availability for dependent animal communities. This resulted in a constant availability of flowers and fruits throughout the year.

There are several reasons for the bad reputation of lianas, all of which might included as indicators in a certification system. The following “nuisance factors” can be distinguished. Large individuals grow from tree crown to tree crown. This habit may exacerbate logging damage when harvested trees pull down others that are connected through liana linkages (Putz 1991, Vidal *et al.* 1997). Apart from damage, this presents a safety hazard to logging personnel. Several liana species have vigorous resprouting capacity and may stifle the regeneration of trees in logging gaps under a blanket of leaves (Putz 1991, Schnitzer *et al.* 2000). Large lianas compete with the trees crowns for light and may thus depress tree growth and fecundity and increase mortality (Putz 1984, Putz *et al.* 1984, Stevens 1987, Clark & Clark 1990, Zuidema *et al.* submitted). Underground competition is another reason for reduced growth of desired species (Dillenburg *et al.* 1993, Pérez-Salicrup & Barker 2000, Schnitzer & Bongers 2002). These effects play a role at different stages of the logging cycle and affect trees of different size and in different parts of the forest.

It is often advocated to apply liana cutting before logging to reduce the problem of large lianas in tree crowns, but there are several problems associated with this: at least notionally high cost (Vidal *et al.* 1997), the questionable effectiveness of liana cutting for reducing logging damage (no effect in van der Hout 1997, Parren & Bongers 2001, reduced damage in Fox 1968, Appannah & Putz 1984, Vidal *et al.* 1997) or for reducing post-harvest liana proliferation through resprouting (Putz *et al.* 1984), potentially negative effects of blanket liana cutting treatments on biodiversity, resources for local populations and for primates (Vidal *et al.* 1997).

Performance indicators associated with criteria regarding reducing nuisance, cost and danger presented by lianas would include the abundance of large diameter lianas and of species with a high resprouting capacity.

1.3.5 Why lianas?

Lianas were selected as a suitable group to study changes in the forest ecosystem as the result of logging, in spite of the reportedly poor performance of species-based indicators in the literature as described above. This is based on the following assumptions and findings of earlier studies of lianas in Central Guyana and elsewhere.

Lianas form a conspicuous component of tropical rain forest ecosystems, typically occupying *c.* 10-25% of the woody stem density (Schnitzer & Bongers 2002). The term “lianas” refers to several types of climbing plants: woody climbing (plants that rely on other plants for support, Putz (1984), woody hemi-epiphytes (plants that rely on support from other plants during part of their life cycle, Benzing (1995) and herbaceous tendril-climbing vines (Gentry & Dodson (1987).

They are favoured by disturbance (Hegarty and Caballé 1991), a finding that is based on their increased abundance in gaps, large-scale disturbances, and forest edges (Oliveira-Filho *et al.* 1997, Schnitzer & Bongers 2002, Schnitzer & Carson 2001, Laurance *et al.* 2001). In a chronosequence of young (20 y) to old (>>100 y) forest, liana abundance and diversity were found to decrease (Dewalt *et al.* 2000). In addition, it is suggested that liana abundance is increasing worldwide in response to increasing tree turnover in tropical forests (Phillips & Gentry 1994, Phillips *et al.* 2002). They rapidly colonise disturbed sites, including logged forests (Putz *et al.* 1984), which suggests that they would be suitable as sensitive indicators for logging-related disturbance.

The taxonomy and field-identification of the liana flora of central Guyana is well known (Ek 1997), which adds to their suitability as a study group. To date, *c.* 280 species have been collected from that area (see http://www.lianas.tmfweb.nl/index_ie.htm for an overview).

For these reasons, it is expected that the abundance and species composition of liana vegetations will be correlated with the degree of disturbance of a forest, and as such, lianas could be used as indicators for unacceptable modifications of the original forest habitat.

1.4 SETUP OF THE REPORT AND RESEARCH QUESTIONS

This study makes use of the results obtained from a series of censuses of liana vegetation in permanent sample plots in commercial Greenheart forest in a logging concession the vicinity of Mabura Hill. These censuses provided information about liana abundance and diversity of undisturbed forest, and of logged forests that differed in logging intensity and the time passed since logging. The impact of different levels of logging intensity was studied in a monitored field experiment with repeated censuses per plot. The medium-term consequences of logging were studied by comparing logged with unlogged sites in a time-series.

The study approach and the methodology are summarised in Chapter 1. An attempt was made not to burden the text with too much methodological and statistical detail. Most of the methodology is therefore described in Appendix A.

In the first part of the results, the composition of the liana community in undisturbed forest will be described (section 3.1). This will be the baseline, against which to judge changes caused by logging. Specific questions to be answered include

- What are liana abundance, diversity and structure of undisturbed Greenheart forest?
- What is the spatial variability in species composition between plots located at different distances from each other (the plots in the study area were located at distances 0.1-30 km)?

In the second part, the impact of increasing levels of logging intensity on liana composition will be assessed (section 1.1).

- How is the liana species pool affected by logging? Are species lost and where do new species come from?
- Is it possible to distinguish direct effects of logging on liana diversity (liana cutting, logging damage) from indirect effects (habitat-related changes in population dynamics)?
- Are post-harvest liana diversity, abundance and structure related to logging intensity and habitats created by logging?
- Are there groups of species with similar response to similar changes in habitat?

In the third part, the persistence of changes in the liana community will be described by comparing plots with a different age since logging (section 1.1).

- What is the development of liana diversity, abundance and structure at different ages since logging?
- Are liana communities in logged forest converging back to pre-harvest composition and abundance?

Finally, in the fourth part, the validity of lianas as indicators for logging damage, biodiversity and “nuisance parameters” will be discussed (section 1.1).

- Are patterns of change in composition/abundance per habitat type consistent between sites?
- What lianas or liana groups can be used to assess logging damage?
- What lianas or liana groups can be used to assess liana diversity?
- What is the development of liana “nuisance indicators” in relation to logging intensity and time since logging?

The results will be discussed immediately, while the general discussion is concerned with the main purpose of the report, i.e. the formulation of liana-based indicators.

2 METHODOLOGY

2.1 APPROACH

2.1.1 Chronosequence versus direct monitoring

Liana communities were repeatedly enumerated in areas with a different logging history in order to collect information about the development of liana abundance and composition after logging. Within each plot, associations between liana occurrence and logging-related habitat patches were examined.

This information was gathered using botanical sample plots (BSPs). BSPs were laid out in areas that were logged at different points in time in order to construct a time series of logging induced changes in liana composition and abundance. In addition to age since logging, these plots also varied in logging method and intensity (Table 2.1). While the study was designed to minimise differences in geography (geomorphology, soil and hydrology) and species composition, such variation cannot be avoided in practice. A subset of the total sample of BSPs was part of a planned experiment in which logging intensity was manipulated and the response of the liana community was monitored (logging intensity experiment).

Temporal changes in liana abundance and composition were thus assessed using two main approaches:

- Chronosequence approach – comparison of clusters of harvested plots (BSPs) of a known age since logging with a nearby, undisturbed reference plot. Chronosequences are commonly used in succession studies if the time span of interest exceeds the time available for research (Eggeling 1947, Saldarriaga *et al.* 1988).
- Monitoring approach – repeated census of harvested plots (PSPs, permanent sample plots) with a known age since logging and undisturbed reference plots over a period of 6-7 years. Monitoring is a more precise method than chronosequences that minimises variation due to site-specific effects.

In some cases, BSPs were used for both chronosequence and monitoring purposes.

2.1.2 Abundance and composition compared between habitat types

In each plot, the extent of the various logging-related habitat types was mapped and linked to the distribution of lianas in order to gain insight in the effect of small-scale habitat diversity on liana abundance and composition. In recently-logged forests this was straightforward; in older plots the extent of, particularly, gaps was more difficult to assess and their area was most likely underestimated.

2.1.3 Abundance and composition at different spatial scales

Spatial components of liana abundance and composition in undisturbed forest were studied at the landscape, site and plot level, approximately corresponding with scales of 30,000, 3,000 and 150 m. The plots were distributed over four 400-500 ha sites in a logging concession, with a maximum distance of *c.* 30 km between sites. This distance was related to the chronology of logging in the concession: sites with a high age since logging were located far from recently logged sites. Each site contained three to fifteen 1 ha BSPs and in each BSP there were twenty-five 0.01 ha subplots. Inevitably, this implies that the gradient in time is confounded with the geographical gradient]

2.2 DESCRIPTION OF THE STUDY SITE

This study of liana composition was conducted in the vicinity of Mabura Hill in Central Guyana on the 350,000 ha timber Mabura Concession (TSA 91/1) leased by Demerara Timbers Ltd. (5°13' N, 58°48' W). The area is characterised by a variety of lowland rain forest types, which are closely associated with soil type and geomorphology (ter Steege *et al.* 1994, 2000a, ter Steege 2000b). The present study was limited to Greenheart-bearing Mixed

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Forest on brown sands (*sensu* ter Steege *et al.* 2000a), which occupy well-drained yellowish brown sands and sandy loams in this region. This forest type is frequently dominated by Greenheart (*Chlorocardium rodiei*), which is one of Guyana's principal commercial timbers. As a result, a large proportion of this forest type in this concession has been selectively harvested for Greenheart and some other species between 1985 and present.

The forest types of central Guyana comprise a distinct forest region in Guyana. They are comparably low in alpha biodiversity, but the regional differences in species composition between forest types growing on different soils are large, resulting in a high regional species diversity (ter Steege 2000b). The proportion of Guyanan endemic species is high, and many tree species are characterised by high wood density, large seed size, animal assisted or autochorous dispersal modes and slow growth rates (ter Steege & Hammond 2001, Hammond & Brown 1995). It is unknown whether the strong regional identity of the tree community is also found among the liana community of central Guyanan forests.

The landscape in the Mabura Concession is part of the White Sand Plateau, in which hills, footslopes, erosional plains, sedimentary plains and alluvial plains are distinguished (van Kekem *et al.* 1996). All sites of the current study are located in the sedimentary plains, which are characterised by unconsolidated sandy and loamy sediments. The topography is rolling to hilly (van Kekem *et al.* 1996) and the altitude does not exceed 50 m above sea level. Within these plains, a number of soil types can be distinguished. The soils of the Greenheart-dominated mixed forests belong to the Brown Sand Series. They are classified as ferralic Arenosols (Tabela loamy sand), haplic Ferralsols (Kasarama sandy loams) and haplic Acrisols (Ebini sandy clay loams) in the FAO and Guyana soil classification systems, respectively (Khan *et al.* 1980, van Kekem *et al.* 1996). These soils, which cover *c.* 43% of the concession (van Kekem *et al.* 1996), are characterised by low nutrient contents, particularly available phosphorous, high aluminium concentrations (van Kekem *et al.* 1996, Brouwer 1996, van Dam 2001), and they are well-drained (Jetten 1994). Data from the Pibiri Field station in the main study site indicate a total annual rainfall of around 2750 mm. Rainfall is bimodally distributed over the year, with maxima generally in May and December (van Dam 2001). Mean monthly temperature oscillates between 24.5° and 27.0°, while mean relative humidity (measured in a large gap) is just below 90% (van Dam 2001).

The Greenheart-dominated mixed forest on brown sand (also called Mixed forest on gently undulating terrain, FAO code 1e) in the study area has been described by Ek (1997) and ter Steege *et al.* (2000a). Their occurrence is largely restricted to the sedimentary plains, but a minor area is also recorded from the erosional plains (ter Steege *et al.* 2000a). This forest type covers about 34% of the concession (ter Steege *et al.* 2000a). The stem density of trees >10 cm DBH in this forest type was 402-668 ha⁻¹ (experimental plots in Pibiri, van der Hout 1999) while tree species richness (all sizes) varied from 71-98 ha⁻¹ (same plots, Ek 1997). The average canopy height is 30-40 m (van der Hout 1999). Lianas are common and abundant while understorey trees (dbh<10 cm) are abundant but rather species-poor compared with other sites (Ek 1997). Legumes (principally Caesalpiniaceae), Chrysobalanaceae, Sapotaceae, Annonaceae and Lauraceae dominate the tree component of the flora (Ek & ter Steege 1998, Thomas 2001). The species composition of Greenheart-dominated mixed forests on brown sand varies over intermediate spatial scales (10-50 km). Nearby sites show a higher similarity in species composition than more distant sites (Ek 1997).

Logging in the concession started around 1985 along the northern boundary close to the sawmill site in the Mabura Hill township. By the time of the final censuses in 2001 most of the suitable areas in the concession had been entered at least once. Logging intensity and frequency of re-entry is highly variable; depending on available volumes of commercial species, market conditions at the time of logging and constraints imposed by the terrain. The average logging intensity is quoted as 5-6 m³ ha⁻¹ (van der Hout 1999) but locally much higher intensities of 60-110 m³ ha⁻¹ can be recorded (van der Hout 1999, Zagt 1997). Logging methods can be characterised as “conventional” *sensu* van der Hout (1999), although the majority of the current research was conducted in experimental plots where reduced impact

logging techniques were employed (van der Hout 1999). Reduced impact logging in this area is characterised by a more regular distribution of, on average, smaller gaps than in conventionally logged areas, selective pre-harvest liana cutting, reduced skid-trail lengths and generally reduced physical damage to the residual stand (van der Hout 1999).

2.3 METHODS OF DATA COLLECTION

2.3.1 Definition of lianas

Lianas were defined as described in section 1.3.5.

2.3.2 Locations of botanical sample plots

Twenty-nine one ha Botanical Sample Plots were laid out in clusters in several areas with different logging history in the DTL concession. The largest cluster (15 plots) was located in the West Pibiri Compartment at *c.* 35 km south of Mabura Hill township. This area was logged during the study. Three clusters of three plots each were located in areas that were harvested 6-10 years prior to the first census: one at Waraputa Compartment at *c.* 20 km south-west of Mabura Hill; another at km 2 along the Kurupukari Main Road at *c.* 5 km south of Mabura Hill and one at the Mabura Hill Forest Reserve at *c.* 15 km south of Mabura Hill. The BSPs in two of the latter three clusters were re-established at the recensus, resulting in a total of 29 plots (details in Table 2.1).

2.3.3 Experimental design and plot characteristics

A different approach was taken to study liana diversity in relation to logging intensity in recently logged forest (logging experiment) and in relation to age since logging (chronosequence approach).

The Logging Experiment

The logging experiment was carried out as a randomised block design, in Pibiri. Five different reduced impact logging treatments were applied over 5.76 ha treatment areas in three blocks (replicates), giving a total of 15 treatment areas (van der Hout 1999). The four treatments¹ used to study the impact of logging differed in logging intensity: 0, 4, 8 and 16 trees/ha. Before logging, the climbers were cut around the trees to be harvested. Harvesting took place in 1994. Permanent one hectare plots were laid out in the centre of each treatment area. In these plots, lianas were censused before logging and 2, 4 and 6 years after logging, but not each plot was remeasured in all these years (Table 2.1). In this report, only the logging experiment contains plots for which pre- and post harvest species composition can be directly compared.

Chronosequence study

Chronosequence studies were carried out using clusters of three plots, one unlogged reference plot and two logged plots, at three different sites: Waraputa, MHFR and 2KM. In addition, three plots of the logging experiment provided a fourth cluster (Table 2.1). The plots selected in the logging experiment represent the heaviest treatment of 16 trees.ha⁻¹, which were most comparable in intensity and total impact to conventional operations (*cf.* van der Hout 1997). Logging at the remaining three sites took place at different times before the start of the study using conventional techniques and at a logging intensity that was only limited by the occurrence of harvestable trees. Details of the logging intensity and damage of the chronosequence are provided in Table 2.1. The date of logging was determined through interviews with company officials. The censuses in the chronosequence represented a time series spanning a period of 16 years since the harvest (Table 2.1).

¹ A fifth treatment consisted of a harvest followed by liberation of potential crop trees. In this study, only the pre-harvest enumeration of the plots in this treatment was used for descriptive purposes. The lianas of the post-harvest vegetation were not enumerated.

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Table 2.1 Census history and damage data of 29 Botanical Sample Plots used for the study of liana populations near Mabura Hill. For notes, see next page, top.

Plot	Site	Logged ^s	Treatment [*]	Census history [†]							Purpose [‡]		Year of harvest	Harvest intensity [§]		Gap area [¶] (%)	Skid trail area [¶] (%)	Skidded gap area [¶] (%)	Comment	
				P	+2	+4	+6	+7	+10	+12	+16	LE		CS	N (ha ⁻¹)					BA (m ² .ha ⁻¹)
1	Pibiri	L _R	RIL 8	+		+						•	•	1994	9	2.0	26/32	5/7	1.3/2.1	
2	Pibiri	L _R	RIL 16	+	+	+	+					•	•	1994	14	2.3	28/22	6/6	1.4/1.6	
3	Pibiri	L _R	RIL 4	+		+						•	•	1994	4	1.2	7/4	5/3	0.0/0.0	
4	Pibiri	L _{R-s}	(-)	+								•	•	(1994)	-	-	-	-	-	Only pre-logging census
5	Pibiri	C	0	+		(+)	(+)					•	•	-	0	0	0/0 ^l	0/0	0/0	
6	Pibiri	C	0	+		(+)						•	•	-	0	0	0/0	0/0	0/0	
7	Pibiri	L _R	RIL 16	+	+	+	+					•	•	1994	15	3.8	36/31	9/10	2.2/2.6	
8	Pibiri	L _R	RIL 8	+		+						•	•	1994	9	1.7	12/9	10/9	1.0/2.0	
9	Pibiri	L _{R-s}	(-)	+								•	•	(1994)	-	-	-	-/-	-	Only pre-logging census
10	Pibiri	L _R	RIL 4	+		+						•	•	1994	5	0.8	13/10	6/8	0.1/0.3	
11	Pibiri	L _R	RIL 4	+		+						•	•	1994	6	1.7	8/8	5/7	0.6/0.9	
12	Pibiri	C	0	+		(+)						•	•	-	0	0	0/0 ^l	0/0	0/0	
13	Pibiri	L _{R-s}	(-)	+								•	•	(1994)	-	-	-	-	-	Only pre-logging census
14	Pibiri	L _R	RIL 16	+		+						•	•	1994	16	4.1	21/23	14/17	4.0/4.7	
15	Pibiri	L _R	RIL 8	+		+						•	•	1994	9	2.0	15/16	6/7	0.3/0.0	
16	2 Km	C					(+)					•	•	-	0	0	0/0 ^l	0/0	0/0	No recensus - destroyed by logging
17	2 Km	L _C					+					•	•	c. 1985	17	3.3	41/39	16/16	9.9/9.5	
18	2 Km	L _C					+					•	•	c. 1985	12	3.5	35/38	22/22	9.7/10.1	
19	2 Km	L _C									+	•	•	c. 1985	N/A	N/A	41/39*	16/16*	9.9/9.5*	=plot 17, position shifted
20	2 Km	L _C									+	•	•	c. 1985	19 [‡]	N/A	35/38*	22/22*	9.7/10.1*	=plot 18, position shifted
21	MHFR	C					(+)					•	•	-	0	0	0/0 ^l	0	0	
22	MHFR	L _C					+					•	•	c. 1988	20	6.5	28/28°	18/18°	5.1/5.1°	
23	MHFR	L _C					+					•	•	c. 1988	21	5.4	40/40°	17/17°	6.8/6.8°	
24	Waraputa	C					(+)					•	•	-	0	0	0/0 ^l	0/0	0/0	
25	Waraputa	L _C					+					•	•	1989	13	5.3	36/34	17/23	10.5/14.1	
26	Waraputa	L _C					+					•	•	1989	19	5.7	36/43	16/16	7.8/8.6	
27	Waraputa	C									(+)	•	•	-	0	0	0/0 ^l	0/0	0/0	=plot 24, Position shifted
28	Waraputa	L _C									+	•	•	1989	16 [‡]	N/A	36/34*	17/23*	10.5/14.1*	=plot 25, Position shifted
29	Waraputa	L _C									+	•	•	1989	28 [‡]	N/A	36/43*	16/16*	7.8/8.6*	=plot 26, Position shifted

Plot 29 was 1.2 ha- 5 subplots (20*20 m) removed from dataset; plot 23 was 1.02 ha; 1 subplot removed

[§]Logged – L_R, plot was logged using reduced impact logging techniques; L_C, plot was logged using conventional logging; C, plot was not logged and used as a control; (L_{R-s}), plot was logged and silviculturally treated but only prelogging data were used.

[¶]Treatment – Design criteria for the Logging Experiment, expressed as number of trees logged per hectare, applied over 5.76 ha. Actual harvest intensity in the 1 ha census plot is in column Harvest intensity.

[†]Census history – P is pre-harvest enumeration (t-1); +2, +4 etc is the number of years since harvest. (+) refers to control plots which were enumerated in the same years as harvested plots even though it is impossible to speak of “years since harvest”.

[‡]Purpose – Purpose for which these plots were used in this study. LE plots were monitored for the Logging Experiment; CS plots were used for the Chronosequence. Three plots in Pibiri had a dual purpose; silviculturally treated plots were used for descriptive purposes only.

[§]Harvest intensity – actual number of trees and basal area felled in the census plot; dbh ≥35 cm.

[¶]Overestimate; this total includes individuals <35 cm dbh

[†]Logging damage – First figure, percentage of area affected in the 1 ha census plot; second figure, percentage area affected in 25 10*10 m subplots (Sample A) used for most of the analysis in this report. Post-harvest gap outlines were not available immediately after logging in CS plots. Gaps are defined as vertical projections of canopy opening enclosed by crown edges of surrounding trees (Ek 1997). Gap outlines as measured at the youngest census (since logging) was used for all censuses. Figure includes natural gaps if present.

[‡]No gaps were measured in undisturbed plots. Gap percentage was set to 0% in all undisturbed and control plots.

[§]Recensus of plots outside Pibiri suffered from difficulties with relocation of the original plots. Some were shifted with regard to their original positions. Gap and skidtrail distributions were taken as identical to the earliest census.

[¶]In MHFR, no data were available for 10*10 m subplots; same data were used as for the entire plot. Skidded gap percentages were obtained as the product of skidtrails and gaps.

Plots were laid out at 2KM, MHFR and Waraputa in the same way as in Pibiri. The clusters in 2 Km (twice), Waraputa (twice) and Pibiri (three-four times) were re-censused (Table 2.1). However, because the plots in 2 KM and Waraputa were not permanently marked, there were difficulties in relocating the exact plot outlines in the field. This led to shifts of the original plot outlines for most of these plots. Although each re-census was largely overlapping with the first census, these cannot be considered true remeasurements as in Pibiri. The plots in MHFR were only censused once, while the unlogged plot at 2 Km was logged in 2001 and therefore not recensused.

2.3.4 Plot outline

Each 100 m x 100 m (1 ha) botanical sample plot was physically subdivided in twenty-five 20 m x 20 m recording units which were used to locate individuals. Smaller subplots, nested in each of the recording units, were used to subsample individuals belonging to smaller size classes (Figure 2.1, Table 2.2). Each subplot was identified by a unique number. The subplots in the logging experiment in Pibiri were permanently marked with plastic stakes, while the subplots in the other areas were temporarily marked with wooden stakes. The plot layout in Pibiri is described in Ek (1997) and van der Hout (2000).

2.3.5 Species identification

Each censused individual was assigned a field name, which was either an existing vernacular name or a morphospecies name based on salient characteristics. All field identifications were done by experienced field guides or staff trained in taxonomy. For all species, vegetative voucher collections were made and deposited in Utrecht (U) and Guyana (BRG at University of Guyana). Vouchers were also collected when there was doubt about the species identification and to create a reference collection for each census. Identifications were carried out by R. Ek, N. Raes and other specialists as listed in Ek & ter Steege (1998).

The composition of the teams that carried out the inventories varied between censuses, resulting in the possibility of variations in field name nomenclature. Three species complexes were distinguished for species that provided inconsistencies in the field between but not within plots. All named species within the complex were actually identified in the reference collection, but the assignment of individuals to one of these species is considered unreliable. The three complexes are *Abuta* spp. (*A. imene*, *A. obovata* and *A. sp. 1*), *Memora* spp. (*M.*

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flavida and *M. racemosa*) and Malpighiaceae/Hippocrateaceae complex (*Tontelea attenuata*, *Cheiloclinium cognatum* and *Salacia multiflora*). Complexes and partially identified species are not included in the analysis. Together, individuals of these species make up *c.* 11% of total liana abundance, running up to *c.* 20% for individuals ≥ 2.5 cm dbh, so the results must be affected by not including these species and individuals.

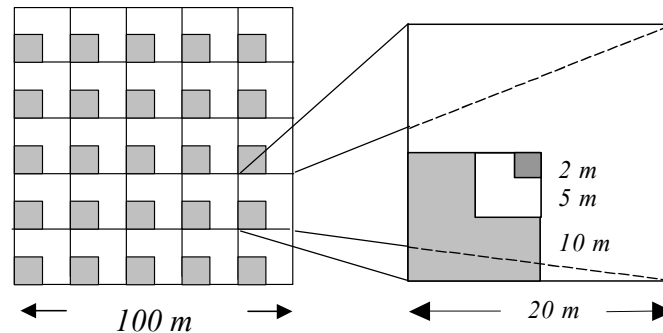


Figure 2.1 Layout of a one ha BSP with subdivision in 25 enumeration units (left) and nested enumeration unit used to enumerate lianas of different size classes (*cf.* Table 2.2, right). The gray area in the left-hand panel represents the area used to obtain Sample A, the basis for most analysis in this report.

In rare cases, variation in species identity may have been retained in the final dataset. Their presence is apparent in the unexpected decrease and increase of pairs of species between censuses of the same plot.

2.3.6 Measurements

Lianas

All liana individuals were measured in nested subplots depending on their size (Table 2.2). Individuals, which were rooted outside the subplot but grew into it, were excluded. Members of a clonal group with above-ground connections were regarded as a single individual. In that case the largest sprout was measured. Lianas that looped back to the ground and produced adventitious roots in the subplot were excluded (unless the main root system was also located in the subplot)

The following data were recorded for each individual:

- Species name, usually a morphospecies name;
- X and Y coordinates of the stem base relative to the plot origin, calculated from compass readings taken from two corner pegs;
- Stem length in 0.05 m intervals for individuals < 2 m, in 0.5 m intervals for individuals < 10 m; for larger individuals the position of the crown was estimated in m above the ground. For most individuals smaller than 15 m, stem length corresponds with position of the crown above ground level.
- Diameter, measured at a fixed distance from the base of the stem, being 1.3 m (dbh) for individuals ≥ 2 m (“10 m” and “20 m” subplots) and *c.* 0.1 m for individuals < 2 m (“2 m” and “5 m” subplots). The point of measurement was shifted up if the stem showed irregularities at the designated point. For hemi-epiphytes that were established in the canopy and sent down aerial roots, the diameter of the root was taken using the same criteria as stems. This concerns *Clusia* spp., *Heteropsis flexuosa*, *Ficus* spp. and *Coussapoa microcephala*.
- Host diameter at breast height (not used in this report)

Individuals were not tagged, so it was not possible to monitor individuals over time. Changes in species composition had to be done by assessing changes at subplot (enumeration unit) and plot level.

Table 2.2 Categorisation of lianas and subplot sizes used for sampling in the field and for analysis. See 2.4, p.18 for explanation of Sample A and Sample B.

	Subplot dimensions (m)	Area sampled per plot (m ²)	Size class (field procedure)	Sample A	Sample B
Large adults	20 x 20	10,000	≥10 cm dbh	Only in 10 x 10	Only in 5 x 5
Adults	10 x 10	2,500	≥2 m height, <10 cm dbh	All ≥2 m height	Only in 5 x 5
Saplings	5 x 5	625	0.5 m ≤ height < 2 m	Omitted	All ≥0.5 m
Seedlings	2 x 2	100	< 0.5 m height	Omitted	Omitted

Habitats

In separate measurements, forest structure was described in order to quantify the intensity of logging in each plot. Skidtrails were mapped using signs of tyres, physical damage to trees and low secondary vegetation. Gap area was determined in the field using an octangular method, measuring the distance from gap centre to gap edge at 45° intervals. The gap edge was identified in the field as the vertical projection of the canopy opening (Putz 1984). Gaps and skidtrails were remeasured at some but not all remeasurements.

It should be noted that in plots 16-29, skidtrails and gaps were measured several years after their creation. Gap outlines were often hard to see due to obstructing secondary vegetation and may have changed due to post-logging gap extension or lateral gap closure caused by ingrowth of neighbouring tree crowns into the gap (shown in the Pibiri plots by Rose 2000). Single-pass skidtrails may have been difficult to recognise. To minimise this problem, gap and skidtrail outlines as found during the first available census after logging were used to characterise logging-related changes in habitat (also in Pibiri). Where plots were shifted at the recensus, the data of the first census were used to characterise habitats at the plot level. Where subplots were used as units for data-analysis, only those were used that were in the overlapping area between the census and the recensus. In one plot (plot 19 at 2KM, 16 year after logging), this could not be done and recensus subplot data were excluded from analysis at subplot level.

The occurrence of natural gaps posed an additional challenge. Natural gaps are unavoidably included in the figures for the logged plots. The gap definition used will be imply the inclusion as gap in the data of natural gaps of a range of ages. Logging gaps are usually created in the course of a just a few weeks after which no additional gaps are created for many years. Although natural gaps must have a significant impact on liana abundance and composition in unlogged forest, their contribution to abundance and composition in logged plots will probably be dwarfed by the impact of logging. Gaps in undisturbed forest in Pibiri (6.1% of the forest, van Dam 2001) and the lowest RIL logging intensity (8.5%, van der Hout 1999) were smaller and covered a smaller relative area than conventionally logged forest and intermediate to high RIL treatments (15.7-30.1%, van der Hout 1999). Unfortunately, it is not possible to distinguish logging gaps from natural gaps in this study and the gap area in several undisturbed and control plots was not measured. In order to avoid creating artefacts in the dataset due to differences in gap area and gap definition between undisturbed plots with known and unknown plot area, the gap area of undisturbed plots was arbitrarily set to zero. This is not correct, but the data does not allow a better resolution of gap area in undisturbed habitats.

No data were available of the distribution of habitats for site MHFR.

2.4 ANALYSIS

2.4.1 Data preparation

Data storage

The data were initially stored in separate databases for plots (plot database, containing the information from Table 2.1), species (species database, containing information about names), individuals (individuals database, containing the information obtained from the field measurements, see “measurements”) and habitats (habitat database, containing identifiers and coordinates of the polygons describing skidtrails and gaps). Subplots were used as identifiers to relate censuses from different years in the Pibiri plots, while this was not possible in the remaining plots due to shifts in plot locations. Information on individuals measured in each census could not be related to each other, as they were not individually tagged.

The individuals database and the habitat database were spatially linked using the PCraster GIS package. Before this was done, habitats were mapped and 5 m border zones were defined inside and outside gaps. This was done for two reasons: the methodological uncertainty associated with determining gap edges in the field, and to cater for possible ecological edge effects of gaps into forest surrounding gaps and of surrounding forest into gaps. Possible ecological edge effects include the micro-climatological effects of shading or insolation into the gap and forest, respectively (van Dam 2001), the different probability of propagule arrival close to edges as compared to gap centres and other differences such as litterfall (van Dam 2001). In the data analysis, when gap size is described this was based on the gap definition as used in the field. However, when subplots were assigned to habitat-categories (gap/non-gap), the 5 m zone into the forest was included in the gap definition, for the reasons described above.

In the database, individuals can be linked to habitats in two ways. Either the coordinates of each individual and the coordinates of the various habitat categories can be linked to give individual habitat assignments, or subplots can be assigned a code on the basis of the most extensive habitat. There were two habitat variables coding for ground-level disturbance (on or off a skidtrail) and for canopy-level disturbance (location in forest, forest edge, gap edge and gap interior; both edge zones are 5 m wide). Habitat categories were merged for analysis if necessary (*e.g.* gaps were defined as forest edge + gap edge + gap interior for some analysis).

For analysis, given the uncertainty associated with determining coordinates in the field, preference was given to the second method of assigning habitat codes to individuals, *i.e.* by means of uniform codes at the subplot level. All subplots were classified in one of four habitat categories: skidded gap (canopy and soil disturbance), skidtrail (soil disturbance), gap (canopy disturbance) or forest interior (no disturbance).

Selection of data – Sample A and Sample B

In the individuals database, individuals were selected for analysis based on a number of criteria:

- Seedlings as enumerated in the 2 x 2 m subplots were retained for descriptive purposes of population size distribution only. They were not included in the analysis of compositional change and species responses to logging.
- The size criterion for large adult lianas (dbh>10 cm) made that few individuals were measured at the level of the 20 x 20 m subplot (Table 2.2). Before the logging, only 1.9% of the total measured population in Pibiri consisted of individuals of this size (average 0.8 per subplot or 21 per ha, range 7-34). Therefore, this spatial level was only used for descriptive purposes but not most analysis. Instead, two samples were created at different spatial levels of analysis (Table 2.2). Sample A includes all lianas > 2m sampled within the 10 x 10 m subplots. Sample B includes all lianas ≥ 0.5 m height within the 5 x 5 m subplots. All lianas satisfying the criteria for inclusion in

larger subplots but with coordinates outside the 100 m² and 25 m² subplots, respectively, were rejected for inclusion in these two samples. Sample A contains 30,456 liana individuals belonging to an accepted taxon; Sample B contains 17,090 liana individuals. The choice of “scaling down” (selecting only the larger individuals physically located in subplots of a lower category), rather than “scaling up” (giving a heavier weight to individuals from smaller size classes and subplots than larger individuals and bigger subplots) was made because the species-area implications of scaling up is not compatible with the purpose of this study (measurement of biodiversity). The consequence of scaling down is that fewer species are represented in the sample. For methodological reasons, no Sample B could be established for logged plots in MHFR (plots 22 and 23).

- Botanically unidentified individuals with a clear identity (as apparent from a morphospecies name) were retained for analysis. Unidentified individuals without identity (no such name) were rejected. Taxa were accepted for further analysis if they represented consistent and identifiable botanical units. If there was doubt about the consistency of field name assignation, or fieldnames were demonstrated to contain several botanical species in the plots, then taxa were not included in further species-based analysis. Of all 187 accepted taxa, 82.4, 89.9 and 98.4 % could be identified to the species, genus and family level, respectively, while 1.6 % of the taxa were readily identifiable in the field but remained without taxonomic name. Thirty additional taxa, including three species complexes and nine names in these complexes, were not accepted as valid because each probably represented several unknown species. Of all 50,528 individuals identified as a liana in the field, 89.7, 91.6 and 93.4 % could be identified to the species, genus and family level, respectively, while 6.6 % were not identified.

2.4.2 Data analysis

A detailed description of the methods used for data analysis is provided in Appendix A. Below, a brief summary is provided.

Diversity and abundance

The main measure for species diversity used in this report is Fisher’s α . Contrary to the more “natural” measure of species richness (called “species density” in this report), Fisher’s α is little dependent on the number of individuals in a sample, and therefore suitable to detect differences in diversity between two samples which vastly differ in abundance (as happens frequently in this report). Abundance, N , is also used to characterise liana communities, while Simpson’s index (expressed as its inverse, $1/D$) provides an idea of the degree to which a community is dominated by some species.

Rarefaction

While Fisher’s α is suitable to compare diversity between samples of different size, several replicates need to be sampled in order to evaluate statistical differences between two treatments. If only single samples are available, rarefaction techniques can be used to evaluate to what extent differences in species richness between two samples of unequal size are “real”. This was done to compare the species richness of different habitat patches. Each of these patches was too small to calculate reliable Fisher’s α values. Instead, the data were aggregated over all available habitat patches per logging intensity treatment. Assuming that the smallest sample contained n_1 individuals, differences in richness between pairs of habitat patches were compared on the basis of 1000 random drawings of n_1 individuals from the larger sample.

Species-Area curves

Diversity of undisturbed forest was studied at three spatial levels: region, site and plot, whereby region is the entire dataset. Species-area curves – the accumulation of species as more and more area is sampled – were constructed to assess to what extent the total regional

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species pool was sampled in samples of different size and what percentage of diversity was sampled by individual plots.

Size class distributions

Liana size class distributions were based on height classes for individuals ≤ 2 m (≤ 0.5 m; ≤ 1 m and ≤ 2 m), and dbh size classes for larger individuals (1 cm classes up to 5 cm dbh, followed by 5.1-10, 10.1-20 and 20.1-50 cm). This is the only analysis that was conducted on all lianas regardless the subplot in which they were sampled. For some types of analysis, this would mean that some size classes would contain a very large number of individuals and others just a few. Therefore, an alternative size classification was used with classes of increasing width: two height classes and five diameter classes of doubling width (details in Table A.1). This alternative size classification was only done for Sample B, or a mixture of Sample A and Sample B.

Anova analysis of the logging experiment

The logging experiment was set up as a randomised block design, with four harvesting treatments in three replicate blocks. Each plot was measured twice, before and four years after logging. The effects of logging on diversity at the community level were investigated using four different parameters: species density (S), total abundance (N), diversity (Fishers α), and dominance (Simpson's index, $1/D$), and this was analysed with analysis of variance (anova). Models were constructed that were based on a randomised block design, with two fixed factors (L-Logging intensity and S-Size, using the alternative size classification) and two random factors (B-Block and T-Time = census). The specific tests that were conducted were to assess whether the interaction between Logging intensity and Size depended on Time (LST), or whether the effect of Logging Intensity depended on Time (LT). In both cases, a significant effect would imply that there would be an effect of logging intensity on the parameter of interest, either dependent on liana size class (LST) or independent of size (LT).

Similarity

The similarity between pairs of plots was expressed using Sorenson's index and the Morisita-Horn index. The former is a measure for the relative number of shared species between two sites, while the latter also takes similarities in abundance into account.

Correspondence analysis and canonical correspondence analysis

Differences in species composition between undisturbed plots were analysed using correspondence analysis. The variation in species composition between plots is expressed as scores on imaginary axes. The first axis represents an ordering of plots that corresponds with the highest variation in the abundance of species present within the data and thus represent the main trend in the data. The second axis does the same with the remaining variation after axis 1 has been extracted.

In logged forest (both in the logging experiment and in the chronosequence), these axes describing the main variation in the dataset were constrained by factors thought to be responsible for changes in species composition related to logging. This was done for plots (providing an idea of changes due to plot-level variability, such as logging intensity or age since logging) and subplots (providing an idea of changes due to the existence of different logging-related habitats). Environmental factors were expressed per (sub)plot and included parameters describing logging intensity (N or Basal area felled), logging damage (% of (sub)plot with canopy damage, with ground damage, with both), age (years since logging) and space (replicate block in which the (sub)plot was located, site coordinates).

Chronosequence

The problem of chronosequence studies is that plots differ in more than just age since logging. Species composition varies from place to place and therefore, strictly, it is not possible to unambiguously attribute differences in diversity between plots to logging. The basic

assumption was that the control plot represented the pre-logging situation for each logged plot in the chronosequence. To minimise differences between the four sites caused by differences in species composition, all diversity and abundance variables in the chronosequence were expressed as differences between logged and unlogged control plots. At two points in the chronosequence no control plots were available to be compared with logged plot censuses: at $t=2$ years after logging (Pibiri) and $t=16$ years after logging (2KM). In these cases, the control plots for $t=0$ (Pibiri) and $t=10$ (2KM) were used as a reference. The census of logged plots at $t=0$ in reality concerned yet unharvested plots.

Due to these uncertainties, no formal analysis was conducted for the chronosequence study, but trends were assessed visually, assuming that the relation between a parameter value (diversity or abundance) and age since logging would be unimodal, increasing or declining just after logging and then returning to background (control plot) values.

Ecological species groups

The study was designed to evaluate the existence of species or groups of species that would respond predictably to logging and that could potentially be used as indicators. Species responses to logging were assessed in two ways: by comparing species scores in the correspondence analysis and by comparing species abundance between plots and habitats that differed in logging history. Several patterns were expected to occur among the species when subjected to logging: increase or decrease related to logging intensity, increase or decrease related to logging but independent of logging intensity, and indifferent to logging. In order to determine whether species belonged to one of these groups, the abundance of each was tested at the plot and the habitat level. An important requirement was that species responses be consistent. For instance, a species was only considered to have a positive response to logging, if its abundance increased significantly with increasing logging intensity and if that increase was caused by increases in habitats created by logging. If the increase would be confined to unlogged habitat in otherwise heavily logged plots, the response of this species would be deemed inconsistent.

Indicators

In the final part, the relation between the abundance of species with a consistent response to logging and direct measures of logging damage (*i.e.* skidtrail area) will be analysed using simple regression analysis. The usefulness of indicators thus derived was assessed by their ability to successfully predict logging damage. No independent dataset was available for which the relations found can be validated, so that is where the analysis stops.

2.5 DIFFERENCES BETWEEN THE LOGGING EXPERIMENT AND THE CHRONOSEQUENCE STUDY

As is evident from the information presented so far, the basic data collection and analysis is very similar between the two major components of the study, the logging experiment and the chronosequence study. In spite of these similarities, there are a number of major differences, which affect the interpretation and strength of the conclusions. It should be borne in mind that the first 6 years of the chronosequence actually concerns plots that were set up and measured in the framework of the logging experiment.

The principal differences between logging experiment and chronosequence study are:

- The chronosequence data cover a much longer period (0-16 years in stead of 0-4 years).
- Logging in the plots of the chronosequence was generally not controlled as it was in the reduced impact logging experiment in Pibiri. Logging method and intensity, therefore, were variable. Logging in the plots outside Pibiri was likely most like (but not the same as) the RIL 16 treatment in Pibiri. The RIL 16 treatment is used to assess short term changes (0-6 years) in the chronosequence dataset. There is no information

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on medium-term changes in liana diversity and abundance in lightly to moderately logged forest. In heavily logged plots, there are differences in habitat distribution between Pibiri and the other sites (Table 2.1). This difference is particularly large for the extent of area with canopy and soil damage (skidded gaps): 2.5% of plot area in RIL 16 plots in Pibiri vs. 8.3% outside Pibiri. It is associated with the use of Reduced Impact Logging in Pibiri and Conventional Logging techniques elsewhere. For the interpretation of the Chronosequence study (which includes 2 high intensity plots in Pibiri), it is relevant to realise that the effects of logging intensity and age are confounded. The younger plots in the sequence are in Pibiri and relatively little damaged given the intensity of logging, while the older plots are located outside Pibiri and relatively heavily damaged. There are no “old” plots with low levels of logging damage.

- The pre-harvest liana composition of the plots in the chronosequence is not known. Instead, nearby unharvested plots were enumerated to obtain an idea of the pre-harvest species composition of the forest. As it will be shown later (Figure 3.6, Figure 3.7) that there is spatial variation in species composition between plots, there is uncertainty whether changes between the control and harvested plots are attributable to logging (time) or to spatial variation. There might be a reason why the unharvested controls were not harvested: their species composition might have been different (unattractive for loggers) or logging conditions might have been different (difficult terrain). Care has been taken to find plots that were as similar as possible to the harvested plots, but the possibility of these pre-harvest differences in composition and site conditions cannot be excluded.
- “Treatments” (years since logging) were not randomly distributed over plots in the chronosequence approach. The younger treatments were all in Pibiri while the older treatments were scattered over 3 other sites. There is no replication of “treatments” over sites (except for t=6)
- More people were involved in the censuses of the chronosequence. If observer-effects existed in the dataset, their impacts are expected to be larger in the chronosequence dataset.
- For most unharvested control plots (all except those in Pibiri and Waraputa, which were measured repeatedly over the same time period as the harvested plots) it is unknown whether and to what extent liana composition changed over the same period as the harvested plots. It is attractive to think that species composition in undisturbed forest is relatively constant and this is largely confirmed by the Pibiri plots (see, *e.g.*, Figure 3.13). However, there is no certainty that this is always the case, particularly if logging and road building have occurred in close vicinity of these plots.
- Species composition between the four main sites of investigation is slightly different and some species that are good associates of logging-related changes in one site might be rare or absent in another. The window of opportunity to respond to logging may be short for some species and sometimes, logging comes at such a time or in such a place that responsive species are not capable of responding, *e.g.* at a time that there are no seeds or when the weather is unfavourable.

3 RESULTS

3.1 PRE LOGGING DIVERSITY AND COMPOSITION

3.1.1 Species density and diversity

In plots in undisturbed Greenheart-bearing Mixed forest near Mabura Hill a total of 137 valid liana taxa (from here called “species”) were found. If the species in the three species complexes (see section 2.3.4) would be added, the species count is 146. In the two samples used in this study, the number of species was 132² (Sample A; individuals >2 m tall in 100 m² recording units) and 103³ (Sample B; individuals > 0.5 m in 25 m² recording units). Pibiri, which was most intensively studied, harboured the largest number of species: 101 and 75, respectively (pre-harvest data). Thirty to forty percent of the regional species pool is found in any 1 ha plot (*cf.* Table 3.1), while *c.* 5% of the regional species pool is found in any 100 m² (25 m² for Sample B) recording unit. At the best-studied site (Pibiri 1993), plot level species richness was at about 40%, and subplot level species richness at *c.* 8% of the local species pool.

A floristic analysis of the Mabura Hill region, including the liana flora, was made previously by Ek (1997) and Ek & ter Steege (1998).

Table 3.1 Species density of undisturbed liana communities in Greenheart-bearing Mixed forest near Mabura at three spatial scales: regional (all research sites jointly), plots and subplots. Means and standard deviations are provided. The area enumerated per region, plot and subplot differs between Sample A and B. The regional area sampled was 5.75 ha (Sample A) and 1.4375 ha (Sample B) The same data are provided for the pre-harvest census of the largest single site, Pibiri (3.75 and 0.9375 ha, respectively). All undisturbed and control plots were used for this overview.

Scale	All sites					Pibiri pre-harvest				
	n	mean	s.d.	mean	s.d.	n	mean	s.d.	mean	s.d.
Region/Site		132	-	103	-		101	-	75	-
Plot	23	39.9	5.8	29.3	5.8	15	41.1	5.3	30.1	5.0
Subplot	575	8.1	3.5	5.3	2.5	375	8.7	3.6	5.7	2.6

A summary of key biodiversity parameters of the liana community in undisturbed Greenheart forest is provided in Table 3.2; the individual plot data are provided in Appendix C. The difference between Sample A and Sample B in Fisher’s α is not real. It is due to the difference in area sampled between the two samples. If compared at equal sample area, Fisher’s α is almost the same (see also 3.1.5).

Table 3.2 Summary of key diversity parameters[†] for the liana community based on 23 undisturbed (pre-harvest and control) plots in Greenheart bearing forest near Mabura Hill. Mean standard deviation and range are given. All indices are expressed per plot.

		Sample A (height >2 m in 100 m ² subplots)			Sample B (height >0.5 m in 25 m ² subplots)		
		mean	s.d.	range	mean	s.d.	range
Abundances							
Species density	S	39.9	5.8	27-50	29.3	5.8	13-40
Number of individuals	N	554	184	169-957	371	135	126-678
Diversity indices							
Fishers’ alpha	α	10.1	1.4	6.9-13.5	7.7	1.7	3.1-11.6
Shannon-Wiener index	H’	2.4	0.2	1.9-3.0	2.0	0.3	1.3-2.6
Shannon’s evenness	E	0.6	0.1	0.6-0.8	0.6	0.1	0.4-0.8
Dominance indices							
Simpson’s index	1/D	5.0	2.1	3.4-11.1	3.6	1.2	2.0-6.7
Berger-Parker index	1/d	2.4	0.6	1.9-4.3	1.9	0.4	1.4-2.9

[†]excluding species/individuals of uncertain taxonomic status and species complexes.

² 140 including species in species complexes

³ 112 including species in species complexes

3.1.2 Species-area relations

The data in Table 3.1 show that only a relatively small percentage of the total diversity in the region or site is sampled within any 1 ha plot. This suggests that many plots need to be sampled to encounter all species belonging to the regional species pool. This is illustrated in the species-area curves in Figure 3.1, in which the increase in mean expected number of species with enumerated area is given for the undisturbed forest plots. The curve for all 23 plots is above the curve for the pre-harvest census of Pibiri alone (compare left and right hand panels) because the regional species pool (all species found in undisturbed and control plots) exceeds the pre-harvest species pool of Pibiri by 32 species (Sample A, Table 3.1). The increase in the number of species does not level off quickly as more plots are sampled so more species are expected to accumulate if more plots are added.

The species–area relations for Sample A and B appear to be different in Figure 3.1, but this is an artefact caused by large differences in the number of individuals per unit area between the two Samples. The curves for Fisher’s α (triangles), which is relatively insensitive to the number of individuals, are almost overlapping. However, with increasing area sampled, Fisher’s α is not as stable as would be expected in communities with random mixing of species, but it increases slowly. This suggests that larger samples are more diverse. This could point to a non-random but patchy occurrence of species, both within Pibiri (right hand panel) and at the regional scale captured in the left hand panel of Figure 3.1.

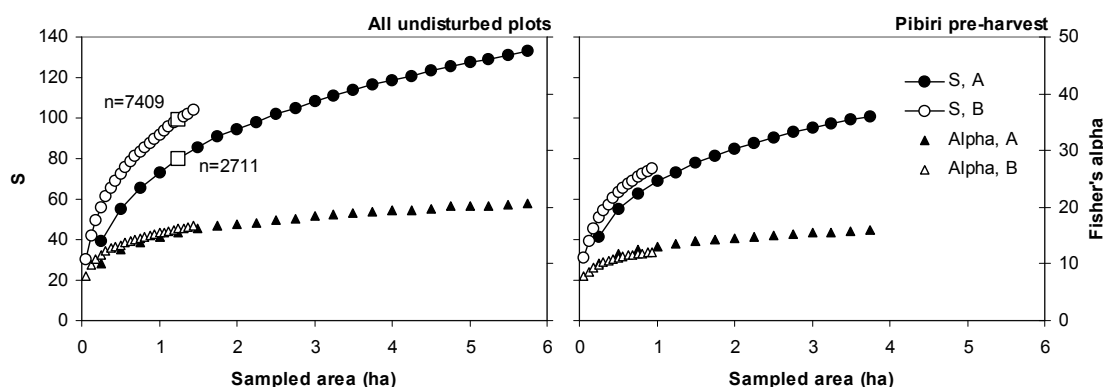


Figure 3.1 Relation between sampled area and number of liana species, S (left hand axis) and Fisher’s α (right hand axis) for all undisturbed plots (left hand panel, $n=23$) and for Pibiri’s pre-harvest plots (right hand panel, $n=15$) near Mabura Hill. The curves are based on means of 50 random samples of 1, 2, 3 ... n plots (dots and triangles). The squares in the left hand panel illustrate that – at a sample area of 1.25 ha – the difference in species density between sample A (closed dots) and Sample B (open dots) is related to the larger number of individuals per unit area (insets) of Sample B, not by true differences in diversity (because Fisher’s α of both Samples is almost identical at that point).

3.1.3 Species abundance distribution in Pibiri

The distribution of species over abundance classes in the pre-harvest census at Pibiri is shown in Figure 3.2. Classes of doubling abundance (octaves) were defined and all 15 plots were taken together. As many as 20% of all species were represented by a single individual, even though the total population consisted of almost 9000 individuals (in the case of Sample A). One species, *Conarus perrottetii*, stands out because it was found to be almost nine times as abundant as the second most abundant species. This species made up *c.* 50% of the pre-harvest liana population in Pibiri. This dominance is unusual and causes low values of the Berger-Parker index (which is the reciprocal proportion of the commonest species) and the Simpson index (Table 3.2).

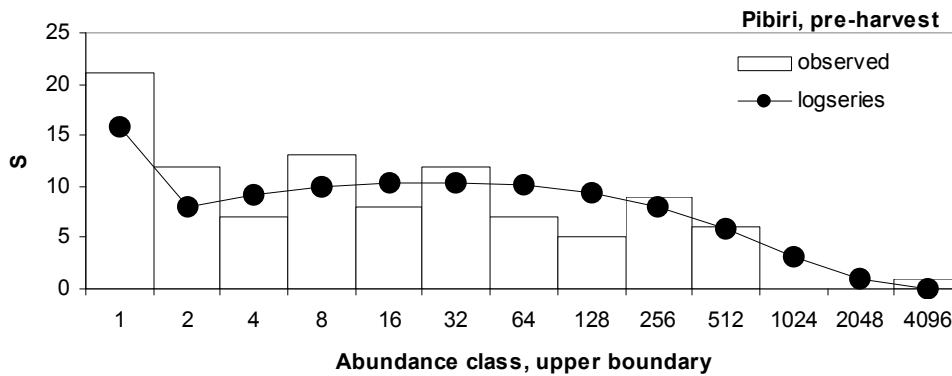


Figure 3.2 Distribution of liana species abundances in the pre-harvest census of Pibiri (data from all 15 plots combined), Sample A. S is the number of species per abundance class. The dots and line give the distribution predicted by the log series. $S_{\text{total}} = 101$. Sample B also followed a log series.

The distribution of species over abundance classes in the pre-harvest plots in Pibiri is adequately described by a log series. It is an underlying assumption for the calculation of Fisher's α , that species are distributed as in a log series. The distribution expected in a log series was not statistically different from the observed distribution ($\alpha=15.95$; $x=0.99823$; $\chi^2_{10}=11.34$, n.s.). The expected log series distribution is shown by a line in Figure 3.2.

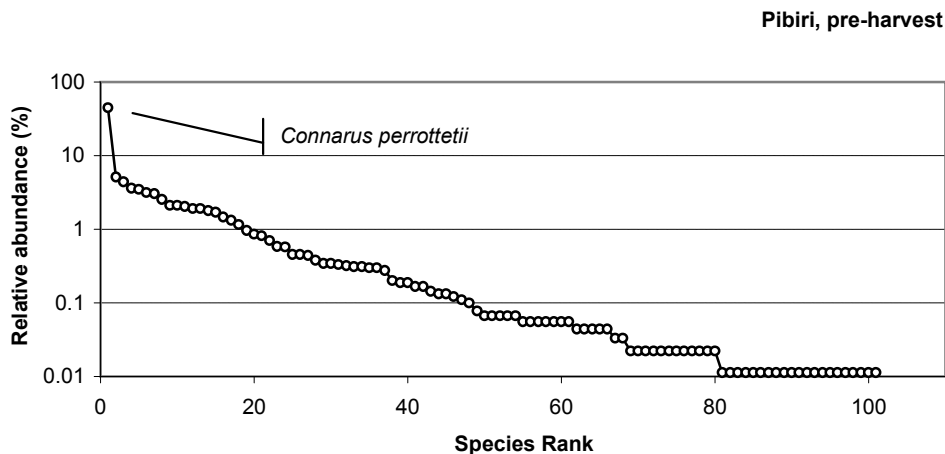


Figure 3.3 Rank-abundance plot of the 101 species present in Sample A in the pre-harvest plots at Pibiri. Abundance (in %) is plotted on a log scale, and is fitted by $\log(\text{relative abundance}) = 0.52 - 0.066 * (\text{rank})$; $R^2=0.952$. *Connarus perrottetii* is by far the commonest species in Pibiri.

Essentially the same information as in Figure 3.2 is provided by the rank-abundance plot, in which species are ranked from highest to lowest abundance and their proportion in the total population plotted on a log scale (Figure 3.3). Of 101 species found in the 8989 individuals of Sample A in Pibiri prior to harvest, eighteen species each accounted for more than 1% of the individuals, while 21 species were represented by a single individual.

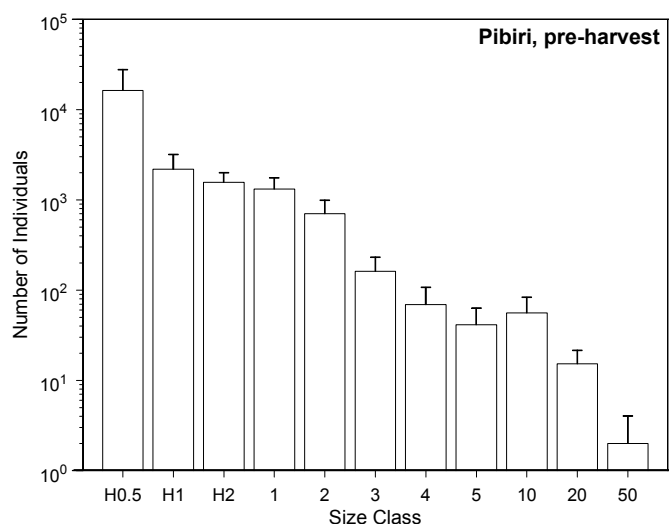
3.1.4 Size class distribution

Most natural populations show a highly skewed distribution of individuals over the various size classes. This was no different for the liana communities near Mabura Hill. Undisturbed populations (pre-logging and control plots) showed a high abundance of small individuals (Figure 3.4), whereas large lianas were scarce. On average, fewer than 20 lianas with a diameter of >10 cm were present per hectare. The number of seedlings (height <0.5 m) is estimated to be in the order of thousands to tens of thousands per ha. Even though the shape of the population size class distributions was very similar between plots ($>50\%$ of correlations between pairs of plots was >0.99), the number of individuals per size class varied markedly between plots. Apart from seedling numbers, which are always variable due to local

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variations in seed dispersal and germination, the highest variability was found among lianas 3-4 cm dbh. Further analysis showed that differences in population size distribution were not geographically determined, i.e. plots that were located close together were as different from each other as plots further apart (data not shown). Differences in response to logging are therefore probably not systematically related to differences in pre-harvest size class distributions.

Figure 3.4 Size class distribution of lianas in undisturbed rain forest in Pibiri. Means and standard deviation of 15 one ha plots,



based on all data. Note log scale on Y-axis. Classes preceded by 'H' are based on height

3.1.5 Diversity-size trends

Species differ in maximum size, which suggests that diversity in the larger size classes would be different from lower size classes. Indeed, species density peaks at *c.* 1 cm dbh, after which it decreases with increasing size (Figure 3.5). Because of the decreasing trend in liana abundance with increasing size (Figure 3.4), the reduced number of species in the large size classes can be explained as a density or sample effect rather than a real decrease in species richness. As a result, Fisher's α fluctuates a bit without trend (Figure 3.5, middle). In all size classes based on dbh, Fisher's α is approximately constant between 11 and 15 (Sample A, calculated for the aggregated pre-harvest data from Pibiri), but smaller size classes (based on height and Sample B) appear to be less diverse than the dbh-classes. This reduced diversity in smaller size classes is somewhat counterintuitive, as these classes are very abundant and are, in principle, expected to contain individuals of each regenerating species found in the plot. Their lesser diversity can be understood if the species-abundance pattern of small individuals is very much different from large individuals, if seedling populations are ephemeral: irregular regeneration events followed by rapid mortality and growth into larger size classes and thus have a low "detection probability" in a single census, or if species are missed in the census due to identification problems.

The trend in Simpson's index, which is a measure of dominance, shows much stronger fluctuations. Classes with a low value of the index (Figure 3.5, right) are highly dominated by *Conarus perrottetii*. (This is illustrated by its abundance in Figure 3.5, right hand panel). Curiously, this dominance shows a dip in diameter classes less than 0.5 cm, coinciding with a near absence of *C. perrottetii*. A low Simpson's index, i.e., a high dominance of *C. perrottetii*, in the 1-2 cm classes might be due to an accumulation of shrub phase individuals of *C. perrottetii*. This species grows up as a freestanding shrub before it starts climbing. If climbing opportunities (suitable supports, trellises) are limiting for the growth of *C. perrottetii* into larger size classes, then individuals may accumulate in the shrub-class and thus depress Simpson's index.

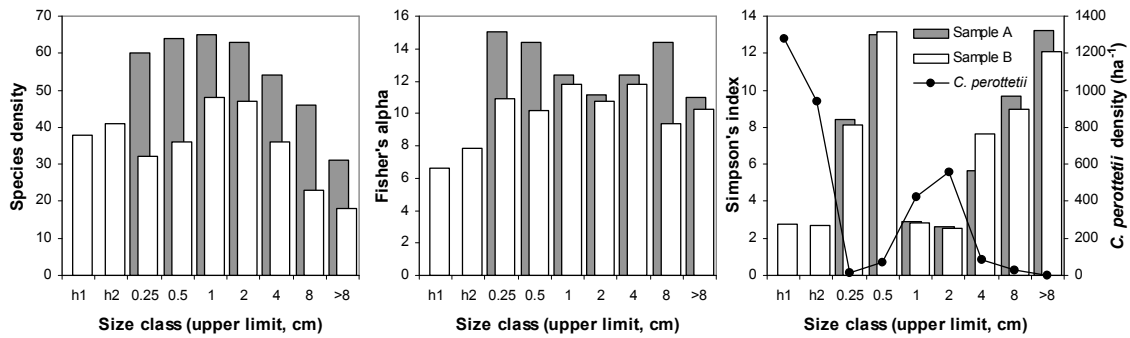


Figure 3.5 Size-dependence of liana species density (left), Fisher's α (middle) and Simpson's 1/D (right) for Sample A (gray, height >2m) and Sample B (white, height >0.5 m), in 15 plots of undisturbed forest in Pibiri. Size classes are of doubling width (unlike Figure 3.4) and data of all plots were aggregated to ensure sufficient individuals for calculating the parameters in each class. Abundance of *Connarus perrottetii* (Sample B) is plotted in the right-hand panel.

3.1.6 Species composition and similarity

Liana communities in unharvested forest showed relatively minor differences in species composition between plots. Even though any given 1 ha plot contained less than 40% of the regional species pool (Table 3.1), this was not due to clear variation in composition caused by, e.g., variation in habitats or growth conditions but rather to random "sampling" from a large species pool. The only trend that could be detected was a trend for plots to be more different in composition when they were located farther apart.

Differences in species composition per plot were investigated using correspondence analysis. In this analysis, variation in species composition between plots is expressed as scores on imaginary axes. The first axis represents an ordering of plots that corresponds with the highest turnover in the abundance of species present within the data (Jongman *et al.* 1987). The second axis does the same with the remaining variation after axis 1 has been extracted, etc.

This exercise was conducted on 23 undisturbed plots on untransformed species abundances per plot; rare species were downweighted. The abundance data are provided in Appendix D.

In Figure 3.6, the scores of the plots on axes 1-3 have been plotted. The total variation accounted for by these axes was 45%. The analysis revealed strong geographic patterns in the dataset. In general terms, axis 1 separated plots located in Pibiri from those away from Pibiri. Axis 2 singled out MHFR (positive score) Waraputa (negative scores). Finally, axis 3 appears to correspond with differences between plots that were enumerated before logging was conducted in the area and plots that were used as controls after neighbouring plots had been logged. The non-Pibiri plots (all located near harvested forest) were scattered over these two categories on axis 3.

Plotting of species scores on these axes enabled the identification of species that contributed much to the observed differences between plots. The many rare species in the dataset contributed heavily to these differences but that is little informative for the analysis of spatial pattern. Of the 20 commonest species in the dataset, six (*Anomospermum grandifolium*, *Memora moringifolia*, *Pinzona coriacea*, *Petrea volubilis*, *Rourea ligulata* and *Heteropterys multiflora*) contributed disproportionately to differences between plots. Even in these species, this was usually due to one or two plots with a disproportionately high abundance, such as in the case of *Heteropterys multiflora*, of which 75% of all 164 individuals in Sample A were recorded from the control plot at 2KM. *Pinzona coriacea* (n=217) and *Petrea volubilis* (195) were typical of Pibiri plots, while *Rourea ligulata* (153) was almost confined to Waraputa. *Connarus perrottetii* (5704) did not display strong geographical preferences.

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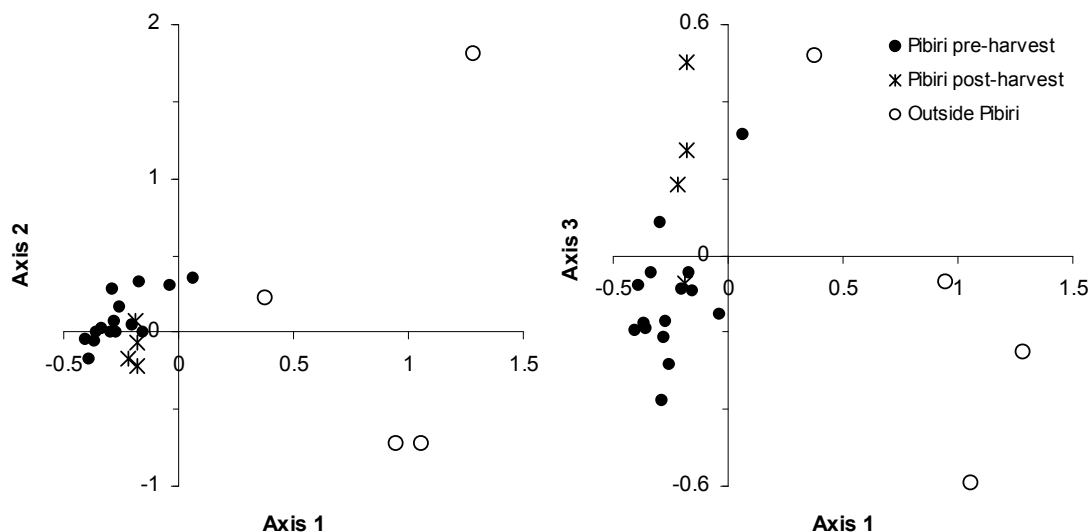


Figure 3.6 Results of Correspondence Analysis of liana abundance scores in 23 undisturbed plots near Mabura Hill. Scores on the three main axis are plotted. Plots in Pibiri (measured prior to and after harvest of surrounding plots) and outside Pibiri are identified by different symbols. Data are from Sample A (100 m² subplots, lianas >2 m). Results from Sample B are comparable (not shown).

The analysis confirms the conclusions obtained for these plots by Ek (1997) using cluster analysis, i.e. that geographic patterns appear to be responsible for differences between sites and that the apparently homogeneous Greenheart-bearing mixed forest in reality varies in (liana) species composition from place to place. This is visualised by calculating similarity for all 253 combinations of plots and plotting that against the distance between plots (Figure 3.7). The similarity was calculated using the Sorenson index (based on absence/ presence data) and the Morisita-Horn index (based on abundance data). As the latter is highly sensitive to the abundance of the most common species, *Connarus perrottetii* was removed from the calculation of the Morisita-Horn index. The similarity of plots within the Pibiri area was high and decreased to low values at *c.* 30 km, the maximum distance present in the dataset. The decrease in similarity with distance was much more pronounced in the Morisita-Horn index than in the Sorenson index. Exclusion of *Connarus perrottetii* indeed had a large influence on the Morisita-Horn index, and affected similarity of the MHFR plot with the others. This plot had a relatively low abundance of *Connarus perrottetii*.

Several plots were enumerated repeatedly in a period of 5-7 years. If the assumption is true that there is very little change in species composition in control plots, a very high similarity index (close to 1) between these plots would be expected. However, within Pibiri, the mean Sorenson similarity of five pairs of plots that represent recensuses equals 0.67, which is the same as the mean of all other pairs of plots in Pibiri. Hence, variation between plots is caused by “real” spatial variation in composition of the liana community cannot be distinguished from temporal variation in occurrence of (rare) species in this dataset.

The same comparison with acknowledgement of species abundance gives the same result: even though, as expected, the Morisita-Horn similarity between identical plots at different moments in time is higher (0.77) than between different plots at the same moment (0.71), this difference is not significant when tested with a *t* test ($p=0.17$, ns)

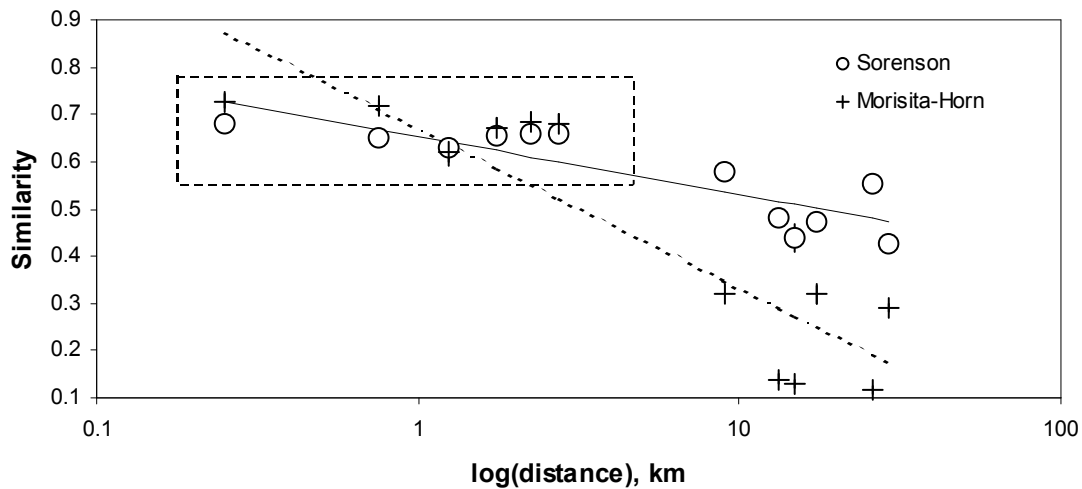


Figure 3.7 Relation between the distance between plots and similarity, as expressed by the Sorensen and Morisita-Horn indices, for lianas in undisturbed plots near Mabura Hill, using Sample A. Points in Pibiri (in the box) are means (\pm s.e.) for pairs of plots per zone of 500 m. For each other distance, all combinations involving Pibiri were averaged. The R^2 of the regression lines are 0.74 and 0.80, respectively. For the Morisita-Horn index, the dominant *Connarus perrottetii* was removed from the data prior to analysis.

3.1.7 Evaluation of assumptions of the study based on analysis undisturbed plots.

The following conclusions can be drawn:

- One ha sample plots in this forest type sample only 40% of the local liana species pool. Twelve plots are needed to sample 95% of the species.
- The liana vegetation in this forest type is heavily dominated by a single species, *Connarus perrottetii*. This species alone accounts for much variation between plots, particularly of Simpson's Index of dominance and to a lesser extent also Fisher's α .
- Large lianas are rare, with just 20 individuals >10 cm dbh per ha.
- Plots vary geographically in composition, mainly due to the occurrence of many relatively rare species. The larger the distance between two areas in similar forest type, the larger the difference in liana species composition.

The data give some confidence in the important assumption underlying chronosequence studies, i.e. that the pre-harvest species composition and size class distribution of the liana vegetation, while not the same, was relatively similar for all plots. In all but one case (MHFR) the control plot was located in the immediate neighbourhood of the logged plots used for the chronosequence, suggesting that similarity in species composition was likely to be high. Unlogged plots that were censused repeatedly differed little in population size distribution and diversity, although the analysis also showed that undisturbed plots are not unchanging. The analysis presented in this section also permits to identify species that appear to vary in a geographical manner. In this dataset, these taxa are less suitable to evaluate the effects of logging at least over larger geographic scales

3.2 CHANGES IN DIVERSITY AND SPECIES COMPOSITION: THE LOGGING EXPERIMENT

3.2.1 The logging experiment - general trends

In Pibiri, a direct comparison of biodiversity before and four years after logging is possible because the same plots were monitored. The values of several basic diversity parameters of these plots are presented in Table 3.3 and Table 3.4. The total number of species encountered in Pibiri increased by 16% (Sample A) and even 32% (Sample B). Similar increases were also found at the plot and subplot levels (Table 3.3), but this varied with the logging intensity treatment that was applied to each plot (Table 3.4, plot level). The percentage of species of the total site species pool that was found at plot and subplot levels barely changed between pre- and post-logging censuses.

Table 3.3 Pre- and post-harvest species density in liana communities in Greenheart-bearing Mixed Forest forest in the logging experiment at Pibiri, at three spatial scales: site (all plots jointly), plot and subplot. Means and standard deviations are given. The pre-harvest data exclude the 3 plots that were not re-enumerated (see Table 2.1; compare Table 3.1). The total site area sampled was 3.75 ha (Sample A) and 0.9375 ha (Sample B).

Scale	n	Pibiri pre-harvest				Pibiri post -harvest			
		Sample A		Sample B		Sample A		Sample B	
		mean	s.d.	mean	s.d.	mean	s.d.	mean	s.d.
Site	1	100		75		115		98	
Plot	12	41.8	5.4	30.9	5.0	54.3	10.2	42.3	8.3
Subplot	300	9.1	3.5	6.0	2.6	10.9	5.1	7.1	3.3

In general, biodiversity parameters summarised in Table 3.4 tend to increase in value with increasing logging intensity. For species density and Fisher's alpha (Sample B) this was supported statistically (mixed model Anovas, see Table 3.4), but not for abundance, Fisher's alpha (Sample A) and the Simpson's index. The pattern emerging from this table is that part of the increase in species counts is explained by an increase in liana abundance (even though this increase was not significant, it affects the calculation of the other parameters), because the increase in Fisher's α is not as strong as in species count (and only significant for Sample B). There is a difference in the effect of logging intensity between Sample A and Sample B, suggesting that the effect of logging intensity on smaller lianas (height 0.5-2 m, included in Sample B, but not Sample A) must be larger than on larger lianas (height >2 m). In this analysis it is unclear to what extent slight pre-logging differences could have contributed to the observed effects. These effects, and those of liana size, are incorporated in the more elaborate statistical analysis below.

3.2.2 Species losses and gains

From Table 3.3 it follows that at the scale of site the net species density changed by 15⁴ and 23 between the pre- and post-harvest census of the plots in Pibiri for Sample A and Sample B, respectively. The dynamics in the number of species encountered during the censuses is larger than these net figures suggest. Table 3.5 shows that in the combined Samples, 35 species were encountered that did not occur prior to logging, while 19 species disappeared from the population.

The pattern of species gains and losses appears largely random. Only 8 out of 35 newly appeared species are unique to logged plots in the entire dataset (i.e. no records exist of such species in any of the undisturbed or pre-harvest plots), so these species could, in principle, be specialists of habitats not available in undisturbed forest. Ten newly appeared species have also been recorded in undisturbed plots either outside Pibiri or appeared in one of the control plots of the logging experiment. Hence, these species are capable of growing in undisturbed forest and their absence in the pre-harvest census may simply be a sampling artefact.

⁴ 14, if the RIL 8+L treatment is included.

Logging intensity and liana diversity

Table 3.4 Summary of key diversity parameters* for the liana community based on the logging experiment in Pibiri plots. Means (s.d.) are given for n=3 plots per treatment, and for Sample A (top, sample area 2500 m² in each plot) and Sample B (bottom, sample area 625 m² in each plot). N is expressed per plot, not per ha. Pre-harvest data exclude the RIL 8+L plots (Table 2.1). The last column gives the results of statistical tests for differences in parameter values in the post-logging census[†]. Parameters in pre-logging censuses did not differ statistically.

		Treatment: Logging Intensity								Test
		Control		RIL 4		RIL 8		RIL 16		
Sample A		mean	(s.d.)	mean	(s.d.)	mean	(s.d.)	mean	(s.d.)	
<i>Abundances</i>										
Species density S	pre	42.0	(4.6)	40.7	(7.6)	41.7	(8.5)	42.7	(2.9)	●
	post	43.0	(1.7)	51.3	(4.9)	57.7	(10.2)	65.0	(7.0)	
Abundance N	pre	726	(40)	628	(321)	589	(121)	598	(167)	○ [†]
	post	593	(115)	580	(257)	687	(273)	1108	(133)	
<i>Diversity indices</i>										
Fisher's α	pre	9.7	(1.2)	9.9	(1.0)	10.4	(2.9)	10.7	(1.3)	○ [†]
	post	10.7	(0.8)	13.9	(0.3)	15.5	(3.9)	15.1	(1.6)	
Shannon-Wiener H'	pre	2.3	(0.1)	2.4	(0.1)	2.6	(0.4)	2.4	(0.2)	
	post	2.3	(0.1)	2.8	(0.4)	2.9	(0.5)	2.9	(0.3)	
Shannon's E	pre	0.61	(0.00)	0.66	(0.07)	0.70	(0.08)	0.63	(0.04)	
	post	0.60	(0.01)	0.70	(0.11)	0.72	(0.09)	0.70	(0.06)	
<i>Dominance indices</i>										
Simpson's 1/D	pre	3.9	(0.1)	4.8	(1.0)	6.8	(3.1)	4.3	(1.1)	○
	post	3.6	(0.1)	7.5	(5.0)	9.3	(5.0)	8.2	(2.7)	
Berger-Parker 1/d	pre	2.0	(0.0)	2.3	(0.3)	2.8	(0.8)	2.2	(0.3)	
	post	1.9	(0.0)	2.9	(1.2)	3.5	(1.4)	3.2	(0.7)	
Sample B		mean	(s.d.)	mean	(s.d.)	mean	(s.d.)	mean	(s.d.)	
<i>Abundances</i>										
Species density S	pre	29.3	(3.8)	30.7	(6.8)	34.0	(7.2)	29.7	(2.1)	●
	post	33.3	(2.5)	38.7	(7.1)	45.3	(3.1)	51.7	(4.9)	
Abundance N	pre	491	(49)	418	(255)	429	(81)	392	(58)	○
	post	421	(112)	408	(200)	477	(134)	554	935	
<i>Diversity indices</i>										
Fisher's α	pre	6.9	(1.3)	7.9	(0.7)	8.9	(2.9)	7.5	(0.8)	●
	post	8.6	(1.1)	11.0	(2.9)	12.6	(2.1)	13.9	(1.6)	
Shannon-Wiener H'	pre	1.9	(0.3)	2.1	(0.0)	2.1	(0.7)	1.9	(0.1)	
	post	1.9	(0.1)	2.5	(0.4)	2.4	(0.6)	2.7	(0.3)	
Shannon's E	pre	0.57	(0.06)	0.63	(0.06)	0.60	(0.16)	0.57	(0.04)	
	post	0.55	(0.04)	0.67	(0.08)	0.62	(0.14)	0.68	(0.07)	
<i>Dominance indices</i>										
Simpson's 1/D	pre	3.3	(1.0)	3.8	(0.2)	4.5	(2.3)	3.0	(0.4)	○
	post	3.1	(0.4)	5.9	(2.9)	5.3	(2.7)	6.1	(1.8)	
Berger-Parker 1/d	pre	1.9	(0.4)	2.0	(0.0)	2.2	(0.7)	1.8	(0.1)	
	post	1.8	(0.2)	2.7	(1.0)	2.5	(0.9)	2.6	(0.4)	

*excluding species/individuals of uncertain taxonomic status and species complexes.

[†]Significance of logging intensity effect in random factor anova of post-harvest parameter values with treatment (fixed) and block (random) as factors. ●=Logging intensity on this parameter is significant (p-levels vary); ○[†], not significant (p=0.07); ○, not significant. Remaining parameters were not tested. Simpson's index was ln-transformed before testing.

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Table 3.5 Balance of species gains and losses between pre- and post logging censuses of the logging experiment in Pibiri. “Net Result” is the net result of Sample A and Sample B. Sample A and B do not sum up to the total in Both Samples as species lost (gained) in either Sample might still be present (might already have been present) in the other Sample.

	Sample A	Sample B	Both Samples
Present in pre-logging census [†]	101	75	102
Present in post-logging census	115	98	118
Net change	+14	+23	+16
Species gained	34	34	35
Unique to logged plots	20	13	8
Belonging to species pool of undisturbed forest	8	11	10
Species lost	20	11	19
Unique to undisturbed forest	10	6	2
Belonging to species pool of logged forest	10	3	8
Summed abundance of species gained, per ha (% of overall post-harvest liana abundance)	73 (2.4%)	200 (2.7%)	121 [‡] (1.6%)
Summed abundance of species lost, per ha (% of overall pre-harvest liana abundance)	12 (0.5%)	20 (0.3%)	12 [‡] (0.2%)

[†]Figure for Sample A includes 1 species only found in the RIL 8+L treatment, which was not re-enumerated after harvest.

[‡]Abundance based on Sample B data.

Of the 19 species lost after harvest in the logging experiment, only 2 are unique to undisturbed forest in this dataset, i.e. only present in at least one of the 23 censuses of undisturbed forest in the entire dataset and absent in any of the 23 post-harvest censuses. Both species were limited to a single plot before harvest. In contrast, eight species, which outside Pibiri were observed to be growing in harvested plots, disappeared in the logging experiment. In all cases, these were rare species with a few individuals in a one to at most three plots, so it is unlikely that these losses have anything to do with unsuitable growth conditions. There is one remarkable loss, i.e. *Clitoria sagotii*, of which the single individual growing in Pibiri disappeared after logging, even though this species is very common in logged forest in Waraputa (and absent in unlogged forest there). In this species and two others (*Clusia myriandra* and *Mimosa myriadenia*), the absence in the post-logging censuses might be (partly) related to liana-cutting before logging. The few individuals that were present were big lianas of 5-13 cm dbh that may have been cut to prepare trees for harvest.

All species that were lost were rare species; their joint abundance represented a mere 0.2% of the total liana abundance in Pibiri prior to logging. The species that appeared were also quite rare (1.6% of post-logging liana abundance), but some species appeared in numbers and in several plots. These species are the most likely ones to have responded to logging-induced changes in the plots. Five species achieved an average density of 3 individuals per plot (on ha basis). One of these appeared in a single plot, but four achieved a relatively high abundance in several plots. The commonest, *Clytostoma sciuripabulum*, achieved an average density of 25.3 individuals.ha⁻¹ (Sample B), a presence in 8 of 12 plots and ranked 32nd in abundance in the post-logging census (of 118 species). It was not limited to logged plots, but also occurred in all undisturbed reference plots in the logging experiment. The other three, *Hiraea affinis*, *Mezia includens* and *Stigmaphyllon sinuatum*, did not avoid the reference plots either, but were found in relatively high numbers in several logged plots.

At the level of plot, the patterns of gains and losses were much more dynamic. Given the spurious nature of most changes at the site level, these data were not further analysed.

3.2.3 Logging effects on abundance and diversity in the logging experiment

The effects of logging on diversity at the community level were investigated using four different parameters: species density *S*, total abundance *N*, Fishers α , and the Simpson’s index $1/D$ in an Anova-design. Logging intensity, time (pre- and post-harvest), space (block in which plots were located) and liana size were used as factors in the analysis. Size classes were defined logarithmically as in section 3.1.5, and consisted of data from the “hybrid” Sample (a mixture of Sample A and Sample B). The definition of the hybrid sample, the setup of the model and the hypotheses tested were described in section Appendix A (p. 90).

Table 3.6 Effects of logging intensity on liana species diversity in the logging experiment. Significant results imply an effect of logging intensity (column LT) or of logging intensity in dependence of size (LST) on four diversity parameters. Summary of results of Anova tests, original analysis results are presented in Appendix F. Meaning of symbols: ○ effect not significant; ● effect significant at $p < 0.05$. The results are given for the “hybrid” Sample (see text).

Effect> Factor		Logging Intensity x Size x Time		Logging Intensity x Time	
			LST		LT
Species density	S		○		●
Abundance	N		●		●
Fisher’s α	α		○		●
Simpson’s Index	$\ln(1/D)$		●		●

The results of the tests (Table 3.6, Table 3.7, Figure 3.8) suggest that:

- There is an effect of the intensity of logging on both species density and Fisher’s α ; this effect is independent of liana size;
- This effect is caused by high post-harvest values for species density and Fisher’s α in the plots with the highest logging intensity, RIL 16, and by a moderately high post-harvest values of species density and Fisher’s α in the plots with low and intermediate logging intensity, RIL 4 and RIL 8.
- Logging intensity affects abundance and Simpson’s index, but only in certain size classes.
- The effect on abundance is related to a high post-harvest abundance of individuals 0.5-2 cm dbh in treatment RIL 16 and a low pre-harvest abundance of individuals 1-2 cm dbh in treatment RIL 8. The latter result is not a logging effect but caused by a somewhat different population size distribution in unharvested forest in those plots.
- The effect of logging intensity on Simpson’s index varies per size class, but significantly higher values are usually associated with post-harvest censuses in RIL 4, RIL 8 and RIL 16 (in 3 of 5 size classes with significant differences).
- Parameter values for pre-harvest logging effects (in practice all undisturbed plots) and post-harvest control plots were not different. For these four parameters, the pre-harvest plots were well comparable, and the control treatment did not change significantly as a result of logging in the immediate vicinity.
- Only in four comparisons (species density, Fisher’s α , abundance/size class 1 and Simpson’s index/class h2) a logical alternative to the null hypothesis can be proposed. In all these cases, this is that mean parameter values in (some or all) harvested plots are higher than in pre-harvest and control plots. In all other cases there was no clear-cut alternative to the null hypothesis, as is evident from the many parameter means that seemed to belong to different “groups” (as evident from double or triple letters in Table 3.7).

Although in some cases an alternative hypothesis could be proposed, the alternative proposal is different from the previously formulated expectation that Fisher’s α and *N* would be dependent on size. Fisher’s α increased with logging and increased more with increasing

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logging intensity, but this was independent of size class. Diversity was increased to the same extent among small lianas as among large lianas, even though new recruits into the community are mainly expected among the smaller size classes. So, even if this is the case, this is not reflected in diversity.

As expected, liana abundance did increase with logging, with logging intensity and this depended on size class. However, the increase in abundance did not occur in the smallest size classes as expected, but in size class 0.5-2 cm in RIL 16. From the evidence presented in 3.2.4, below, the “wave” of new recruits in RIL 16 had reached a size of *c.* 1-2 cm by the time of the post-logging census (4 years after logging), so this explains why these classes show an effect of logging. In the smaller size classes, positive (recruitment, faster ingrowth) and negative effects (density-dependent mortality, faster outgrowth, reduced recruitment in gap understories) may have balanced causing an apparent lack of effect.

Table 3.7 Results of multiple comparisons between parameter means of combinations of logging intensity and time (pre-/post-logging)[†]. For each row, effects sharing the same letter are not different at $\alpha=0.05$. Species counts and Fisher’s α were tested over all size classes as size did not interact with LT (Table 3.6).

Parameter	Size class	Pre-harvest				Post-harvest			
		C	RIL 4	RIL 8	RIL 16	C	RIL 4	RIL 8	RIL 16
Species density	(all)	a	a	a	a	a	b	b	c
Fisher’s α	(all)	a	a	a	a	a	b	b	c
Abundance	h1	a	a	a	a	a	a	a	a
	h2	a	a	a	a	a	a	a	a
	0.25	a	a	a	a	a	a	a	a
	0.5	a	a	a	a	a	a	a	a
	1	a	a	a	a	a	a	a	b
	2	bc	ab	a	ab	ab	ab	ab	c
	>2	a	a	a	a	a	a	a	a
Simpson’s index	h1	a	a	a	a	a	ab	b	b
	h2	a	a	a	a	a	b	b	b
	0.25	a	a	a	a	a	a	a	a
	0.5	ab	ab	a	ab	ab	b	ab	ab
	1	ab	ab	ab	a	ab	c	bc	c
	2	ab	abc	bc	abc	a	abc	c	abc
	>2	a	a	a	a	a	a	a	a

[†]Student-Newman-Keuls post-hoc procedures.

3.2.4 Changes in population size distribution in the logging experiment

Population size distributions four years after logging were slightly different from pre-harvest population size distributions, but the general shape of the distributions did not change (Figure 3.9). The major patterns of change reiterate the findings of the analysis presented in 3.2.3 and Figure 3.8(b). The main differences between harvest intensities are found in classes 1 and 2, between the highest logging intensity and the rest. The increase in class 1 and 2 in RIL 16 represents a doubling of liana abundance compared to the pre-harvest abundance in the same plots; in RIL 8 this increase is 15-50% and not significant. Although not significant (Table 3.7), the trend in the Control treatment and, to a lesser extent, RIL 4, was that post-logging abundance was lower than pre-logging abundance in most cases. These data were not tested further.

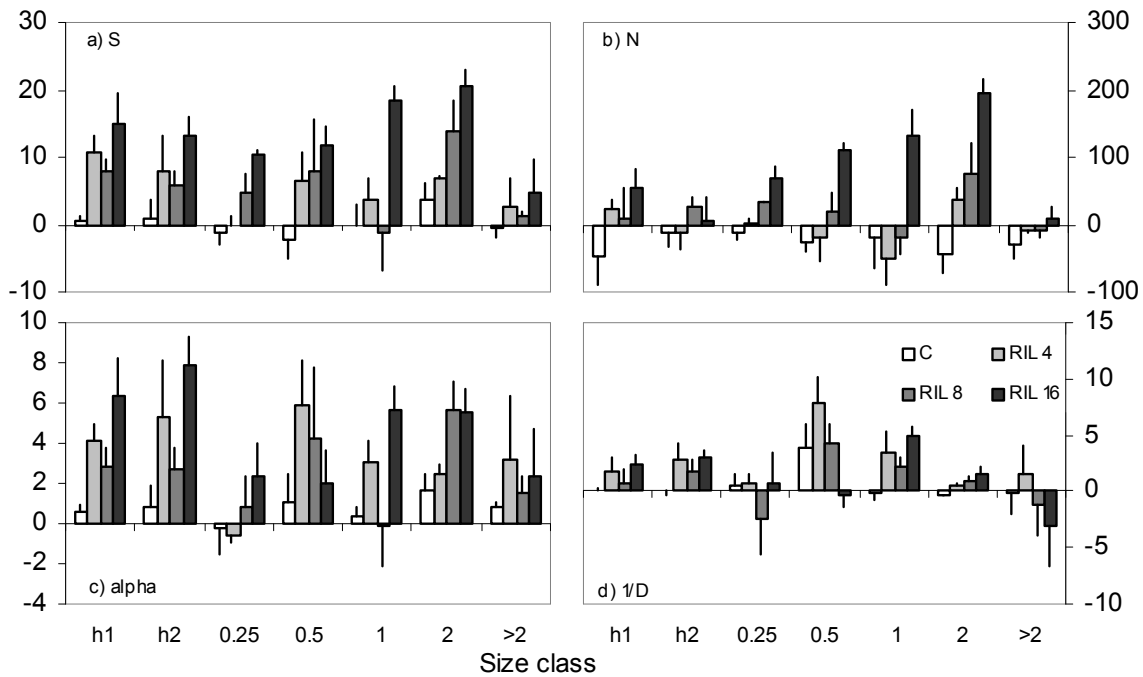


Figure 3.8 Effects of logging on change in a) species density; b) abundance; c) Fisher's α and d) Simpson's index by sizeclass (x-axis) and logging intensity treatment (shades of bars), of harvested liana communities in the logging experiment in Pibiri. Bars give mean (+ 1 s.e.) differences between pre- and post-logging (t+4) values of three replicate plots per logging intensity treatment, for the "Hybrid Sample" (see text). Data based on 625 m² per ha for h1 and h2; 2500 m² per ha for remaining size classes. N is adjusted for area.

Three plots in the logging experiment, one control plot and two RIL 16 plots, were monitored more frequently than the remaining plots, i.e. before logging and 2, 4 and 6 years after logging. If harvesting caused an episode of increased establishment of seedlings or release of previously suppressed lianas, e.g. in the logging gaps, this should be revealed by a "wave" of recruits moving from smaller to larger size classes when comparing the population size distributions. It should also provide an indication of where in the size class distribution of the t+4 year census (as in 3.2.3) these new recruits would be concentrated.

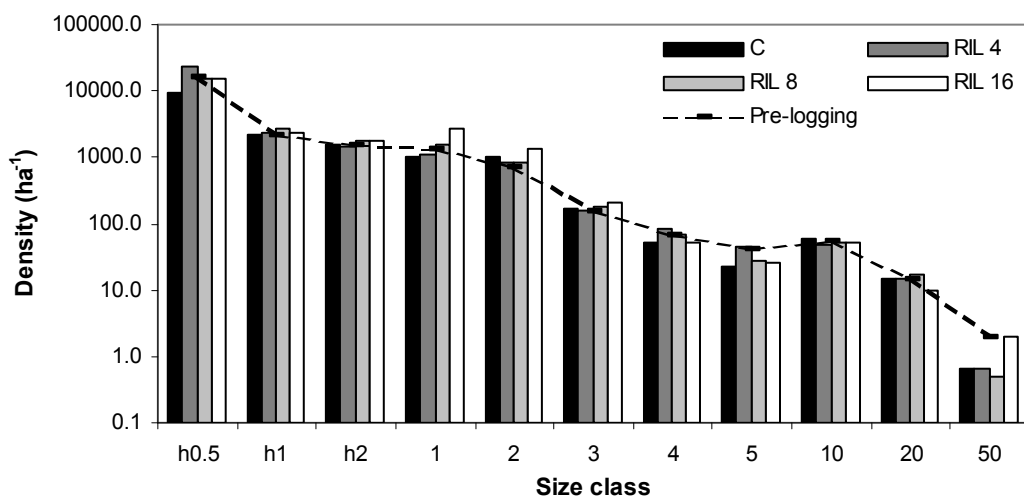


Figure 3.9 Post-logging population size distributions of liana communities in the logging experiment in Pibiri. Means based on 3 plots per treatment, s.d.'s not given (c. 45% of means). The stippled line is the mean pre-harvest population size distribution over all plots. Data based on complete dataset.

A wave of lianas is present in the two harvested plots (shown in Figure 3.10, with modified size classes of 0.5 m height and 0.5 cm dbh). As only two plots were examined, the data cannot be statistically supported and variation between plots is probably high.

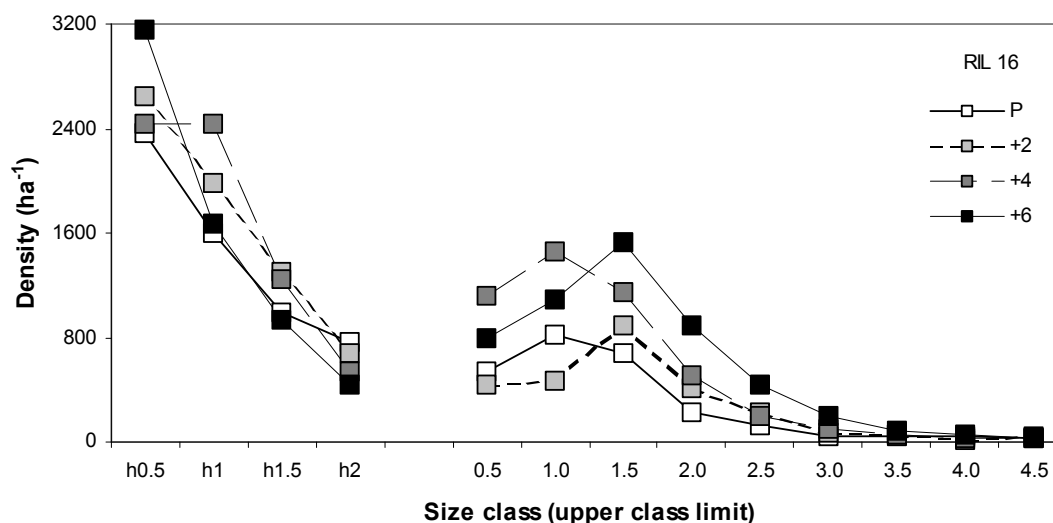


Figure 3.10 Temporal development of population size distributions of lianas at 0, 2, 4 and 6 years after logging in two RIL 16 plots in the logging experiment at Pibiri. Mean abundance per ha ($n=2$) per size class of 0.5 m height (left) and 0.5 cm dbh (right)

In the height classes, data from the pre-harvest census and the census six years after logging are generally below the +2 and +4 censuses, suggesting that for a brief period a higher number of seedlings was present before dropping off again. In the dbh-based classes, a wave of lianas appears to grow through the 1.5 and 2 (-2.5) cm classes during the study period. In the smaller classes, liana abundance goes up and down in a less predictable way. By 6 years after harvest, abundance-related effects of logging appear to be evident in all classes between 1 and 3 cm. In that census, the abundance of all classes smaller than 1 cm dbh (upper size class limit) is decreased as compared to the previous census. One control plot was enumerated 6 years after logging; in that plot, no clear evidence of increased recruitment and growth was present.

This pattern explains why in the analysis presented in section 3.2.3, significant effects in the RIL 16 treatment were encountered in the 1 and 2 cm classes. It is difficult to assess whether the absence of significant changes in abundance per size class in RIL 4 and RIL 8 is due to the absence of a wave of recruits (due to a lighter intervention in the forest) or whether this wave lags behind the one in RIL 16 due to delayed germination and establishment and reduced growth. The latter pattern could, in principle, be detected by a higher abundance of smaller (than 1-2 cm) size classes in these treatments, but this it cannot be supported statistically (Figure 3.8).

3.2.5 Diversity per habitat type

Subplots were assigned to one of four habitat types based on ground and canopy disturbance. Randomised species-individual accumulation curves showed that the number of species present differed between habitat types, but the extent of this difference depended on logging intensity. Gaps and skidtrails were the most species-rich habitats when compared at equal number of individuals. As the density of lianas in gaps is 6 to 9 times as high as on skidtrails, in absolute terms gaps constitute the largest species pools in logged forest. In RIL 8, skidded gaps accumulated species at the same rate as gaps and skidtrails. In all cases where rarefaction showed that forest-interiors differed from other habitats (RIL 8 and RIL 16), they were poorer, while accumulation curves of the control plot were similar to forest-interior. Expressed as Fisher's α (lumping all treatments) diversity decreased in the order gap (20.2^a) > skid trail (19.4^a) > skidded gap (16.2^b) > interior (15.2^{bc}) > control (13.5^c , different letters indicate <5% probability of equal median richness, as determined by rarefaction).

The finding that gaps are relatively rich is not surprising as many pre-established species and individuals will survive the logging and new ones that require gaps will establish. In gaps,

particularly in gap edges, there are many trellises available for the support of lianas (Schnitzer & Carson 2001). Many species will also establish in skidded gaps, but damage to the ground layer in this habitat also means that few pre-established species and individuals will survive the logging, while fewer trellises would be available. The high diversity of skidtrails is somewhat surprising, as pre-established individuals will be destroyed while conditions for establishment of new individuals are not as suitable as in gaps.

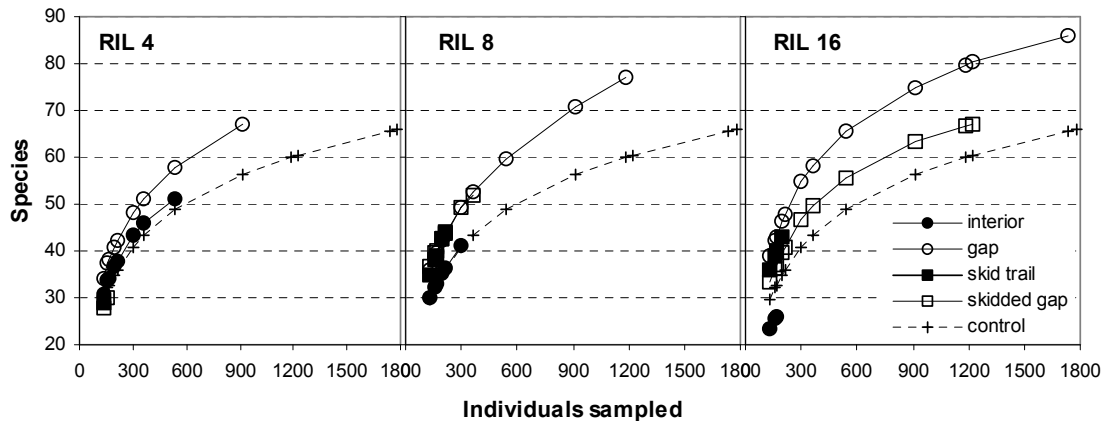


Figure 3.11 Post-harvest species accumulation curves of liana communities growing in four logging related habitats, for each treatment in the Logging Experiment in Pibiri. Subplot data from all three plots per treatment were lumped. The curve for the control treatment (undisturbed forest) has been added in each panel.

3.2.6 Conclusions – diversity and structure

- Species were gained and lost in a largely random manner from Pibiri between the pre- and post-logging censuses.
- All species lost were very rare and were likely lost because of chance.
- In just a few cases, some evidence existed for loss or gain to be (partly) related to logging at this time scale, either because of liana cutting (3 species) or because of the creation of suitable habitat or establishment conditions (4 species). Evidently, many more species may have responded in abundance to liana cutting or habitat creation without disappearing or appearing (see below).
- Liana species density and diversity was increased four years after reduced impact logging.
- This increase was more in heavily logged plots than in moderately and lightly logged plots.
- In heavily logged plots four years after logging, liana abundance was increased, but only in certain size classes.
- In moderately and lightly logged plots, liana abundance did not increase.
- Gaps were generally most species-rich after logging, while forest-interiors were poorest.
- Dominance was decreased in some size classes four years after logging, the more so as logging intensity was higher.
- For all parameters examined, control treatments resembled the pre-harvest situation.
- Past logging events in heavily logged plots are evident from a wave of recruits moving through the population size distribution.

3.2.7 Logging effects on similarity

Logging causes changes in the abiotic environment of the forest and physically removes individual lianas from the vegetation. The species composition of the post-logging stand may therefore be assumed to differ from the pre-logging stand, due to a combination of (accidental) differences in losses between species, and differences in species composition among the newly established lianas and pre-established lianas. These processes occur in harvested and unharvested plots alike, but it may be expected that differences in species composition are larger in heavily logged plots with greater damage and variation in establishment conditions than in lightly logged or undisturbed plots.

If expressed in terms of similarity, similarity between pre- and post-logging species composition of heavily logged forests is expected to be lower than of lightly logged or unlogged plots. For Sample A, this expectation was confirmed for the Morisita-Horn similarity index (which is abundance-weighted) but not for the Sorenson index (which only takes absence and presence of species into account; Figure 3.12). For Sample B it was not. The Morisita-Horn similarity between pre- and post-logging censuses of plots in the RIL 16 treatment was significantly lower than of all other treatments, in Sample A. The species composition of the liana community in this treatment changed markedly, most probably due to logging. In Sample B, this was not the case. There is no a priori reason why patterns present in Sample A would not be present in Sample B. Possibly the smaller size classes were not affected by logging, or they were affected by logging but the composition was converging back to pre-logging conditions.

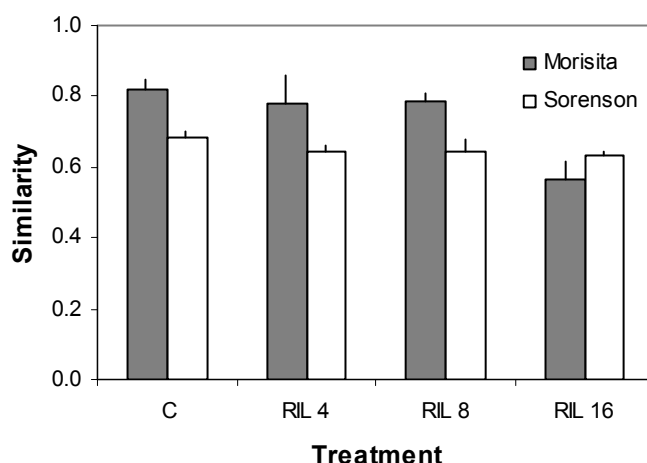


Figure 3.12 Similarity between pre- and post-logging species composition of plots in the logging experiment in Pibiri. Mean and s.e. for n=3 plots per treatment for Sample A. The differences in the Morisita-Horn index are significant (Anova with Logging treatment (fixed) and Block (random); $F_{3,6}=5.90$; $p<0.05$; RIL 16 is different from all other treatments), but in the Sorenson they are not (Anova $F_{3,6}=0.90$; n.s.). Data for Sample B not shown, Morisita overall mean = 0.80; $F_{3,6}=0.70$, Sorenson mean = 0.63; $F_{3,6}=0.5$, $p=n.s.$ for either case. The Morisita-Horn index excludes *Conarus perrottetii*.

In general, similarity in species composition between pre- and post-harvest censuses was high. In the control plot, for Sample A, the Morisita-Horn index averaged 0.82 ± 0.03 between pre- and post-logging censuses, while the within-treatment similarity of (then undisturbed) plots before harvest averaged only 0.68 ± 0.03 (mean \pm s.e. of the 4 treatments). Even for the RIL 4 and RIL 8 treatments similarity between pre- and post-harvest censuses was higher than pre-harvest within-treatment similarity. Apparently, variation in species composition in space is more important than variation in time, even if in this period a light to moderate logging event took place (RIL 4 and RIL 8).

Similarity in species composition of the three post-logging censuses of the two RIL 16 plots that were enumerated repeatedly was very high, suggesting a relatively stable post-harvest species composition. The mean Morisita-Horn similarity of all pairs of censuses involving the

pre-harvest census (3 combinations per plot) was 0.63 for Sample A. The mean of 3 possible post-logging census-pairs was 0.83. For the Sorenson index the patterns were similar (data not shown); the same is true for Sample B.

Most of these patterns also existed for the Sorenson index. However, unlike the Morisita-Horn Index, the species composition of RIL 16 plots after logging was as similar to the pre-logging situation as was the case in the other treatments, and changes due to temporal and/or physical change in the same plot was of the same order as spatial differences between plots before logging.

3.2.8 Patterns in species composition

The effect of the logging treatments on liana composition was further investigated using canonical correspondence analysis. The main objective was to detect whether any environmental variable (such as logging intensity) was correlated with patterns in species composition in the 12 plots and whether there were groups of species corresponding with major environmental trends in the dataset. The environmental variables that were used were time (distinguishing pre- from post logging censuses); space (dummies representing the block into which plots are located), treatment (dummies representing the treatment received) and several correlated damage parameters representing the percentage gaps, skidtrails and the number of trees harvested per ha. Fisher’s α and Simpson’s index were also used, even though they are strictly no environmental variables. It is not expected that the responses of individual species is closely related to the environmental conditions expressed at the plot level, but this analysis provides a good idea of differences in species composition between plots. Species responses are investigated in more detail at the subplot level in section 3.2.10. The analysis was performed on untransformed species abundance values in Sample A per plot with downweighing of rare species in the dataset.

The first two axes of the correspondence analysis explained *c.* 31% of the variation. Several other axes explained 4-7% each (Table 3.8). Because many environmental variables are highly correlated, it is difficult to separate, at the plot level, correlations of, *e.g.*, gap area from those of skidtrail area.

Axis 1 can be interpreted as a logging intensity axis. It is highly correlated with variables related to logging, particularly with the number of trees removed per hectare ($r=0.93$). All pre-harvest plots have similar negative scores on this axis (Figure 3.13, top left panel). The plots of the post-harvest census partition this axis roughly according to the treatment. With a single exception, the Control and RIL 4 plots have negative scores, which positions them close to the pre-harvest plots in terms of species composition. RIL 8 and RIL 16 plots exhibit positive scores on Axis 1, the latter higher than the former. Plots belonging to these two treatments separate on Axis 3, on which RIL 16 plots tend to have negative scores and RIL 8 plots positive scores. For the “undisturbed plots” (negative Axis 1 scores), Axis 3 separates plots of the post-logging from those of the pre-logging census. The precise ecological correlate of Axis 3 is not clear.

Table 3.8 Overview of the first four axes extracted by canonical correspondence analysis of the logging experiment in Pibiri and the main correlates of the plot scores. The strength of the relation is given by *r*, the intraset correlation between the environmental variable and constrained site scores. Based on Sample A results.

Axis	Variation explained	Main environmental correlate (<i>r</i>)	High scores correlate with
1	20.1	N of harvested trees (0.93) and other logging-related variables	Heavily logged plots
2	11.4	Space (0.54)	Block I plots
3	7.7	RIL 8 treatment (0.64)	Plots in treatment RIL 8
4	6.4	Space (-0.66)	Blocks away from Block II

Logging effects on liana diversity and abundance in Central Guyana

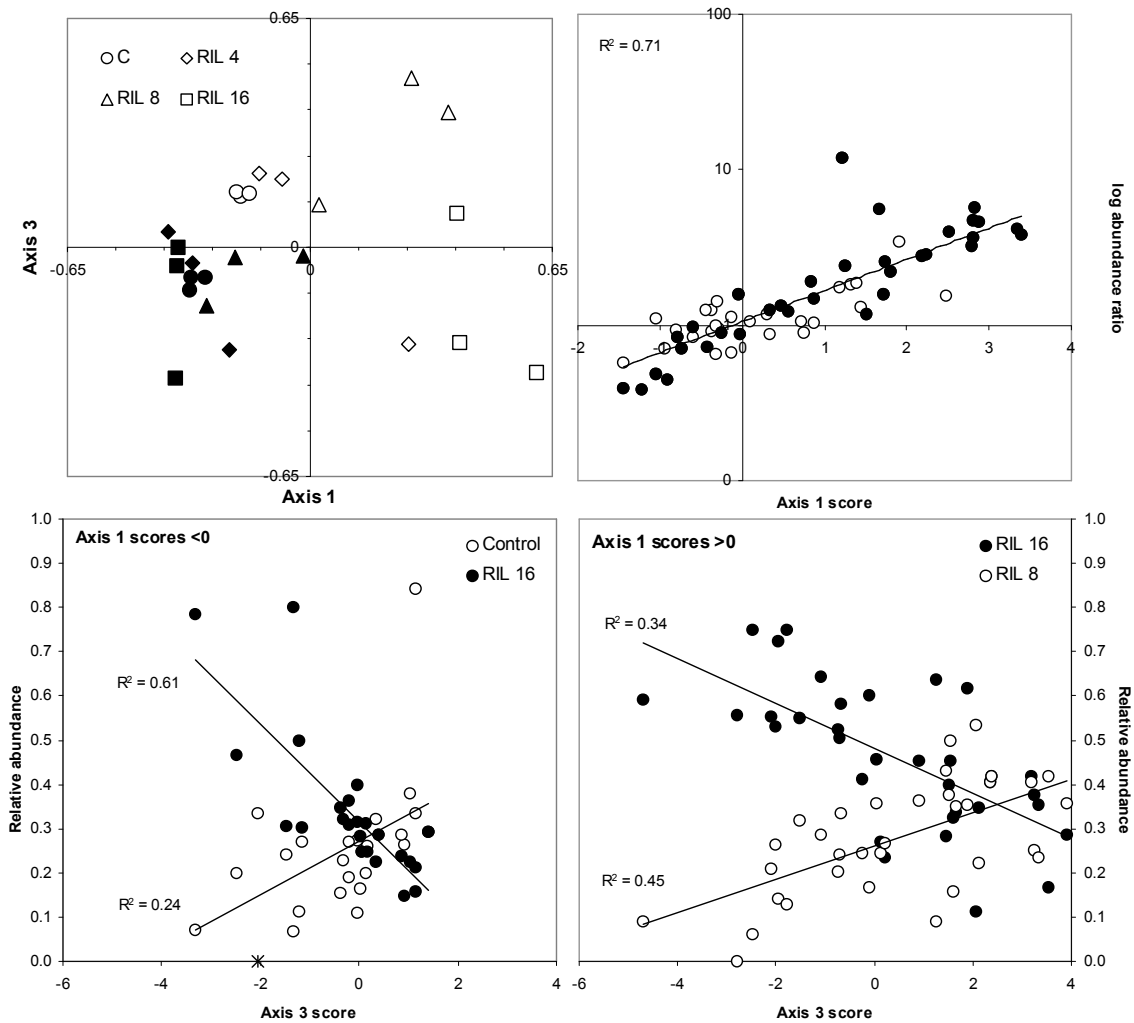


Figure 3.13 Trends in species composition in the logging experiment in Pibiri based on results from Canonical Correspondence Analysis. Top left: plot scores on Axes 1 and 3. Filled symbols denote pre-harvest census; open symbols post-harvest census. The symbols vary per logging treatment as indicated (pre-harvest censuses all refer to undisturbed plots). Top right: relation between Axis-1 score and the ratio of post and pre-harvest abundance for 59 abundant species (log scale). Closed symbols identify species that have a significant treatment or census effect when tested individually (log-linear tests, $p \leq 0.05$), open symbols are species with no significant trend in abundance. Bottom panels: relation between Axis 3 scores and the relative abundance of species in indicated treatments in the post-harvest census. Left: for abundant species with a negative Axis 1 score, $n=25$; Right: for abundant species with a positive Axis 1 score, $n=34$. Star is an outlier caused by one species with no individuals in the Control treatment.

The position of the exceptional RIL 4 plot with a positive Axis 1 score is most probably related to atypically very low post-harvest abundance of *Connarus perrottetii* in this plot rather than a species composition that characterises gaps and skidtrails. In this plot, as in plots in the heavily harvested treatments, *C. perrottetii* comprised *c.* 25% of the liana vegetation, while in control and other RIL 4 plots this percentage is typically *c.* 50%.

Axes 2 and 4 allow spatial separation of the plots by the block in which they are located (Figure 3.14). This spatial variation in species composition partly survives the effects of logging – post-harvest plots still tend to cluster closely with plots located in the same block, even though there are several exceptions.

There is an apparent contradiction to the results of the similarity analysis: that analysis suggested that similarity of pre-and post-harvest censuses of the same plot was larger than of pre-harvest censuses of different plots. Canonical correspondence analysis reveals that the dominant cause for variation in species composition is related to harvesting and that spatial variation is less important.

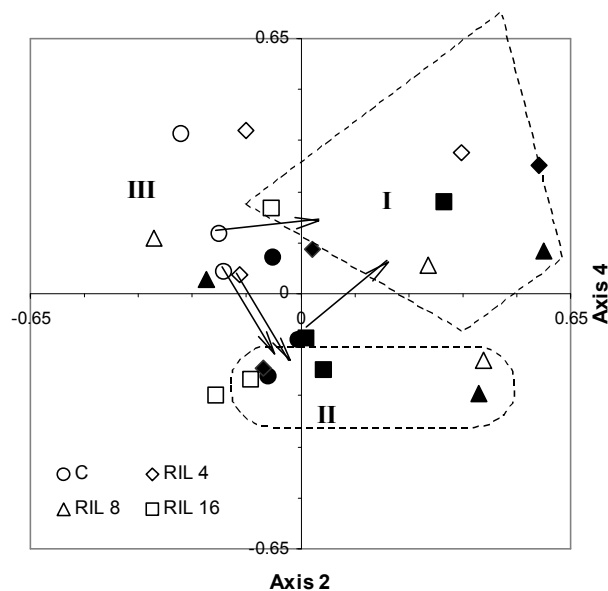


Figure 3.14 Plot of Axis-2 and Axis-4 scores based on canonical correspondence analysis of logging experiment in Pibiri. Open symbols are plots in post-harvest census, closed symbols in the pre-harvest census. Boxes enclose plots located in the same Block (in Roman numerals), arrows indicate membership of plots that are not enclosed by the boxes.

3.2.9 Impact of logging intensity on species distributions

The quite clear separation of plots by census and treatments over Axes 1 and 3 enables identification of the species that are responsible for this partitioning. As Axis 1 clearly separated the heavily logged plots in the post harvest census from the pre-harvest census and lightly harvested plots, species with high positive scores on this axis can be expected to be indicative of logging-related habitats. The quotient of post and pre-harvest abundance (adjusted by 1 to cater for absence of a species in one of the censuses) is strongly exponentially related to the Axis-1 species scores ($r=0.85$, $p<0.001$ for $N=59$ important species⁵; Figure 3.13 top right panel). The higher the Axis-1 score for a species, the larger the increase in abundance between censuses. Hence, in general, a high Axis-1 score implies that a species responds positively to logging, while a low score implies a negative response. However, not always will logging be directly responsible for the trend, as the relation between Axis-1 score and trend in abundance also holds, more weakly, for the control plots alone ($r=0.42$, $p<0.001$, $N=59$; not shown).

For plots with a positive Axis-1 score, Axis 3 separated the RIL 8 treatment from the RIL 16 treatment (Figure 3.13 bottom right). This distinction is less clear than the trend on Axis 1, as it explained less than 8% of the variation compared with 20% for Axis 1. Of the species with a positive Axis-1 score (i.e. responding to logging with an increase in abundance), positive Axis-3 scores distinguish those that showed this increase in both the RIL 8 and RIL 16 treatments from those which only showed this increase in the RIL 16 plots. This is illustrated by plotting the proportion of individuals found in the RIL 8 plots in the second census against Axis-3 scores in the bottom right panel of Figure 3.13. Species with negative values of Axis 3 are concentrated in the RIL 16 plots, while species with high values are approximately equally common in RIL 8 and RIL 16.

Of the species with a negative Axis-1 score (of similar abundance before and after logging, or decreasing in abundance), low Axis 3 scores tend to be correlated with a low relative abundance in the control plots and high scores with a more equitable distribution of individuals over the four treatments, but although this trend is significant, it is not strong. Low

⁵ Important species defined as occurring in at least 5 plots of 24 possible plots and density at least 4 individuals per ha at first or second census.

Logging effects on liana diversity and abundance in Central Guyana

Axis 3 scores are also typical for those few species that in spite of a general decrease in abundance showed a “preference” for the heavily logged plots. This pattern is hard to explain unless it survived from pre-harvest distribution patterns.

The species showing the highest positive scores on Axes 1 and 3 are listed in Table 3.9. As the correlations of trends in abundance with these axes is not perfect, the interpretations of the axes as given in the table do not always hold in the same measure for all species mentioned.

Separation of plots and identification of species based on preference for logging-related habitats (such as gaps or skidtrails) is not possible at the plot level. An analysis at the subplot level is needed for that.

Table 3.9 List of species with high absolute scores on axis 1 and 3 of canonical correspondence analysis performed on the logging experiment in Pibiri and tentative interpretation of their response to logging. Species are listed that were present in at least 5 (of 24) plots with an abundance of at least 4 individuals/ha in the pre or post-logging census. Sample A was used.

Axis 1 score	Axis 3 score	Species*	Interpretation
> +1.5	< 0	PRIO ASPE, HIRA AFFI, CLYT SCIU, PINZ CORI, PASS GLAN, BAUH GUIA, ANEM OLIG, ANEM PARK, PAUL CAPR	Strongly increased, concentration in heavily logged plots (RIL 16)
> +1.5	> 0	HETE MULT, MALP SP5, STIG SINU, DICH RUGO, PASS KAWE, COCC MARG, MACH QUIN, SMIL SCHO	Strongly increased, concentration in moderately and heavily logged plots (RIL 8 and RIL 16)
any	< -1.5	DIOS DODE, PAUL PACH, CLUS PALM, SECU SPIN	No or declining trend in abundance, concentration in heavily logged plots (RIL 16)
any	>+1.5	MACH MYRI, CYDI AEQU, DOLI BREV, MARI SCAN, MEMO MORI, CLYT BINA, DICH PEDU, FORS SCHO	Somewhat increased, concentration in moderately and heavily logged plots (RIL 8 and RIL 16)
< -1	any	TETR VOLU, CLUS GRAN, ARIS DAEM, PLEO ALBI, CAYA OPHT	Strongly decreased

*For acronyms of species, see Appendix B.

3.2.10 Habitat effects on species distributions

The scale that was used in the canonical correspondence analysis of species composition above, the level of plots, was too large to study the relation between habitats or other site factors and the occurrence of species. These habitats vary at a much smaller spatial scale than the plots, causing “dilution” of trends caused by preferences of species for certain habitats or other site factors in plot-level analysis.

In order to assess such relationships, the analysis was repeated at the level of subplots. For each subplot it is known whether it is located on a skidtrail or in a gap⁶, and if species respond to these conditions, it is expected that the analysis differentiates plots by species with preference for certain habitats, and species by their distribution over plots with specific habitat characteristics. The analysis is not perfect – in many cases several habitat types co-occur in the same subplot, causing a reduction in the power of this analysis.

The disadvantage of using the species composition of small subplots to characterise highly diverse plant communities is that each subplot “samples” just a small proportion of this community (see also section 3.1.2). This introduces a large sampling effect. The probability for subplots equal in site conditions to have the same species growing in them will be low if the number of species is high and the number of individuals per subplot is low. As a result, by

⁶ Except for Control plots, see methods

chance two subplots belonging to the same plant community may differ as much as two subplots belonging to entirely different plant communities.

The analysis reflects these problems. The analysis was conducted on a data matrix consisting of species counts in Sample A for each subplot in the post-harvest census of Pibiri (115 species by 300 subplots). The variance explained by the first axis was just 5%, which was much lower than in the plot-level analysis (20%, Table 3.8). Further axes explained 2.1 and 1.1%. The environmental variables that were used to explain the variance in the data matrix were plot-level treatment descriptors (treatment), plot-level spatial descriptors (blocks) and subplot-level estimates of canopy disturbance (gap percentage) and ground disturbance (skid-trail percentage), and the size of the gap, if the subplot was located in a gap. Gaps included the zone of 5 m into the forest.

Table 3.10 Axis-1 scores of subplots by habitat and treatment in the logging experiment in Pibiri. Means (standard error, n of subplots) based on canonical correspondence analysis of subplots, sample A. There was a significant interaction between treatment and habitat (Anova on ln-transformed Axis-1 scores, $F_{(6,213)}=3.13$, $p<0.01$, Control treatment excluded from analysis). Treatments sharing the same letter are not different ($p>0.05$).

Habitat	Control	RIL 4	RIL 8	RIL16	Mean
Forest interior	-0.39 (0.03, 75)	-0.32 ^a (0.03, 27)	-0.42 ^a (0.03, 12)	-0.35 ^a (0.08, 4)	-0.37 (0.02, 118)
Gap	Unknown	-0.22 ^a (0.06, 32)	-0.18 ^a (0.05, 42)	0.01 ^{ab} (0.05, 40)	-0.12 (0.03, 114)
Skidtrail	-	-0.33 ^a (0.09, 8)	-0.17 ^a (0.08, 10)	0.11 ^{ab} (0.20, 6)	-0.15 (0.07, 24)
Skidded gap	-	-0.42 ^a (0.08, 8)	0.01 ^{ab} (0.11, 11)	0.54 ^b (0.13, 25)	0.23 (0.10, 44)

The first axis was positively correlated with any variable describing the amount of logging damage in the subplot. The percentage of area affected by both ground and canopy disturbance (skidtrails through gaps) is the strongest correlate of this axis ($r=0.70$). Gap size was correlated with Axis 1 at $r=0.66$.

The scores per subplot were highly variable but some trends were present. Subplots located in the forest-interior generally had negative scores on Axis 1, subplots with either canopy or soil disturbance had intermediate scores and subplots with both types of disturbance had positive scores (Table 3.10). However, these scores were highly dependent of the logging treatment to which the plot was subjected. In spite of the similar pattern of disturbance, subplots with both ground and canopy disturbance located in RIL 16 plots had, on average, positive scores, while in RIL 4 such plots had negative scores that are similar to interior forest scores. RIL 8 plots were intermediate. In contrast, subplots in the forest-interior had similar (low) scores regardless of the logging treatment. Apparently, the subplot score on Axis 1 partly reflects the logging intensity of the surrounding area, implying that changes in the environment and species composition at the larger scale co-determine the effects at the smaller scale. The low scores of all damaged habitat types in RIL 4 plots suggest that they are mainly recolonised by undisturbed forest species, while similar plots in the RIL 16 are colonised by species with high Axis 1 scores, i.e. species typical of disturbed habitats. The most obvious factor causing this distinction between lightly and heavily logged plots is gap size (gaps in the heavier treatments were larger than in the lighter treatments), but other factors could be related to not measured variables, such as temperature and relative humidity, and soil factors. These factors apparently did not (or not yet) affect species composition in the remnant undisturbed forest area.

In terms of species, the high correspondence between percentage area affected by both ground and canopy disturbance and Axis 1 is expressed in species preference for this habitat. Many species with high Axis-1 scores were over-represented in skidded gaps (Figure 3.15), while species with low Axis-1 scores were over-represented in forest-interiors.

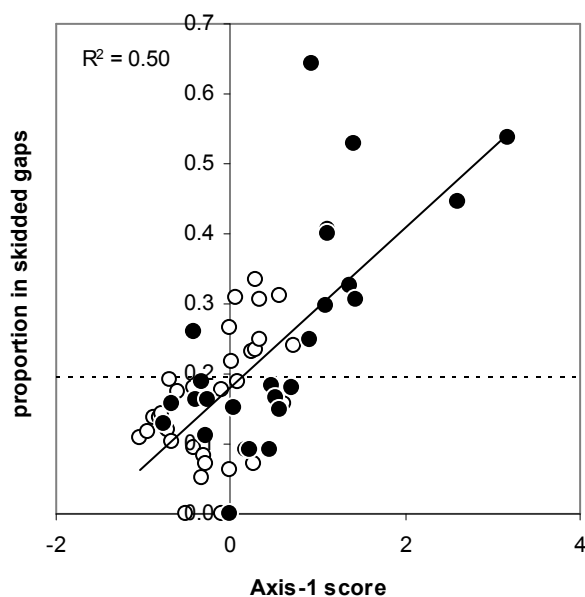


Figure 3.15 Relation between Axis 1 score and preference for skidded gap habitat for 59 abundant species in the post-harvest census of the logging experiment in Pibiri. Filled symbols are all 27 species showing a significant habitat preference (χ^2 test; $p < 0.05$; preference may be for other habitat than skidded gap); open symbols: species that are randomly distributed over habitats. The stippled line is at 0.196, the proportion of liana individuals growing in skidded gaps in the sample. Based on Sample A.

A large majority of species had small positive or negative axis-1 scores but two species stood out from the rest: *Passiflora glandulosa* (2.61) and *Pinzona coriacea* (3.19). Both are common species that were strongly associated with skidtrails in gaps. All other species with an Axis-1 score above 1 showed a similar preference for skidded gaps (Table 3.11). In most cases these are the same species that showed a large increase between the two censuses, but in the case of *Lysiostyles scandens*, a strongly decreasing species, the “preference” for skidded gap environments was achieved by a decrease in forest-interior habitats rather than an increase in skidded gaps. Only one species had a negative Axis-1 score below -1 , *Gnetum cf. schwackeanum*.

Table 3.11 List of species with high absolute scores on axis 1 of canonical correspondence analysis performed on subplots of the logging experiment in Pibiri and tentative interpretation of their response to logging. Species are listed that were present in at least 5 (of 24) plots with an abundance of at least 4 individuals/ha in the pre or post-logging census. Sample A was used.

Axis 1 score	Species*	Interpretation
> +1.0	BAUH GUIA, PASS KAWE, LYSI SCAN, MACH MYRI, STIG SINU, ANEM PARK, PASS GLAN, PINZ CORI	Strong preference for skidded gaps
< -1.0	GNET SCH1	-

*For acronyms of species, see Appendix B.

3.2.11 Ecological species groups

The analysis presented so far provided indications of groups of species showing similar responses to changes in growth conditions induced by reduced impact logging.

A series of tests was performed on species abundances for each of the 59 abundant species to identify groups of species with similar responses. For each species, it was tested whether a census effect (logging), a treatment effect (logging intensity) and/or a habitat effect were present. The test logic is described in 2.4.2, p. 92. A majority of 38 species showed a statistically significant response to at least one of the three criteria (Table 3.12). Positive responses to logging dominated; only nine species decreased significantly between censuses. See Appendix E for a detailed overview of the response patterns per species.

Logging intensity and liana diversity

Table 3.12 Summary of the responses of 59 abundant liana species to logging, logging intensity and habitat in the logging experiment in Pibiri. “Positive” and “negative” imply positive and negative responses in terms of abundance to logging and a preference for heavier treatments and more disturbed habitats.

	Positive	Negative	Erratic	No response
Census (Logging)	23	9	0	26
Treatment (Logging Intensity)	20	0	1	38
Habitat	25	1	1	32
Response to at least 1 of above	29	9	0	21

Species that responded to logging were expected to be in three consistent response patterns, Group A-C in Table 3.13. Group A, species that specifically respond to increasing disturbance and Group B, species that increase regardless of the intensity of logging were indeed well represented. No species were found that showed a decrease that depended on the intensity of logging (Group C). Two other groups of decreasing species were distinguished: species that decreased anywhere (Group E) and species that, while they decreased in abundance, still displayed a preference for heavily logged treatments and skidded gaps (Group D). Group X encompasses species that displayed significant but possibly spurious responses to some aspects of logging, but without a consistent pattern that can logically be linked to establishment and growth in logged forest. A large group did not show any significant response to any test and can be considered indifferent species. *Connarus perrottetii* was included in this group, even though this species displayed significant patterns in most tests. These patterns were mostly due to its high abundance rather than large differences in response to treatments or habitats.

Table 3.13 Species groups among 59 important liana species in the logging experiment in Pibiri. “Specific” implies that the response depends on logging intensity and habitat.

Group	Response pattern	N of species	Species*
A1	Specific positive response to logging, logging intensity, disturbed habitats (skidded gaps)	9	MACH MYRI; BAUH GUIA; PASS GLAN; PINZ CORI; ANEM PARK; PASS KAWE; STIG SINU; MACH QUIN; ANEM OLIG
A2	Dito (gaps)	3	PAUL CAPR; MARI SCAN; COCC MARG
B	Aspecific increase after logging	4	CONN ERIA; MEMO MORI; SMIL SCHO; DICH RUGO
C	Specific negative response related to logging, logging intensity and disturbed habitats	0	
O	Indifferent species	22	CONN PERR; CURA CAND; DIOS DODE; SMIL SYPH; CLUS PALM; CLUS GRAN; LONC NEGR; SCHL VIOL; CAYA OPHT; ODON PUNC; CONN MEGA; MOUT GUIA; STRY MELI; ARRA MOLL; GNET SCH1; COUS MICR; PAUL PACH; SECU SPIN; MALA MACR; CLYT BINA; DICH PEDU; FORS SCHO
D	“Specific negative preference” for skidded gaps and heavily logged treatments in decreasing species	4	COCC PARI; MACH MADE; LYSI SCAN; PETR VOLU
E	Aspecific decrease after logging	3	ANOM GRAN; HETE FLEX; TETR VOLU
X	Inconsistent pattern of responses	14	DIOC SCAB; ROUR PUBE; HIRA AFFI; CLYT SCIU; ARIS DAEM; PLEO ALBI; MALP SP6; HETE MULT; DOLI BREV; FORS ACOU; TELI KRUK; PRIO ASPE; CYDI AEQU; MALP SP5

*For acronyms of species, see Appendix B.

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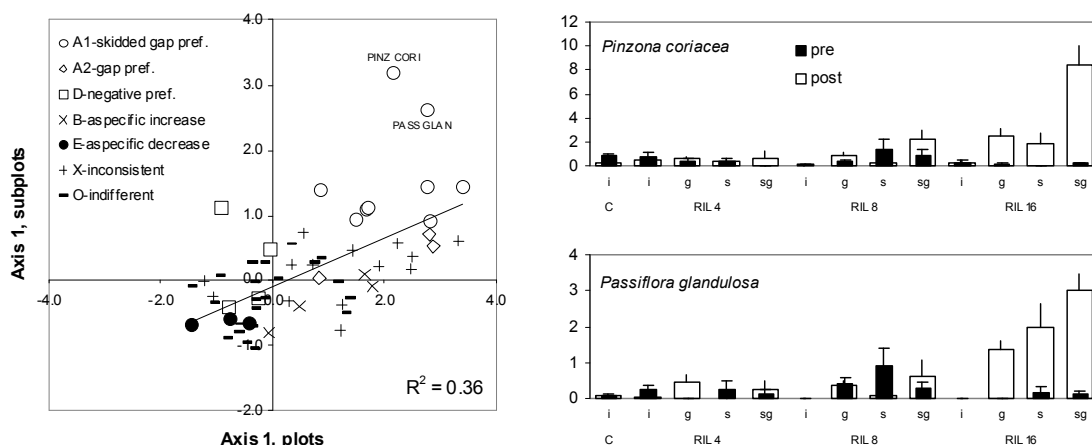


Figure 3.16 (left) Distribution of 59 abundant liana species and species groups in a bi-plot of Axis-1 scores from the plot and the subplot analysis, in the logging experiment in Pibiri. The line is the relation between axis scores for all plots. (right) Mean abundance (n per 100 m² subplot \pm s.e.) of *Pinzonia coriacea* and *Passiflora glandulosa* in forest-interior (i), gaps (g), skidtrails (s) and skidtrails in gaps (sg) in the four logging intensity treatments before and after logging. Note that pre-harvest abundance is based on imaginary (future) habitats.

Group D displays the most intriguing pattern in combining an overall decline in abundance with a preference for habitats most disturbed by logging. A possible explanation could be that these are relatively short-lived species that cannot maintain themselves for a long time in forest-interior habitats but readily colonise disturbances. The difference with the species in Group A would be that the latter maintain themselves for a long time after establishment or that these already disappear from disturbed habitats by the time these return to forest (i.e., abundance in undisturbed forest and control plots would be close to zero).

The strongest group is Group A1 which shows clear positive responses to logging. Only this group can be readily identified in a plot of Axis-1 scores of both canonical correspondence analyses that were conducted (Figure 3.16). The axes are correlated ($r=0.60$), suggesting that the general pattern of species responses is that species with a high Axis-1 score in the plot analysis (species that increase in abundance, Figure 3.13) do so because they do well in the most disturbed habitat, skidded gaps (high Axis 1 score in the subplot analysis, related to relative abundance in skidded gaps, Figure 3.15). *Passiflora glandulosa* and *Pinzonia coriacea* are identified in Figure 3.16 as the two species showing the clearest response. While most other groups show patterns in Figure 3.16, the axis scores of the canonical analyses are no unequivocal guides to the species responses as defined for the groups. Most likely, there are different and more subtle responses to logging that cannot be quantified in simple measures such as relative abundance in a habitat etc. Spatial (block) patterns, which were not considered in the Group definitions, also contribute to the axis scores.

There are some differences between the preliminary groupings based on a single analysis in Table 3.9 and Table 3.11 and the one presented in Table 3.13. These are mainly caused by applying criteria of consistency in the latter. If a species showed incompatible responses between plot and subplot analyses, it was put into group X.

3.2.12 Conclusions – logging effects on species composition

- Harvest intensity is the strongest environmental trend explaining differences in species composition between plots.
- This trend correlates well with the relative change in abundance of species before and after logging.
- The difference in species composition along the harvest gradient is due to differences in species composition between logging-related habitats and differences in the distribution of these habitats in plots of different harvest intensity.

Logging intensity and liana diversity

- Forest interiors and skidded gaps represent the extreme habitats in terms of species composition.
- In spite of these differences, overlap in species composition between habitats is large – it is often not possible to determine the habitat on the basis of species composition alone.
- Species composition of each habitat type is dependent on the logging treatment of the entire plot in which the habitat is located. Habitats located in a heavily logged forests are more likely to contain species that are “typical” for that habitat than the same habitats located in lightly logged forest.
- Spatial patterns of species composition are relatively strong even in the small geographic area of Pibiri.
- Two groups of emerge that show a tendency of increase in logged plots but differ in the minimum logging intensity at which this increase is occurring. This suggests that discrimination of plots subject to different logging intensity would be possible using these groups.
- Sixteen species showed relatively strong and consistent positive responses to logging and logging related habitats, while only three showed negative responses. Twenty-two species can be considered indifferent to logging and logging intensity, while the remaining eighteen species showed variable or inconsistent responses.
- *Passiflora glandulosa* and *Pinzonia coriacea* have high axis scores and are therefore strong determinants of differences between plots and subplots. They are strongly associated with skidded gaps.

3.3 MEDIUM-TERM CHANGES IN DIVERSITY AND SPECIES COMPOSITION – THE CHRONOSEQUENCE STUDY

3.3.1 Introduction

In the previous sections it was shown that liana abundance and diversity responded significantly to changes in the forest habitat associated with the harvesting of trees. Four years after logging, the number of individuals was increased and the number of species was higher as the intensity of the harvest was higher. Very few species, if any, were lost, but logging provided opportunities to several new species or species that were little abundant prior to logging. In the following chapters it will be investigated whether these conclusions, based on a situation four years after logging, are persistent or whether they change if the time perspective is extended from 4 to 16 years. If there is continuous change, it is important to know whether the liana community reverts to pre-harvest abundance and composition, or whether logging was the start of a development that leads to ever more different communities.

The data that are available for this exercise (called the chronosequence data) are different from the data used for the logging experiment. This is important when interpreting the outcomes. The principal differences are reiterated here (see also 2.5, p. 21):

- The chronosequence data cover a much longer period (0-16 years in stead of 0-4 years).
- Logging in chronosequence data was not controlled as in the logging experiment, leading to variable intensity and higher damage. Those plots in the chronosequence that were taken from the logging experiment (the plots in Pibiri, 0-6 years) have much lower damage than the other plots in spite of similar logging intensities (Table 3.14).
- The pre-harvest liana composition of the plots in the chronosequence is not known. It is approached by control plots in nearby undisturbed forest.
- Plots of the chronosequence are spread out over a large area; this introduces a strong geographic element in the species composition. Of a total of 161 species present in Sample A, just 33 were present at all four sites. Conversely, 57 species were unique to a single site, mostly uncommon species but six species were abundant at that single site.
- “Treatments” (years since logging) were not randomly distributed over plots in the chronosequence approach. The younger treatments were all in Pibiri while the older treatments were scattered over 3 other sites.

All these aspects make that the results of the chronosequence need to be interpreted with care. In principle, for the simple quantitative measures, the data of the logged plots will be compared with the control, and the difference between harvested and control will be compared through time.

Table 3.14 Summary of plot characteristics of plots in the chronosequence. Harvest intensity and habitat areas of recensused plots were considered equal (see comments in Table 2.1). Habitat areas refer to Sample A, i.e. 2500 m² per plot.

	Time since harvest								
	0 PIB	2 PIB	4 PIB	6 PIB	6 WAR	7 MHFR	10 2KM	12 WAR	16 2KM
<i>Harvest Intensity</i>									
Stems harvested (ha ⁻¹)	0	14.5	14.5	14.5	11.0	20.5	14.5	11.0	14.5
Basal Area harvested (m ² .ha ⁻¹)	0	3.1	3.1	3.1	5.5	5.9	3.4	5.5	3.4
<i>Habitat (%)</i>									
Gap area	0	27	27	27	39	34	38	39	38
Skidtrail area	0	8	8	8	19.5	18	19	19.5	19
Skidded gap area	0	2.1	2.1	2.1	11.4	6.0	9.8	11.4	9.8

3.3.2 Trends in diversity after logging

The basic diversity data obtained from the censuses in the chronosequence plots are summarised in Table 3.15. Trends in time that are not corrected for differences between control plots are inconsistent, even between Sample A and Sample B. The trend in liana abundance expressed as a difference between harvested plots and the control (corrected data) is much more consistent (Figure 3.17). During the first 6-8 years after logging the number of individuals increased compared with the control plots. After that time it dropped to approximately the level of the control plots by 16 years after logging. The trends in the plots that were censused repeatedly (points connected by lines in Figure 3.17) confirm this general trend: increasing in the first few years, decreasing later on. There appears to be a delay in the increase of liana abundance after logging. At two years after logging, abundance was about the same as in control plots, even though the number of species was already higher. Apparently, the loss of lianas during logging and the gain through establishment were approximately in balance at this time.

Table 3.15 Summary of key diversity parameters* for the liana community during the chronosequence. Plots are identified by year since logging and site. Means of n=2 harvested (except in t=0) plots per year and site, and for Sample A (top, sample area 2500 m² in each plot) and Sample B (bottom, sample area 625 m² in each plot; abundance data refer to these areas). Data for Sample B in MHFR are lacking.

	Time since harvest								
	0	2	4	6	6	7	10	12	16
Sample A	PIB	PIB	PIB	PIB	WAR	MHFR	2KM	WAR	2KM
<i>Abundances</i>									
Species Density S	43.5	54.0	68.5	68.0	35.5	46.5	54.0	43.0	66.5
Abundance N	672	682	1184	1311	880	737	683	480	486
<i>Diversity indices</i>									
Fisher's α	10.5	13.8	15.8	15.2	7.4	11.3	13.8	11.4	21.1
Shannon-Wiener H'	2.4	3.1	3.1	3.1	2.4	2.9	3.2	2.7	3.5
Shannon's E	0.62	0.77	0.74	0.73	0.68	0.75	0.81	0.71	0.85
<i>Dominance indices</i>									
Simpson's 1/D	4.8	9.6	9.7	9.9	7.8	10.5	17.0	8.2	22.7
Berger-Parker 1/d	2.3	3.4	3.5	3.6	4.6	4.9	7.1	4.0	8.0
Sample B	0	2	4	6	6	7	10	12	16
	PIB	PIB	PIB	PIB	WAR	MHFR	2KM	WAR	2KM
<i>Abundances</i>									
Species Density S	28.5	48.0	54.5	50.0	28.5	-	40.5	28.5	48.0
Abundance N	387	438	565	514	311	-	307	213	243
<i>Diversity indices</i>									
Fisher's α	7.1	13.7	14.9	13.7	7.6	-	12.5	8.8	18.0
Shannon-Wiener H'	2.0	2.8	2.9	2.7	2.4	-	3.0	2.3	3.3
Shannon's E	0.58	0.74	0.72	0.70	0.72	-	0.81	0.70	0.85
<i>Dominance indices</i>									
Simpson's 1/D	3.2	7.5	7.1	6.2	7.5	-	13.8	6.1	19.1
Berger-Parker 1/d	1.8	3.0	2.9	2.6	4.0	-	6.1	3.0	7.0

*excluding species/individuals of uncertain taxonomic status and species complexes.

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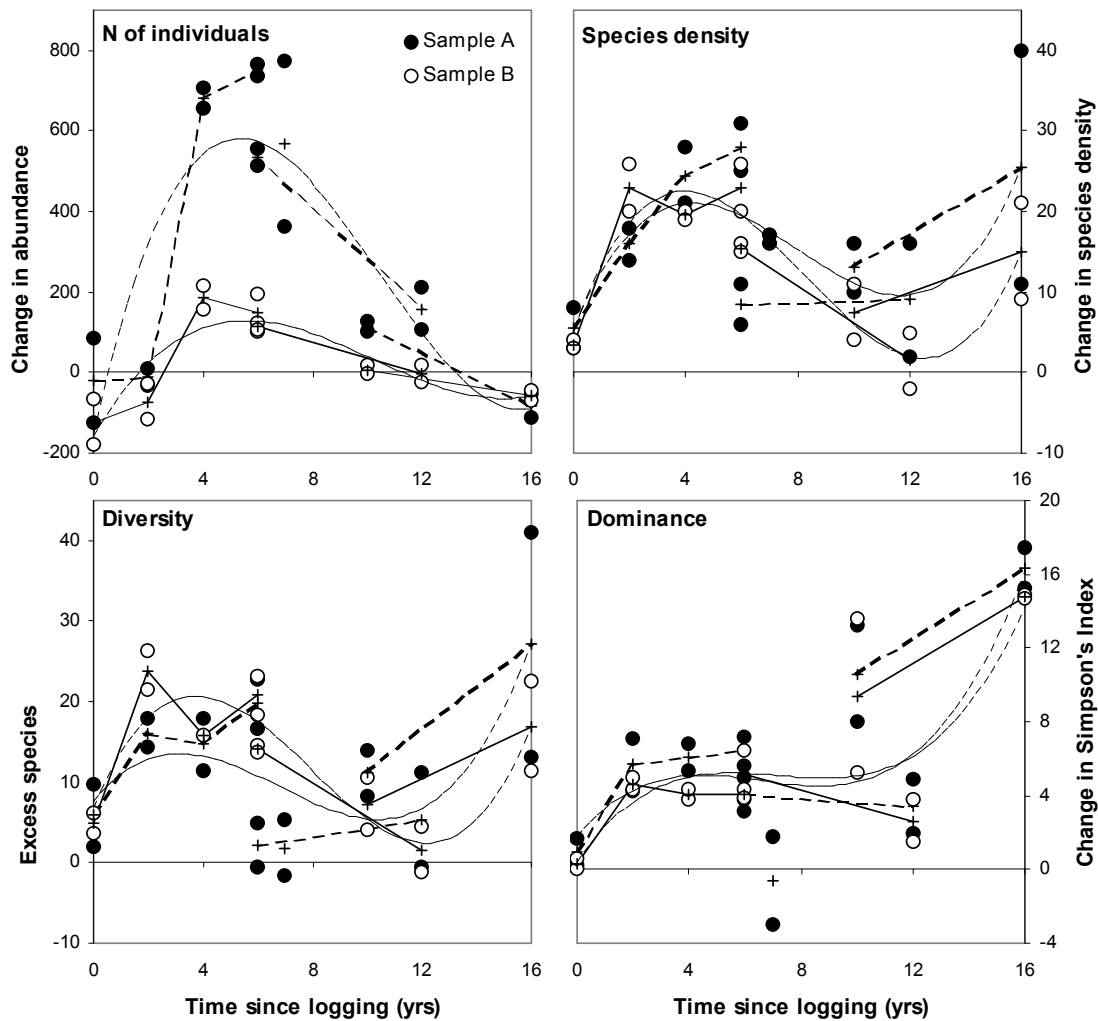


Figure 3.17 Chronosequence of liana abundance (top left), species density (top right) and diversity (Fisher's α , bottom left; Simpson's Index, bottom right) after logging near Mabura Hill. The graphs show differences in these parameters compared with control plots (see text for explanation of "excess species"). Sample A and B are distinguished by closed and open symbols, respectively. Lines connect means (crosses) of recensuses at the same site. Curved dotted lines are the trend in the parameter value based on third order polynomial. Parameter values are based on 2500 m² (Sample A) and 625 m² (Sample B) per plot.

The general trend in species density is similar to abundance. However, this trend is heavily influenced by one plot at the 2KM site, censused at 10 and 16 years after logging. This plot showed a marked increase in species density (from 57 to 81 in Sample A) where stability or a decrease was expected based on the trend in the other plots. It is not clear what could be the mechanism for such an increase so long after logging, particularly as the number of individuals was dropping just as in the other plots. The conditions for establishment of new individuals and species are best just after logging, after which the vegetation becomes closed and competition for space and resources becomes important. It cannot be excluded that an observer effect has caused this increase.

In the bottom panels of Figure 3.17, the chronosequence of two different diversity parameters is depicted. Because it is little insightful to express a change in diversity as the difference in Fisher's α between a logged plot and the control (as this could be due to differences in abundance or species density; or both), the expected number of species was calculated for each logged plot based on the observed number of individuals in the logged plot and Fisher's α in the control. The difference between the actually observed number of species and the expectation ("excess species" in Figure 3.17) is then a measure for the difference in diversity between logged plot and control. The general trend followed an optimum curve – clear in Sample B, less so in Sample A – that is very similar to the trend in species density. It shows a

large excess of species (15-25 more than expected) between 2 and 6 years after logging⁷, while diversity was only slightly higher than or equal to the control plots between 6 and 12 years after logging. The 2KM site, again, is exceptional. The trend in the Simpson's index (dominance) is not clear. While the trend in Pibiri and Waraputa is somewhat reminiscent of the optimum curves found for the other parameters, it is clear that 2KM takes a very different position with regard to dominance patterns in the liana community.

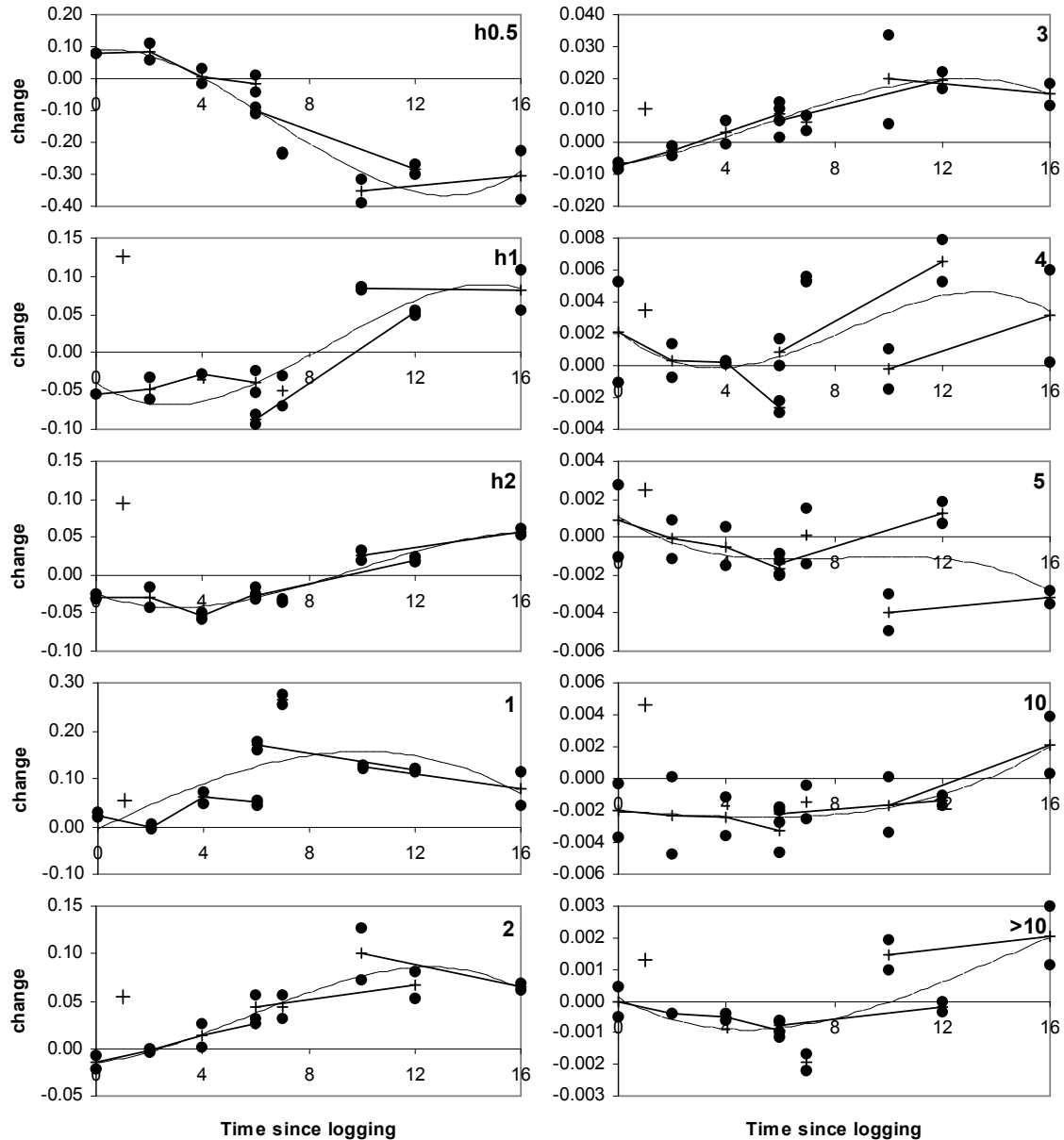


Figure 3.18 Development in relative liana population size class distribution over 16 years after logging in the chronosequence study. The abundance of each size class (identified in the upper right corner of the panel) is plotted separately as the difference in the fraction of lianas in that size class between the each logged and control plot (note the different Y-axes). A positive value implies an increase in the relative abundance of that size class, a negative value a decrease. Dots are values for individual plots. Lines connect means (crosses) of recensuses at the same site. Curved dotted lines are third order polynomial approximations of the trend in relative abundance. To give an idea of the importance of the change in relative abundance of a size class, its relative abundance in undisturbed forest (the mean of 7 control plots) is provided (marked by a +; the value for class h0.5 is 0.65).

⁷ Most of these plots are in Pibiri, so a site effect can't be excluded.

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The expected trend for species diversity in time would be a strong increase in species richness and diversity in the first few years as long as conditions for establishment of new individuals in new habitats are suitable, after which attrition in the number of species but not necessarily diversity would occur as a result of mortality due to competition. The data suggest that it is not likely that diversity drops back to background levels (represented by the control) within 16 years after logging. This would require the loss of a substantial number of species from each plot. The main mechanisms of local extirpation are a short lifespan in combination with the absence of regeneration (*e.g.* short-lived pioneers), “random” loss, mostly of rare species, due to reducing liana abundance in thinning vegetations and displacement of competitively inferior species. Except for the first mechanism, it is hard to imagine how this would lead to substantially lower diversity within the 16 years covered by the study.

3.3.3 Population size distribution

The pattern observed in relative abundance of the various size classes in the post-logging plots is generally consistent with the idea of a “wave” of recruits that gradually moves from smaller to larger size classes through time. Relatively important changes in abundance, with increases by a factor 2-4 compared with the control, took place in size classes 1, 2 and 3 cm dbh (Figure 3.18). Maxima were reached at 6-7, 10 and 10-12 years after logging, respectively. Classes 4 and 5 showed large but erratic changes in relative abundance, probably due to the small number of lianas and differences in abundance between sites in these size classes. Lianas larger than 5 cm dbh started increasing in abundance only after 12 years after logging. The classes that were based on height showed a slightly different pattern. The, in absolute terms, most important changes took place among the smallest individuals (height < 0.5 m) which decreased by as much as 30 percent points after 6-7 years (this coincides with plots away from Pibiri). If these individuals represent recently germinated seedlings, this implies that recruitment may be inhibited and mortality increased in logged forest compared to control plots after 7 years after logging. The reverse pattern is present among height classes 1 and 2 m. The increase in these size classes occurs late, particularly if lianas of 1-3 cm have already peaked by that time. These individuals may actually represent suppressed individuals that have grown just enough to survive, while smaller individuals were weeded out from dark gap understoreys.

3.3.4 Trends in species composition after logging

Correspondence analysis of plots

Three main factors contribute to differences in species composition between plots in these data: plot location, the amount of logging damage and time since they were harvested. It is difficult to distinguish these factors with the few plots available in the chronosequence study, given strong correlations between age since logging and logging damage, and the importance of geographic position in this study. As a result, canonical correspondence analysis of the plots revealed, more than anything else, the existence of geographical patterns in species composition. The environmental variables that were included in this analysis were space (two coordinates for each site), age since logging, and three variables linked to disturbance, *i.e.* total gap area, total skid trail area and basal area removed. The first four axes explained 49% of the variation (Table 3.16).

Table 3.16 Overview of the first four axes extracted by canonical correspondence analysis of the plots in the chronosequence near Mabura Hill and the main correlates of the plot scores. The strength of the relation is given by *r*, the intraset correlation between the environmental variable and constrained site scores. Based on Sample A results at the plot level.

Axis	Variance explained	Main environmental correlate (<i>r</i>)
1	23.1	Space (-0.80)
2	12.8	Skidtrail area (0.72)
3	7.9	Harvest intensity (-0.49)
4	5.4	Skidded gap are (0.54)

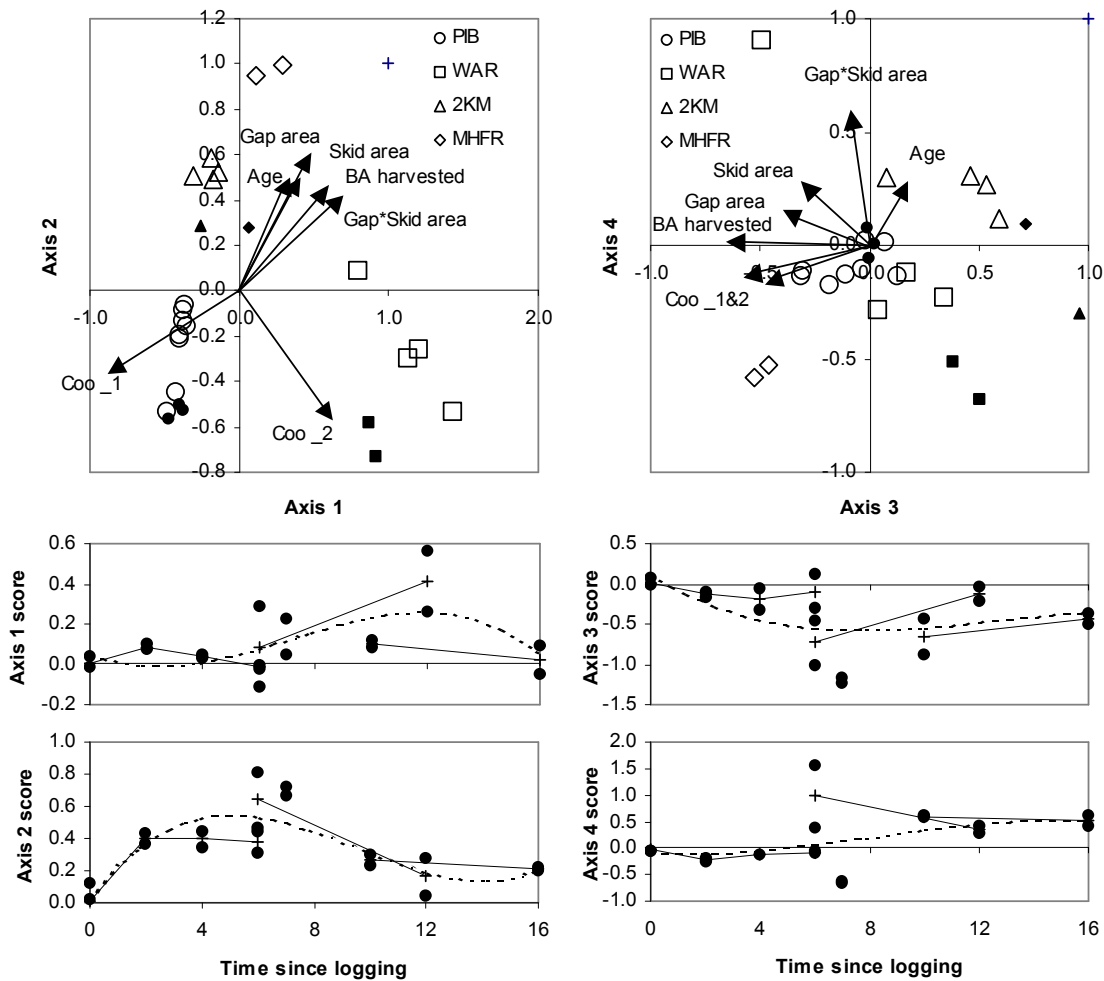


Figure 3.19 Results of Canonical Correspondence Analysis of plots in the chronosequence analysis near Mabura Hill. Biplots of Axis 1 and Axis 2 (top left) and Axis 3 and Axes 4 (top right). The arrows represent the direction of the main environmental trends in the dataset. Coo_1 and Coo_2 are coordinates of the four sites. Each site is represented by a different symbol. Open symbols are logged plots (to be logged in case of Pibiri preharvest at t=0), filled symbols are unlogged controls. In the four bottom panels, adjusted plot scores are plotted against time since logging, for Axes 1-4. Each value (dot) is the difference between the score of a logged plot and its control. Conventions follow those of Figure 3.17

In a biplot of the plot scores of the two main axis, plots located at the same site are usually close together in separate quadrants of the biplot (Figure 3.19, top left). Even though logging causes a clear shift in species composition at each site – in all cases, the logged plots have much higher Axis-2 scores and slightly higher Axis-1 scores – the geographic discrimination remains dominant (see also Figure 3.6).

Axis-2 provides the clearest apparent relationship with the variable of interest in the chronosequence study, i.e. time since logging (Figure 3.19), with a correlation of 0.6. Axis-2 scores, when plotted against time, follow a optimum curve that is similar to the curve found for liana abundance in time in Figure 3.17. As said above, the presence of strong correlations between time since logging and logging damage variables precludes the drawing of more definite conclusions on the cause of this trend: temporal change in community composition or differences in damage between plots.

The analysis was repeated twice in an effort to remove the main geographical effects. First, the species dataset was restricted to 46 main species in terms of abundance and distribution over sites. The results of this analysis were virtually identical to the one described above. Second, the species abundance for each plot was expressed as a difference from abundance in the control plot. This analysis provided quantitatively different results, but qualitatively geographical patterns still dominated. The effects of time since harvest, logging damage and

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geographical site were still confounded and no clear axis related to time since logging emerged.

Subplot analysis

The same analysis performed for species counts at the subplot level should give insight in the temporal development of species composition in each of the habitats that were created during logging. As in the logging experiment, the analysis at the subplot level explained a lower percentage of variation than the plot analysis. The first four axes accounted for 18% of total variation. Geographical variables showed highest correlations with Axis-1 scores, while variables related to logging damage and intensity correlated with Axis-2 scores.

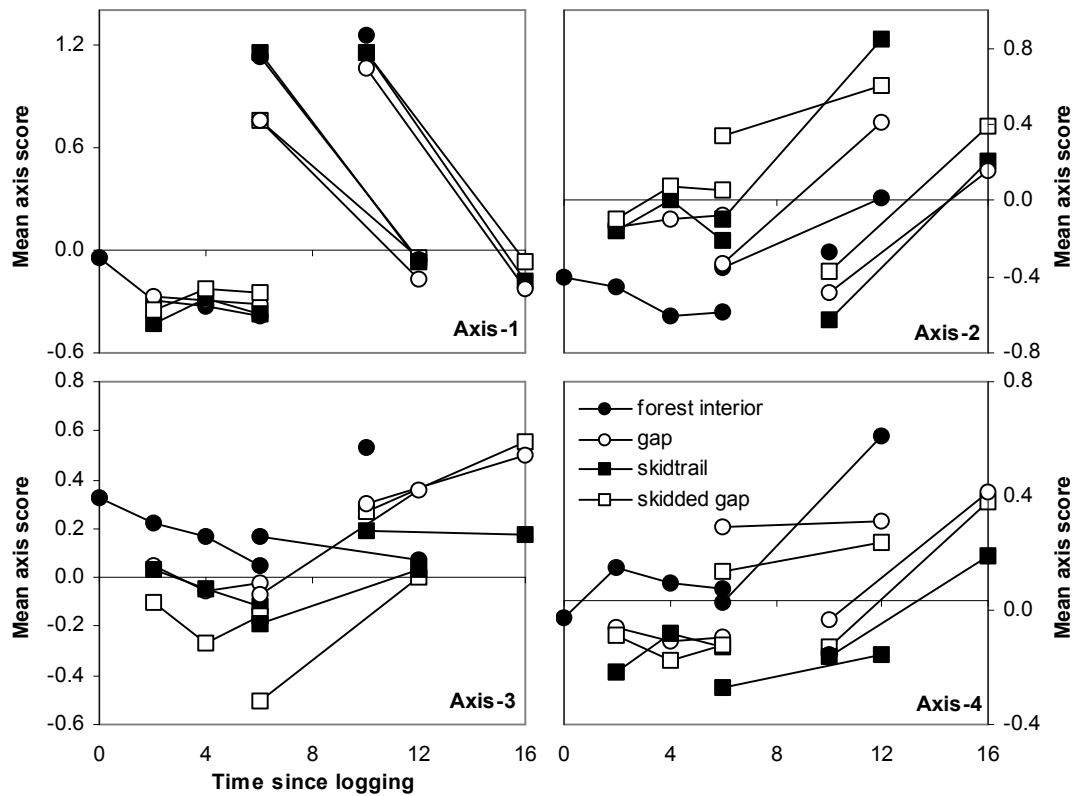


Figure 3.20 Chronosequence of subplot scores (Y-axis) through time for the four principal axes extracted with canonical correspondence analysis of liana species abundance per subplot, near Mabura Hill. Means of axis scores of subplots in forest-interior, gaps, skidtrails and skidded gaps are distinguished by different symbols. Repeated censuses of subplots from the same plot are connected with a line. Based on data from Sample A. Note that, unlike other figures, these scores are not adjusted for values in the control plots (subplots in the control plots were all designated as forest-interior at t=0). No data were available for logging-related habitats at t=0, for subplots at t=7 (site MHFR) and for interior habitat at t=16.

Anova analysis⁸ showed that the four logging-related habitats (forest-interior, gaps, skidtrails and skidded gaps) showed temporal variation in scores on all axes but Axis 1 (Figure 3.20). Of these axes, only Axis 3 appeared to present a temporal trend that can be interpreted. Skidtrails and particularly skidded gaps had lower scores than gaps and forest-interior sites. These scores reached a minimum at *c.* 6 years after logging after which they increased again. There are no data for forest-interior sites at 16 years after logging to confirm it, but there is no clear indication that scores of damaged subplots were converging towards forest-interior scores as time since logging increased. It should be noted that the trend as described here coincides with the transition from subplots located in Pibiri (first 6 years, decreasing Axis-3 scores) to subplots located outside Pibiri (remaining period, increasing Axis-3 scores), so a geographic cause cannot be dismissed.

⁸ The data are not suitable for proper Anova analysis, but a range of anova techniques suggests that the statement is not wrong.

Low Axis-3 scores on skidded gaps are caused by a relatively high abundance of species with low scores. As expected, species in groups A1 (skidded gap preferents) and A2 (gap preferents) contributed strongly to such low scores (mean Axis-3 score for these two groups is -1.064 , -0.523), although there were relatively common species from other groups (D, E and X) that also contributed to low subplot scores. The commonest low-score species – the second commonest species overall – was skidded gap specialist *Pinzona coriacea*, so this species contributed to a large extent to low Axis-3 scores of subplots in skidded gaps. The trend in Axis-3 scores suggests that low score species (i.e., group A1) increase in abundance after logging, but by 10 years after logging they are not common enough any more to cause low subplot scores on Axis 3.

Species trends in time

The finding that group A1 species showed a trend in time was supported by individual species chronosequences. Trends of 20 abundant species that were represented at each site with at least 1 individual (equivalent to 4 individuals per ha) in Sample A were plotted against time since logging (Figure 3.21). Relative abundance of each species was expressed as the difference between abundance in the logged plots and the control plot. For all other species geographic differences in occurrence per site were more important than temporal trends, so these species are not included, even though some of these species may display strong logging-determined habitat preferences⁹.

The trend in liana abundance in time in harvested plots (Figure 3.17) is the result of the summation of individual species trends and therefore the null hypothesis for each species chronosequence is a curve of the same shape as the overall trend. The results from the logging experiment showed that species differed in their response to logging, so if the null hypothesis is rejected, it is expected that the overall trend in liana abundance is due to those species that were shown to respond positively to logging (i.e. groups A1, A2, B and possibly D in Table 3.13), while non-responsive species will show a trend that is unrelated to time since logging or related in a different way (groups E, O, X and possibly D). These trends were evaluated qualitatively.

The abundant species within group A1 (n=3) and A2 (n=1) indeed appeared to follow the general trend in liana abundance while one of two abundant species in group B did so, too (Figure 3.21). Another species in group B, *Memora moringifolia*, showed inconsistent patterns in time. Unlike other common species in groups A1, A2 and B, this species had a strongly positive Axis-3 score in the subplot analysis, which suggests that its ecological behaviour differed between the logging experiment and the chronosequence study. No species in group D was abundant enough for this analysis. In all time intervals over which recensus data of the same plots are available¹⁰, the abundance of all these species rose and declined in parallel to that of the total liana vegetation. Only between 4 and 6 years after logging in Pibiri, some of the species in these four groups showed an opposite (declining) trend compared to overall liana abundance. This is understandable if these species are early successional species that are short-lived, not competitive and/or regenerating only in young gaps. These species will show increased mortality or reduced regeneration relatively soon after logging and decline in abundance.

In contrast, species belonging to groups E (n=2), O (n=7) and X (n=5) showed a variety of trends, which were often partly contrary to the general trend in liana abundance on a particular site. One species, *Rourea pubescens* (group X) showed a pattern that was reminiscent of a species that responds strongly to logging. However, the subplot analysis showed that this species did not show preference disturbed habitats, and also its positive Axis-3 score set it apart from species that do respond to logging.

⁹ Such as *Clitoria sagotiana*, almost confined to Waraputa and very strongly overrepresented in gaps and skidded gaps.

¹⁰ i.e., 0-6 years in Pibiri; 6-12 years in Waraputa and 10-16 years in 2KM.

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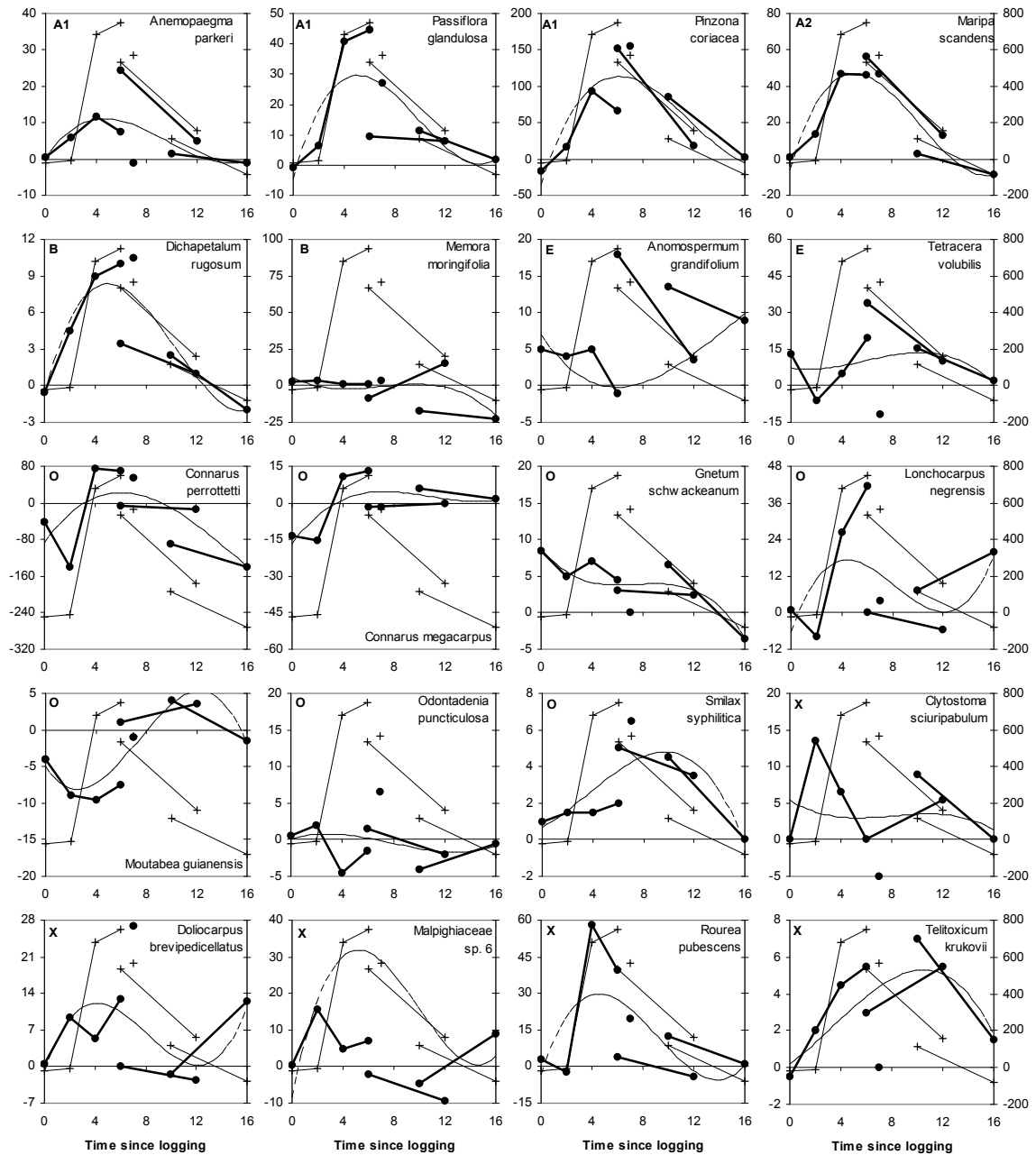


Figure 3.21 Trends in relative abundance of 20 common liana species in a 16-year chronosequence after logging, near Mabura Hill. Closed symbols and left-hand axis give relative abundance (difference between abundance in logged and control plots, mean of two plots per site-year combination) of the species named in the upper right corner. Solid lines connect repeated censuses of the same plots at a site. Interrupted line is the approximation of the trend in time by a third order polynomial. For comparison, the trend in total liana abundance is given by crosses, thin lines and the right hand axis (identical to left-hand panel in Figure 3.17). Letters indicate group membership as defined in Table 3.13. Note that left-hand axes vary for each species and that the X-axis may cross each Y-axis at different points. Data are based on Sample A.

3.3.5 Species groups compared between logging experiment and chronosequence

As indicated above, in general terms the response patterns of the lianas that were identified in the logging experiment in Pibiri were confirmed by the chronosequence study. Without doubt, the fact that the first 6 years in the chronosequence consisted of Pibiri plots contributes to this finding. The three groups with the clearest response pattern (A1, A2 and B) contained 6 species that were abundant at all sites and 12 that were abundant at most sites. Of these, only *Bauhinia guianensis* and *Memora moringifolia* need to be removed because their responses to logging were not confirmed in the other plots of the chronosequence. On a variety of indications in the chronosequence, several other species (*Coccoloba parimensis*, *Heteropsis*

flexuosa, *Rourea pubescens* and *Tetracera volubilis*) might be placed in one of these groups. *Clitoria sagotiana* was restricted to Waraputa, but behaved strongly as a skidded gap specialist there.

Of the species that were indifferent to logging in the logging experiment, most were indifferent in the chronosequence as well. However, the principal species in this group, *Connarus perrottetii*, was consistently underrepresented in logged plots compared to control plots and should probably be placed in group E, decreasing species.

All other groups are much less clearly defined, so it is less informative to assess whether species switch to other groups or not.

3.3.6 Conclusions – medium term changes in liana abundance and diversity

- Liana abundance increased over the first 6-7 years after logging before declining and reaching near-natural abundance by 16 years after logging.
- While liana abundance was similar to the control plot, 16-year old communities were enriched, in relative terms, in larger individuals compared to control plots.
- The number of small seedlings showed a sharp drop after the initial surge caused by logging, and remained low throughout the rest of the chronosequence.
- Trends in species composition related to the age of the forest since logging are obscured by geographic patterns of species occurrence in this dataset. Just 20% of the species was common to all sites, while 35% was confined to one site only;
- These geographic patterns are not only due to species that are limited to one or few sites, but also to differences in abundance of common species;
- Species density and diversity increased over the first 6-7 years after logging. After that, a slight decline appears to occur, but the data is not conclusive;
- Few individuals of strongly gap and skidded-gap preferent species that proliferate immediately after logging survive for 16 years. Yet, post-logging liana communities still have a different composition by 16 years after logging.

3.4 THE POTENTIAL OF LIANAS AS INDICATORS

The analysis presented in 1.1 and 1.1 clearly shows that logging and logging damage create habitats that provide opportunities for a number of characteristic species that are rare or absent in undisturbed forest. The logging of forest in the study region will almost certainly lead to a proliferation of these species, and for some it can be assumed that the larger the changes caused by logging, the more abundant these species will be. Therefore, in principle, such species are suitable candidates to serve as indicator species for forest disturbance.

In this chapter, the value of lianas as indicators will be briefly explored. Three topics will be addressed: indication of damage, indication of biodiversity and indication of detrimental effects related to lianas themselves.

3.4.1 Logging damage

The analysis presented clear evidence that species within Group A responded strongly to the creation of skidtrails and gaps. This is shown in Figure 3.22 as a positive linear relationship between logging damage, expressed as percentage skidtrail in a plot, and the percentage lianas belonging to Group A1 and A2 in Sample A. Percentage skidtrail is a more suitable measure than percentage gaps or skidded gaps in this dataset, due to the uncertainty in the extent of gaps just after logging in the older plots¹¹. Moreover, skidtrail area is easier to plan and manage during a harvesting operation than gap area. In this section, relative Group A abundance will be called “Indicator” and relative skid trail area, “Impact”. The percentage skidtrail explains *c.* 55% of the variation in relative abundance of Group A species, and even 87% of the variation in plots younger than 8 years and undisturbed plots. From the results of the logging experiment it is known that the RIL 4 and RIL 8 led to comparably moderate changes in species density and Fisher’s alpha, and not significant changes in liana abundance (Table 3.7, Figure 3.8), so these treatments can be used to determine a norm for acceptable logging damage. Disregarding one RIL 8 plot with 10% skidtrail area, these plots had less than 7% skidtrail. Using regression analysis on plots aged 7 years since logging or less (incl. undisturbed reference plots), this would correspond to plots with a relative Group A abundance of 17.7%.

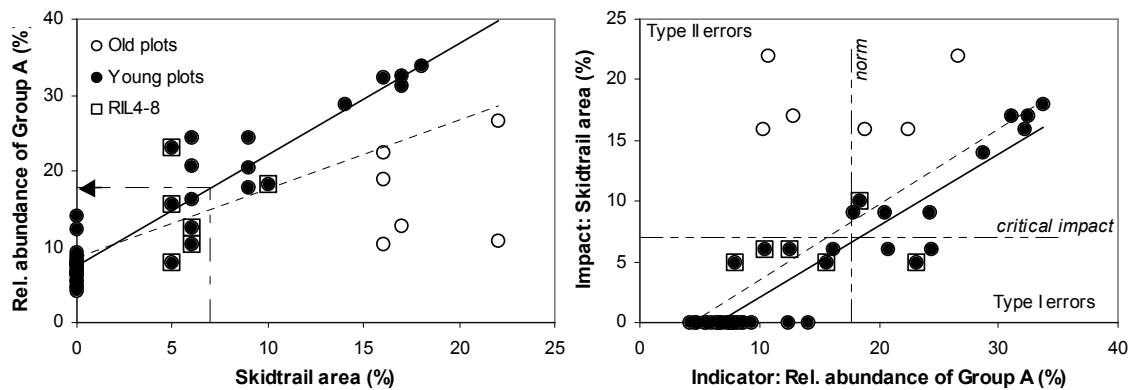


Figure 3.22 Relation between skidtrail area and abundance of Group A lianas in all plots in the dataset (left hand panel) and its reciprocal (right hand panel). Young plots (age <8 years since logging) are distinguished from old plots (age >8 years). Drawn regression lines are for young plots (incl. undisturbed plots): $y=0.015 \cdot x+0.074$ (left), $y=59.12 \cdot x-3.87$ (right), $R^2=0.87$, $p<0.001$; interrupted lines for all plots $y=0.009 \cdot x+0.085$ (left), $y=61.99 \cdot x-2.70$ (right), $R^2=0.57$, $p<0.001$. For explanations of Type I and Type II errors: see text.

¹¹ It is noted that the summed damage area (area damaged by skidtrails and/or gaps) gives a better fit for Group A abundance. However, gap area is unreliable in this dataset due to difference in age since logging between plots, and due to non-measurement of gaps in most undisturbed plots.

For valid indicators, the relation between indicator and response variable should be reciprocal. This is shown in Figure 3.22 (right) by flipping the axes. This does not change the nature of the relation (although the regression equation is not entirely reciprocal) but it gives a better visual impression of the uncertainties associated with determining skidtrail area with knowledge of relative abundance of Group A species alone.

This graph, along with the norm defined, shows the existence of four combinations of outcomes regarding the performance of the Indicator and the actual level of the Impact variable (Table 3.17). The combinations are identified in the graph as regions separated by the norm (related to the Indicator) and critical impact level (related to the Impact). Ideally, an indicator predicts the value of the Impact reliably and no false judgements are made. However, in reality, prediction success is not 100%. Two regions in the graph represent erroneous judgements. “Type I errors”, defined in analogy to statistical terminology, are those plots that fail the norm (the proportion of Group A individuals is higher than the norm) while, in reality, the Impact was below the critical level (there was less than 7% skidtrail). Type I errors are potentially serious in a practical situation of certification as this leads to unfair negative judgement of forest management.

In this specific example, Type I errors might point at a deficiency of the indicator, i.e. it might fail the criterion of unambiguity (section 1.3.1). While this study shows that “a high percentage of skidtrails” reliably leads to “a high abundance of Group A species” (Figure 3.22, left hand panel), it is not necessarily true that the reciprocal, “a high abundance of Group A species” is always and unfailingly associated with “a high percentage of skidtrails” (Figure 3.22, right hand panel). There may be other causes for a high abundance of Group A species, such as, in the case of the RIL 8 plot in the Type I error region in Figure 3.22, right hand panel, a high percentage of gaps (26% vs. 12 and 15% for the two other RIL 18 plots).

Type II errors are plots that satisfied the norm (the proportion of Group A individuals is lower than the norm) but in reality, the Impact was above the critical level (there was more than 7% skidtrail). From a certifiers’ viewpoint these errors are slightly less serious, particularly if the extent of the error is not too large or if other indicators exist that would pick up unacceptable impacts to the forest ecosystem in that particular area.

Table 3.17 Assessment of indicator performance with the four possible combinations of indicator and impact outcomes. An example is given of performance for the Indicator “Relative abundance of Group A species” for Impact I, “Relative skidtrail area” using norms N derived from Figure 3.22 (7% for I and 17.7% for N). Accepted means that a situation (a plot) satisfies the norm, while rejected means that it fails the norm. Prediction success and Cohen’s Kappa are based on n=23 disturbed plots.

	Norm:	Critical	Proportion of plots				Prediction success	Kappa statistic
	N	Impact: I	<N,<I	<N,>I	>N,<I	>N,>I		
Actual Skidtrail area								
Relative abundance of Group A species	17.7	7	5/23	3/23	3/23	12/23	0.739	0.425
Relative abundance of Group A species and Size Index	17.7, see Figure 3.24	7	5/23	1/23	3/23	12/23	0.826	0.593
Interpretation			Correctly Accepted (a)	Incorrectly Accepted (“Type II error”, b)	Incorrectly Rejected (“Type I error”, c)	Correctly Rejected (d)		

Cohen’s kappa: $[(a+d)-((a+c)(a+b)+(b+d)(c+d)/n)]/[n-((a+c)(a+b)+(b+d)(c+d)/n)]$, Manel *et al.* (2001)

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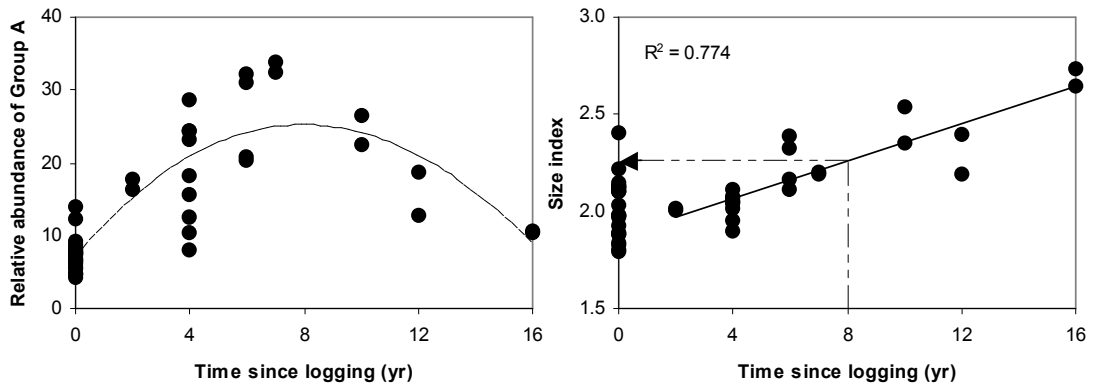


Figure 3.23 Relation between the relative abundance of lianas in Group A and time since logging (left) and between the size index of Group A lianas and time since logging. For definition of size index, see text. Size index (y) is related to time since logging (x) as $y=0.048 \cdot x+1.87$, $R^2=0.77$, $p<0.001$ for 23 logged plots. Line and arrow represent a size index norm for a critical age of 8 years.

In this example, Type II errors point at another deficiency of the indicator – the relation between indicator value and impact is not (always) linear or monotonous (section 1.3.1). In Figure 3.22, right hand panel it is evident that all plots subject to Type II error are old plots, 12-16 years old in this case. This is because Group A abundance has an optimum relationship with time since logging, and 12-16 years after logging most individuals have died (see examples in Figure 3.21). This relationship does not only exist in absolute terms but also in relative terms (Figure 3.23, left). In this example, the deficiency in the Indicator can be accommodated, because in the field a low abundance of lianas in recently logged forest can be distinguished from a low abundance in forest logged long ago by the smaller average liana size in the former (Figure 3.18). A size index¹² was developed that had a positive linear relationship with time since logging (Figure 3.23, right) but not with skidtrail area (addition of skidtrail area to a regression model relating size index to age; $F_{1,20}=0.0017$, $p=0.96$; analysis excluding undisturbed plots). The size index allows the identification of plots that satisfy the norm but are old and thus constitute potential Type II errors. A further norm is required to determine which of these plots should be rejected and which plots satisfy the criterion of limited skidding damage. In the absence of old plots with low skidding damage, this dataset does not allow the definition of this norm, but a graphical solution is proposed in Figure 3.24. Plots are accepted as satisfying the norm if they are below an arbitrary diagonal between the intersection of the abundance norm and size index 2.26 (representing a plot age of *c.* 8 years, Figure 3.23, right) and the y-axis and size index 3. The higher the size index (age) of a plot, the lower the acceptable range of Group A abundances. This is based on the assumption that a moderate Group A abundance in old plots is a relict of very high Group A abundances (heavy logging damage) just after logging. Type I error remains 3/23 in this example, while Type II error is reduced from 3/23 to 1/23. Evidently, there is potential that adding a second indicator introduces new Type I and Type II errors. For example, if the diagonal is drawn differently in Figure 3.24, the undisturbed plot indicated by an arrow could be falsely rejected as a low-damage plot.

¹² The size index is calculated as $\sum_{i=1}^5 i \cdot p_i$, where *i* are 1 cm sizeclasses with upper size limit *i* and *p_i* the proportion of individuals in sizeclass *i* relative to the total number of Group A individuals >1.3 m tall.

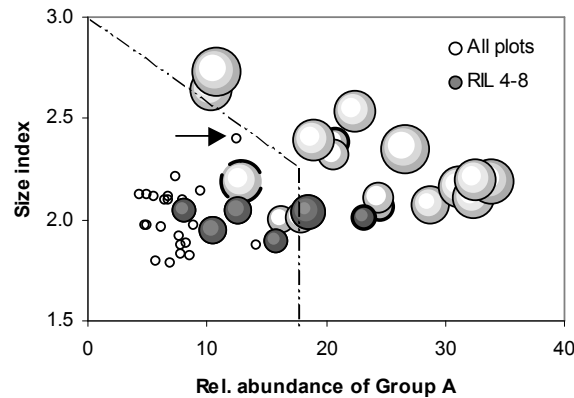


Figure 3.24 Biplot of percentage skidtrail (represented by the size of the symbols) as a function of Relative Group A abundance and the Size Index. RIL 4 and RIL 8 plots are identified by the darker symbols. The line represents the adjusted norm incorporating the size index. Type I errors are symbols with a thick border to the right of the norm line; Type II errors symbols with a thick interrupted border to the left of the norm line.

Norms

The definition of norms eventually determines whether damage is deemed acceptable or not. From the analysis presented above, it is clear that application of different norms leads to different outcomes with different prediction success. In ecology, a clear and well founded threshold will not often be present. In the example above, there is little ecological basis for choosing a norm of 7% skidtrails rather than 6% or 8%. Therefore, the setting of norms will be essentially be a political process leading to a negotiated agreement between stakeholders. Economic and social factors will be as important as ecological factors in determining the norms.

The performance of an Indicator with its associated norm can be estimated by prediction success: the proportion of correct predictions (Table 3.17). Another measure is Cohen's κ , or proportion of specific agreement (Manel *et al.* 2001), which accounts for chance. These measures can be used to compare different indicators. In the current example, the prediction success as measured by Cohen's κ improved from $\kappa=0.43$ to $\kappa=0.59$, when the norm based on Relative Abundance of Group A was refined with a norm based on the Size Index.

A norm as applied in this example is based on a single study and it is not known whether it can be extrapolated to other areas and other periods. The value of the indicator itself (relative abundance of an ecological species group) is probably quite universal, but the norm may differ from place to place. The relation between abundance of lianas in Group A and logging intensity is based on the analysis of the logging experiment and subsequently applied to a dataset comprising these same plots and the plots of the chronosequence. No true validation has been carried out, because no further plots are available to do this. The plots in the chronosequence are all heavily damaged, and generally the (adjusted) norm correctly distinguished acceptable from unacceptable damage. However, no plots with acceptable damage were available in the chronosequence and it remains to be proved that the indicator and norm perform equally well in distinguishing little damaged old plots from heavily damaged old plots. More problems may arise if the indicator with associated norm will be applied in areas where the species composition of Group A will be different. This implies that this indicator can be used only after a pilot study has established

- which species of the local species pool respond strongly to gaps and skidded gaps (this can probably be quickly ascertained in roadside vegetations);
- how abundance of these species is related to logging damage;
- what would be a suitable norm to be applied.

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In the current example it was known what species are member of species Group A, but in other areas that knowledge requires extra research and it might be advantageous to limit to the one or two commonest and most widespread members present. If this exercise would be repeated with *Pinzona coriacea*, the commonest member of Group A, approximately the same results would be obtained, but the analysis would be more sensitive to local variation in the occurrence of this species.

The analysis reported above is based on the current plot design, which is not geared to practical application but to ensuring optimum scientific reliability of outcomes. In a certification situation, conclusions will need to be drawn on the basis of much smaller and fewer samples, preferably without setting up time-consuming plots. In this dataset the effect of reducing the sample size on prediction success can be studied but this is not pursued here. It is likely that prediction success declines with smaller sample sizes, but the extent to which this occurs will depend on the “faithfulness” of Group A species. If individuals of these species grow on each and every skidtrail in logged forest, smaller samples are probably still quite powerful. If the proportion of skidtrails without individuals of such species is high, or if many non-skidtrail plots contain Group A individuals, a much larger margin of error should be accepted. Regardless of the sampling procedure, the spatial arrangement of logging damage should be acknowledged in the sampling design. Skidtrails are heterogeneously distributed through the landscape, so sampling few plots will not be sufficient to obtain a reliable estimate of logging damage. Instead, laying out of several line transects of reasonable length (>50 m but preferably longer) in different compass directions in an area of at least 1 ha logged forest (i.e., without patches of non-commercial forest) will be required for an adequate sample of logging damage.

3.4.2 Biodiversity

As stated in the introduction (1.3.4, p. 8), it is much harder to find appropriate indicators for biodiversity, even liana biodiversity, than for logging damage. The main reason is that for most biodiversity parameters, it is difficult to meet the condition that indicators should have a direct and measurable relationship with the underlying ecological process or variable. Biodiversity, expressed as Fisher’s α , is an information parameter, not a physically measurable parameter. Individual species or plants do not vary predictably in size, occurrence or abundance with biodiversity parameters. At most, indicators might be defined that co-vary with underlying causes of biodiversity. At the small spatial scale of this study and the type of impact examined (logging), habitat heterogeneity caused by logging damage might be the best correlate of biodiversity.

There is also a conceptual problem with biodiversity and logging in this study. The purpose of sustainable forest management is to reduce impacts, principally through reducing logging damage. In this study, it was demonstrated that logging, through its effect on increasing habitat heterogeneity, leads to increased biodiversity. Increased biodiversity is an unintentional consequence of logging at this particular site (it may be different at other places in the world). There is no benefit to finding indicators for biodiversity above those that are meant to measure logging impacts. In samples with a high Group A abundance it is likely that there has been a high level of logging-damage, which is indicative of a high habitat diversity. High habitat diversity, in its turn, is correlated with high diversity.

One of the reasons for reducing impacts of logging is to conserve species and ecosystems that are characteristic for rain forest in a near-natural state. The appropriate indicator would therefore not be “the level of biodiversity” but rather “the biodiversity and abundance of species of undisturbed systems”. Forests, which maintain many species that are characteristic for undisturbed forest but disappear in heavily intervened forests, are closer to satisfying sustainable forest management principles than forests which don’t. Damage itself cannot be easily used to assess whether forests satisfy this condition or not, as it is the result of reducing damage, i.e. the presence of such species, that determines whether the criterion has been met or not. Taking the current study on lianas as a case, a suitable indicator would measure the

number and abundance of species characteristic to undisturbed forest and sensitive to logging. As was shown before, few species were strongly negatively affected by logging, and Group C (species with specific negative responses related to logging, logging intensity and disturbed habitats) contained no species (Table 3.13). The three species in Group E showed a negative response to logging, but this was regardless of logging intensity or habitat. They will not be suitable to detect unacceptable loss of undisturbed-forest biodiversity in relation to logging intensity.

If a measure is needed to compare biodiversity between similar sites with similar floras, abundance would be the best guess for species density (*cf.* Figure 3.1). In addition, in the dataset there is a number of species that correlate relatively well with species density and abundance and to a certain extent also with Fisher’s α . The strongest correlate of species density and Fisher’s α is the abundance of *Rourea pubescens*, an abundant species in almost all plots (Table 3.18). While the cause for its quite strong relationship with diversity is unknown, it is pointed out here that the nature of the relationship with species density is very similar for undisturbed plots, logged plots in Pibiri and logged plots outside Pibiri (compare regression coefficients in Table 3.18; for Fisher’s α the relationship does not hold when subsets of plots are examined). There are several other species that correlate fairly well with diversity and/or Fisher’s α ; not surprisingly, these are all Group A species.

Table 3.18 Correlations between liana diversity (species density and Fisher’s α) and abundance of all lianas and *Rourea pubescens*, respectively. Slopes a (\pm s.e.) of *R. pubescens* abundance in regression $y=ax+b$, where y =species density, x =*R. pubescens* abundance, for three subsets of plots are also given. Regression coefficients are not different at $p=0.05$. Analysis based on Sample A in $n=45$ plots, excluding one outlier (plot at 2KM, 16 years after logging).

	Number of plots	Fisher’s α	Species density	
		Correlation coefficient	Correlation coefficient	Slope
Abundance, all species	45	0.34*	0.70***	
Abundance, <i>Rourea pubescens</i>	45	0.53***	0.74***	0.391 \pm 0.054
–, undisturbed plots	23	0.36 ^{ns}	0.72***	0.273 \pm 0.057
–, logged plots Pibiri	13	0.23 ^{ns}	0.77**	0.332 \pm 0.083
–, logged plots outside Pibiri	9	0.44 ^{ns}	0.64 ^{b=0.06}	0.239 \pm 0.109

3.4.3 Detrimental effects of lianas

Detrimental effects of lianas on logging are related to the potential of large individuals to increase logging damage and reduce safety by pulling down trees and the potential of regenerating lianas to blanket tree regeneration. In addition, lianas in tree crowns may compete with trees for light. Below, results related to effects of the cutting of large lianas prior to logging and the proliferation of potentially blanket-forming species are reported. No information is available of competition between lianas and trees.

Large individuals

About 6 months prior to logging, liana cutting was carried out around the trees selected for logging. Van der Hout (1999, p. 87) reported no effect of liana logging on the size of (single) tree fall gaps created. There is no record of which liana species and individuals were cut.

If a liana of 5 cm dbh or more would be considered a large liana with the potential to interconnect tree crowns, then 4% of all individuals taller than 1.3 m in undisturbed forest would fall in this category (based on Sample A). Only a small proportion of species is capable of achieving this size: just 22 species of the 127 present in undisturbed plots made up 88% of all large individuals; three of these were hemi-epiphytes that don’t grow from tree crown to tree crown. Some species (Table 3.19) tend grow to a large size while others are frequent as large lianas simply because they are very common (such as *Connarus perrottetii*).

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Table 3.19 Most important species of large lianas in rainforest near Mabura Hill.

Large species (>10% of population ≥ 5 cm dbh)	Quantitatively important species (>5% of large individuals)	Large hemiepiphytes
<i>Anemopaegma oligoneuron</i> (31%*)	<i>Anomospermum grandifolium</i> (13% [†])	<i>Clusia grandiflora</i>
<i>Anomospermum grandifolium</i> (28%)	<i>Connarus megacarpus</i> (6%)	<i>Clusia palmicida</i>
<i>Aristolochia daeminoxi</i> (11%)	<i>Connarus perrottetii</i> (14%)	<i>Heteropsis multiflora</i>
<i>Bauhinia guianensis</i> (28%)	<i>Moutabea guianensis</i> (11%)	<i>Noranthea guianensis</i>
<i>Curarea candicans</i> (29%)	<i>Tetracera volubilis</i> (6%)	
<i>Cydista aequinoctialis</i> (11%)		
<i>Doliocarpus brevipedicellatus</i> (14%)		
<i>Machaerium myrianthum</i> (19%)		
<i>Moutabea guianensis</i> (21%)		
<i>Pinzona coriacea</i> (11%)		
<i>Strychnos bredemeyeri</i> (33%)		
<i>Strychnos melinoniana</i> (10%)		
<i>Tetracera volubilis</i> (13%)		

*Proportion of population of this species (>1.3 m tall) that is ≥ 5 cm dbh.

[†]Proportion of individuals ≥ 5 cm dbh belonging to this species.

From Table 3.7 it is clear that there is no effect of logging or logging intensity on the abundance of lianas >2 cm dbh. If the data for large lianas (dbh>5 cm) is analysed separately, a census effect but not a logging intensity effect is detected¹³ (compare Figure 3.9; the census effect in this figure, which is based on the entire plot, is weaker than in Sample A). There is a general decline in abundance, which does not depend on logging intensity. Decline in the control plots (unharvested and no liana cutting) is of the same order as in the other treatments. Hence, no effect of liana cutting on the abundance of large lianas is present in the data. It is unclear why large lianas are decreased in abundance even in the control plot.

Blanket formers

Blanket-forming lianas are lianas that respond to disturbance or physical damage by the development of many sprouts which can grow out to veritable carpets. Not all species possess that quality, but it is relevant to monitor their abundance in logging operations as such liana carpets may retard regeneration of gaps (*e.g.*, Schnitzer *et al.* 2000).

Species that were observed in the field to be capable of forming many sprouts and blankets are listed in Table 3.20. This table shows that most species with a blanket-forming potential are in Group A1, while another few are in the group with inconsistent responses. These species had at least some 'positive' responses to either logging or logging intensity. This suggests that, in general terms, blanket-forming lianas follow the behaviour of Group A lianas. This is illustrated in Figure 3.25 for the two main species with a blanket-forming potential, showing a strong increase in the RIL 8 and RIL 16 treatments in the Logging Experiment, and a preference for skidded gaps and gaps.

Table 3.20 Species observed to be capable of forming liana blankets, along with their ecological group affinity (*cf.* Table 3.13).

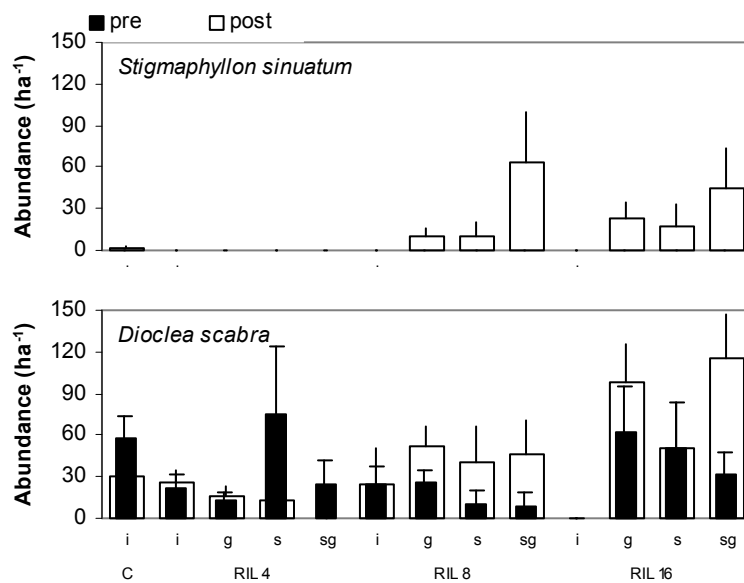
Name	Ecological Species Group	Name	Ecological Species Group
<i>Bauhinia guianensis</i>	A1	<i>Machaerium quinata</i>	A1
<i>Clitoria sagotii</i>	(A1)*	<i>Mezia includens</i>	- [†]
<i>Dalechampia olympiana</i>	- [†]	<i>Moutabea guianensis</i>	O
<i>Dioclea scabra</i>	X	<i>Passiflora glandulosa</i>	A1
<i>Doliocarpus brevipedicellatus</i>	X	<i>Prionostemma aspera</i>	X
<i>Machaerium madeirense</i>	D	<i>Stigmaphyllon sinuatum</i>	A1
<i>Machaerium myrianthum</i>	A1		

[†] Species not classified in ecological species group due to low occurrence in Pibiri.

**Clitoria sagotii* was not classified as it was rare in Pibiri, but certainly belongs to this group.

¹³ Mixed effects anova of random factors block and census and fixed factor treatment on abundance of large individuals per plot. Census effect $F_{1,2}=240.1$, $p<0.01$; treatment*census effect $F_{3,6}=0.62$, not significant.

Figure 3.25 Response pattern of two blanket-forming species, *Stigmaphyllon sinuatum* and *Dioclea glabra*, to logging intensity and habitat in the Logging Experiment in Pibiri. *Stigmaphyllon* did not occur before logging.



3.4.4 Conclusions – indicators

The value of lianas as indicators is mainly based on their ability to respond to changes in the physical environment of the habitat in which they are growing and their ability to respond rapidly to it. The following main conclusions can be drawn based on the results presented above:

- There is a clear positive relationship between the abundance of pioneer lianas belonging to Group A (A1 and A2) and the area of skid trails per plot, at least for forest that was logged less than 8 years before the measurement.
- For these plots, Group A liana abundance could form a reasonable indicator of logging damage (skidtrail area), even though application of this indicator will lead to a small number of wrong conclusions.
- If this method is to be applied in forest older than 8 years since logging, an indicator must be added that estimates the age of the forest based on the size of the lianas.
- This indicator would only be of value in conditions where direct measurement of skidtrail area proves to be difficult, or in conditions where a direct estimate of the consequence of unacceptably high skidtrail area is required.
- The value of Group A abundance is probably universal but this requires validation. The species composition of Group A varies from site to site and must be established prior to applying the indicator.
- The norms associated with this indicator are not universal and must be established prior to applying the indicator.
- There is little evidence that lianas will contribute useful indicators for biodiversity or liana biodiversity.
- There are no lianas in this study that have indicative value for the condition (abundance, species diversity) of liana communities that are characteristic for undisturbed old growth forest, mainly because few lianas appear to be strongly negatively affected by logging.

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- In this study, there was little evidence that pre-harvest liana cutting was responsible for the observed reduced abundance of large lianas after logging. Liana cutting was restricted to individuals growing in trees earmarked for harvesting.
- Potentially blanket-forming species predominantly belong to ecological species Group A1 (pioneers). There is little benefit to distinguishing indicators that measure risk for liana blankets, above the indicator for disturbance (which is also based on Group A abundance).

4 BIODIVERSITY AND LOGGING-COMPARISON WITH OTHER STUDIES

4.1 UNDISTURBED FOREST

4.1.1 Diversity of liana communities in undisturbed tropical rain forest

Comparison of liana diversity with other published data in the literature is marred by a lack of standards for plot size and structure, minimum size cut-off, liana definition (hemi-epiphytes are sometimes included, sometimes they are not) and sample strategy (treatment of clonal individuals, treatment of individuals growing into the plot). The use of Fisher's α to express diversity will address some of these problems quite well, provided samples are laid out in homogeneous areas. However, often plots are not contiguous and possibly laid out over environmental gradients in an effort to maximise species richness, leading to inflated values for Fisher's α . Notwithstanding these problems, the data from Table 4.1 show that liana diversity in Pibiri is generally below values recorded for other sites in tropical lowland forests. The large dataset provided in Gentry (1991) stands out for its (very) high values of α of some plots¹⁴ and also, remarkably, for much higher liana abundance figures than reported in other studies, including Pibiri. Possibly all lianas growing into the very narrow sample strips were included in the sample in Gentry (1991); in any case, there is probably little value in directly comparing Gentry's (1991) data with other studies reported in the table. If strip samples are excluded, one ha of tropical lowland forest is tentatively expected to contain 1000-1500 lianas >1 cm dbh, of which 325-425 are >2.5 cm dbh. Pibiri appears to be relatively rich in small lianas (1-2.5 cm) but poor in large lianas (>2.5 cm). Generally, Fisher's α of these liana communities appears to be within the range 10-30 with exceptional sites up to 40 (Yasuní, Ecuador). Pibiri occupies the lower end of that range. The very limited data available are in agreement with the finding that Guyanan forests tend to be less diverse than central and western Amazonian forests (ter Steege *et al.* 2000c).

4.1.2 Diversity of trees and lianas in undisturbed forest in Pibiri

Along with lianas, diversity of trees has been determined in the experimental plots in Pibiri and in other comparable forests in Guyana. The problem here is that trees are usually enumerated from 10 cm dbh and up and no logical equivalent exists for lianas. Leaving this apart, Fisher's α for trees >10 cm dbh in one ha plots (including Pibiri) in Central Guyana ranges from 11.9-29.3 (ter Steege 2000b). This implies that liana diversity (6.9-13.1, Table 3.2) overlaps with the lower end of that range, but that in general lianas are less diverse than trees. In Pibiri, species density per life form decreased from trees (51% of all species found) via lianas (39%) to herbs and shrubs (11%; Ek 1997).

¹⁴ see, e.g. Faber-Langendoen & Gentry (1991) for a much lower estimate of liana diversity in the site at Bajo Calima, Colombia, using a different plot design (contiguous instead of "exploded")

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Table 4.1 Overview of liana abundance and diversity data from sites in tropical lowland forests. Data are grouped by minimum liana dbh used in the census. Some data are calculated on the basis of the author's information, as indicated in notes. Data from Gentry (1991) only include mainland tropical lowland rain forest sites (precipitation > 1750 mm; elevation < 500 m). In all cases, only plots in primary tierra firme or comparable forests were included; forests on swamp, floodplain, white sand and other aberrant soil types were not included.

Location	Plot layout	Size (cm dbh)	Replicates	N (ha ⁻¹ ; s.d.)	Fisher's α (s.d.)	Notes	Source	
a. Individuals ≥ 2.5 cm dbh								
PIBIRI PRE-HARVEST	Guyana	2,500 m ² : 25 subplots @ 10*10 m in 1 ha	≥ 2.5	15	344 (123)	10.1 (1.9)	N based on all indiv. incl. unidentified species and species complexes, α is based on valid species and individuals only (incl. hemi-epiphytes)	This study
Los Tuxtlas, Veracruz	Mexico	1,000 m ² : 10 strips @ 2*50 m, 20 m apart	≥ 2.5	1	560	24.8		Gentry 1991
Corcovado	Costa Rica	—,—	≥ 2.5	1	560	36.7		Gentry 1991
Curundu	Panama	—,—	≥ 2.5	1	590	15.1		Gentry 1991
Madden Forest	Panama	—,—	≥ 2.5	1	760	18.3		Gentry 1991
Pipeline Road	Panama	—,—	≥ 2.5	1	680	35.5		Gentry 1991
Bosque de la Cueva	Colombia	—,—	≥ 2.5	1	650	14.9		Gentry 1991
Tutunendo	Colombia	—,—	≥ 2.5	1	700	84.6		Gentry 1991
Bajo Calima	Colombia	—,—	≥ 2.5	1	640	116.4		Gentry 1991
Cerro Neblina	Venezuela	—,—	≥ 2.5	2	295	19.1		Gentry 1991
Rio Palenque	Ecuador	—,—	≥ 2.5	2	565	19.9		Gentry 1991
Jauneche	Ecuador	—,—	≥ 2.5	1	1230	24.5		Gentry 1991
Jatún Sacha	Ecuador	—,—	≥ 2.5	1	940	67.9		Gentry 1991
Saul	Fr. Guiana	—,—	≥ 2.5	1	500	42.3		Gentry 1991
Mocambo, Para	Brazil	—,—	≥ 2.5	1	490	24.7		Gentry 1991
Sucursari	Peru	—,—	≥ 2.5	1	680	40.7		Gentry 1991
Yanamono (upland)	Peru	—,—	≥ 2.5	2	625	69.6		Gentry 1991
Bosque v. Humboldt	Peru	—,—	≥ 2.5	1	660	32.4		Gentry 1991
Cabeza de Mono	Peru	—,—	≥ 2.5	1	620	24.7		Gentry 1991
Shiringamazu	Peru	—,—	≥ 2.5	1	790	51.9		Gentry 1991
Indiana	Peru	—,—	≥ 2.5	1	900	60.1		Gentry 1991
Jenaro Herrera	Peru	—,—	≥ 2.5	1	730	43.9		Gentry 1991
Cocha Cashu	Peru	—,—	≥ 2.5	1	810	39.4		Gentry 1991
Tombopata (lateritic)	Peru	—,—	≥ 2.5	2	775	36.6		Gentry 1991
Makokou	Gabon	—,—	≥ 2.5	2	925	31.3		Gentry 1991
Omo Forest	Nigeria	—,—	≥ 2.5	1	730	15.5		Gentry 1991
Mt. Cameroon	Cameroon	—,—	≥ 2.5	1	1170	31.7		Gentry 1991

Location	Plot layout	Size (cm dbh)	Replicates	N (ha ⁻¹ ; s.d.)	Fisher's α (s.d.)	Notes	Source	
Korup NP	Cameroon	—,—	≥2.5	1	710	52.8	Gentry 1991	
Pasoh	Malaysia	—,—	≥2.5	2	1145	44.2	Gentry 1991	
Baitete	Papua New Guinea	—,—	≥2.5	1	800	50.7	Gentry 1991	
Semengoh NP	Sarawak	—,—	≥2.5	1	250	139.8	Gentry 1991	
Bako NP	Sarawak	—,—	≥2.5	1	560	18.9	Gentry 1991	
Yasuní	Ecuador	1,000 m ² : 2 strips with 2 plots @ 2*50 m, 1 km apart	≥2.5	4	330 (152)	23.1	Results calculated from means of 2 replicates of 2 pseudoreplicated plots provided by author	Nabe-Nielsen (2001)
Yasuní	Ecuador	1,000 m ² : 20*50 m	≥2.5	10	428 (128)	18.4 (4.3)	Tierra firme plots only	Duque <i>et al.</i> (in prep)
Middle Caquetá	Colombia	1,000 m ² : 20*50 m	≥2.5	11	386 (131)	12.8 (2.7)	Tierra firme plots only	Duque <i>et al.</i> (in prep)
Maynas province	Peru	1,000 m ² : 20*50 m	≥2.5	5	332 (108)	34.8 (16.4)	Tierra firme plots only	Duque <i>et al.</i> (in prep)
b. Individuals ≥1 cm dbh								
PIBIRI PRE-HARVEST	Guyana	2,500 m ² : 25 subplots @ 10*10 m in 1 ha	≥1	15	1454 (482)	8.3 (1.4)	N is based on all individuals including unidentified species and species complexes, α is based on valid species and individuals only (incl. hemiepiphytes)	This study
Yasuní	Ecuador	2,000 m ² : 5 strips @ 4*100 m, 16 m apart	≥1	12	1812 (285)	39.1 (12.4)	Sample excl. hemi-epif.; including individuals growing into the sample plot; this probably does not affect α , but would affect N.	Burnham (2002)
Yasuní	Ecuador	1,000 m ² : 2 strips with 2 plots @ 2*50 m, 1 km apart	≥1	4	945 (280)	32.5	Results calculated from means of 2 replicates of 2 pseudoreplicated plots provided by author	Nabe-Nielsen (2001)
Lacandon Forest, Chiapas	Mexico	1,500 m ² : 30 subplots 5*10m within 20*250 plot	≥1	2	1260	18.0	Data from 2 Alluvial terrace sites	Ibarra-Manríquez & Martínez-Ramos (2002)
Lambir National Park, Sarawak	Malaysia	5,000 m ² : 5 plots @ 20*50 m	≥1	2	710	20.3	2 sites, ridge and valley; assuming that all recorded species were in class ≥1 cm dbh.	Putz & Chai (1987)

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Location		Plot layout	Size (cm dbh)	Replicates	N (ha ⁻¹ ; s.d.)	Fisher's α (s.d.)	Notes	Source
c. Other minimum sizes								
Oquiriquia concession	Bolivia	1,080 m ² : 12 plots @ 900 m ² within 25 ha	≥2	1	2471	9.2	Site in liana forest, calculated from information provided in paper on the basis of aggregated data of 12 plots, i.e. 1 replicate	Pérez-Salicrup <i>et al.</i> (2001)
Ebom	Cameroon	10,000 m ²	≥2	33	408 (200)	?		Parren (2002), Parren & Bongers (2001)
Manaus	Brazil	400 m ² : 20*20 m	≥2	36	298 (222)	12.8 (8.3)		Laurance <i>et al.</i> (2001)
Barro Colorado National Monument	Panama	800 m ² : 8 plots @ 5*10 m in 2 transects ≥20 m apart	≥0.5	2	1569	7.7	Data from 2 old growth sites; α is lower than reported by authors	Dewalt <i>et al.</i> (2000)
Northwest District	Guyana	1,000 m ² : 10 plots @ 10*10 m 90 m apart in 1000 m transect	<10; ≥1.50m height	3	1132 (498)	15.1 (8.2)	Two primary sites and one 60 year old secondary forest; N includes indiv. >10 cm dbh	Van Andel (2000)
Makokou	Gabon	16,000 m ² : 20 plots @ 40*20 m in strip	≥5	2	137	25.1	Averaged from two censuses 13 years apart; each census is aggregate of 20 plots; including indiv. growing into the sample plot; this probably does not affect α , but would affect N.	Caballé & Martin (2001)

4.2 TRENDS IN DIVERSITY AND ABUNDANCE IN LOGGED FOREST

As a larger proportion of the world's tropical rain forests are logged, it is crucial to establish to what extent logged forests can play a role in biodiversity conservation. In this study, this was studied using lianas as a model group. A principal finding of this study is that liana diversity is higher but of different composition in selectively logged forest than in undisturbed forest in central Guyana, and that it is higher as logging intensity increases.

Comparisons of community responses to logging are made for three types of studies found in the literature: responses by liana communities to logging elsewhere in the tropics; responses by communities of other organisms in similar forests in Guyana, and finally general responses of various communities of other organisms in other tropical forests. In all cases, the effect of logging is considered in isolation, even though in practice forests logged once have a high chance of being disturbed again by further logging and harvesting, hunting, settlement, fire and/or fragmentation. This may have more impacts on species diversity than the initial logging event itself.

4.2.1 Lianas in other forests

Accounts of the response of liana diversity to logging are rare. Of the studies reported in Table 4.2, only one addresses liana diversity after selective logging. Woody climber species-richness was not significantly different between 45 year old logged and unlogged forests at Pasoh, Malaysia, but there was a strong difference in the frequency distribution of various size classes in the logged and unlogged rain forest. Large lianas were scarce in logged forest. In this study, liana diversity depended on stem diversity but not disturbance history (Gardette 1998). The time scale of this study is much longer than the one in Central Guyana. It suggests that liana diversity eventually returns to background levels. In Guyana, large lianas started to increase after 12 years as the effects of increased regeneration short after logging became to be felt. This might be a temporary increase if this wave of recruits is not sustained by younger regeneration. The study at Pasoh found that mammal and bird-dispersed species were under-represented in logged forest. It is unknown whether this trend was also present in Central Guyana.

In Panama, liana diversity and abundance were examined over a chronosequence from 20 to *c.* 500 years since disturbance (Dewalt *et al.* 2000), *i.e.*, the youngest stand is slightly older than the oldest stand in the study in Central Guyana. Liana abundance (>1.3 m tall; >0.5 cm dbh) decreased over the chronosequence examined, which is a somewhat different result from Central Guyana, where liana abundance had already returned to background level at 16 years. The difference might be in differences in regional liana abundance, or in the nature of the disturbance that set off the succession (complete clearing for agriculture in Panama, selective logging in Guyana). Size class distributions did not differ greatly among stand ages. Nonetheless, small-diameter lianas were most abundant in the 20-y stands and the largest lianas were found in the forests older than 70 y.

In a study in Brazil, forest edges were the source of disturbance. Sites within 100 m from forest fragment edges were considered disturbed while sites beyond 100 m were less disturbed. All sites were located within recently (max 20 years) isolated 10 ha forest fragments, which is a different situation than the continuous forest present at the Central Guyanan study site. Forest edges are continuously dynamic environments, while gap edges in logged forest gradually return to more stable conditions as the gap fills in (even though they may be more dynamic than intact forest for a number of years, Young & Hubbell 1991). The results of that study were in accordance with Central Guyana in that liana diversity and abundance at edges was higher. Apparently, liana abundance remained higher at edges even after 20 years because of ongoing disturbance. Liana communities were not significantly different in composition at forest edges, however, and very few species were more abundant at edges than in the interior.

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In spite of these few and rather varied studies, some tentative general conclusions may be drawn. Increased abundance of lianas after disturbance, whether or not caused by logging, has been documented extensively, also in other studies than the three quoted (Schnitzer & Bongers 2002). Forests, which are not further disturbed after initial disturbance, tend to show diminishing liana density after an initial peak, but the time scale varies from rapid (16-20 y) in Guyana and to at least 70 y in Panama. (The sites of 20 and 70 years are both succession after slash and burn). Liana size structures are slower to recover to pre-disturbance levels than abundance per se and even in the longest timeseries, there is still mention of reduced density of large lianas and increased density of small lianas. Pibiri's increase in large lianas towards the end of the chronosequence may thus be a transient effect of increased recruitment just after disturbance.

Increased diversity of lianas after logging is a more difficult issue because several processes interact to produce higher species density. At patch level (gaps), species richness is increased because of a higher liana stem density and because of a higher diversity (higher species per stem ratio; higher Fisher's α) than in forest-interiors. A higher diversity (as shown by rarefaction analysis) in gaps was also demonstrated for lianas growing in natural gaps in Barro Colorado Island (Schnitzer & Carson 2001), even though for tree saplings that was not the case there (Hubbell *et al.* 1999). At plot level (scale of hectares), species richness is increased because logged landscapes consist of habitat patches, which differ not only in diversity but also in species composition. Most studies are conducted at this level and it appears that liana diversity (Fisher's α) tends to be increased some years after logging and then declines very slowly in the course of decades. However, this finding is not as strong as the similar finding about liana density and requires further study. For example, the 20 y old forest at Barama River in North-west Guyana was less diverse than the nearby intact forest site. No other studies were found supporting or refuting the finding, that diversity is correlated with logging intensity.

4.2.2 Other species groups in Guyana

The response to logging of species diversity depends on the characteristics of the forest and of the logging operations. These vary largely over the world, so responses of plants and animals may vary accordingly. Within (central) Guyana, variation due to variation in forest characteristics and logging operations should be less, so differences in response will be attributable largely to the type of organism involved. The main question asked is: is temporary increased abundance and diversity in logged forests only found among lianas or is it a feature held in common with other groups of organisms.

Published studies on diversity in central Guyana are available for several groups of organisms: trees, herbs and shrubs, and insects (see Table 4.2 for references). In all cases, except herbs and shrubs, species diversity increased in recently (1-5 years) logged forest or in logging gaps compared to intact forest or forest-interiors. For trees increased diversity is only shown for saplings (Arets *et al.*, in prep.) and (weakly) seedlings (*cf.* Rose, 2000), while diversity among adult trees and poles is not or less increased in the first few years after logging. The presence of a response in saplings and its absence in adults in the short to medium term is similar to reports from other sites. At the level of individual gaps, diversity is reported to be equal (Hubbell *et al.* 1999, Schnitzer & Carson 2001) or higher (Molino & Sabatier 2001, except in the most heavily disturbed sites). Differences in composition between habitat patches leads to higher diversity at the plot level (Webb 1998), but if only large trees are included in the analysis, little change in diversity is usually apparent (*e.g.*, Verburg & van Eijk in press; Slik *et al.*, 2002). In Malaysia, c. 45 years after logging and silvicultural treatment, a lower diversity than in unlogged forest was reported (Okuda *et al.* in press).

Insect diversity was increased in logged forest in Guyana, too, a finding that is at odds with other accounts of insect diversity in logged forests (Basset *et al.* 2001, Putz *et al.* 2000). This points at a particular feature of central Guyanan forests, which are hypothesised to be in a late

successional stage with a high abundance of slow-growing and poorly dispersed species (ter Steege & Hammond 2001). The intermediate disturbance theory predicts that disturbance in such forests is associated with a (temporary) increase in species diversity (*e.g.*, Sheil and Burslem *in press*), but that is only possible if the species that make up that increased diversity are present in the regional species pool and capable of responding to the increased disturbance (ter Steege *et al.* *in press*). On a large scale and a time span of 75 y since first logging, large tree diversity remains similar to pre-harvest levels (ter Steege *et al.* 2002). This was attributed to the relatively low proportion of forest actually affected and the absence in the regional species pool of a large number of species that invade logged forests. The large area (*c.* 1150 km²) considered in this study included mainly primary forest but inevitably also successional patches, so most species of the regional species pool must have been present in the pre-logging forest already. At local levels as in Pibiri (which was selected to be as undisturbed in appearance as possible) such species, even though they may be rare compared with other, more dynamical forest regions, do invade in gaps and increase local species richness.

4.2.3 Other species groups in other forests

General conclusions about responses in diversity to logging are not easily drawn. Different intensities and patterns of logging will affect different groups of organisms in different ways. Some groups will be more sensitive to logging than others (Putz *et al.* 2000). The literature reveals contrasting responses even within species groups. An important but somewhat trivial factor is whether logging specifically targets the community or not (relevant for trees) and whether this creates opportunities for other, competing groups (such as lianas that will be released from competition for light). Sessile and relatively immobile species, including plants, cannot move away from logged areas and will continue to contribute to the diversity of logged forests as long as they are not physically removed. There might be an indirect consequence on diversity if such organisms stop reproducing, but this is a long-term consequence that will be important only if logging is heavy, frequent or leads to permanent changes in the forest ecosystem (*cf.* Tilman *et al.* 1994). Species with relatively short lifecycles or small home ranges may respond rapidly to the habitat patches that are created by logging, particularly if they are well-adapted to the more extreme conditions of those patches (compared with forest-interiors). These species may be gone as quickly as they came as succession proceeds towards closed forest. Species with long life cycles and large home ranges may be less sensitive in response, may avoid unsuitable habitat patches (spatial avoidance for mobile organisms, lack of regeneration for sessile organisms) but any change in community composition may persist much longer.

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Table 4.2 Overview of responses to logging of lianas and other groups of organisms reported in the literature. Data from other life forms in tropical forests (c.) taken from Putz *et al.* (2000).

Lifeform and source	Context of the study	Diversity	Composition	Abundance	Population structure
THIS STUDY	Experimental RIL 0-16 trees/ha, 0-4 years after logging; Chronosequence approach over 16 yrs; selective logging of mostly <20 trees/ha; min. size 2m tall	Increased with LI; peaks at 6 yrs but not back to normal by 16 yrs (?); diversity highest in gaps	Different, especially on skidded trails in high LI; difference appears to be largest at 6 years but persists at least 16 yrs	Increased in highest LI; highest after 6 yrs, normal by 16 yrs	Wave of recruits in highest LI; deficiency of seedlings after 8 yrs; increase in large individuals after 8 yrs
a. Studies on liana diversity					
Barro Colorado Island, Panama (deWalt <i>et al.</i> 2000)	Chronosequence over 20-100 (-500) yrs; min. liana size 0.5 cm dbh; disturbance caused by clearfelling/shifting cultivation	Fisher's α declines between 20-70 yrs, then constant at level of control plot	Qualitatively similar between stand ages, but relative abundance of some species correlated with stand age	Decreased with increasing age, while in CG abundance had returned to background level by 16 yr	Mean liana size increasing with age
Pasoh, Malaysia (Gardette 1998)	Comparison unlogged with logged and silviculturally treated area aged 45 yrs; Only woody lianas	No difference in Fisher's α between sites	Reduction in mammal and bird dispersed species in logged forest	No information	Logged forest deficient in large lianas
Manaus, Brazil (Laurance <i>et al.</i> 2001)	Comparison of plots at forest fragment edges and interiors aged 14-20 years. Disturbance caused by fragmentation	More disturbed edges have higher Fisher's α than less disturbed forest-interior	No significant differences; some species increased at edges	Increased at edges compared with forest-interior	Edge plots enriched in small individuals < 3 cm dbh compared with interior
Barama River, Guyana (van Andel, 2000)	Comparison of intact forest site with secondary forest 20 y after shifting cultivation.	Fisher's α reduced in sec. forest site		No difference	No information
b. Studies in comparable forest in Guyana on other plant life forms and animals					
Trees (Arets <i>et al.</i> in press; Rose 2000)	c. 3-6 yrs after logging over a gradient of logging intensity in Pibiri and North-west Guyana; mostly low intensity selective logging ; partially the same plots in the logging experiment in Pibiri	Positive relation between Fisher's α and LI (% basal area removed) for saplings (2m– 5 cm dbh); no effect on large trees; Seedling diversity shows weak maximum in small gaps (6-15% canopy openness)	Lightwood species increased at expense of large seeded heavy hardwood species		
Herbs and shrubs (Ek, 1997)	Comparison of logged and unlogged plots (same as in chronosequence study in this report)	Species richness in logged and control sites similar	No information	No information	No information

Lifeform and source	Context of the study	Diversity	Composition	Abundance	Population structure
Herbivorous insects (Basset <i>et al.</i> 2001)	Comparison logged and unlogged patches before and 1 yr after logging	Increased (not typical of arthropod responses to logging); reduced evenness	Generalists increased more than specialists	Abundance of most species increased but large differences between species	No information
Insects (Charles 1998)	Comparison of gaps differing in size	Increased in large compared to small gaps	No information	No information	No information

5 THE VALUE OF LIANAS AS INDICATORS

This study has shown that the relative abundance of certain lianas – Group A lianas, interpreted as pioneers – has a predictable relationship with damage – expressed as skid trail area – at the study site, at least during the first *c.* 8 years after logging. Could lianas be used to measure whether forest management has met performance targets as specified in standards of sustainable forest management? Of the national certification standards that are currently available for tropical forests (Bolivia, Brazil, Cameroon, Costa Rica, Indonesia, Malaysia, Mexico, Peru, Ghana; http://www.gtz.de/forest_certification/english/standards.asp), none introduce lianas as indicators of damage caused by logging. Most are fairly general in their requirement to limit logging related damage as much as possible and apply reduced impact logging techniques, and only one (Costa Rica, Ministerio del Ambiente y Energía 1998) is specific in providing norms for each type of damage.

Realistically, in the view of the general absence of output and performance indicators in current standards of forest management, it is unlikely that lianas will be introduced as an indicator for forest damage in the near future. If norms are defined, they will be based on direct measures of impact in terms of percentage area damaged and gap sizes. Liana abundance may play a role in indirectly measuring the area disturbed by skidding if an assessment needs to be done several years after logging, when a secondary vegetation has grown up in the logging gaps and visibility and accessibility will be drastically reduced. Even then, direct sampling of area damaged (using line sampling methods) may still prove to be easier than sampling lianas.

Therefore, the only way in which lianas could be usefully employed in certification standards could be when they are used as a basis for setting norms, i.e. the reverse operation as used in section 1.1. Once it is accepted that “limited logging damage” is an indicator for assessing the criterion “critical ecological functions of forest ecosystems maintained” (*cf.* FSC criterion 6.3), a norm must be set to distinguish acceptable from non-acceptable damage. The setting of norms is largely a political decision, but requires a firm footing in ecology. Using lianas as one of the contributing factors to deciding this norm may present several advantages in this respect, because lianas show a relatively sensitive, rapid and unambiguous response to logging, as shown in this study, and a norm supported by changes in liana abundance may appeal to several groups of stakeholders involved in setting the norms. Environmentalists are interested to maintain forest biodiversity as closely as possible in diversity and composition to undisturbed forest, while forest managers are interested in avoiding the risk, that tree regeneration is retarded by liana tangles and that large lianas will link tree crowns during future harvests. These interests run largely parallel.

Using this logic, stakeholders first need to agree on acceptable and unacceptable levels of liana diversity and abundance (specifically of Group A pioneers), and then establish the associated level of logging damage. In field assessments of logging performance, logging damage is used as the indicator; liana abundance and composition are only used to provide convincing support for choosing the norm. Most likely, this needs to be validated for each forest region where the norm is to be applied.

In the example of Pibiri, it is clear that liana diversity is always increased when the forest is logged, and that an intensity of 16 tree.ha⁻¹ yields higher diversity than 4 and 8 trees.ha⁻¹, which did not differ from each other (Table 3.7). So the highest acceptable logging intensity would then be 8 trees.ha⁻¹, if reduced impact logging techniques are employed. This study does not answer the question how the liana abundance and diversity will develop in RIL 8 plots as time passes on (the chronosequence study concerns heavily damaged plots), but it is assumed that lianas would be less abundant and more similar in composition to intact forest compared with RIL 16 plots. Disregarding one of the RIL 8 plots with a very high abundance of Group A pioneer species (23% *vs.* 24-28% in RIL 16 plots), a norm could be tentatively based on the RIL 8 plot with the highest remaining Group A abundance, i.e. 18%. From

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Figure 3.22 the associated maximum acceptable skidtrail area can be read at *c.* 7% (6.77%), using the relation for plots <8 years of age. For comparison: the maximum allowable skidtrail area in the Costa Rican certification standard is 8%. In the practice of conventional logging near Pibiri in Guyana (i.e. unplanned skidtrails and no winching of logs) the area disturbed by skidding ranged from 12 (8 trees.ha⁻¹) to 20% (16 trees.ha⁻¹; van der Hout 1999). A review of skidding impact studies showed that world-wide a vast majority of studies reported skidding damage above 7% of forest area, with little apparent relation to logging intensity (van der Hout, 1999).

6 SUMMARY OF CONCLUSIONS

This report described the abundance and composition of liana communities in undisturbed and logged forests in Central Guyana. Four main issues were addressed:

- What is liana abundance and composition of undisturbed forests?
- What is the impact on liana abundance and composition of different intensities of logging (reduced impact logging)?
- How do liana abundance and composition of logged forests develop as the time since logging progresses?
- Are lianas suitable indicators of forest disturbance and or biodiversity?

The first question was researched by describing plots in undisturbed forest, the second by comparing liana communities before and after logging in an experiment whereby logging intensity was varied and the third question by comparing plots of different age since logging. The main conclusions are summarised in the following sections.

6.1 LIANA ABUNDANCE AND COMPOSITION OF UNDISTURBED FOREST

A total of 23 plots of one hectare in undisturbed Greenheart-bearing Mixed Forest were available to describe intact liana communities, of which 3 were measured several times. In all, 146 liana taxa were described from these plots. The specific questions and conclusions were:

- What are liana abundance, diversity and structure of undisturbed Greenheart forest?
 - Liana species diversity was somewhat lower than values reported for tree diversity in Central Guyana.
 - Liana diversity as found in these plots is mostly below values reported from other areas in tropical lowland forests.
 - One ha plots in this forest type sample only 40% of the local liana species pool. Twelve plots are needed to sample 95% of the species.
 - The liana vegetation in this forest type is heavily dominated by a single species, *Conarus perrottetii*. This species alone accounts for much variation between plots.
 - Large lianas were rare, with just 20 individuals >10 cm dbh per ha.
- How does liana composition vary in space?
 - Plots vary geographically in composition, mainly due to the occurrence of many relatively rare species. The larger the distance between two areas in similar forest type, the larger the difference in liana species composition.

6.2 LOGGING IMPACTS ON LIANA COMMUNITIES

Liana communities were compared before and four years after logging in 12 one ha plots, which were harvested at four levels of reduced impact logging. The main questions and conclusions were:

- How is the liana species pool affected by logging? Are species lost and where do new species come from?
 - Species were gained and lost in a largely random manner from Pibiri between the pre- and post-logging censuses.
 - All species lost were very rare and were likely lost because of chance.

Summary of conclusions

- Most species gained were not exclusive to logged forest but can be found in undisturbed forest outside the experimental area.
- Are post-harvest liana diversity, abundance and structure related to logging intensity and habitats created by logging?
 - Liana species density and diversity was increased four years after reduced impact logging.
 - This increase was more in heavily logged plots than in moderately and lightly logged plots.
 - In heavily logged plots, liana abundance was increased, but only in certain size classes.
 - In moderately and lightly logged plots, liana abundance did not increase.
 - Gaps were generally most species-rich after logging, while forest-interiors were poorest.
 - Forest interiors and skidded gaps represent extremes in terms of species composition, although the overlap is large.
 - Species composition of each habitat type is dependent on the logging treatment of the entire plot in which the habitat is located. Habitats located in a heavily logged forests are more likely to contain species that are “typical” for that habitat than the same habitats located in lightly logged forest.
 - Measured increases in liana species density are caused by a combination of increased abundance (more individuals lead to a higher probability of sampling rare species) and increased habitat heterogeneity.
- Is it possible to distinguish direct effects of logging on liana diversity (liana cutting, logging damage) from indirect effects (habitat-related changes in population dynamics)?
 - In just a few cases, some evidence existed for loss or gain to be directly related to logging, either because of liana cutting (3 species lost) or because of the creation of suitable habitat or establishment conditions (4 species gained). Evidently, many more species may have responded in abundance to liana cutting or habitat creation without disappearing or appearing.
- Are there groups of species with similar response to similar changes in habitat?
 - Of 59 common species, sixteen showed relatively strong and consistent positive responses to logging and logging related habitats, while only three showed negative responses. Twenty-two species can be considered indifferent to logging and logging intensity, while the remaining eighteen species showed variable or inconsistent responses. Other species were not abundant enough to draw conclusions.
 - A small number of species, exemplified by the common species *Passiflora glandulosa* and *Pinzonia coriacea*, are strongly associated with skidded gaps. Another set is more strongly associated with gaps. Together these species demonstrate pioneer-like ecological behaviour.
 - Pre-existing spatial patterns of species composition remain relatively strong after logging, even in the small geographic area of Pibiri.

6.3 SUCCESSIONAL DEVELOPMENT OF LIANA COMMUNITIES AFTER LOGGING

Liana communities were compared among 18 plots that differed in age since they were logged. Plot age varied from 0-16 years. As is usual in chronosequence studies, species composition of liana communities of the plots varied with other environmental and site parameters and with logging method along with plot age. This problem was partly overcome by comparing logged plots at each site with nearby unlogged controls. The main questions and conclusions were

- What is the development of liana diversity, abundance and structure at different ages since logging?
- Are liana communities in logged forest converging back to pre-harvest composition and abundance?
- Liana abundance increased over the first 6-7 years after logging before declining and reaching near-natural levels by 16 years after logging.
- While liana abundance was similar to the control plot, 16-year old communities were, in relative terms, enriched in larger individuals compared to control plots.
- The number of small seedlings showed a sharp drop after the initial surge caused by logging, and remained low throughout the rest of the chronosequence.
- Species density and diversity increased over the first 6-7 years after logging. After that, a slight decline appears to occur, but the data is not conclusive.
- Strongly gap and skidded-gap preferent species that proliferate immediately after logging are rare after 16 years. Yet, post-logging liana communities still have a different composition, and heavily disturbed habitats are still different from interior forest habitats by 16 years after logging.
- Trends in species composition related to the age of the forest since logging are obscured by geographic patterns of species occurrence in this dataset. Just 20% of the species were common to all sites, while 35% were confined to one site only;
- As plots in Pibiri dominated the first 6 years of the chronosequence, and three sites outside Pibiri the final 10 years, it is difficult to separate site-specific patterns from age-dependent patterns in this study. Hence, the results of the chronosequence analysis must be treated with caution.

6.4 INDICATORS

Liana-based indicators were on beforehand suspected to be useful for assessing the amount of damage inflicted to forests by logging. This was because liana communities show clear responses to new habitats created by logging. This assumption was tested on the dataset. In addition to logging damage, the indicative value of lianas for assessing biodiversity was also examined, and the development of lianas that may present problems for logging or regeneration of logged forests.

- Are patterns of change in composition/abundance per habitat type consistent between sites?
- Pioneer lianas belonging to ecological groups A1 and A2 showed consistent preferences for heavily disturbed habitats across sites, even though membership of this group may vary.
- What lianas or liana groups can be used to assess logging damage?

Summary of conclusions

- Pioneer lianas belonging to Group A (A1 and A2) could form a reasonable indicator of logging damage (area damaged by skid trails per plot), at least for forest that was logged less than 8 years before the assessment.
 - If this method is to be applied in forest older than 8 years since logging, an indicator must be added that estimates the age of the forest based on the size of the lianas.
 - This indicator would only be of practical value in conditions where direct measurement of skidtrail area proves to be difficult, or in conditions where a direct estimate of the *consequence* of unacceptably high skidtrail area is required
 - The value of Group A abundance as an indicator is probably universal but this requires validation. The species composition of Group A varies from site to site and must be established prior to applying the indicator.
 - The norms associated with this indicator are not universal and must be established prior to applying the indicator.
- What lianas or liana groups can be used to assess liana diversity?
- There is little evidence that lianas will contribute useful indicators for biodiversity or liana biodiversity.
 - There are no lianas in this study that have indicative value for the condition (abundance, species diversity) of liana communities that are characteristic for undisturbed old growth forest, mainly because few lianas appear to be strongly negatively affected by logging.
- What is the development of liana “nuisance indicators” in relation to logging intensity and time since logging?
- There was little evidence that pre-harvest liana cutting was responsible for the observed reduced abundance of large lianas (> 5 cm dbh) after logging in the logging experiment. Liana cutting was restricted to individuals growing in trees earmarked for harvesting.
 - Large lianas (> 5 cm dbh) increased in relative abundance from *c.* 12 years after logging.
 - Potentially blanket-forming species predominantly belong to ecological species Group A1 (pioneers). There is little benefit to distinguishing indicators that measure risk for liana blankets, above the indicator for disturbance (which is also based on Group A abundance).

7 ACKNOWLEDGEMENTS

This study benefited of the work of numerous persons. Special thanks are due to all. Treepotter Sam Roberts, field assistants George Roberts, Maurice Nathan, Martin Williams, Julian Williams, Marlon Peters, Lindsey Nathan and students Barbara Gravendeel, Karl Eichhorn, Lonneke Versteeg, Arjan Stroo, Ferry Slik, Juul van Dam, Cornel van der Kooij, Menno de Lind van Wijngaarden, Else Hesse, Martin Smeets, Geertje van der Heijden, Linda Rockx en Thijs van der Velden assisted with collecting the field data. Thanks to staff and management of the Tropenbos-Guyana Programme and Tropenbos International, staff and management of the National Herbarium of the Netherlands, Utrecht Branch, staff and management of the Department of Plant Ecology, Utrecht University, staff and management of Demerara Timbers Ltd. and the numerous persons who provided for species identifications. Many colleagues at the Tropenbos-Guyana Programme and the National Herbarium, in

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particular Marinus Werger, Pauline Hogeweg, Peter van der Hout, Paul Maas, Marion Jansen-Jacobs and Hans ter Steege have contributed time, knowledge, insight, plots and information that have tremendously benefited this study. Alvaro Duque (University of Amsterdam) contributed unpublished data. Financial support by the European Union under contract B7-6201/98-13/FOR and by Tropenbos International and Utrecht University is gratefully acknowledged.

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APPENDIX A. METHODS – DATA ANALYSIS

A.1 Diversity indices

The effect of logging on liana species diversity was expressed using species density, Fisher's α and Simpson's index (Magurran 1988, Fisher *et al.* 1943). The term "species density" is preferred here to emphasise that the number of species encountered in samples is intended rather than species richness (which should be standardised for the number of individuals sampled). Fisher's α is a measure for diversity based on the assumption that the number of individuals per species follows a log-series and is estimated from S , the number of species, and N , the number of individuals in a sample. Fisher's α is commonly used as it is relatively insensitive to sample size. In this report, however, it was avoided to calculate α for small samples based on subplots. Simpson's index D is also a measure for diversity, but it explicitly incorporates information about the distribution of individuals over species. It is a measure of dominance. To avoid confusion, $1/D$ was preferred, which means that a high value of the index can be interpreted as high diversity. A Visual Basic algorithm by H. ter Steege was used to calculate α .

Other indices of diversity and dominance are in common use and these are presented for comparison, but not used for analysis. They are: Shannon-Wiener index, Shannon's evenness (diversity indices) and Berger-Parker index (dominance).

A.2 Similarity

The similarity between pairs of plots was expressed using Sorenson's index and the Morisita-Horn index (Magurran 1988). The former is a measure for the relative number of shared species between two sites, while the latter also takes similarities in abundance into account. While the Morisita-Horn index is relatively insensitive to species richness and sample size, it is highly sensitive to the abundance of the most abundant species (Magurran 1988). As this dataset is characterised by dominance by one species (see section 3.1.2), the Morisita-Horn index was calculated with exclusion of the dominant species. This analysis was performed to detect geographic effects in similarity of plots (undisturbed plots) and to interpret the magnitude of change in pairs of pre- and post harvest censuses in the logging experiment.

Similarity indices were calculated using EstimateS 6.0b1 (Colwell 2000).

A.3 Species-area curves

Diversity of undisturbed forest was studied at three spatial levels: region, site and plot, whereby region is the entire dataset. Species-area curves were constructed to assess to what extent the total regional species pool was sampled in samples of different size and what percentage of diversity was sampled by individual plots. Species-area curves (based on 50 randomisations) were calculated using EstimateS 6.0b1 (Colwell 2000).

A.4 Species-individual curves

Differences in diversity between the four habitat types in the logging experiment could not be studied in the randomised block design as habitats could only be assigned *a posteriori* and the relative contribution of the different habitat types was not equal between the logging intensity treatments. Instead, subplots belonging to the different habitats in the logged plots, and the control plot were lumped across the replicates of each logging intensity treatment and differences in species density were evaluated using rarefaction, i.e. the species density of each possible pair of samples was compared at the lowest common sample size. If the smaller sample contained more or fewer species than estimated in the central 950 of 1000 random samples drawn from the larger sample, it was considered to be significantly richer or poorer in species. This procedure was done sequentially going down from the two largest samples to the two smallest. Fisher's α was also calculated for these samples, but this does not provide

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information about the statistical significance of differences between habitats. Ecosim 7.0 (Gotelli & Entsminger 2001) was used to perform the rarefaction analysis.

A.5 Size class distributions

Liana size class distributions were based on height classes for individuals ≤ 2 m (≤ 0.5 m; ≤ 1 m and ≤ 2 m), and dbh size classes for larger individuals (1 cm classes up to 5 cm dbh, followed by 5.1-10, 10.1-20 and 20.1-50 cm). This size class definition is slightly different from the one used for anova analysis (see below). Only individuals belonging to valid taxa were included in the analysis.

Size class distributions were compared between treatments in the logging experiment. In the chronosequence, the proportion to the total of each individual size class was plotted against time since logging. In both cases, these data were not formally tested.

A.6 Analysis of the logging experiment

The logging experiment was set up as a randomised block design, with four harvesting treatments in three replicate blocks. Each plot was measured twice, before and four years after logging. The effects of logging on diversity at the community level were investigated using four different parameters: species density (S), total abundance (N), diversity (Fishers α), and dominance (Simpson's index, $1/D$).

It was expected that logging would affect communities in several different ways. Some individuals and species will be affected by the direct effects of logging, such as the use of heavy machinery and the pre-logging liana cutting. On the other hand, new habitats will be created (large gaps, skid trails) and changing environmental conditions for growth, survival and reproduction will lead to shifts in patterns of abundance and even establishment of new species. The result will be changes in diversity, abundance and patterns of dominance. It was expected that negative effects of liana cutting and harvest would be rather independent of individual size of the lianas, while establishment of new species and individuals would become apparent first in the smaller size classes. Therefore, liana size was included as a factor in the analysis.

An Anova model was formulated to find out whether these patterns existed in the dataset, based on the Sample A and Sample B. The data were analysed per plot, i.e. the recordings from 25 subplots per one ha plot were aggregated. To enable a better analysis, the size classification used was different than the one used in section 2.4.2 p. 90, above. The individuals were classified in octaves (classes of doubling height and diameter), which ensured that each class contained a reasonable number of individuals, allowing the calculation of the relevant parameters (Table A.1). The two Samples were merged into a hybrid Sample, i.e. Class H1 and H2 were based on Sample B, and the other classes were based on Sample A. These data are derived from subplots of different area, which could pose a problem if factors driving differences in the parameters to be tested would vary over that spatial scale¹⁵. It is not possible to use the Hybrid Sample to compare abundance between size classes within the same census (either pre or post-harvest census). However, even though size is a factor in the test, no specific hypotheses were formulated regarding differences in between-size class, within-time abundance (i.e., size class distributions). Fisher's α and Simpson's index are relatively insensitive to N, but a higher N allows better estimates. Species density S is sensitive to N, as in all analysis presented, but will not be used to draw conclusions about diversity. It is presented here as it is the most "natural" index of diversity and gives information about absolute species numbers.

¹⁵ The main environmental variables affecting species composition, %gaps and %skidtrail, are reasonably well correlated at the two scale levels, 25 m² subplots and 100 m² subplots: $r=0.81$ for gaps and $r=0.73$ for skidtrail; based on 225 subplots (in 9 logged plots) in Pibiri; $p<0.001$ for both habitat types.

Table A.1 Size classification used for Anova analysis, and composition of the "Hybrid Sample" membership of size classes for both Samples and n, mean number of individuals per plot (pre-and post-logging censuses averaged) from which test parameters were calculated.

Size class	Based on	Limits	Data based on:	n
H1	Height	<0.5-1 m]	Sample B	155
H2	Height	<1-2 m]		101
0.25	DBH	≤0.25 cm	Sample A	56
0.5	DBH	<0.25-0.5 cm]		85
1	DBH	<0.5-1 cm]		161
2	DBH	<1-2 cm]		224
2+	DBH	>2 cm		106

Models were constructed that were based on a randomised block design, with two fixed factors (L-Logging intensity and S-Size) and two random factors (B-Block and T-Time = census). The dependent variables were S, N, Fisher's α , and natural log transformed Simpson's index ($\ln(1/D)$). The model was analysed using a repeated measures Anova. Because in this type of design there is no within block or within time replication, not all possible effects can be tested. In addition, the tests that can be carried out assume that there is not interaction LSTB between the four factors Logging Intensity, Size, Block and Time. This assumption cannot be tested. The effects of interest to the analysis are LST (the effect of the interaction between Logging intensity and Size depends on Time) and LT (the effect of Logging Intensity depends on Time), which both are indicative of an effect of logging. The effect of LST was tested as an F test on the ratio between the mean squares of LST and LSTB. If this effect was not significant, the analysis proceeded by testing the ratio of mean squares of LT and LTB. If found to be significant, post-hoc tests were carried out using the Students-Newman Keuls procedures (Underwood 1997) to detect which plots differed from each other.

A.7 Correspondence analysis and canonical correspondence analysis

Differences in species composition between undisturbed plots were analysed using correspondence analysis and by calculating similarity. In correspondence analysis, a species-plot matrix consisting of species abundances per plot was analysed. The variation in species composition between plots is expressed as scores on imaginary axes. The first axis represents an ordering of plots that corresponds with the highest turnover in the abundance of species present within the data (Jongman *et al.* 1987) and thus represent the main trend in the data. The second axis does the same with the remaining variation after axis 1 has been extracted. Correspondence analysis was performed using the MVSP 3.12a package (Kovach Computing Services 2000), with untransformed abundance data and downweighing of rare species.

In logged forest (both in the logging experiment and in the chronosequence) factors that were responsible for changes in species composition were investigated using correspondence analysis that was constrained by environmental factors related to logging. This analysis was conducted for Sample A at two spatial levels: plot level and habitat level (approximated by subplots). The data matrix consisted of species abundances per (sub)plot, with different sets of plots used for the analysis depending of the analysis (logging experiment or chronosequence). Environmental factors were expressed per (sub)plot and included parameters describing logging intensity (N or Basal area felled), logging damage (% of (sub)plot with canopy damage, with ground damage, with both), age (years since logging) and space (replicate block in which the (sub)plot was located, site coordinates). Many of these variables showed moderate to high degree of correlation. This was left as it was.

For several environmental factors, notable those related to gaps, data were lacking for the control plots. No gaps were measured in some of these plots, even though they must have been present. In all analysis, parameters related to gaps have been set to 0 for control plots.

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The data were examined and interpreted through plots of (sub)plot and species scores on the main axes that were extracted by this analysis and by summarising these scores by geographical area, time or habitat.

A.8 The chronosequence study

Given the strong geographical patterns that were present in the dataset and the correlation between age since logging and logging damage, rigorous testing of the data in the chronosequence study was not possible. Instead, a nominal inspection of trends was made based on expected trends in abundance and diversity of lianas. In all cases the data obtained per logged plot were presented as deviations from the data in the associated control plot. In this way, as much of the geographical variation as possible was removed from the data. Trends were approximated by third-order polynomials fitted to the data. This procedure assumes that all points (plots) are independent, which is evidently not true: pairs of plots are located at the same site (spatial dependence) and almost each plot was recensused 2-4 times (temporal dependence). To address this, the parameter of interest (i.e. the deviations in that parameter from the control) per site-year combination were averaged and points representing recensuses were connected by lines. If these lines run approximately parallel to the third-order fitted line, the fit was considered reliable. It should be stressed again that recensuses in Pibiri were much more accurate than elsewhere due to somewhat shifted plot positions outside Pibiri.

At two points in the chronosequence no control plots were available to be compared with logged plot censuses: at $t=2$ years after logging (Pibiri) and $t=16$ years after logging (2KM). In these cases, the control plots for $t=0$ (Pibiri) and $t=10$ (2KM) were used as a reference. The census of logged plots at $t=0$ in reality concerned yet unharvested plots.

A.9 Species grouping

This study was designed to find patterns in species response related to logging. The results of the canonical correspondence analysis at the two scales, the plot level and the subplot level, should provide strong indications of groups of species showing similar responses to changes in growth conditions induced by logging. The following logic was applied to detect these patterns. It is mainly based on the results of the logging experiment, which were later validated with the results of the chronosequence.

The effect of treatment and time (pre- and post-harvest census) on species abundance was tested using log-linear analysis of species counts with independent variables Time, Block and Treatment. This test provides evidence which of these three factors affect species abundance. This was followed, if necessary, by similar analysis only for the post harvest census, and a random-factor Anova on Time and Block. These tests provide evidence whether a species responds to treatment (logging intensity), to time alone or neither. If there are trends, the direction of the trend is inspected visually. The test logic is described in Table A.2.

This series of tests was followed by a series of three χ^2 -tests to determine whether a significant habitat effect was present in the subplot data (“habitat analysis”). First, the distribution of individuals over the four habitats in the post-harvest census was compared with a random distribution based on the distribution of all individuals over these habitats in the same census. If the test detected a significant difference, the species was concluded to show a habitat preference. To confirm that this preference was related to logging and not a chance distribution or a “legacy” of an existing pre-harvest pattern, the same test was conducted to assess the absence of “habitat preference” in the pre-harvest census by comparing the pre-harvest species distribution over future habitats with the random distribution of pre-harvest individuals over these habitats. A final χ^2 -test was done to confirm that a species’ post-harvest distribution differed significantly from a pattern expected from its pre-harvest distribution. The results of these tests were interpreted as in Table A.3. If habitat preference was

established, nominal inspection of abundance per habitat type and contribution to the χ^2 -statistic were used to judge the pattern of preference.

Table A.2 Logic of tests used to determine whether species showed significant responses to Time (logging) and Treatment (logging intensity).

Test	Effect of interest	Result	Conclusion	Next step
1 Loglinear Time, Treatment, Block on species counts per plot	Partial association of Time*Treatment (Effect of adding this interaction to a model including all other two-way interactions)	Significant	Treatment effect	Examine pattern of abundance per treatment and year, see 5
		Not significant	Continue	Examine time effect, see 2
		No test (insufficient observations, eg if pre-harvest abundance is very low)	Continue	Examine treatment effect in post-harvest census, see 3
2 Loglinear Time, Treatment, Block on species counts per plot	Partial association of Time	Significant	Logging but no treatment effect	Test direction of logging effect, see 7
		Not significant	No effect	Stop
3 Loglinear Treatment, Block on species counts in post-harvest census per plot	Partial association of Treatment	Significant	Treatment effect	Examine pattern of abundance per treatment, see 6
		Not significant	Continue	Examine logging effect, see 4
		No test	Continue	Examine logging effect, see 4
4 Anova on random factors Time, Block	Effect of Time	Significant	Logging but no treatment effect	Test direction of logging effect, see 7
5 Visual inspection of trend per treatment, taking year into account	C≤4≤8≤16 in post-harvest census; AND (C<>4<>8<>16 in pre-harvest census OR significant difference (by Chi2) with pre-harvest distribution)	Significant	Positive relation between abundance and logging intensity	Check control plots, see 8
		Not significant	No effect	Stop
		Other patterns	Erratic relation	Check control plots, see 8
6 Visual inspection of trend per treatment, in post harvest census	C≤4≤8≤16 in post-harvest census;	Significant	Positive relation between abundance and logging intensity	Check control plots, see 8
		Not significant	No effect	Stop
		Other patterns	Erratic relation	Check control plots, see 8
7 Visual inspection of trend in time	Difference in abundance	Post-harvest >pre-harvest	Increase	Check control plots, see 8
		Post-harvest <pre-harvest	Decrease	Check control plots, see 8
8 Mann-Whitney U test on species counts by year per plot in RIL C Treatment	Control shows no difference between pre- and post harvest censuses	Significant	Possible positive or negative logging effect in control treatment	Suspect result; conduct habitat analysis
		Not significant	Control is good control	Conduct habitat analysis

Table A.3 Interpretation of the series of three χ^2 -tests conducted to assess habitat preference among liana species. Meaning of symbols: s-significant; ns-not significant. Two combinations of test results unambiguously support the hypothesis of habitat preference, while one (ns-s-s) requires further examination. Tests were evaluated at $\alpha=0.05$ without Bonferroni correction. Excessive type-I error was avoided by requiring consistency in serial test results (e.g., the combination s-ns-ns led to rejection of the hypothesis due to apparently spurious post-harvest habitat preference)

Observed distribution	Expected distribution generated from	Results							
		Supporting hypothesis of habitat preference			Rejecting hypothesis of habitat preference				
Post-harvest species abundance	Post-harvest distribution of all individuals	s	s	ns	s	s	ns	ns	ns
Pre-harvest species abundance	Pre-harvest distribution of all individuals	ns	s	s	ns	s	ns	ss	ns
Post-harvest species abundance	Pre-harvest species abundance	s	s	s	ns	ns	ns	ns	s

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APPENDIX B. ALPHABETICAL SPECIES LIST

Acronym	Name	Family	Valid taxon used in analysis (1) and reason for rejection (0)
ABUT BARB	<i>Abuta barbata</i> Miers	Menisperm.	1
ABUT BULL	<i>Abuta bullata</i> Moldenke	Menisperm.	1
ABUT CPLX	<i>Abuta</i> complex	Menisperm.	0 in complex; ID unclear
ABUT IMEN	<i>Abuta imene</i> Eichler	Menisperm.	0 in species complex
ABUT OBOV	<i>Abuta obovata</i> Diels	Menisperm.	0 in species complex
ABUT RUFE	<i>Abuta rufescens</i> Aubl.	Menisperm.	1
ABUT SP1	<i>Abuta</i> sp. 1	Menisperm.	0 in species complex
ANEM OLIG	<i>Anemopaegma oligoneuron</i> (Sprague & Sandw.) A. Gentry	Bignoni.	1
ANEM PARK	<i>Anemopaegma parkeri</i> Sprague	Bignoni.	1
ANOM GRAN	<i>Anomospermum grandifolium</i> Eichler	Menisperm.	1
ANOM SP1	<i>Anomospermum</i> sp. 1	Menisperm.	1
APOC X	Apocynaceae x	Apocyn.	0 unidentified
ARIS CONS	<i>Aristolochia consimilis</i> Mast.	Aristolochi.	1
ARIS DAEM	<i>Aristolochia daemoninoxia</i> Mast.	Aristolochi.	1
ARIS RUGO	<i>Aristolochia rugosa</i> Lam.	Aristolochi.	1
ARRA EGEN	<i>Arrabidaea egensis</i> Bureau ex K.Schum.	Bignoni.	1
ARRA FANS	<i>Arrabidaea fanshawei</i> Sandw.	Bignoni.	1
ARRA MOLL	<i>Arrabidaea mollis</i> (Vahl) Bureau ex K.Schum.	Bignoni.	1
ASCL SP1	Asclepiadaceae sp. 1	Asclepiad.	1
BANI MART	<i>Banisteriopsis martiniana</i> (A. Juss.) Cuatrec.	Malpighi.	1
BAUH GUIA	<i>Bauhinia guianensis</i> Aubl.	Leguminosae (Caes.)	1
BAUH SCAL	<i>Bauhinia scala-simiae</i> Sandw.	Leguminosae (Caes.)	1
BAUH SP1	<i>Bauhinia</i> sp. 1	Leguminosae (Caes.)	1
BAUH SUR1	<i>Bauhinia surinamensis</i> Amsh.	Leguminosae (Caes.)	1
BIGN SP10	Bignoniaceae sp. 10	Bignoni.	1
BIGN SP7	Bignoniaceae sp. 7	Bignoni.	1
BIGN SP8	Bignoniaceae sp. 8	Bignoni.	1
BIGN SP9	Bignoniaceae sp. 9	Bignoni.	1
BIGN X	Bignoniaceae x	Bignoni.	0 identified to family level
CAYA OPHT	<i>Cayaponia ophthalmica</i> R.E. Schultes	Cucurbit.	1
CHEI COGN	<i>Cheiloclinium cognatum</i> (Miers) A.C. Sm.	Hippocrate.	0 belongs to complex
CHEI HIPPO	<i>Cheiloclinium hippocrateoides</i> (Peyr.) A.C. Sm.	Hippocrate.	1
CLIT SAGO	<i>Clitoria sagotii</i> Fantz	Leguminosae (Pap.)	1
CLUS GRAN	<i>Clusia grandiflora</i> Splitg.	Guttiferae	1
CLUS MYRI	<i>Clusia myriandra</i> (Benth.) Planch. & Triana	Guttiferae	1
CLUS PALM	<i>Clusia palmicida</i> Rich.	Guttiferae	1
CLUS X	<i>Clusia</i> x	Guttiferae	0 identified to genus level
CLYT BINA	<i>Clytostoma binatum</i> (Thunb.) Sandw.	Bignoni.	1
CLYT SCIU	<i>Clytostoma sciuripabulum</i> Bureau & K. Schum.	Bignoni.	1
COCC LUCI	<i>Coccoloba lucidula</i> Benth.	Polygon.	1
COCC MARG	<i>Coccoloba marginata</i> Benth.	Polygon.	1
COCC PARI	<i>Coccoloba parimensis</i> Benth.	Polygon.	1
COCC X	<i>Coccoloba</i> x	Polygon.	0 identified to genus level
CONN CONN	Connaraceae conn'	Connar.	0 identified to family level
CONN CORI	<i>Connarus coriaceus</i> Schellenb.	Connar.	1
CONN ERIA	<i>Connarus erianthus</i> Benth. ex Baker	Connar.	1
CONN MEGA	<i>Connarus megacarpus</i> S.F. Blake	Connar.	1
CONN PERR	<i>Connarus perrottetii</i> (DC.) Planch.	Connar.	1
CONN PUNC	<i>Connarus punctatus</i> Planch	Connar.	1
CONV SP1	Convolvulaceae sp. 1	Convolvul.	1
CONV X	Convolvulaceae x	Convolvul.	0 identified to family level
COUS MICR	<i>Coussapoa microcephala</i> Trécul	Cecropi.	1
CUCU SP1	Cucurbitaceae sp. 1	Cucurbit.	1
CUER KAPP	<i>Cuerva kappleriana</i> (Miq.) A.C. Smith	Hippocrate.	1
CURA CAND	<i>Curarea candicans</i> (Rich.) Barneby & Krukoff	Menisperm.	1
CYDI AEQU	<i>Cydista aequinoctialis</i> (L.) Miers	Bignoni.	1
DALE OLYM	<i>Dalechampia olympiana</i> Kuhl. & Rodr.	Euphorbi.	1
DALE PARV	<i>Dalechampia parvibracteolata</i> Lanj.	Euphorbi.	1
DESM MACR	<i>Desmoncus macroacanthos</i> Mart.	Palmae	1
DICH PEDU	<i>Dichapetalum pedunculatum</i> (DC.) Baill.	Dichapetal.	1
DICH RUGO	<i>Dichapetalum rugosum</i> (Vahl) Prance	Dichapetal.	1
DICR AMPL	<i>Dicranostyles ampla</i> Ducke	Convolvul.	1
DILL X	Dilleniaceae x	Dilleni.	0 identified to family level
DIOC SCAB	<i>Dioclea scabra</i> (Rich.) R.H. Maxwell	Leguminosae (Pap.)	1

Acronym	Name	Family	Valid taxon used in analysis (1) and reason for rejection (0)
DIOS DODE	Dioscorea dodecaneura Vell.	Dioscore.	1
DIOS MEGA	Dioscorea megacarpa Gleason	Dioscore.	1
DIST ELON	Distictella elongata (Vahl) Urb.	Bignoni.	1
DOLI BREV	Dolioscarpus brevipedicellatus Garcke	Dilleni.	1
DOLI GUIA	Dolioscarpus guianensis (Aubl.) Gilg.	Dilleni.	1
DOLI MACR	Dolioscarpus macrocarpus Mart. ex Eichler	Dilleni.	1
DOLI MAJO	Dolioscarpus major J.F. Gmel.	Dilleni.	1
DOLI PARA	Dolioscarpus paraensis Sleumer	Dilleni.	1
EUPH SP1	Euphorbiaceae sp. 1	Euphorbi.	1
EVOD FUNI	Evodianthus funifer (Poit.) Lindm.	Cyclanth.	1
FICU GUIA	Ficus guianensis Desv.	Mor.	1
FICU SP1	Ficus sp. 1	Mor.	1
FORS ACOU	Forsteronia acouci (Aubl.) A. DC.	Apocyn.	1
FORS FOST	Forsteronia fost?'	Apocyn.	0 identified to genus level
FORS GRAC	Forsteronia gracilis (Benth.) Muell. Arg.	Apocyn.	1
FORS GUYA	Forsteronia guyanensis Muell. Arg.	Apocyn.	1
FORS SCHO	Forsteronia schomburgkii A. DC.	Apocyn.	1
GESN SP1	Gesneriaceae sp. 1	Gesneri.	1
GNET NODI	Gnetum nodiflorum Brogn.	Gnet.	1
GNET PANI	Gnetum paniculatum Spruce ex Benth.	Gnet.	1
GNET SCH1	Gnetum schwackeanum/nodiflorum ???	Gnet.	1
GNET UREN	Gnetum urens (Aubl.) Blume	Gnet.	1
GURA ACUM	Gurania acuminata Cogn.	Cucurbit.	1
GURA BIGN	Gurania bignoniacea (Poepp. & Endl.) C. Jeffrey	Cucurbit.	1
HELM LEPT	Helmontia leptantha (Schlechtend.) Cogn.	Cucurbit.	1
HETE FLEX	Heteropsis flexuosa (Kunth) Bunting	Ar.	1
HETE MULT	Heteropterys multiflora (DC.) Hochr.	Malpighi.	1
HETE SIDE	Heteropterys siderosa Cuatrec.	Malpighi.	1
HIPP SP1	Hippocrateaceae sp. 1	Hippocrate.	1
HIPP SP2	Hippocrateaceae sp. 2	Hippocrate.	0 belongs to complex
HIPP SP3	Hippocrateaceae sp. 3	Hippocrate.	1
HIPP SP5	Hippocrateaceae sp. 5	Hippocrate.	1
HIPP X	Hippocrateaceae x	Hippocrate.	0 identified to family level
HIRA ADEN	Hiraea adenophora Sandw.	Malpighi.	1
HIRA AFFI	Hiraea affinis Miq.	Malpighi.	1
INDE T1	indet 1		1
INDE T2	indet 2		1
INDE T4	indet 4		1
LIAN SPEC	xx		0 unidentified
LOGA TWIN	Loganiaceae 'twining hook'	Logani.	0 identified to family level
LONG NEGR	Lonchocarpus negrensis Benth.	Leguminosae (Pap.)	1
LYGO VOLU	Lygodium volubile Sw.	Pteridophyta	1
LYSI SCAN	Lysiosyles scandens Benth.	Convolvul.	1
MABE PULC	Mabea pulcherrima Müll. Arg	Euphorbi.	1
MACH MADE	Machaerium madeirense Pittier	Leguminosae (Pap.)	1
MACH MULT	Machaerium multisii Killip ex Rudd	Leguminosae (Pap.)	1
MACH MYRI	Machaerium myrianthum Spruce ex Benth.	Leguminosae (Pap.)	1
MACH OBLO	Machaerium oblongifolium Vogel	Leguminosae (Pap.)	1
MACH QUIN	Machaerium quinata (Aubl.) Sandw.	Leguminosae (Pap.)	1
MACH SP1	Machaerium sp. 1	Leguminosae (Pap.)	1
MACH SP2	Machaerium sp. 2	Leguminosae (Pap.)	1
MALA MACR	Malanea macrophylla Bartl. ex Griseb.	Rubi.	1
MALA SP2	Malanea sp. 2	Rubi.	1
MALP CPLX	Malpighiaceae/Hippocrateaceae complex		0 ID unclear
MALP HIPP	Malpighiaceae / Hippocrateaceae		0 In complex
MALP SP3	Malpighiaceae sp. 3	Malpighi.	1
MALP SP4	Malpighiaceae sp. 4	Malpighi.	1
MALP SP5	Malpighiaceae sp. 5	Malpighi.	1
MALP SP6	Malpighiaceae sp. 6	Malpighi.	1
MALP X	Malpighiaceae x	Malpighi.	0 identified to family level
MARC PARV	Marcgravia parviflora Rich. ex Wittm.	Marcgravi.	1
MARI GLAB	Maripa glabra Choisy	Convolvul.	1
MARI MAR	Maripa 'maripa lp'	Convolvul.	0 identified to genus level
MARI RETI	Maripa reticulata Ducke	Convolvul.	1
MARI SCAN	Maripa scandens Aubl.	Convolvul.	1
MARI T4LP	Maripa 't4 lp'	Convolvul.	0 identified to genus level
MARK COCC	Markea coccinea Rich.	Solan.	1

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Acronym	Name	Family	Valid taxon used in analysis (1) and reason for rejection (0)
MARK PORP	Markea porphyrobaphes Sandwith	Solan.	1
MARK SESS	Markea sessiliflora Ducke	Solan.	1
MASC LOUR	Mascagnia lourteigii ??	Malpighi.	1
MASC SEPI	Mascagnia sepium (A. Juss.) Griseb.	Malpighi.	1
MEMO BRAC	Memora bracteosa (DC.) Bureau & K. Schum.	Bignoni.	1
MEMO CPLX	Memora complex	Bignoni.	0 in complex; ID unclear
MEMO FLVD	Memora flavida (DC.) Bureau & K. Schum.	Bignoni.	0 belongs to complex
MEMO FLVF	Memora flaviflora (Miq.) Pulle	Bignoni.	1
MEMO MORI	Memora moringifolia (Miq.) Pulle	Bignoni.	1
MEMO RACE	Memora racemosa A. Gentry	Bignoni.	0 belongs to complex
MEMO SP1	Memora sp. 1	Bignoni.	1
MEND SQUA	Mendoncia squamuligera Nees	Acanth.	1
MENI X	Menispermaceae x	Menisperm.	0 identified to family level
MEZI INCL	Mezia includens (Benth.) Cuatrec.	Malpighi.	1
MICR LYCO	Microgramma lycopodioides (L.) Copel.	Pteridophyta	1
MIKA GLEA	Mikania gleasonii B.L. Rob.	Aster.	1
MIKA PSIL	Mikania psilostachya DC.	Aster.	1
MIMO MYRI	Mimosa myriadenia (Benth.) Benth.	Leguminosae (Mimos)	1
MOUT GUIA	Moutabea guianensis Aubl.	Polygal.	1
MUSS PRIE	Mussatia priuriei (DC.) Bureau ex K. Schum.	Bignoni.	1
NORA GUIA	Norantea guianensis Aubl.	Marcgravi.	1
ODON PUNC	Odontadenia puncticulosa (A. Rich.) Pulle	Apocyn.	1
ODON SP1	Odontadenia sp. 1	Apocyn.	1
PASS AURI	Passiflora auriculata Kunth	Passiflor.	1
PASS CIRR	Passiflora cirrhiflora A. Juss.	Passiflor.	1
PASS COCC	Passiflora coccinea Aubl.	Passiflor.	1
PASS FUCH	Passiflora fuchsiflora Hemsl.	Passiflor.	1
PASS GARC	Passiflora garckeii Masters	Passiflor.	1
PASS GLAN	Passiflora glandulosa Cav.	Passiflor.	1
PASS KAWA	Passiflora kawensis Feuillet	Passiflor.	1
PASS VESP	Passiflora vespertilio L.	Passiflor.	1
PASS X	Passifloraceae x	Passiflor.	0 identified to family level
PAUL CAPR	Paullinia capreolata (Aubl.) Radlk.	Sapind.	1
PAUL INGA	Paullinia ingaefolia Rich.	Sapind.	1
PAUL PACH	Paullinia pachycarpa Radlk.	Sapind.	1
PAUL SP1	Paullinia sp. 1	Sapind.	1
PETR MACR	Petrea macrostachya Benth.	Verben.	1
PETR VOLU	Petrea volubilis L.	Verben.	1
PHIL RUDG	Philodendron rudgeanum Schott	Ar.	0 not a liana
PINZ CORI	Pinzona coriacea Mart. & Zucc.	Dilleni.	1
PIPE FOVE	Piper foveolatum Kunth ex C. DC.	Piper.	1
PIPE HOST	Piper hostmannianum (Miq.) C. DC.	Piper.	1
PLEO ALBI	Pleonotoma albiflora (Salzm. ex DC.) A. Gentry	Bignoni.	1
PLEU FLAV	Pleurisanthes flava Sandw.	Icacin.	1
PRIO ASPE	Prionostemma aspera (Lam.) Miers	Hippocrate.	1
PRIS NERV	Pristimera nervosa (Miers) A.C. Smith	Hippocrate.	1
PSEU MACR	Pseudoconnarus macrophyllus (Poepp. & Endl.) Radlk.	Connar.	1
RAND ASPE	Randia asperifolia (Sandw.) Sandw.	Rubi.	1
ROEN SORD	Roentgenia sordida (Bureau & K. Schum.) Sprague & Sandw.	Bignoni.	1
ROUR FRUC	Rourea frutescens Aubl.	Connar.	1
ROUR LIGU	Rourea ligulata Baker	Connar.	1
ROUR PUBE	Rourea pubescens (DC.) Radlk.	Connar.	1
SABI ASPE	Sabicea aspera Aubl.	Rubi.	1
SABI SURI	Sabicea surinamensis Bremek.	Rubi.	1
SALA INSI	Salacia insigne A.C. Smith	Hippocrate.	1
SALA JURU	Salacia juruana Loes.	Hippocrate.	1
SALA MABU	Salacia maburensis A.M. Mennega	Hippocrate.	0 not a liana
SALA MULT	Salacia multiflora (Lam.) DC.	Hippocrate.	0 belongs to complex
SCHL VIOL	Schlegelia violacea (Aubl.) Griseb.	Bignoni.	1
SCIA CAYE	Sciadotenia cayennensis Benth.	Menisperm.	1
SCLE SP1	Scleria sp. 1	Cyper.	0 not a liana
SECU SPIN	Securidaca spinifex Sandw.	Polygal.	1
SENN SP1	Senna sp. 1	Leguminosae (Caes.)	1
SERJ PAUC	Serjania paucidentata DC.	Sapind.	1
SMIL CUMA	Smilax cumanensis Willd.	Smilac.	1

Appendices

Acronym	Name	Family	Valid taxon used in analysis (1) and reason for rejection (0)
SMIL POEP	<i>Smilax poeppigii</i> Kunth	Smilac.	1
SMIL SANT	<i>Smilax santaremensis</i> DC.	Smilac.	1
SMIL SCHO	<i>Smilax schomburgkiana</i> Kunth	Smilac.	1
SMIL SP.	<i>Smilax</i> sp.	Smilac.	1
SMIL SYPH	<i>Smilax syphilitica</i> Willd.	Smilac.	1
SOUR GUIA	<i>Souroubea guianensis</i> Aubl.	Marcgravi.	1
STIG SINU	<i>Stigmaphyllon sinuatum</i> (DC.) A. Juss	Malpighi.	1
STRY BRED	<i>Strychnos bredemeyeri</i> (Schult.) Sprague & Sandw.	Logani.	1
STRY DIAB	<i>Strychnos diabolii</i> Sandw.	Logani.	1
STRY ERIC	<i>Strychnos erichsonii</i> M.R. Schomb.	Logani.	1
STRY HIRS	<i>Strychnos hirsuta</i> Spruce ex Benth.	Logani.	1
STRY MELI	<i>Strychnos melinoniana</i> Baill.	Logani.	1
STRY SUBC	<i>Strychnos subcordata</i> Spruce	Logani.	1
TELI KRUK	<i>Telotoxicum krukovii</i> Moldenke	Menisperm.	1
TELI MINU	<i>Telotoxicum minutiflorum</i> (Diels.) Moldenke	Menisperm.	1
TETR SP1	<i>Tetrapterys</i> sp. 1	Malpighi.	1
TETR SP2	<i>Tetrapterys</i> sp. 2	Malpighi.	1
TETR VOLU	<i>Tetracera volubilis</i> L.	Dilleni.	1
TONT ATTE	<i>Tontelea attenuata</i> Miers	Hippocrate.	0 belongs to complex
TONT CORI	<i>Tontelea coriacea</i> A.C. Sm.	Hippocrate.	1
TONT NECT	<i>Tontelea nectandrifolia</i> (A.C. Smith) A.C. Smith	Hippocrate.	1
UNDE T	undet.		0 unidentified
VANI CRIS	<i>Vanilla cristato-callosa</i> Hoehne	Orchid.	1
VANI SP.	<i>Vanilla</i> sp.	Orchid.	1
XXXX XXXX	Not a liana		0 not a liana

APPENDIX C. LIANA DIVERSITY SCORES BY PLOT

Key diversity parameters per sample plot and census. Plot numbers correspond to Table 2.1. Only valid species included (see Appendix A).

Sample A:		Individuals >2m height in 25 subplots of 10*10 m per ha														
Site	Census		Plot			CS	LE	S	N	N _c	Fisher's α	Shannon Wiener H'	Shannon's H'	Simpson's 1/D	Berger-Parker 1/d	
	Nr	Year	Nr	Age	Treatm.											
PIB	1	1993	1	0	RIL 8	0	1	42	727	248	9.69	2.73	0.73	7.22	2.93	
PIB	2	1993	2	0	RIL 16	1	1	46	566	224	11.82	2.57	0.67	5.58	2.53	
PIB	3	1993	3	0	RIL 4	0	1	32	315	123	8.90	2.54	0.73	5.84	2.56	
PIB	4	1993	4	0	RIL 8+L	0	0	40	542	191	9.96	2.66	0.72	6.75	2.84	
PIB	5	1993	5	0	C	1	1	38	692	341	8.64	2.21	0.61	3.88	2.03	
PIB	6	1993	6	0	C	0	1	41	715	354	9.44	2.27	0.61	3.87	2.02	
PIB	7	1993	7	0	RIL 16	1	1	41	778	373	9.21	2.31	0.62	4.09	2.09	
PIB	8	1993	8	0	RIL 8	0	1	50	533	149	13.51	2.98	0.76	9.79	3.58	
PIB	9	1993	9	0	RIL 8+L	0	0	42	503	234	10.89	2.38	0.64	4.31	2.15	
PIB	10	1993	10	0	RIL 4	0	1	46	957	462	10.07	2.31	0.60	4.01	2.07	
PIB	11	1993	11	0	RIL 4	0	1	44	611	279	10.87	2.45	0.65	4.48	2.19	
PIB	12	1993	12	0	C	0	1	47	770	370	11.03	2.36	0.61	4.06	2.08	
PIB	13	1993	13	0	RIL 8+L	0	0	33	325	166	9.18	2.19	0.63	3.67	1.96	
PIB	14	1993	14	0	RIL 16	0	1	41	449	241	10.97	2.21	0.60	3.37	1.86	
PIB	15	1993	15	0	RIL 8	0	1	33	506	262	7.90	2.12	0.61	3.54	1.93	
PIB	16	1996	2	2	RIL 16	1	1	56	703	188	14.30	3.17	0.79	10.96	3.74	
PIB	17	1996	7	2	RIL 16	1	1	52	661	213	13.22	2.96	0.75	8.17	3.10	
PIB	18	1998	1	4	RIL 8	0	1	65	989	267	15.60	3.15	0.76	10.44	3.70	
PIB	19	1998	2	4	RIL 16	1	1	65	1158	307	14.88	3.13	0.75	10.34	3.77	
PIB	20	1998	3	4	RIL 4	0	1	48	402	94	14.21	3.20	0.83	13.16	4.28	
PIB	21	1998	5	4	C	1	1	44	501	260	11.61	2.26	0.60	3.58	1.93	
PIB	22	1998	6	4	C	0	1	44	722	365	10.32	2.34	0.62	3.76	1.98	
PIB	23	1998	7	4	RIL 16	1	1	72	1209	364	16.77	3.09	0.72	8.96	3.32	
PIB	24	1998	8	4	RIL 8	0	1	61	458	95	18.89	3.23	0.79	13.61	4.82	
PIB	25	1998	10	4	RIL 4	0	1	57	875	425	13.64	2.44	0.60	4.03	2.06	
PIB	26	1998	11	4	RIL 4	0	1	48	464	196	13.44	2.63	0.68	5.20	2.37	
PIB	27	1998	12	4	C	0	1	41	556	292	10.21	2.21	0.59	3.47	1.90	
PIB	28	1998	14	4	RIL 16	0	1	58	958	392	13.58	2.57	0.63	5.19	2.44	
PIB	29	1998	15	4	RIL 8	0	1	46	613	305	11.52	2.38	0.62	3.87	2.01	
PIB	30	2000	2	6	RIL 16	1	1	71	1297	346	16.14	3.14	0.74	10.63	3.75	
PIB	31	2000	5	6	C	1	1	40	560	294	9.85	2.15	0.58	3.46	1.90	
PIB	32	2000	7	6	RIL 16	1	1	65	1325	384	14.32	3.00	0.72	9.11	3.45	
2KM	33	1996	16	10	C	1	0	41	568	175	10.14	2.48	0.67	6.39	3.25	
2KM	34	1996	17	10	CL	1	0	51	670	84	12.83	3.31	0.84	19.59	7.98	
2KM	35	1996	18	10	CL	1	0	57	696	111	14.69	3.18	0.79	14.37	6.27	
2KM	36	2001	19	16	CL	1	0	52	456	55	15.12	3.37	0.85	21.61	8.29	
2KM	37	2001	20	16	CL	1	0	81	515	67	27.00	3.69	0.84	23.85	7.69	
MHFR	38	1995	21	7	C	1	0	30	169	39	10.60	2.79	0.82	11.11	4.33	
MHFR	39	1995	22	7	CL	1	0	47	533	100	12.42	3.10	0.80	12.85	5.33	
MHFR	40	1995	23	7	CL	1	0	46	941	210	10.12	2.66	0.70	8.15	4.48	
WAR	42	1994	24	6	C	1	0	27	344	157	6.86	1.92	0.58	3.73	2.19	
WAR	43	1994	25	6	CL	1	0	33	900	219	6.73	2.33	0.67	6.84	4.11	
WAR	44	1994	26	6	CL	1	0	38	859	170	8.13	2.54	0.70	8.69	5.05	
WAR	45	2001	27	12	C	1	0	34	322	125	9.59	2.23	0.63	4.75	2.58	
WAR	46	2001	28	12	CL	1	0	36	428	119	9.36	2.46	0.69	6.66	3.60	
WAR	47	2001	29	12	CL	1	0	50	532	121	13.52	2.85	0.73	9.68	4.40	

PIB – Pibiri; 2 KM – 2 Kilometer; MHFR – Mabura Hill Forest Reserve; WAR – Waraputa; RIL x – Reduced Impact Logging treatment + logging intensity; C – unharvested Control; CL – Conventionally Logged plot; CS – plot is member of Chronosequence Study; LE – plot is member of Logging Experiment; S – Species density; N – abundance, number of individuals; N_c – abundance of commonest individual.

Sample B: Individuals >0.5m height in 25 subplots of 5*5 m per ha

Site	Census		Plot			CS	LE	S	N	N _c	Fisher's α	Shannon Wiener H'	Shannon's H'	Simpson's 1/D	Berger-Parker 1/d
	Nr	Year	Nr	Age	Treatm.										
PIB	1	1993	1	0	RIL 8	0	1	36	420	182	9.42	2.43	0.68	4.87	2.31
PIB	2	1993	2	0	RIL 16	1	1	29	329	190	7.66	1.91	0.57	2.91	1.73
PIB	3	1993	3	0	RIL 4	0	1	23	168	83	7.20	2.18	0.69	3.92	2.02
PIB	4	1993	4	0	RIL 8+L	0	0	30	324	150	8.07	2.27	0.67	4.33	2.16
PIB	5	1993	5	0	C	1	1	25	510	292	5.50	1.79	0.56	2.89	1.75
PIB	6	1993	6	0	C	0	1	31	528	327	7.19	1.76	0.51	2.54	1.61
PIB	7	1993	7	0	RIL 16	1	1	28	444	232	6.63	2.04	0.61	3.45	1.91
PIB	8	1993	8	0	RIL 8	0	1	40	353	124	11.60	2.60	0.70	6.54	2.85
PIB	9	1993	9	0	RIL 8+L	0	0	29	342	202	7.56	1.74	0.52	2.72	1.69
PIB	10	1993	10	0	RIL 4	0	1	36	678	336	8.11	2.09	0.58	3.73	2.02
PIB	11	1993	11	0	RIL 4	0	1	33	409	207	8.46	2.09	0.60	3.61	1.98
PIB	12	1993	12	0	C	0	1	32	435	190	7.96	2.22	0.64	4.44	2.29
PIB	13	1993	13	0	RIL 8+L	0	0	22	204	112	6.26	1.85	0.60	3.11	1.82
PIB	14	1993	14	0	RIL 16	0	1	32	403	245	8.16	1.81	0.52	2.63	1.64
PIB	15	1993	15	0	RIL 8	0	1	26	514	365	5.77	1.38	0.42	1.95	1.41
PIB	16	1996	2	2	RIL 16	1	1	51	482	166	14.40	2.85	0.72	7.20	2.90
PIB	17	1996	7	2	RIL 16	1	1	45	394	128	13.09	2.85	0.75	7.88	3.08
PIB	18	1998	1	4	RIL 8	0	1	48	540	178	12.72	2.82	0.73	7.45	3.03
PIB	19	1998	2	4	RIL 16	1	1	55	594	213	14.79	2.88	0.72	6.82	2.79
PIB	20	1998	3	4	RIL 4	0	1	40	234	62	13.87	2.82	0.76	9.12	3.77
PIB	21	1998	5	4	C	1	1	35	379	211	9.40	1.94	0.54	3.05	1.80
PIB	22	1998	6	4	C	0	1	33	548	328	7.71	1.80	0.52	2.68	1.67
PIB	23	1998	7	4	RIL 16	1	1	54	536	181	14.97	2.90	0.73	7.42	2.96
PIB	24	1998	8	4	RIL 8	0	1	46	323	105	14.66	2.62	0.68	6.29	3.08
PIB	25	1998	10	4	RIL 4	0	1	45	627	258	11.10	2.46	0.64	5.03	2.43
PIB	26	1998	11	4	RIL 4	0	1	31	364	189	8.09	2.10	0.61	3.50	1.93
PIB	27	1998	12	4	C	0	1	31	337	171	8.32	2.06	0.60	3.54	1.97
PIB	28	1998	14	4	RIL 16	0	1	46	531	250	12.08	2.31	0.60	4.07	2.12
PIB	29	1998	15	4	RIL 8	0	1	42	567	373	10.47	1.72	0.46	2.27	1.52
PIB	30	2000	2	6	RIL 16	1	1	53	561	223	14.36	2.79	0.70	5.86	2.52
PIB	31	2000	5	6	C	1	1	27	366	249	6.72	1.47	0.45	2.11	1.47
PIB	32	2000	7	6	RIL 16	1	1	47	467	171	13.03	2.70	0.70	6.44	2.73
2KM	33	1996	16	10	C	1	0	33	300	134	9.46	2.20	0.63	4.38	2.24
2KM	34	1996	17	10	CL	1	0	44	317	39	13.87	3.22	0.85	17.96	8.13
2KM	35	1996	18	10	CL	1	0	37	297	74	11.14	2.81	0.78	9.60	4.01
2KM	36	2001	19	16	CL	1	0	42	231	32	15.02	3.21	0.86	19.21	7.22
2KM	37	2001	20	16	CL	1	0	54	255	38	20.94	3.37	0.84	19.03	6.71
MHFR	38	1995	21	7	C	1	0	23	126	43	8.24	2.44	0.78	6.75	2.93
MHFR	39	1995	22	7	CL	1	0	-	-	-	-	-	-	-	
MHFR	40	1995	23	7	CL	1	0	-	-	-	-	-	-	-	
WAR	42	1994	24	6	C	1	0	13	197	126	3.12	1.33	0.52	2.28	1.56
WAR	43	1994	25	6	CL	1	0	29	320	82	7.74	2.26	0.67	6.19	3.90
WAR	44	1994	26	6	CL	1	0	28	302	74	7.53	2.53	0.76	8.71	4.08
WAR	45	2001	27	12	C	1	0	27	216	109	8.14	1.92	0.58	3.46	1.98
WAR	46	2001	28	12	CL	1	0	25	193	76	7.65	2.19	0.68	4.94	2.54
WAR	47	2001	29	12	CL	1	0	32	233	67	10.04	2.51	0.72	7.23	3.48

PIB – Pibiri; 2 KM – 2 Kilometer; MHFR – Mabura Hill Forest Reserve; WAR – Waraputa; RIL x – Reduced Impact Logging treatment + logging intensity; C – unharvested Control; CL – Conventionally Logged plot; CS – plot is member of Chronosequence Study; LE – plot is member of Logging Experiment; S – Species density; N – abundance, number of individuals; N_c – abundance of commonest individual.

APPENDIX E. ECOLOGICAL SPECIES GROUPS IN THE LOGGING EXPERIMENT

Qualitative results of tests carried out to determine ecological species groups among the 59 commonest lianas in the logging experiment. Three criteria were used to determine a response to logging, while two conditions were to be met to determine the validity of controls (post-harvest control plots and lack of census effect in control plots). The test logic is described in Table A.2. Results are provided in the RESULT columns, with T=true (criterion/condition met as defined at $\alpha=0.05$), F=false (criterion/condition not met). (T) implies that criterion is met but interacts with another criterion. Result is specified in the columns that follow, as stated in the header row. Axis scores are from canonical correspondence analysis as reported in Figure 3.13 (plot analysis) and Figure 3.15 (subplot analysis). LI=Logging Intensity; p-l=post-logging; int=forest-interior habitat; sk.g=skidded gap. See Table 3.12 for interpretation of Group codes. This analysis was based on Sample A plot and subplot abundances.

Species	Criterion 1: Abundance depends significantly on habitat (series of χ^2 -tests)					Criterion 2: Abundance depends significantly on logging intensity (log-linear test/anova)					Criterion 3: Abundance depends significantly on census (pre or post-logging) (log-linear test/anova)					Condition: Abundance in control trt not affected by logging		Condition: Abundance in interior is same as control (p-l)		Plot analysis		Subplot analysis			
	RESULT	best: most in sk.gap and least in int or vv	most in skidded gap	most in gap or skid	most in interior	RESULT	LI	positive relation with LI	dominant in RIL 16, other LI mixed	negative relation with LI	RESULT	increase	decrease	increase dependent on LI	decrease dependent on LI	erratic	RESULT	increase	decrease	RESULT	increase (int>RIL C)	decrease (RIL C>int)	GROUP	Axis-1 score	Axis-3 score
ANEM OLIG	T	x	x			T	x	x		T	x					T			T			A1	1.510	-1.085	0.931
ANEM PARK	T	x	x			T	x	x		T	x					T			T			A1	2.799	-0.726	1.426
ANOM GRAN	F					F				T		x				T			T			E	-0.427	-0.321	-0.678
ARIS DAEM	T				x	F				T		x				F		x	T			X	-1.230	-1.207	-0.011
ARRA MOLL	F					F				F						T			T			O	-0.452	0.920	-0.953
BAUH GUIA	T	x	x			T	x			(T)	(x)		x			T			T			A1	1.709	-1.519	1.100
CAYA OPHT	F					F				F						T			T			O	-1.043	1.155	-0.336
CLUS GRAN	F					F				F						T			T			O	-1.443	-2.051	-0.104
CLUS PALM	F					F				F						T			T			O	-0.331	-2.470	-0.008
CLYT BINA	F					F				F						T			T			O	1.176	3.246	-0.014
CLYT SCIU	F					T		x		T	x					F	x		T			X	3.339	-2.108	0.610
COCC MARG	T				x	T	x			T	x					F	x		T			A2	2.880	2.391	0.516
COCC PARI	T				x	T	(x)			(T)	(x)				x	F		x	T			D	-0.027	-0.033	0.473
CONN ERIA	F					F				T	x					T			T			B	-0.052	1.042	-0.806
CONN MEGA	F					F				F						T			T			O	-0.379	0.396	-0.713
CONN PERR	T		x			T				(T)	(x)					T			T			O	-0.593	-0.025	-0.676
COUS MICR	F					F				F						T			T			O	0.097	0.141	0.020
CURA CAND	F					F				F						T			T			O	-0.369	1.157	0.279

Logging effects on liana diversity and abundance in Central Guyana

Species	Criterion 1: Abundance depends significantly on habitat (series of χ^2 -tests)					Criterion 2: Abundance depends significantly on logging intensity (log-linear test/anova)					Criterion 3: Abundance depends significantly on census (pre or post-logging) (log-linear test/anova)					Condition: Abundance in control trt not affected by logging		Condition: Abundance in interior is same as control (p-l)		Plot analysis		Subplot analysis
	RESULT	best: most in sk gap and least in int or vv	most in skidded gap	most in gap or skid	most in interior	RESULT	positive relation with LI	dominant in RIL-16, other LI mixed	negative relation with LI	increase dependent on LI	decrease dependent on LI	erratic	RESULT	increase	decrease	RESULT	increase (int>RILC)	decrease (RILC>int)	GROUP	Axis-1 score	Axis-3 score	Axis-1 score
CYDI AEQU	T		x		F				F			T			T			X	1.442	1.557	0.450	
DICH PEDU	F				F				F			T			F	x		O	1.314	3.527	-0.501	
DICH RUGO	F				F				T	x		F	x		T			B	1.660	2.119	0.091	
DIOC SCAB	F				T	x			(T)	(x)	x	T			T			X	0.564	-0.700	0.730	
DIOS DODE	F				F				F			T			T			O	-0.132	-3.312	0.265	
DOLI BREV	T			x	F				T	x		F	x		F	x		X	1.221	1.596	-0.772	
FORS ACOU	T		x		F				F			T			T			X	0.293	1.452	-0.324	
FORS SCHO	F				F				F			T			T			O	1.381	3.922	-0.272	
GNET SCH1	F				F				F			T			T			O	-0.318	0.047	-1.029	
HETE FLEX	F				F				T	x		T			F	x		E	-0.744	0.145	-0.612	
HETE MULT	T		x		F				T	x		T			F	x		X	2.234	0.046	0.566	
HIRA AFFI	F				T		x		T	x		F	x		T			X	2.507	-2.794	0.345	
LONC NEGR	F				F				F			T			T			O	-0.125	-0.373	-0.278	
LYSI SCAN	T	x	x		T	x	x		(T)	(x)	x	F		x	T			D	-0.918	-1.334	1.116	
MACH MADE	T			x	T	x			(T)	(x)	x	T			T			D	-0.251	-0.215	-0.282	
MACH MYRI	T	x	x		T	x			(T)	(x)	x	T			T			A1	0.871	1.512	1.376	
MACH QUIN	T	x	x		T	x			T	x		F	x		T			A1	2.825	3.202	0.908	
MALA MACR	F				F				F			T			T			O	0.877	-0.695	0.341	
MALP SP5	T		x		F				F			T			T			X	1.909	1.250	0.211	
MALP SP6	T		x		F				T	x		F	x		T			X	1.257	0.214	-0.390	
MARI SCAN	T		x		T	x			(T)	(x)	x	T			T			A2	0.839	1.671	0.034	
MEMO MORI	F				F				T	x		T			F		x	B	0.480	2.050	-0.411	
MOUT GUIA	F				F				F			T			T			O	-0.608	0.342	-0.792	
ODON PUNC	F				F				F			T			T			O	-0.298	0.870	-0.421	
PASS GLAN	T	x	x		T	x	x		(T)	(x)	x	T			T			A1	2.782	-1.790	2.608	
PASS KAWE	T	x	x		T	x			T	x		T			F	x		A1	1.732	2.360	1.111	
PAUL CAPR	T			x	T	x	x		(T)	(x)	x	T			T			A2	2.804	-0.102	0.709	
PAUL PACH	F				F				F			T			T			O	0.337	-2.487	0.562	
PETR VOLU	T	x	x		T	x			(T)	(x)	x	T			T			D	-0.782	0.016	-0.427	
PINZ CORI	T	x	x		T	x	x		(T)	(x)	x	F		x	T			A1	2.177	-1.966	3.186	

Species	Criterion 1: Abundance depends significantly on habitat (series of χ^2 -tests)		Criterion 2: Abundance depends significantly on logging intensity (log-linear test/anova)		Criterion 3: Abundance depends significantly on census (pre or post-logging) (log-linear test/anova)		Condition: Abundance in control trt not affected by logging	Condition: Abundance in interior is same as control (p-l)	Plot analysis		Subplot analysis	
	RESULT	most in skidded gap best: most in sk gap and least in int or vv	RESULT	most in interior most in gap or skid	RESULT	negative relation with LI dominant in RIL16, other LI mixed positive relation with LI	increase decrease increase dependent on LI decrease dependent on LI erratic	RESULT	increase (int>RILC) decrease (RILC>int)	GROUP	Axis-1 score	Axis-3 score
PLEO ALBI	T	x	F		T	x	T	T	X	-1.056	-1.467	-0.269
PRIO ASPE	T		F	x	F		T	T	X	2.473	-4.686	0.178
ROUR PUBE	F		T		(T)	(x)	T	T	X	0.338	-0.242	0.241
SCHL VIOL	F		F		F		T	T	O	-0.287	1.406	-0.303
SECU SPIN	F		F		F		T	T	O	0.749	-2.007	0.279
SMIL SCHO	F		F		T	x	F	x	B	1.804	3.335	-0.089
SMIL SYPH	F		F		F		T	T	O	-0.938	-0.198	0.062
STIG SINU	T	x	T	x	T	x	F	x	A1	3.396	1.904	1.417
STRY MELI	F		F		F		T	T	O	-0.806	0.155	-0.889
TELI KRUK	T		F	x	F		T	T	X	0.723	0.912	0.226
TETR VOLU	F		F		T	x	T	T	E	-1.447	-1.149	-0.699

APPENDIX F. ANOVA RESULTS LOGGING EXPERIMENT

Unreplicated randomised block design:

Code	Factor	Type	# levels	
L_i	Logging intensity	fixed	$i = 1..4$	C, RIL4, RIL8, RIL16
S_j	Size class	fixed	$j = 1..7$	$h_1, h_2, 0.25, 0.5, 1, 2, >2$
T_k	Time (census)	random	$k = 1..2$	Pre and post-harvest
B_l	Blocks	random	$l = 1..3$	3 blocks
	Replicates	nested in LSB	$m = 1$	1 plot per block*census*logging intensity

Model: diversity and abundance after logging depends on logging intensity and size class (see 2.4.2, p. 90 and 3.2.3), hence the effect of interest is LST. If LST is not significant, the LT is tested to determine the existence of a census effect (census affects the parameter but independent of logging intensity). In all tests below: bold lines concern the effects of interest, and italics are significant effects ($p < 0.05$). d.f. 1 and d.f. 2 refer to degrees of freedom for numerator and denominator of the F-ratio, respectively. The denominator varies for each F-ratio as explained in the first table.

a. Dependent variable = Fisher's α

Factor	d.f.	SS	MS	F-ratio versus	F-ratio	p-value	d.f.1	d.f.2
T_k	1	327.99	327.99	TB	21.72	<i>0.043</i>	1	2
B_l	2	58.53	29.26	TB	1.94	0.340	2	2
L_i	3	91.30	30.43	-	-			
S_j	6	534.36	89.06	-	-			
TB_{kl}	2	30.21	15.10	Residual (n/a)	-			
LT_{ik}	3	83.13	27.71	LTB	11.66	0.006	3	6
LB_{il}	6	95.07	15.85	LTB	6.67	<i>0.018</i>	6	6
ST_{jk}	6	56.72	9.45	STB	2.87	0.057	6	12
SB_{jl}	12	57.21	4.77	STB	1.45	0.266	12	12
LS_{ij}	18	101.80	5.66	-	-			
LTB_{ikl}	6	14.26	2.38	Residual (n/a)	-			
STB_{jkl}	12	39.57	3.30	Residual (n/a)	-			
LST_{ijk}	18	71.67	3.98	LSTB	1.03	0.454	18	36
LSB_{jil}	36	164.52	4.57	LSTB	1.18	0.310	36	36
$LSTB_{ijkl}$	36	139.34	3.87	Residual (n/a)	-			
$e_{(ijkl)m}$	0	n/a						

b. Dependent variable = species density, S

Factor	d.f.	SS	MS	F	p	d.f.1	d.f.2
T_k	1	1603.34	1603.34	15.93	0.057	1	2
B_l	2	404.01	202.01	2.01	0.333	2	2
L_i	3	872.88	290.96				
S_j	6	2689.58	448.26				
TB_{kl}	2	201.32	100.66				
LT_{ik}	3	934.92	311.64	19.91	0.002	3	6
LB_{il}	6	813.04	135.51	8.66	<i>0.009</i>	6	6
ST_{jk}	6	349.37	58.23	4.19	<i>0.017</i>	6	12
SB_{jl}	12	204.24	17.02	1.23	0.365	12	12
LS_{ij}	18	246.75	13.71				
LTB_{ikl}	6	93.92	15.65				
STB_{jkl}	12	166.60	13.88				
LST_{ijk}	18	275.54	15.31	1.18	0.327	18	36
LSB_{jil}	36	606.71	16.85	1.30	0.219	36	36
$LSTB_{ijkl}$	36	467.50	12.99				
$e_{(ijkl)m}$							

c. Dependent variable = abundance, N

Factor	d.f.	SS	MS	F	p	d.f.1	d.f.2
T_k	1	11733.40	11733.40	4.05	0.182	1	2
B_l	2	23051.00	11525.50	3.97	0.201	2	2
L_i	3	29188.50	9729.50				
S_j	6	597453.80	99575.63				
TB_{kl}	2	5800.60	2900.30				
LT_{ik}	3	62473.90	20824.63	11.39	0.007	3	6
LB_{il}	6	120193.60	20032.27	10.95	0.005	6	6
ST_{jk}	6	21506.70	3584.45	5.67	0.005	6	12
SB_{jl}	12	41139.10	3428.26	5.42	0.003	12	12
LS_{ij}	18	78770.00	4376.11				
LTB_{ikl}	6	10973.10	1828.85				
STB_{jkl}	12	7586.00	632.17				
LST_{ijk}	18	39596.30	2199.79	3.51	0.001	18	36
LSB_{ijl}	36	96903.60	2691.77	4.29	0.000	36	36
$LSTB_{ijkl}$	36	22591.00	627.53				
$e_{(ijk)m}$							

d. Dependent variable = Simpson's index, ln-transformed, $\ln(1/D)$

Factor	d.f.	SS	MS	F	p	d.f.1	d.f.2
T_k	1	2.47	2.47	8.82	0.097	1	2
B_l	2	2.03	1.01	3.61	0.217	2	2
L_i	3	1.41	0.47				
S_j	6	43.69	7.28				
TB_{kl}	2	0.56	0.28				
LT_{ik}	3	0.93	0.31	8.47	0.014	3	6
LB_{il}	6	2.86	0.48	12.99	0.003	6	6
ST_{jk}	6	1.44	0.24	1.95	0.153	6	12
SB_{jl}	12	2.98	0.25	2.01	0.120	12	12
LS_{ij}	18	3.42	0.19				
LTB_{ikl}	6	0.22	0.04				
STB_{jkl}	12	1.48	0.12				
LST_{ijk}	18	1.57	0.09	2.29	0.017	18	36
LSB_{ijl}	36	6.07	0.17	4.43	0.000	36	36
$LSTB_{ijkl}$	36	1.37	0.04				
$e_{(ijk)m}$							