LAND-USE HISTORY AND THE OR IGINS AND EFFECTS OF LIANAS ON TREE-COMMUNITIES

The case of secondary forests in Northeastern Yucatan Peninsula, Mexico

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Summary: Economic problems generate large secondary tropical forests due to crop abandonment; lianas (woody vines climbing upon trees) proliferate there. Lianas generally retard the growth and carbon capture of trees, potentially enhancing global change. It is not known whether all liana species play such a role and which land-use disturbances determined the current species composition of liana communities. We surveyed all lianas ≥1cm diameter at ground level and all trees ≥ 3.16 cm diameter at 1.3 m above ground in twelve plots 20 x 20-m each in semi-evergreen tropical forests in Northeastern Yucatan Peninsula, Mexico, re-measuring the trees 15 mo later. Lianas were classified into two anatomic types: "hard" (typical stem with compact xylem masses) and "soft" (with much parenchyma and wide xylem vessels). History, archaeology, anthropology, and remote sensing studies, as well as non-formal interviews were used to determine the land-use history of each stand. Increasing densities of the hard liana *Dalbergia glabra* (Leguminosae), but not of soft lianas —*Arrabidaea spp*, *Cydista sp*, *Melloa spp* (Bignoniaceae) and *Serjania sp* (Sapindaceae), were related to more rapid relative growth rates of trees (Linear regression, $R^2 = 0.680$, $P = 0.001$). Where *D. glabra* dominated, the trees hosting it grew more rapidly, but trees with large liana-tangles grew more slowly where soft lianas were dominant (Kruskall Wallis, $P > 0.01$ in both cases). The anatomy of soft lianas suggests that they are less able to survive burn after slash during shifting cultivation than *D. glabra* – the previous land use where *D. glabra* dominated. Soft-liana dominated stands were not burnt but subjected to liana-cut during logging and extraction of lianas, palm leaves and latex from *Manilkara zapota* trees. Our results suggest that some lianas enhance carbon capture mitigating global change, whereas others do not and that the dominance of one liana species is a legacy of previous land use, which is better understood by combining natural and social sciences.

Zusammenfassung: Ertrags- und Bewirtschaftungsprobleme im traditionellen Wechselfeldbau führt zur Entwicklung umfangreicher Sekundärwälder in den Tropen, die zunehmend von Lianen kolonisiert sind. Im Allgemeinen verlangsamen Lianen das Wachstum der Bäume und damit die C-Assimilation mit indirekten Wirkungen auf den CO_2-Kreislauf. Wenig bekannt ist, ob alle Lianenarten diese Rolle spielen und welche Landnutzungsstörungen der Vergangenheit die aktuelle Artenzusammensetzung bestimmen. Auf zwölf Plots (20 x 20 m) im teilimmergrünen Tropenwald im Nordosten der Yucatan-Halbinsel wurden alle Lianen ≥ 1 cm Durchmesser am Boden und alle Bäume ≥ 3,16 cm Durchmesser in Brusthöhe identifiziert und vermessen. Fünfzehn Monate später erfolgte eine Wiederholung der Messungen. Zwei anatomische Lianentypen wurden gefunden: „hart" (typischer Stamm mit kompaktem Xylem) und „weich" (Entwicklung des Stammes mit viel Parenchym und breiten Xylemleitgefäßen). Historische, archäologische, anthropologische, fernerkundliche Quellen und informelle Interviews wurden kombiniert, um die historischen Phasen der Landnutzung abzuleiten. Zunehmende Bestandsdichte der „harten" Liane *Dalbergia glabra* (Leguminosae), aber nicht der „weichen" Lianen *Arrabidaea spp, Cydista spp, Melloa sp* (Bignoniaceae) und *Serjania sp* (Sapindaceae) korrelieren mit einem schnelleren Wachstum der Bäume (lineare Regression, $R^2 = 0,68$, $P = 0,001$). Auf Plots mit *D. glabra*-Dominanz ist das Wachstum der Bäume größer, im Gegensatz zu Plots mit einer Dominanz „weicher" Lianen bei hohem Kronenbesatz (Kruskall Wallis, $P > 0,01$). Während holzige Lianen wie *D. glabra* besser an Brandeinwirkung angepasst sind, ist die Überlebensrate bei den „weichen" Lianen nur gering. In slash & burn Plots dominiert daher *D. glabra*. „Weiche" Lianen dominieren dort, wo nicht durch Feuer Nutzungsstörungen auftraten, sondern durch Logging (Holzeinschlag), Lianen- und Palmblätternutzung und wo Kaugummilatex von *Manilkara zapota* Bäumen gewonnen wurde. Unsere Ergebnisse zeigen, dass einige Lianen die C-Assimilation der Bäume verbessern, andere jedoch nicht. Die Dominanz einzelner Lianenarten ist ein Ergebnis der historischen Landnutzungsentwicklung in Verbindung mit dem Sekundärwaldwachstum, was über die Verknüpfung von Landnutzungsgeschichte und vegetationsgeographischen Analysen besser erklärt werden kann.

Keywords: Burn, slash, injury-recovery, relative abundance, lianas, tree growth, secondary forest, Yucatan

1 Introduction

Lianas are climbing woody vines considered disturbance specialist plants but also are a characteristic of tropical forests (Photo 1). They proliferate in secondary vegetation and along the edges of mature forests (CABALLÉ and MARTIN 2001; LAURANCE et al. 2001; DE WALT et al. 2000). Land use and land cover transformation are global phenomena (POTTHOFF 2007; MIEHE et al. 2008) of increasing importance and in the last 50 years the world-wide coverage of secondary vegetation increased from less than 50 million hectares to more than 200 million hectares (CRAMER et al. 2008). This shift is primarily due to field abandonment resulting from social and economic problems (ZHAO et al. 2006; AIDE and GRAU 2004). In the tropics, a by-product of this is an increase in liana abundance and the accompanying effects. Other disturbances favoring lianas have been attributed to the increase of atmospheric carbon dioxide (PHILLIPS and GENTRY 1994). These authors suggest that this latter condition makes trees grow and die faster, producing gaps that are more rapidly colonized by lianas (BABWETEERA et al. 2000; SCHNITZER and CARSON 2001; SCHNITZER et al. 2000). Thus, landscape transformation and global change are related to an increasing role of lianas throughout the tropics (SCHNITZER and BONGERS 2002). However, these roles and the factors shaping liana communities remain poorly studied.

The long-standing problem of why some species are more abundant than others (e.g. HUBBELL 2001, 30–47 and 76–112) also includes lianas. Many disturbances are induced by agriculture and the extraction of forest resources. This circumstance makes local history a source of explanations of current liana species composition. There is a paucity of studies exploring the relationship between different land uses and those liana characteristics, which enable them to persist after disturbance. This article is a first attempt to rectify this deficit.

Many researches have shown a reduction in tree growth – and hence less carbon capture by trees – due to liana competition. Successful competition can occur because the wide vessels of lianas conduct more water than the narrow ones of trees (PHILLIPS et al. 2005; SCHNITZER et al. 2005; PHILLIPS et al. 2002; PÉREZ-SALICRUP 2001; PÉREZ-SALICRUP and BARKER 2000; CLARK and CLARK 1990; PUTZ 1984). Wide vessels are responsible for the light, cellulose-poor bodies of lianas. Because

Photo 1: Liana *Bauhinia sp* (Leguminosae, Caesalpinioideae). Photo by © Stefan A. Schnitzer.

cellulose results from carbon dioxide assimilation during photosynthesis, rich-cellulose plants like trees accumulate more of such carbon when they grow better. In contrast, the poor-cellulose bodies of lianas do not capture enough carbon to compensate for the reduction in carbon capture by trees when lianas delay tree-growth. This could potentially cause liana-induced changes in the global carbon balance (SCHNITZER and BONGERS 2002).

Liana anatomy varies widely among the more than 1,700 liana species of the world (CARLQUIST 1991; FISHER and EWERS 1991; GENTRY 1991), but no study has explored whether this diversity results in different effects on trees. Thus, we hypothesize that the growth of trees changes depending on the abundance and species composition of surrounding lianas. In addition, if lianas are "disturbance specialist plants", today's liana-abundance and species compositions should be historical legacies of past land uses.

We address the following questions: (1) What are the changes of liana-communities among forests of different successional ages and land-use histories? (2) Does tree-growth change according to the abundance and diversity of surrounding lianas?

Also, FISHER and EWERS (1991) classified lianas into different types according to their stem anatomy, where some lianas have wider xylem vessels than others. Thus: (3) What types of lianas are associated with changes in tree growth? Finally, we explore (4) Which land uses resulted in the prevalence of certain liana types in some forest stands compared to others.

2   Study site

The peasant community of Ejido Solferino (Municipality of Lázaro Cárdenas, Quintana Roo, México) has less than 800 inhabitants. It is close to the Yum Balam Reserve of Flora and Fauna (21°26'N, 87°28'W; 10 m a.s l.; INEGI 1993, Fig. 1).

The soils, 10–20 cm in depth, are poorly developed Rendzines and Vertisols on calcareous bedrock, which emerged after the Pleistocene (FAO soil classification before 2006 used in MUNICIPIO DE LÁZARO CÁRDENAS 1987). As for the entire peninsula, groundwater levels at 2–8 m of depth (BAUTISTA-ZÚÑIGA et al. 2003; OLMSTED et al. 2000; even less several days after strong rainfalls, E. I. GARRIDO-PÉREZ, pers. obs.). The topography is mainly flat, and the life zone belongs to Semi-Evergreen Tropical Forest (Selva Mediana Subperennifolia, sensu MIRANDA and HERNÁNDEZ 1963; Tropical Dry Forest, sensu HOLDRIDGE et al. 1971), with a canopy height of between 15 and 20 m in the older forests around the village. Rainfall averages 1,250 mm.y⁻¹; the dry season lasts from December to April, and the wet season, from May to November. A period of cold temperatures locally known as "nortes" lasts from December to February (DUPUY et al. 2007; ORELLANA et al. 1999). More than 30 major hurricanes have affected the region in the last 100 y (SÁNCHEZ and ISLEBE 1999) and even earlier (DE LANDA 1556). They open tree fall gaps in the forest,

which favors liana proliferation (GARRIDO-PÉREZ et al. 2008; BABWETEERA et al. 2000; SCHNITZER et al. 2000). The village is surrounded by small fields and a mosaic of recently abandoned fields of different forest ages and land uses. All these are embedded in a larger matrix of older vegetation (Fig. 2). Since we wanted to assess the effects of lianas on trees, we took exhaustive walks and surveyed preliminary transects to find liana-abundant patches having similar ages of abandonment and belonging to farmers interested in our research to choose where to establish our study plots.

3   Materials and methods

3.1 Survey of trees and lianas

Between November 2003 and March 2004, twelve 20 x 20-m plots were established in areas with high liana density in forests of different ages of abandonment subsequent to shifting agriculture (Fig. 2). The distance between proximate plots was ≥ 20 m, no branches of lianas and trees in a plot extended into any other plot. Inside plots, all trees ≥ 10 cm girth (3.16 cm diameter) at 1.3 m above ground (dbh) were tagged with unique code numbers and their diameters were measured as were all climbers ≥ 1 cm diameter at ground level. Measurement points on trees were marked with paint for further re-measurements. Trees were classified into species
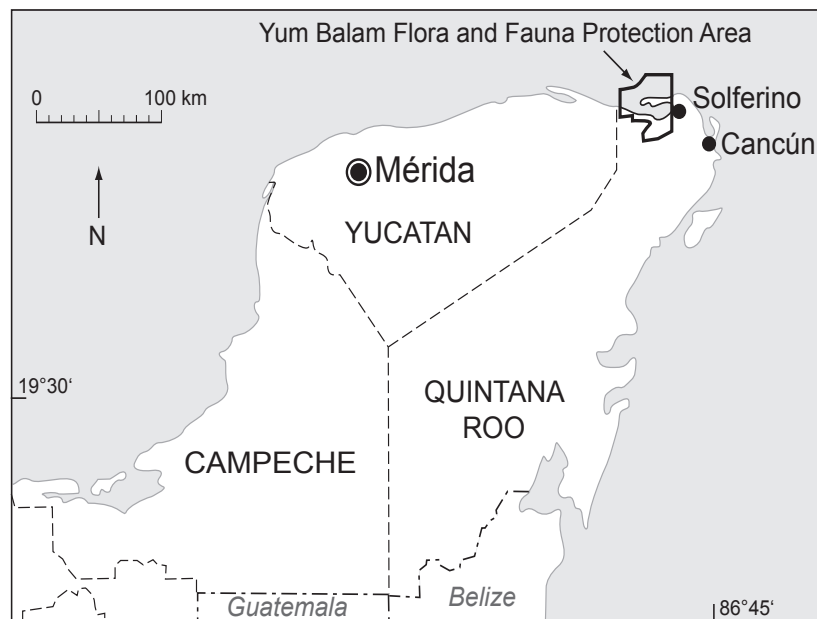

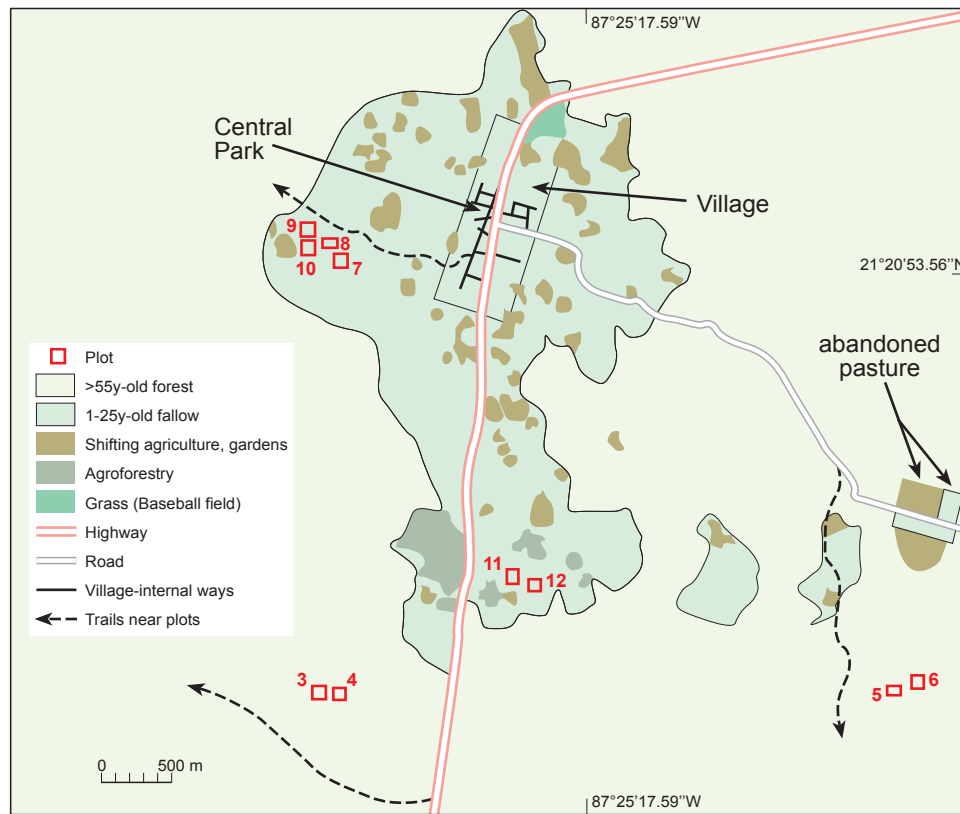Fig. 1: Study site: Ejido Solferino, Quintana Roo, Mexico.

Fig. 2: Map of the study area in Ejido Solferino, Quintana Roo, Mexico. Plots 1 and 2 are about 3 km south of plots 3–4 but do not appear in this figure.

and lianas into their lowest possible taxon. In order to avoid recording any liana more than once, all hand-reachable liana-branches were marked with the same code number. When liana branches emerged directly from the ground, the surrounding soil was manually excavated down to 10 cm of depth in order to reach and measure the main stem. If this was not possible, each branch was considered to be a separate individual. When the main stem was reached but impossible to measure – due to stones or branches emerging directly above ground – the width of each branch was measured and the sum of basal areas of the branches was considered to the basal area of the individual. Each tree was visually classified according to the percentage of its woody area covered by lianas as follows (based on Cʟᴀʀᴋ and Cʟᴀʀᴋ 1990): zero = no-lianas, one = 1–25% of coverage, two = 25–75%, and three = more than 75%. Trees were re-measured at their marked points using the same tape during August 18–20, 2005, i.e., 15 months (two growing seasons) after the end of the first census. Dead trees found in this census were excluded from tree-growth calculations.

3.2 Determining the age and land-use history of the forests

Plot positions were determined using a Global Positioning System (GPS) device and located on aerial photographs from 1979, 1985 and 2001; and on satellite images from 1997 and 2005 in order to assess whether and when they were covered by vegetation. Such images were consulted in the Centro de Investigación Científica de Yucatán, Mérida, México and are "younger" than many Solferino farmers, which implies earlier land uses and landscape transformations. Many of these land uses do not produce changes detectable by remote sensing, but may affect liana species abundances (Photo 2a-c; see also Bᴜ̈ʀɢʜɪ and Gɪᴍᴍɪ 2007). Indeed, to determine the land-use histories of our plots more accurately we combined the following: plant measurements; interviews made while living in the area from 2002 to 2005; consultation of history, anthropology and linguistics texts; fast visits; information on archaeological sites (Tab. 1).
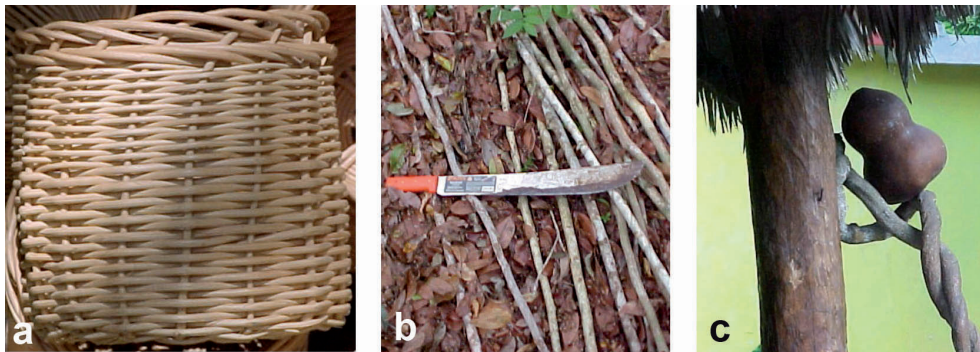
Photo 2: Some forest resources extracted by farmers in Ejido Solferino, Quintana Roo, México. (a) A basket made out of the liana *Arrabidaea sp* (Bignoniaceae). (b) Tree-saplings for fencing. (c) Column made with a selectively extracted tree, roof made of palm leaves, ornamentally used liana (*Petrea sp*, Boraginaceae) and hollow fruit of a vine (*Lagenaria sp*, Cucurbitaceae). These land uses alter species abundances but remote sensing cannot detect their impact. All photos by © E. I. Garrido-Pérez.

3.3 Data analysis

3.3.1 Changes of liana-communities and their effects on tree-growth

Shannon diversity indices (H´) of lianas and trees were calculated for each plot using the formula: $H´ = -\Sigma_{pi} \ln_{pi}$, where pi = proportion of all individuals corresponding to the ith species. High values of H´ show high diversity; low values show trends to the dominance of a few species (modified from Krebs 1999). Cluster analyses (Weighted Pair group Average (WPGA) with the so-called Manhattan distances) were used to detect species composition similarities. Plots sharing shorter Manhattan distances have similar species compositions with respect to other plots (Krebs 1999).

The following indicators of liana and tree abundances were also determined: (a) density and basal area of lianas and trees, (b) liana/tree ratios of density and basal area, (c) percentage of trees hosting lianas and (d) liana density/liana basal area ratio (where low values indicate large lianas with respect to their number). In addition to Shannon indices, all these structural indicators were used as explanatory variables; each plot was considered to be a separate experimental unit. Since many explanatory variables are correlated, multiple and simple linear regressions were used to test the effects of all explanatory variables on the growth of trees. The annual relative growth rate of tree-basal area (RGR_{BA}) was used as the response variable. It is calculated on a per hectare basis and conventionally used for whole tree-community descriptions (e.g. Schnitzer and Bongers 2002; Laurance et al. 2001). For our study, $RGR_{BA} = [(BA_i-BA_f)/BA_i] \div 1.25$, where BA_i and BA_f are the initial and final basal areas of trees, respectively, in square meters (assumed as cylinders) per hectare of terrain. Division by 1.25 was performed in order to standardize the values to an annual basis (since trees grew per 15 mo = 1.25 y).

Trunks are deposits of energy-rich substances (Mauseth 2008); thus, thicker trees can use these reserves to grow more rapidly. In order to ensure that this did not bias our results, we performed linear regressions using the first census-circumference of each tree vs. tree-circumference growth per year: if there is no relationship there is no bias.

3.3.2 Effect of different lianas on tree-growth

We classified the most abundant liana-species into two of the eight anatomical categories of Fisher and Ewers (1991). Because the density and basal area of each liana taxon was determined, it was possible to quantify the abundances of these liana anatomical groups by summing the abundances of their taxa. Specifically, the first group was composed of hard-and-heavy wooded lianas with a compact, "typical" (more similar to trees) arrangement of vascular tissues (hereafter "hard lianas"). The second group comprised lianas which were soft, flexible-and-light wooded having lobed xylem, continuous or disjunctive cambium, and with separated vascular cylinders (hereafter "soft lianas"). Six plots were dominated by one hard liana-species and the other six plots by five soft liana-species (see results). Student's t-tests were used to compare the abundances of such dominant species between the two groups of plots. Compared variables were: (a) density, (b) basal area, and (c) dominant hard/dominant soft lianas ratio.

Table 1: Sources of information for the reconstruction of the land-use history of 12 plots (20 x 20 m) in Solferino, Quintana Roo, Mexico.

Source and method	Information achieved
Aerial pictures, satellite images, transects inside forests	Forest ages, appearance of different vegetation in picture of 2001 to compare to older pictures
Non-formal field interviews ("walk in the woods method", Nᴇsʜᴇɪᴍ et al. 2006)	Use of fire, cattle, tillage, fertilizer and other agents. Observation of non-planned disturbances (e.g. liana-cut during the walks)
Home interviews	Aspects forgotten by the farmer; for example, by asking the ages of children and if they helped to work a target land
Conversation with elder men whose forests were not under research	Independent confirmation of current land uses (e.g. methods to climb upon trees). Relations about land uses before images
History-Archaeology and Anthropology books and journals	Procedures and impact of land uses (e.g. number of people inhabiting camps and the row materials of their facilities). Ages of forests existing before consulted aerial pictures
Visit to two ancient Maya archaeological sites (Kantunilkín and San Ángel) and one XIX century abandoned estate	Possibility of pre-Hispanic land use; confirmed existence of large-scale agro-industry (sugar) and transport (railway)

These variables were also used as explanatory variables plotted against RGR_{BA} in order to assess the effect of the mentioned types of lianas on tree growth (linear regressions).

3.3.3 Effect of liana-cover on tree-growth

Another relative growth rate of tree circumference (RGR_C) was calculated for each tree. Its formula was similar to the one for RGR_{BA} but used the circumferences of trees. Conventionally, similar formulas are used to describe individuals (e.g. Pᴇ́ʀᴇᴢ-Sᴀʟɪᴄʀᴜᴘ and Bᴀʀᴋᴇʀ 2000). The obtained RGR_C values were compared among liana-cover categories (Kruskall-Wallis test) twice: once for plots 1–6 and once for plots 7–12 (the two main plot groups after cluster analysis, see section 3.3.1). In order to obtain sample sizes large enough for comparisons among liana-cover categories, the data for all plots per group were pooled. However, lianas hosted on one tree facilitate colonization by other lianas on the same tree by using the first liana as a climbing aid (Pɪɴᴀʀᴅ and Pᴜᴛᴢ 1994) implying spatial autocorrelation. In order to reduce such risks the RGR_C of all individuals per tree species were averaged; this average being the response variable for KW test.

3.3.4 Correlating land-use history to liana anatomy

Land-use disturbance, such as logging and burning, produce direct injuries to plant bodies. It also alters the plants' environment physically and chemically, affecting the anatomy, physiology and survival of plants. The results are spatial changes of plant mortality, dispersion, settlement, diversity and distribution (Dᴇɴsʟᴏᴡ 1987; Mᴀʀᴛɪ́ɴᴇᴢ-Rᴀᴍᴏs 1994; Bᴏɴᴅ and Kᴇᴇʟᴇʏ 2005). However, no measurements of fire intensity, shape of cuts, healing of lianas and size of tree fall gaps and other processes during past human use were available to us and no manipulative experiments were possible. For these reasons, we decided to rely on the widely accepted biological principle of the relationship between form, function and vulnerability of plant organ designs resulting from natural selection (Nɪᴋʟᴀs 1997; Mᴀᴜsᴇᴛʜ 2008). Specifically, we examined the literature on liana-stem anatomies and propagules of our more abundant taxa (Aᴄᴇᴠᴇᴅᴏ-Rᴏᴅʀɪ́ɢᴜᴇᴢ 2003; Cᴀʀʟϙᴜɪsᴛ 1991; Fɪsʜᴇʀ and Eᴡᴇʀs 1991; Pᴜᴛᴢ and Hᴏʟʙʀᴏᴏᴋ 1991) and plants in general (Bᴏɴᴅ and ᴠᴀɴ Wɪʟɢᴇɴ 1996) while inferring which lianas are more vulnerable and resilient to the main injuring agents applied by people across the land-use history of our study site: cutting and fire.

4   Results

A total of 1717 live lianas and 1826 live trees were found on all plots during the first census, and 1770 live trees during the second census made 15 months later. More than 85% of all trees were < 12 cm dbh and virtually all of them were < 20 cm dbh. Consequently, RGR_C was not associated to the initial size of trees (linear regressions, P > 0.05 for all plots). Plots 1–6 belonged to ≥ 55 y-old forest, plots 7–10 belonged to an 18 y-old stand, and plots 11–12 to a 10 y-old stand (see details in table 2).

4.1   Changes of liana and tree communities

Shannon's liana-diversity index ranged from 0.78 (Plot #12) to 2.11 (Plot #8, Tab. 2). However, cluster analysis showed that liana-species composition of plots in the 10- and 18 y-old stands are more similar to each other than to the ≥ 55 y-old forest; the trees also exhibited these two main clusters (Fig. 3).

Plots 1–6 were dominated by soft lianas with relatively abundant parenchyma and wide vascular vessels (green, blue, yellow and pink colors in Fig. 4). There, the genera *Cydista*, *Arrabidaea*, *Melloa* (Bignoniaceae) and *Serjania* (Sapindaceae) were the more abundant soft liana taxa. Averaged for plots 1–6, such genera represented 83.4% of all liana-individuals (SE = 2.737, n = 6). In contrast, plots 7–12 were largely dominated by one hard liana species: *Dalbergia glabra* Standl. (Leguminosae Papilionoideae, see grey color in figure 4). For plots 7–12, this single species averaged 51.3% (SE = 5.016, n = 6) of all liana individuals.

The density of soft lianas in plots 1–6 averaged 3354.17 indiv.ha^{-1} (SE = 23.488, n = 6). This value was just slightly higher than the density of *D. glabra* in plots 7–12 (average = 1958 ind.ha^{-1}, SE = 38.922, n = 6; Student's t = 4.500, P = 0.06). A similar result was achieved for comparisons using the basal area of soft lianas in plots 1–6 (average = 1.200 m²ha^{-1}, SE = 0.789) with the basal area of *D. glabra* in plots 7–12 (average = 2.220 m²ha^{-1}, SE = 1.123, Student's t = 3.160, P = 0.1059), suggesting roughly similar abundances of the dominant liana-types of both plot clusters (≥ 55 y-old forest, on the one hand, and 10-18y-old forest, on the other hand) though their species compositions are different.

4.2   Diversity, abundance and types of lianas vs. tree-community growth

Trees grew faster on plots with lower liana diversity (plots dominated by few species; simple linear

Table 2: Characteristics of twelve 20 x 20-m plots of secondary semi-evergreen tropical forest in Solferino, Quintana Roo, Mexico (trees ≥ 3.16 cm diameter at breast height and lianas ≥ 1 cm diameter at ground level).

| Plot	Density (ind.ha^{-1})		Basal area (m²ha^{-1})		Percentage of trees hosting lianas	Shannon's Diversity (H')	
	lianas	trees	lianas	trees		lianas	trees
(a) ≥ 55 y-old forest							
1	4475	4200	1.32	37.86	58.6	1.27	3.29
2	4625	3825	1.15	27.27	56.9	1.72	2.61
3	2325	3200	1.03	16.30	50.0	1.28	2.64
4	4600	3225	2.59	28.23	65.0	1.84	2.83
5	4225	3975	1.37	19.17	61.0	2.03	2.82
6	3500	2775	1.65	25.11	76.6	1.73	3.08
(b) 18 y-old forest							
7	3175	4875	2.12	15.21	72.3	1.07	2.63
8	2050	4650	0.66	16.53	52.7	2.11	2.78
9	2125	2775	2.10	12.88	82.0	1.95	2.71
10	2475	4300	3.37	24.32	91.3	1.79	2.34
(c) 10 y-old forest							
11	3675	2800	4.06	11.10	100.0	1.28	2.70
12	4900	3650	3.92	11.32	94.0	0.78	2.66
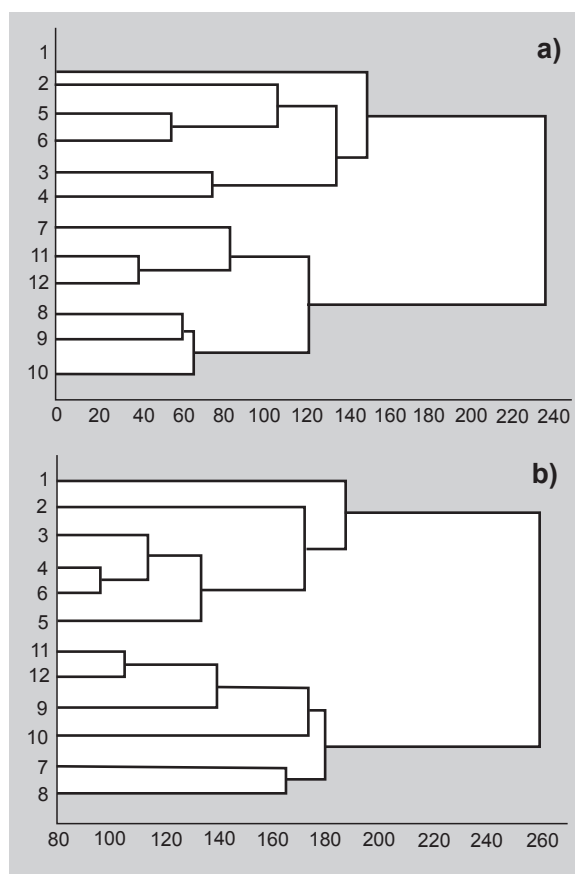
Fig. 3: Cluster dendrograms of 12 plots (20 x 20-m) in Ejido Solferino, Quintana Roo, México according to their species compositions of (a) lianas and (b) trees. See text for full explanation.

regression, $R^2 = 0.370$, P = 0.036, n = 12 Fig. 5a). Consistent with this, the inclusion of the densities of *D. glabra* in the model resulted in a non-significant effect of liana-diversity (Multiple –"double" linear regression, P = 0.830, n = 12), whereas the effect of *D. glabra* density on RGR_{BA} remained significant (P = 0.016). In contrast, when the densities of soft lianas were included instead of *D. glabra*, the effect of liana-diversity remained significant (multiple linear regression, P = 0.053, n = 12), whereas the densities of soft lianas had no effect RGR_{BA} (P = 0.111). Thus, changes of the density of a single species (*D. glabra*) described the changes of RGR_{BA}. Alone, *D. glabra* density explains almost 70% of the variation of RGR_{BA}: (Simple linear regression, $R^2 = 0.680$, P = 0.001, n = 12, Fig. 5b).

The basal area of *D. glabra* is strongly correlated to its density (Spearman correlation, R = 0.894, P = 0.0001, n = 12) since both depend on the number of individuals. Such a dependence is not total (some individuals are thicker than others); thus, 80% of the

variation of the density of *D. glabra* is related to its basal area but 20% is not ($R^2 = 0.798$). Consequently, including *D. glabra*'s basal area in a regression in addition to liana density showed no-significant effects of the former on RGR_{BA} (multiple linear regression, for *D. glabra*'s basal area: P = 0.177, for liana-diversities: P = 0.172, n = 12), in contrast to the result for *D. glabra*'s density described above. Nevertheless, a significant effect of the basal area of *D. glabra* was achieved when it was the only explanatory variable for RGR_{BA} (simple linear regression, $R^2 = 0.368$, P = 0.036, n = 12). In contrast, the basal area of soft lianas had no effect on RGR_{AB}; neither when it was the only explanatory variable (simple linear regression, P = 0.392, n = 12), nor when included in the same model with liana-diversity (multiple linear regression, for density of soft lianas: P = 0.396) although the effect of liana-diversity remained in this multiple regression (P = 0.045, n = 12). None of the other indicators of liana and tree abundance mentioned in 3.3.1 had any significant effect on tree-growth (multiple and simple linear regressions, P > 0.10 for all tests).

4.3 Liana-cover vs. growth of individual trees

For the ≥ 55y-old stands, which were dominated by soft lianas, tree individuals with liana cover > 25% had lower RGR_C than other trees (Kruskall-Wallis test, $KW_{3, 354} = 4.300$, P < 0.001, Fig. 6a). In contrast, for the 10 - 18 y-old stands, which were dominated by *D. glabra*, trees with lianas grew faster than trees hosting no lianas ($KW_{3, 301} = 11.100$, P = 0.01, Fig. 6b).

5 The land-use history of Solferino and the origins of current lianas there

The high liana-abundance and different liana-species composition between plots 1–6, on the one hand, and plots 7–12, on the other hand, (Figs. 3–4) are well understood in the framework of the different land-use histories between such stands. Specifically, plots 1–6 were repeatedly and intensively subjected to liana-cutting and other mechanical injuries but not to fire. Therefore, we propose that Bignoniaceae and Sapindaceae lianas were able to survive and proliferate under such a regime of disturbances. In contrast, plots 7–12 were burnt after slashing during agriculture and this may have killed many Bignoniaceae and Sapindaceae but not *D. glabra*. In order to explain all these factors, we de-
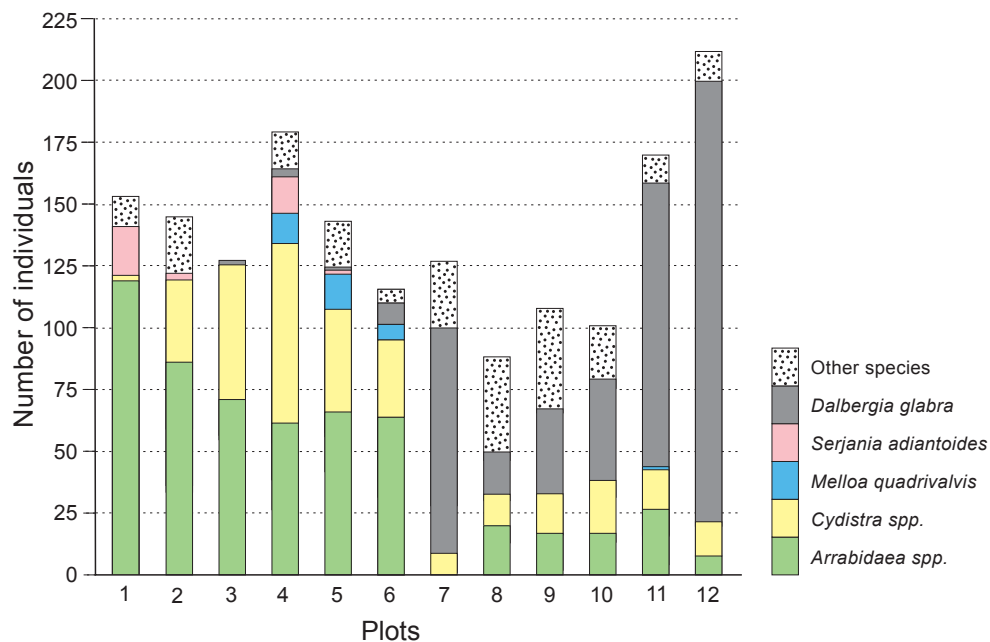
Fig. 4: Number of individuals of the most abundant liana taxa in 12 plots (20 x 20 m) in Ejido Solferino, Quintana Roo, México.

scribe the land-use history of our studied landscape in the context of liana anatomy and morphology.

5.1 Plots one to six

Today's plots 1–6 were already covered by old forest in the aerial picture of 1979. One map from 1776 (ARCHIVO GENERAL DEL ESTADO DE QUINTANA ROO 2006) shows that our study area – near Hol Box Island – was covered by forest. REED (1971) explains that the forest of the region sheltered rebelling Mayas during the Caste War of Yucatan (1847–1912). Much earlier (1511) the whole Peninsula had villages and cities scattered through the forests. At that time many houses were made using resources taken from the forests: hard-wood for columns, light-wood and palm leaves for roofs and lianas for tightening such structures (DE LANDA 1556). Until today, many of these lianas belong to the genera *Arrabidaea* and *Cydista* (Bignoniaceae, DE LA TORRE 2003) implying that they are usually cut. All described land uses are widespread practices still used today (TOLEDO et al. 2003; JIMÉNEZ-OSORNIO et al. 2003). In addition to traditional agroforestry, slash-and-burn agriculture – which produces corn, hot chili, and many other products (*milpa* agriculture) – has been the most common method of producing food at least since the XVI century (DE LANDA

1556). Including Kantunilkín and San Ángel, at least 67 major archaeological sites dating from the year 100 BC (pre-classic) exist in the region, suggesting a dense population using forest resources in that time (agroforestry was an important activity, FEDICK and MORRISON 2004). Agroforestry implies proximity to forests (sources of plants), with gap-opening by logging (enabling lianas to colonize them). Thus, archaeological evidence indirectly supports the hypothesis that today's Solferino has been subjected to all of the mentioned land uses that favor lianas since pre-Columbian times (Fig. 7a; see also CAREAGA 1994). Whether our plots 1–6 were covered by forests during pre-Columbian times remains unclear. However, the low canopy height contrasts with the larger height of remnant trees of the area (> 20 m). This, combined with the small diameter of most of our trees, and the abundance of lianas, suggests that the area was cleared in recent times.

Current land uses of stands including plots 1–6 include selective logging, cutting of treelets (e.g. for fencing, Photo 2b), extraction of palm leaves, using Bignoniaceae lianas for basketry, and the extraction of latex from *Manilkara zapota* (L.) Royen (chewing gum trees) by the approx. 200 Mayan and Mestizo families (MUNICIPIO DE LÁZARO CÁRDENAS 2008; 1987; DUPUY et al. 2007; DE LA TORRE 2003; KIERNAN 2000; INEGI 1993). All these imply: the opening of tree fall gaps favouring liana-proliferation
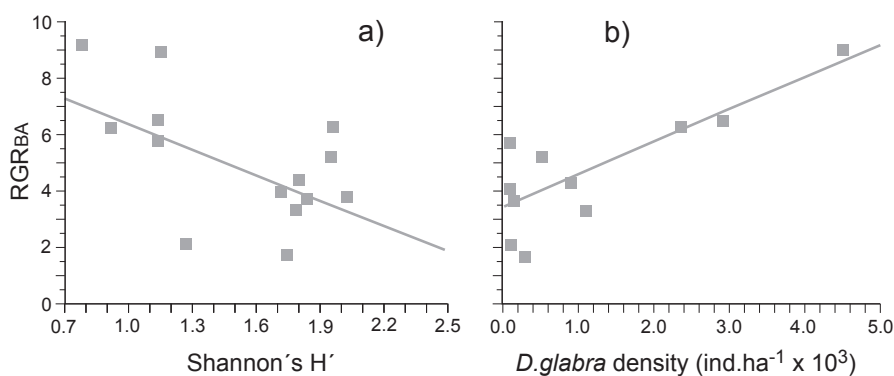
Fig. 5: Relative growth rate of the basal areas of trees for 12 plots (20 x 20-m) in Ejido Solferino, Quintana Roo, Mexico related to: (a) Shannon's liana-diversity index (H') and (b) Density of the legume liana species *Dalbergia glabra* (individuals per hectare).

(e.g. SCHNITZER et al. 2000), on the one hand, but also mechanical damage to lianas when they are cut before logging or climbing upon target *M. zapota* trees (see below), and torsions, binding and even tearing of lianas when trees fall. Burning is not practiced as part of such land uses (Fig. 7a, b).

During 1875–1920, the *Compañía colonizadora de la costa* and the *Compañía agrícola* (*Hacienda El Cuyo*) produced corn, sugar, hot chili, cotton, cacao, bananas and other products in great quantities (Fig. 7a; CAREAGA 1994). The abandoned facilities became an archaeological site, which includes an old railway connecting Labcah (today's Solferino) to *El Cuyo* (E. I. GARRIDO-PÉREZ, pers. obs.). Railways require heavy wood from old trees; materials obtained from neighboring, old forest, using no fire and generating gaps favoring liana colonization without burning soft lianas. Other railways have been reported by archaeologists around the area (FEDICK et al. 2000) suggesting that such land use was wide spread and intense.

Another use of the forest where plots 1–6 are located was the extraction of latex from *M. zapota* trees to produce chewing gum. The latex flows when a man (called a *chiclero*) cuts v-shaped incisions in live tissue from the highest to the lowest sections of the bole (Photo 3). Before climbing, each chiclero cuts all lianas around target *M. zapota* individuals in order to avoid entangling himself while moving upwards (chicleros HERIBERTO TAH and DAVID MORALES, pers. com. interviewed separately). For our study site, large, but unknown, quantities of latex were extracted from circa 1890 to 1938, as part of what we call the *chewing gum rush*. In 1938 President Lázaro Cárdenas took the lands out of the control of large companies to put them under peasant's administration (see asteriks in Fig. 7a; ARCHIVO GENERAL DEL ESTADO DE QUINTANA ROO 2006; KIERNAN 2000; see also REED 1971). Thus, 1938 is the most clear and recent date of the interruption of large-scale land uses at our study site before of our first aerial picture (1979). Indeed, we conservatively state that current forests there began to regenerate at that time. Because we established the age of our studied plots with respect to the beginning of our survey (2003), we deduce that such forest is ≥ 55 y-old (referred to 2003).

During the chewing gum rush, many groups averaging 45 people (ranging from 25–100) camped in ca. 0.25–0.5 hectare open areas located within old forests (deduced from pictures and text in VADILLO 2001). Housing materials were taken from the forest; this produced gaps, which enhanced liana abundance. However, slash-and-burn agriculture and any other large-scale fires were strictly prohibited because the company sold to the employees all of the food consumed by them and their families (VADILLO 2001). In addition, each chiclero abandoned the main camp for several days each week in order to reach and extract latex from trees located further away. For sleeping, such men built-up a so-called *hato*. Hatos are small beds made with narrow trunks of treelets supported by relatively wider wood-columns and covered by a roof of narrow trunks and palm leaves; all them connected by means of lianas (VADILLO 2001; chiclero DAVID MORALES, pers. com.). The existence of *hatos* and chiclero-camps, and all other above-mentioned land uses imply tree fall gaps, wider open areas and mechanical injuries to lianas, but lianas were rarely burnt.

The liana genera *Arrabidaea*, *Cydista* and *Melloa* (Bignoniaceae), produce hundreds of wind-dispersed seeds (Photo 4a), which are able to reach open areas exposed to direct solar radiation. In addition to *Serjania* (Sapindaceae), these lianas grow well where
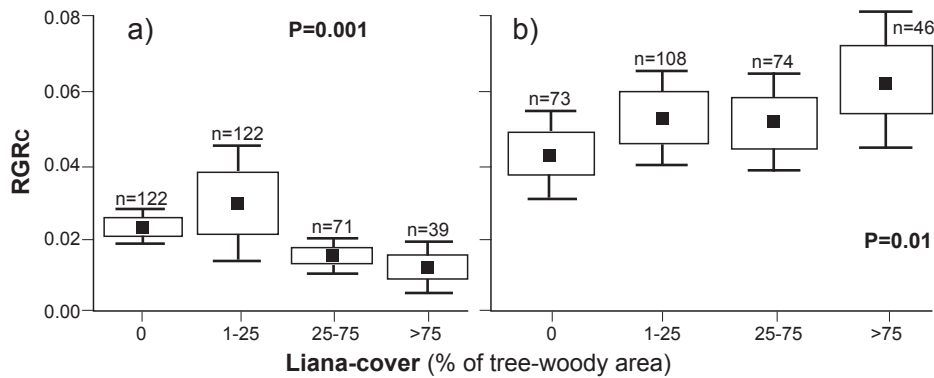
Fig. 6: Relative growth rate of circumference (RGRC) of trees having different liana coverages in Solferino, Quintana Roo, Mexico. (a) ≥ 55y-old- and (b) 10–18y-old forests. Boxes and whiskers represent 1 and 1.98 standard errors, respectively (P-values after Kruskall-Wallis tests).

high incident light is available (AVALOS and MULKEY 1999). They use flexible, narrow tendrils to attach to slender trees. Such tendrils are relatively fragile compared to tendril-like spines of other lianas (Photo 4c-d). Thus, they are only able to support a relatively light liana body (see also PUTZ and HOLBROOK 1991). Both the seeds and the tendrils are very thin and clearly susceptible to fire (Photos 4a and 4c).

The light body of soft lianas is related to their wide xylem vessels (pipe-like tissues conducting water from the roots to the top). Collectively, such vessels together are what we know as the wood of woody plants. If the xylem vessels are wide and are not com-

pactly arranged, the resulting wood is soft. Thus, for soft-wooded lianas like *Arrabidaea* and *Serjania*, these xylem "pipes" are not very compact, (Photo 4e) and alternate with series of live cells organized as columns moving photosynthesis products (called phloem), and with energy (e.g. starch) rich tissues called parenchyma. All these, as well as the cortex and external peridermis, are produced by other tissues called cambium (Photo 4e; MAUSETH 2008; CARLQUIST 1991; FISHER and EWERS 1991). For *Arrabidaea* (the most common soft liana) this arrangement of tissues seems like a "cross" formed by lobules of xylem "penetrated" by phloem and other tissues. In other taxa such as *Serjania* and *Paullinia*, the arrangement consists of joint, but independent groups of all of the above-mentioned tissues (Photo 4e). In both cases, wide xylem vessels may conduct more water than trees, thus reducing the growth of latter (probably the case in Fig. 6a). All live tissues present are also able to heal and produce new sprouts after mechanical injuries such as those caused by tree-felling and liana-cutting during all land uses that occurred on our plots 1–6 (FISHER and EWERS 1991; see also ACEVEDO-RODRÍGUEZ 2003). However, if rooted fragments of these cut lianas are allowed to dry, as during slash-and-burn agriculture, many of these tissues die and their cell walls become "hollow" and occupied by air. This makes them more flammable, and thus reduces the chances of soft-wooded lianas to survive and resprout after agricultural shifts (see also BOND and VAN WILGEN 1996).

5.2 Plots 7-10 and 11-12

Aerial pictures and interviews with farmers suggest that plots 7–10 were slashed and burnt for milpa-agriculture just once (in 1984) and abandoned from

Photo 3: V-shape cuts for latex extraction from the trunk of a chewing-gum tree (*Manilkara zapota*, Sapotaceae; photo by © E. I. Garrido-Pérez).
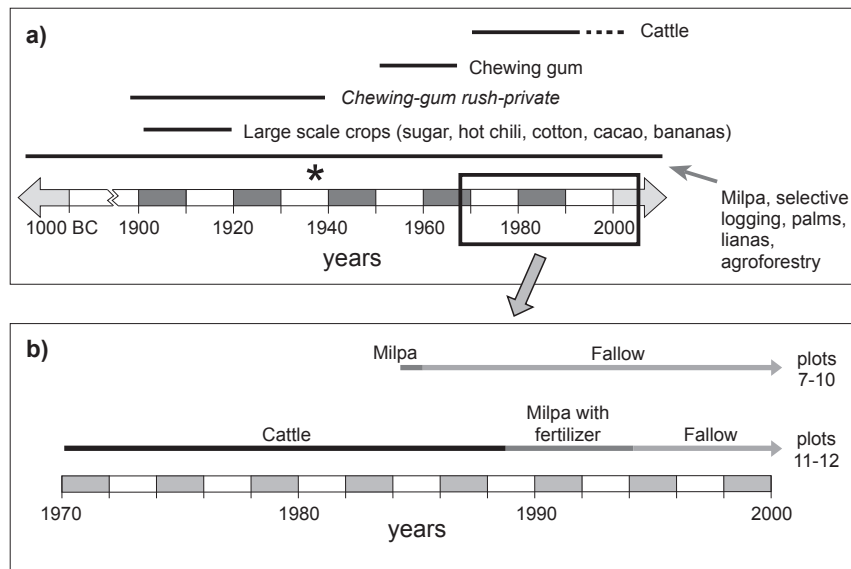
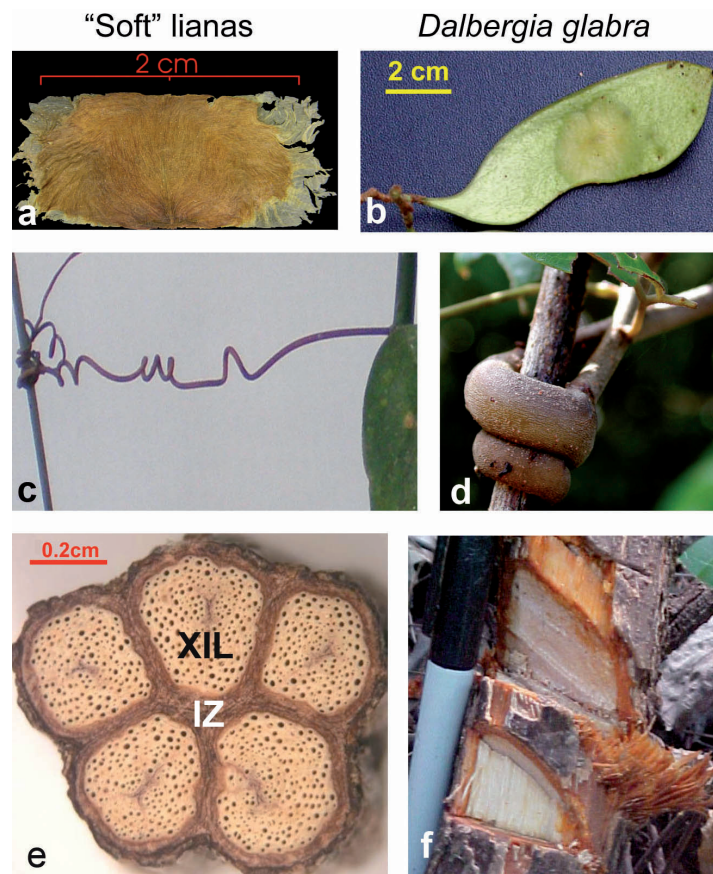Fig. 7: The land-use history of Ejido Solferino, Quintana Roo, Mexico. (a) Plots 1–6, (b) Plots 7–12.

Photo 4: Comparison of soft lianas with anomalous growth vs *Dalbergia glabra*, a "hard liana" with typical growth. (a) Winged seed of *Arrabidaea sp* (Bignoniaceae) vs (b) winged, one-seeded fruit of *D. glabra*. (c) Tendril of *Passiflora sp* (Passifloraceae) vs (d) tendril-like spine of *D. glabra*. (e) Cross section of *Serjania sp* (Sapindaceae) stem, showing Xylem masses (XIL) surrounded by the Intermediate zones (IZ) made of parenchyma and phloem vs (f) stem of *D. glabra*. Copyrights: (a) S. Patton (Smithsonian Tropical Research Institute), (b) and (d): W. John Hayden, (c) and (f) E. I. Garrido-Pérez, and (e) G. U. C. Araújo and C. G. Costa.

1985. The forest there was 18 y-old in 2003 (Fig. 7b). After being cleared, plots 11 and 12 were part of a cooperative cattle range until the end of 1988 when cattle husbandry began to decline in Solferino (see also DUPUY et al. 2007). In order to enhance soil recovery for wood and fruit trees, the land owner (JOSÉ QUINTAL, pers. com.) burnt the grass as part of a "milpa" agriculture using fertilizer, repeating this procedure annually for four years (1989–1992). From 1993 the land was allowed to lie fallow; thus, the forest was 10 years old during our visit in 2003. Milpa agriculture implies allowing the cut plants to dry for several months; this has been the practice from pre-Columbian times (DE LANDA 1556) until today (OKOSHI and GARCÍA-QUINTANILLA 2003).

Dalbergia glabra produces light, winged fruits with just one seed. The fruit (and its seed) are wind dispersed able to reach open areas. The seed enclosed in each fruit of *D. glabra* is thicker than the seeds of Bignoniaceae lianas (Photo 4b). Seed X-ray and other studies suggest that these characteristics increase seed-resistance to damage (KAMRA 1976), including fire (BOND and VAN WILGEN 1996). After coming in contact with a host tree, the tendril-like spines of *D. glabra* (Photo 4d) become rapidly covered by a thick bark. The stem has a densely compact arrangement of narrow xylem (Photo 4f; "typical growth" *sensu* FISHER and EWERS 1991) making its wood much harder than soft lianas; the stem has also a relatively thick bark. Post-cut dehydration and the penetration of air into the slashed body of *D. glabra* are less severe than in soft lianas. All this results in better protection of the parenchyma and cambium during fire. While excavating large *D. glabra* individuals to measure their diameters, we found wide trunks below ground, where they are protected against surface fire (BOND and VAN WILGEN 1996). They are also rich in storage products (MAUSETH 2008). All these differences makes *D. glabra* better adapted – than soft lianas – for re-sprouting and proliferation after fire.

6   Discussion

Our results contribute to making current generalizations on lianas and their role more accurate (SCHNITZER and BONGERS 2002). First, there is evidence that liana species composition changes throughout secondary succession, during which tendril-anchoring lianas are replaced by twisting lianas because of the increase of tree-diameters over time (DE WALT et al. 2000; CABALLÉ and MARTIN 2001). Moreover, our results suggest that the land-use his-

tory also changes liana-species composition. Liana species with similar climbing organs have different abundances depending on the previous use of fire. Thus, for example, increased use of fire favor *D.glabra* over Bignoniaceae and Sapindaceae.

Second, many studies have found that lianas retard the growth of trees thereby reducing the aboveground carbon capture of the latter (SCHNITZER et al. 2005; PÉREZ-SALICRUP 2001; VIDAL et al. 2002; GERWING 2001; PÉREZ-SALICRUP and BARKER 2000; CLARK and CLARK 1990; PUTZ 1984; WHIGHAM 1984; see also DILLENBURG et al. 1993). Our results suggest that the "liana effect" depends on the dominant liana taxa: the legume *D. glabra* was associated to a better tree-growth (and carbon capture) at our study site. Another way in which the same species "conserves" carbon dioxide is by reducing the fall of trees during hurricanes at our study site (GARRIDO-PÉREZ et al. 2008).

Third, there is evidence that large liana-coverages on tree crowns reduce the growth of tree-individuals compared to those with low liana coverage (KAINER et al. 2006; CLARK and CLARK 1990). Our results confirmed this for the $\geq$ 55 y-old stands dominated by soft lianas, but the 10–18 y-old stands dominated by *D. glabra* showed improved growth in those trees hosting lianas. We have not tested whether this was due to soil nitrogen fixation by microorganisms associated to *D. glabra* as is the case with other legumes (e.g. ALPÍZAR et al. 1986). Alternatively, larger liana-coverages may be just an indicator of higher incidence of light, which actually enhances tree-growth.

Fourth, it is currently accepted that lianas affect tree-species turnover by reducing the growth and reproduction of some tree species more than others (WRIGHT et al. 2005; SCHNITZER and BONGERS 2002; PÉREZ-SALICRUP 2001; CLARK and CLARK 1990). Our results suggest that liana effects can also be positive and neutral depending on the wide spatial variation of liana abundances and species compositions resulting from previous natural disturbances and land-use types. This makes liana effects on forest communities less predictable than assumed.

Finally (fifth), there is a long standing discussion on the role of local plant diversity in forest functions (NAEEM and WRIGHT 2003). At our study site, the high abundances of one liana species (*D. glabra*) seemed to be more related to the enhancement of CO_2-capture by trees than liana diversity in itself. The liana-stem categories of FISHER and EWERS (1991) fit into the concept that functional groups of "redundant species" determine ecosystem functions

(Naeem and Wright 2003; Diaz and Cabido 2001) and should allow a better understanding of liana effects on ecosystems.

Because of its long history of disturbances, many areas of the Yucatan Peninsula have abundant lianas (see also Whigham et al. 1991). Other *liana forests* resulting from pre-Columbian land use comprise many thousands of square kilometers in the Bolivian Amazon and Brazil (Balée and Campbell 1990; Thomas et al. 1998). A wide variety of traditional land uses is still practiced in the tropics (e.g. Toledo et al. 2003; Herzog 1994), and such manipulations generate a gradient of disturbances, biodiversities and species compositions. Thus, farmers are unintentionally conducting a world-wide, millenary experiment testing the abilities of different plants such as lianas to persist after disturbances and to affect other plants (see also Gómez-Pompa 1987). Combining natural and social sciences facilitates the understanding of such experiments to enrich basic sciences such as geobotany (Bürghi and Russell 2001) by means of helping to explain why some plant species are more common than others in different locations.

Acknowledgements

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