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**A ten-year decrease in plant species richness on a neotropical inselberg:
detrimental effects of global warming?**

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Abstract

The census of vascular plants across a ten-year interval (1995-2005) at the fringe of a neotropical rainforest (Nouragues inselberg, French Guiana, South America) revealed that species richness decreased, both at quadrat scale (2 m^2) and at the scale of the inselberg (three transects, embracing the whole variation in community composition). Juvenile stages of all tree and shrub species were most severely affected, without any discrimination between life and growth forms, fruit and dispersion types, or seed sizes. Species turnover in time resulted in a net loss of biodiversity, which was inversely related to species occurrence. The most probable cause of the observed species disappearance is global warming, which severely affected northern South America during the last 50 years ($+2^\circ\text{C}$), with a concomitant increase in the occurrence of aridity.

Introduction

Threats to biodiversity in tropical forests have largely been attributed to deforestation and associated events such as habitat loss (Soares-Filho *et al.*, 2006) and climate drift (Wright, 2005). Fires attributed to El Niño Southern Oscillation (ENSO) dry climate anomalies have also been invoked as a cause of present-day losses of biodiversity (Barlow *et al.* 2003), similarly to fires involved in past extinctions (Charles-Dominique *et al.*, 2001; Anderson *et al.*, 2007). In unmanaged tropical forests, major changes are expected to stem from global warming as a chief result of the anthropogenic greenhouse effect (Rosenzweig *et al.*, 2008), but recent observations show divergences between continents, Africa being most and South America least threatened by associated aridity (Malhi & Wright, 2004). However, recent climate studies established that northern South America, which is still more or less preserved

from massive destruction (Eva *et al.*, 2004), was subject to altered precipitations resulting from a southward switch in the location of the Inter-Tropical Convergence Zone (ITCZ), possibly leading to severe biodiversity losses (Higgins, 2007). Moreover updated simulation models predict a 4°C warming during the 21th century over Chilean and Peruvian coasts, Central Amazon and Guianas Shield (Boulanger *et al.*, 2006).

Forest fringes in the tropics ('low forests') are more prone to shifts in biodiversity than adjoining environments such as savannas and tall-tree rain forests (Favier *et al.*, 2004), even without any marked advance of ecotone limits (Noble, 1993). Our aim was to compare across a ten-year interval (1995-2005), encompassing a severe ENSO dry event in 1997-98 (Laurance, 2000; Paine & Trimble, 2004; Wright & Calderon, 2006), the botanical composition of a neotropical forest fringe, free of human activity for centuries, embracing a wide floristic and environmental gradient (Sarhou *et al.*, submitted). Our main expectation was that, as predicted by Jump & Peñuelas (2005), present-day global warming in the wet neotropics is too fast for the long-term maintenance of species-rich communities at the forest limit, as this has been shown to occur in more temperate zones of South America (Villalba & Veblen, 1998). Juvenile forms of plants are expected to suffer more than reproductive stages from severe El Niño years (Engelbrecht *et al.*, 2002), resulting in a deficit of recruitment directly related to scarcity of the species. If this hypothesis is verified, then threats to biodiversity due to global warming itself (Thomas *et al.*, 2004) should add to those stemming from fragmentation and shrinkage of tropical forested areas (Curran *et al.*, 1999; Laurance, 2000).

Materials and methods

Study site

The study site is included in a forest reserve located in French Guiana (northern South America, 4°5'N, 52°41'W) around the Nouragues inselberg, a granitic whaleback dome (altitude 410 m) protruding from the untouched rain forest which covers the Guianas plateau (Poncy *et al.*, 1998). The climate is perhumid (4000 mm annual rainfall) and warm (mean temperature 27°C). Climate data were recorded over fifty years in a nearby meteorological station (Regina) and show seasonal changes in monthly precipitation, with a long rainy season from December to June (more than 300 mm per month) and a short dry season from July to November (Fig. 1). A regular increase in temperature was observed over the last 50 years amounting to 1.6°C, corresponding to a mean increase of 0.32°C per ten-year period. No decrease in annual precipitation was observed over the same period, but four years (1958, 1976, 1997 and 2005) experienced a severe water deficit during the dry season, as exhibited by the Aridity Index which reached a value of 2 or more during the dry season (Fig. 1). The year 1997 was in the range of our botanical record (1995-2005), but the strong drought recorded in 2005 occurred several months after the completion of our study. The same warming trend was depicted by other meteorological stations in French Guiana, including coastal (open) as well as widely forested areas (Table 1), thus it could not be ascribed to potential effects of deforestation upon local climate (Marland *et al.*, 2003).

Soils are enriched in water and nutrients around the granitic outcrop (Sarhou & Grimaldi, 1992; Dojani *et al.*, 2007), supporting a lush species-rich vegetation in the low forest, involving abundant epiphytes in the understory (Larpin, 2001). The low forest borders the inselberg and is also established on its summit (Larpin *et al.*, 2000). This vegetation has been described as a specific community, comprised of plant species from adjoining

communities (the savanna rock and the tall-tree rain forest) along with numerous species exclusive to the low forest (Théry & Larpin, 1993). Multi-stemming and vertical stratification of the vegetation are prominent features of the low forest, which was considered to be an ecocline according to transient relationships between botanical composition and shift from organic to mineral soil (Sarhou *et al.*, submitted).

The rock savanna covers the southern and western sides of the inselberg. Vegetation clumps of the rock savanna are sparsely distributed on slopes and become denser and taller in the vicinity of the low forest (Sarhou & Villiers, 1998). The rock savanna is dominated by epilithic wind- and bird-disseminated herb species and shrubs, which are established directly on the granite (on medium slopes or pools) or in the organic matter accumulated under woody vegetation (Sarhou, 2001; Kounda-Kiki *et al.*, 2006). Primary and secondary successional trends have been described in the savanna rock, fires followed by biological attacks (fungi, termites) being mainly responsible for the destruction and renewal of shrub thickets (Kounda-Kiki *et al.*, 2008; Sarhou *et al.*, 2009).

The tall-tree rain forest is comprised of a variety of late- and early-successional tree species growing isolated or in small clumps (Poncy *et al.*, 2001), mostly disseminated by rodents (Dubost & Henry, 2006), monkeys (Julliot, 1997) and bats (Lobova & Mori, 2004). Due to the absence of hurricanes, a peculiarity of the ITCZ (Liebmann *et al.*, 2004), single tree-fall gaps, rapidly invaded by pioneer plant species, are mainly responsible for the renewal of the rain forest (Riéra, 1995; Van der Meer & Bongers, 2001). Dry periods, accompanied by forest fires and severe erosion, occurred in the past three millenaries (Granville, 1982) and shaped more open landscapes, the last dry event at the site of our study being dated around

118 1000-600 years B.P. (Ledru *et al.*, 1997; Charles-Dominique *et al.*, 1998; Rosique *et al.*,
119 2000).

120

121 *Sampling*

122

123 Three gradient-directed transects (Gillison & Brewer, 1985) were established across the low
124 forest, located at the summit (T6) and along the southern slope (T4, T5). All transects started
125 in the rock savanna on bare rock and their length varied from 52 to 89 m, so that they ended
126 in the first metres of the tall-tree rain forest. The slope was nil or slight in the summit forest
127 (T6), but reached almost 40% in transects T4 or T5. In April 1995 and April 2005, the
128 vegetation was identified at the species level according to Funk *et al.* (2007) and surveyed
129 every metre in adjacent 1x2 m quadrats. For each woody species the diameter and height of
130 individual stems were measured as well as the number of specimens per quadrat. In case of
131 multi-stemming, stems were pooled for each individual for the calculation of species
132 abundance per quadrat. Woody species were classified into two groups according to their
133 height (higher or lower than 50 cm). The same species could fall within both size categories,
134 according to developmental stage or suppression state. The cover percentage of herb and
135 suffrutescent plant species was estimated visually in each quadrat area. Biological traits
136 (Raunkiaer's life form, fruit type, dispersion mode, seed size) were established for the whole
137 set of 164 plant species (Appendix).

138

139 *Data processing*

140

141 Given that sampling was done along transect lines across variable environments,
142 autocorrelation was expected (Legendre, 1993; Legendre & Legendre, 1998). Paired t-tests

were used for the detection of trends from 1995 to 2005, using a specific procedure in order to keep pace with autocorrelation. First, signed differences between years were calculated for each quadrat, and the normality of their distribution was verified using Shapiro-Wilk's test (Shapiro & Wilk, 1965). Second, product-moment (Pearson) autocorrelation coefficients of increasing order (first-order = one lag, second-order = two lags, etc.) were calculated. If first-order autocorrelation coefficients did not display any significant deviation from null expectation at 0.05 level (tested by t-test) then all quadrats of the same transect were used in further calculations. If the first-order autocorrelation coefficient was significant at 0.05 level, then the lag was increased until non-significance was reached. According to the order of the first non-significant coefficient, one or more quadrats were discarded for further calculations, thereby increasing the distance between successive samples and decreasing the effective sample size until autocorrelation was no longer found. This procedure, although prone to some loss of information, was preferred over tedious calculations of the 'effective sample size' (Clifford *et al.*, 1989; Dutilleul, 1993; Dale & Fortin, 2002) which have been shown by Wagner & Fortin (2005) not to be fully applicable to any kind of data.

Fractal dimensions were calculated for each transect using the slope of log-log curves relating the semi-variance $\gamma(h)$ of the series to the lag (h) of autocorrelated data (Burrough, 1983; Gonzato *et al.*, 2000; Dale *et al.*, 2002). We used the linear portion of the log-log curve to compute the fractal (Hausdorff) dimension according to the formula $D = 2 - m/2$, D being the fractal dimension of the series and m the slope of the log-log curve.

Series of plant species present in both years were compared between 1995 and 2005 in order to check for possible changes in density (trees and shrubs), percent cover (herbs and suffrutex) and basal area over the whole set of 258 quadrats. Differences between both years

were tested using the Wilcoxon signed-rank test (Sokal & Rohlf, 1995). The effect of frequency of species on their disappearance expectancy was tested by logistic regression (Sokal & Rohlf, 1995).

All abovementioned calculations were done using XLSTAT (Addinsoft®) statistical software.

Species accumulation or rarefaction curves (Simberloff, 1978; Colwell & Coddington, 1994) were calculated for the whole set of quadrats, in order to check for the representativeness of our sampling effort, using EstimateS version 8.0 for Windows (<http://viceroy.eeb.uconn.edu/estimates>). The expected number of species was calculated using the first-order jackknife richness estimator JACK1, which is considered as the most precise estimator for large sample sizes (Palmer, 1990).

Results

Species accumulation curves of woody plant species for the years 1995 and 2005 show that (i) threshold values were nearly reached in both years, (ii) woody species total richness (inselberg scale) was lower in 2005 compared to 1995 (Fig. 2). Over the three transects, 205 quadrats (2 m² each, totalling 410 m²) harboured a total of 19,591 individuals belonging to 102 species in 1995, compared to 14,871 individuals and 80 species in 2005, representing a decrease of 24% for individuals and 22% for species. The expected species richness (JACK1 estimator) was 116.9 species in 1995 and 89.95 in 2005, thus not much higher than the cumulative species richness.

Quadrat species richness (all species included) decreased from 1995 to 2005, whatever the transect (Fig. 3). The mean decrease observed at the quadrat level was 12%, 17% and 16% in transects T4, T5 and T6, respectively. This net decrease resulted from the combination of additions and subtractions of species, as shown by Figure 4. It can be seen from this figure that increases and decreases are not independent and that communities with many species per quadrat seem to be less stable than poorer ones.

The semi-variance of species richness series was higher in 2005 than in 1995 at short lags (1 to 3 m distance), but lower for longer distances, whatever the transect (Fig. 5). This resulted in a higher fractal dimension in 2005 than in 1995 for all transects, which suggests that the change in species richness between adjacent quadrats increased from 1995 to 2005 whereas the net loss of species caused homogenization at the transect scale.

All major species traits were affected by the observed decrease in plant species richness (Fig. 6). Only minor species traits did not follow the general trend, which was not judged significant: lianas and megaphanerophytes (among Raunkiaer's life forms), climbing plants (among growth forms) and follicles (among fruit types) marginally increased in mean density per quadrat but all of them were poorly represented in the study area. Table 2 shows that growth forms, life forms, fruit types, dispersion modes and seed classes did not display any significant shift in species trait distribution.

At the quadrat scale, the observed trend of decreasing species richness affected mainly juveniles and only to a weak and insignificant extent adults of the same woody species, and basal area did not decrease significantly (Table 3). This result points to a deficit of

recruitment rather than to adult increased mortality. Herbs and suffrutex were not affected at all by this phenomenon.

The probability of disappearance of plant species was strongly dependent on their abundance, as ascertained by logistic regression (Fig. 7). The model predicted that rarest species (species present in only one quadrat in 1995) showed 50% disappearance, while the rate of disappearance of species present in more than 60 quadrats was nil.

Discussion

The decrease in plant species richness observed in ten years at the scale of three transects representative of the Nouragues inselberg as well as at the scale of individual quadrats was accompanied by a small-scale instability of species richness, thereby indicating a severe disturbance. The distribution of species traits was not affected, but most concern was on juveniles of woody species, pointing to a random process at species level and to a non-random process at individual level. The recruitment of species was affected all the more they were scarcely distributed. Neutral models (Hubbell, 2001; Ulrich, 2004; Gotelli & McGill, 2006) make similar predictions but it can be postulated that in the long term the higher sensitivity of juvenile stages would affect the composition of the whole plant community, by privileging species with a low turnover rate (Gourlet-Fleury *et al.*, 2005). The warming trend observed in northern South America can be invoked to explain our results, in particular the severe dry season which occurred two years after the first census done in 1995. We suspect that following a wave of moisture deficit, known to affect more seedlings and saplings than adult trees and shrubs (Poorter & Markesteijn, 2008), further recruitment by seed production (Wright & Calderón, 2006), seed dispersal to safe sites (Janzen, 1970; Julliot, 1997; Dalling *et*

al., 2002) and germination of the soil seed bank (Dalling *et al.*, 1998) never compensated for impoverishment of the plant community, which did not recover its original level at the end of the following eight years.

Other hypotheses for the observed collapse in plant species richness could be proposed, but none is satisfactory. From the last dry period with wildfire events, which ended 600 years ago, the forest ecosystem could be in a phase of development, still far from equilibrium (Odum, 1969). A decrease in plant species richness is commonly advocated in late stages of ecosystem development, following competition for light and nutrients by a few dominant species (Connell, 1979). In this case, development of the forest ecosystem following a major disturbance is accompanied by an increase in basal area (Chazdon *et al.*, 2007), which was not supported by our data. It would also be accompanied by a change in the distribution of species traits, in particular shade-tolerant tall tree species, with big seeds and autochory, should be increasingly represented (Swaine & Whitmore, 1988; Whitmore, 1989; Ter Steege & Hammond, 2001), which was not the case. The effects of CO² fertilization issued from fossil fuel combustion would be similar, by stimulating the growth of dominant species and increasing the basal area (Laurance, 2000). This hypothesis can be discarded too, for the same reasons. Interestingly, recent results by Wardle *et al.* (2008) showed that retrogression of forest ecosystems could occur in the absence of disturbance, displaying a pronounced decrease in basal area, accompanied, or not, by concomitant changes in plant species richness. Such a decrease in basal area was not observed, thus retrogression is not supported by our data either.

Another possible cause for the observed phenomenon could be the worldwide increase in infectious diseases and parasite outbreaks caused by climate warming (Harvell *et al.*, 2002;

Rosenberg & Ben-Haim, 2002; Mouritsen *et al.*, 2005). This can be thought to affect juvenile stages of all plant species, a number of which currently die from damping-off (Hood *et al.*, 2004). Such an explanation cannot be considered as antagonist to the hypothesis of a severe moisture deficit affecting all plant species. Rather, it should be considered as an additional cause of mortality, affecting indiscriminately the whole array of plant species living in the low forest.

Dramatic declines in plant species diversity were observed in temperate, boreal and mountain areas, following forced or actual climate warming (Klein *et al.*, 2004; Walker *et al.*, 2006), but such trends had not been demonstrated in species-rich neotropical forests yet, where most changes in tree growth, mortality and recruitment were attributed to rising CO² (Laurance *et al.*, 2004) and only more recently to global warming (Feeley *et al.*, 2007). Studies done at Barro Colorado, Panama, concluded that seedlings of common tree species were not affected by the severe 1997-98 ENSO dry event (Engelbrecht *et al.*, 2002), although previous studies on the same sites demonstrated long-term effects of severe El Niño years on drought-sensitive species (Condit *et al.*, 1995). However, the same 1997-1998 ENSO event was shown to be a main cause of biodiversity loss in tropical rain forests of Southeast Asia (Harrison, 2001), and decelerating growth rates of tropical trees are now recorded worldwide (Feeley *et al.*, 2007). Experimental studies showed that warming trends could result in changes in species trait distribution, by privileging species better adapted to warmer climate (Post *et al.*, 2008) or reaching dominance through increased growth (Harte & Shaw, 1995), and it is now admitted that the rapidity of present-day climate warming is likely to affect the capacity of adaptation of most plant communities (Walther, 2003; Jump & Peñuelas, 2005). In American and African rain forests lianas have been shown to increase in species trait representation (Phillips *et al.*, 2002; Wright & Calderón, 2005; Swaine & Grace, 2007; but

see Caballé & Martin, 2001). Neither increase nor decrease in lianas species could be demonstrated in our study because of the poor abundance of this growth form in the low forest. We suspect that none of the low forest species are clearly adapted to drought, except for those composing the rock savanna (Sarhou & Villiers, 1998). Surprisingly, no shift towards a better representation of rock savanna species was observed along our three transects (Sarhou *et al.*, submitted). Species typical of rock savanna are always associated with the presence of organic soil and the concomitant absence of any mineral soil, even when established within the low forest (Sarhou *et al.*, submitted). Thus, it is possible that any displacement of the whole plant community, as reported in other transition areas (Camill *et al.*, 2003; Sanz-Elorza *et al.*, 2003; Shiyatov *et al.*, 2005), is prevented by the absence of adequate soil conditions, which may constitute an ecological barrier to community drift in the presence of a rapid environmental change (Higgins, 2007). In this case, erosion events with total removal of the mineral soil (Rosique *et al.*, 2000), as may have occurred in the past, should be a prerequisite for any development of a community better adapted to dry environments.

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665

Table 1. Mean warming trends on the longest possible record period in ten meteorological stations of French Guiana

Meteorological station	Recording period	Mean 10-yr increase	Coefficient of determination R ²
Cacao	1981-2005	0.78°C	0.71***
Camopi	1955-2005	0.26°C	0.47***
Kourou	1967-2005	0.33°C	0.71***
Maripasoula	1955-2005	0.26°C	0.64***
Regina	1955-2005	0.32°C	0.67***
Rochambeau	1950-2005	0.16°C	0.44***
Saint-Georges	1956-2005	0.30°C	0.73***
Saint-Laurent du Maroni	1950-2003	0.19°C	0.44***
Saül	1955-2005	0.36°C	0.61***
Sinnamary	1955-2006	0.13°C	0.16**

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667

Table 2. Variation in species trait distribution from 1995 to 2005 on the whole study area

	1995	2005	
Woody	100	78	
Herb	33	22	$\chi^2 = 0.88$
Suffrutex	4	5	P = 0.83
Palm	2	2	
Therophyte	1	0	
Geophyte	1	1	
Chamaephyte	4	5	
Hemicryptophyte	28	20	$\chi^2 = 2.18$
Liana	9.5	7	P = 0.98
Nanophanerophyte	5	5	
Microphanerophyte	31.5	29	
Mesophanerophyte	37	27	
Megaphanerophyte	8	8	
Berry	34	33	
Capsule	35	23	
Achene	5	5	
Drupe	24	20	
Fleshy	7	7	$\chi^2 = 2.09$
Pod	9	8	P = 0.99
Follicle	3	4	
Samara	3	2	
Caryopsis	7	5	
Sporangium	2	1	
Zoochorous	81	71	
Anemochorous	42.5	31	$\chi^2 = 0.92$
Barochorous	2	1.5	P = 0.92
Autochorous	6	3	
Hydrochorous	0.5	0.5	
Creeping	4	2	
Rosette	8	7	
Erect	79	67.5	$\chi^2 = 0.79$
Leaning	21	19.5	P = 0.98
Climbing	10	7	
Multi-stemmed	13	13	
Seed class 1	48	34.5	
Seed class 2	47.5	46.5	
Seed class 3	18.5	15	$\chi^2 = 1.23$
Seed class 4	8	8	P = 0.94
Winged seed	8	7	
Plumose seed	3	2	

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Table 3. Variation in mean number of adults and juveniles (trees and shrubs), mean percent cover (herbs and suffrutex) and basal area per plant species from 1995 to 2005 on the whole study area

	1995	2005	Wilcoxon signed test
Adults (> 50 cm)	23.5	20.8	P = 0.13
Juveniles (< 50 cm)	261	192	P = 0.0006
Herbs and suffrutex	1.2	1.2	P = 0.53
Basal area (m ²)	250	202	P = 0.99

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Figure legends

Figure 1. Climate data at Regina meteorological station (nearest from study site). Left: mean annual temperature over the previous 50 years. Right: mean monthly aridity index (mean temperature in °C divided by monthly rainfall in mm) over the previous 50 years and individual curves for the four most arid years, i.e. years with a monthly aridity index higher than 2

Figure 2. Species accumulation curves of woody plant species for 1995 and 2005. These curves being based on a random resampling of all individuals, only species which were recorded at the individual level (woody species) were accounted for

Figure 3. Mean plant species richness (trees, shrubs, herbs and suffrutex included) at quadrat scale in the three transects. Comparisons between census years (1995 vs 2005) were done by *t*-test. The number of degrees of freedom (d.f.) takes into account autocorrelation (see text for more details). *n* = number of quadrats in each sample

Figure 4. Increases and decreases in the number of plant species in each quadrat in the three transects (left scale). The broken line indicates the total number of species in 1995 (right scale)

Figure 5. Semivariogram of species richness on the three transects. Abscissa (lag) and ordinate (semivariance) were in logarithmic scale, in order to show the straight line used for the calculation of fractal distance (see text for more details)

Figure 6. Changes in plant species traits (in mean number of species per quadrat) from 1995 to 2005

Figure 7. Logistic regression modelling the relationship between the disappearance of species from 1995 to 2005 (0 = persistence, 1 = disappearance) and their frequency (number of quadrats where the species was present) in 1995. Black dots indicate the species which were still present (bottom line) or had disappeared (upper line) in 2005

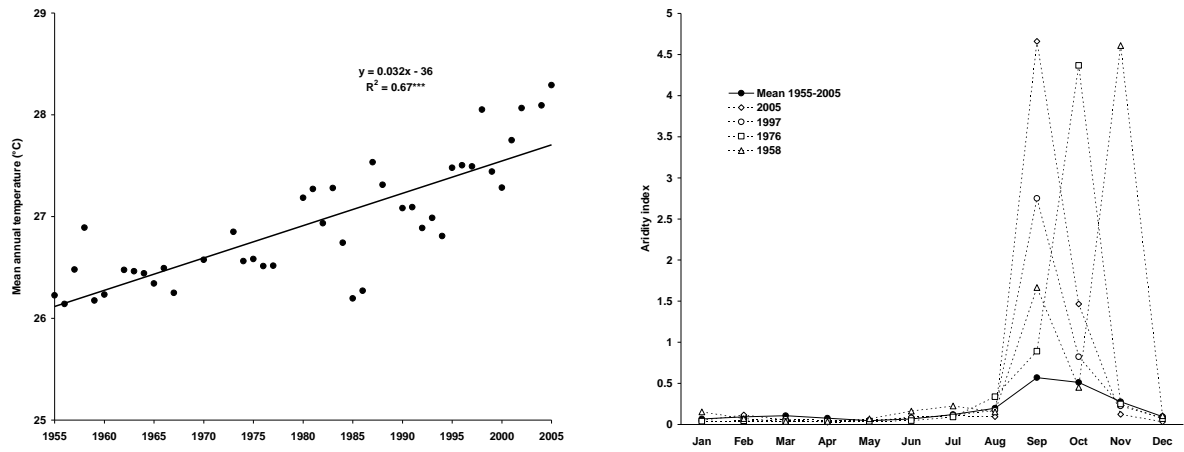
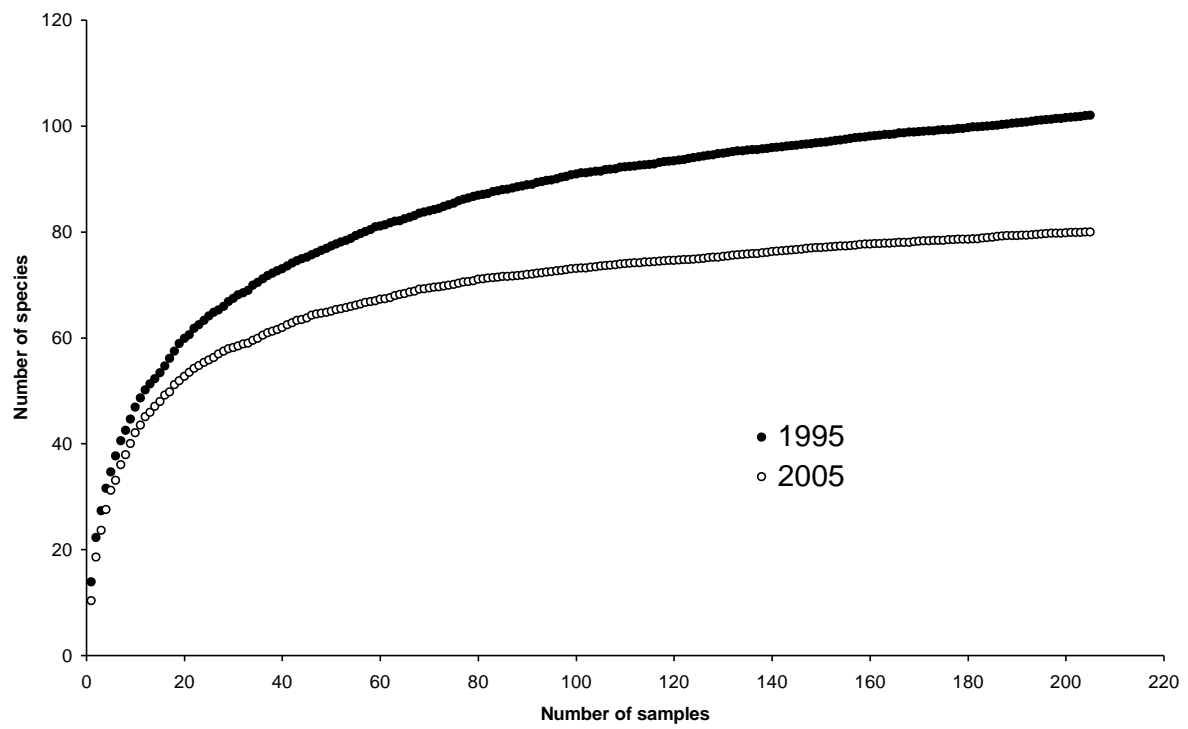


Fig. 1

**Fig. 2**

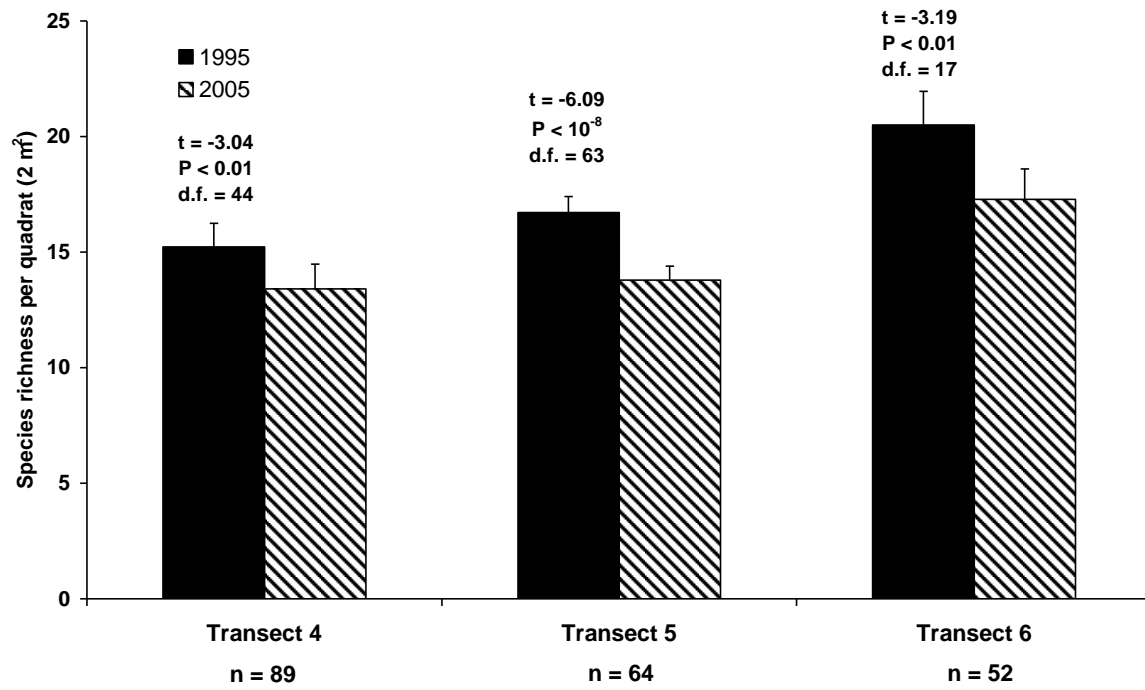


Fig. 3

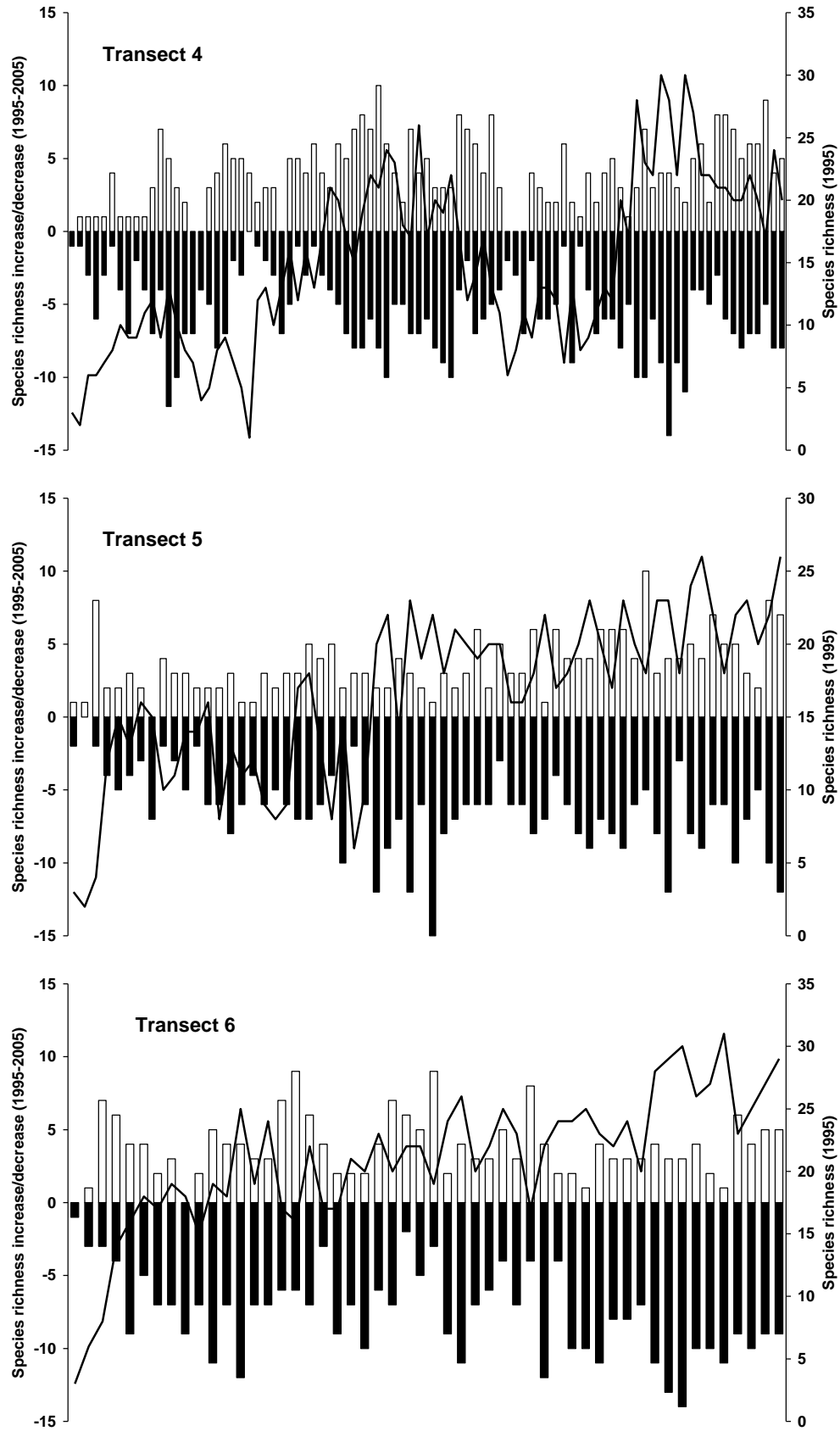


Fig. 4

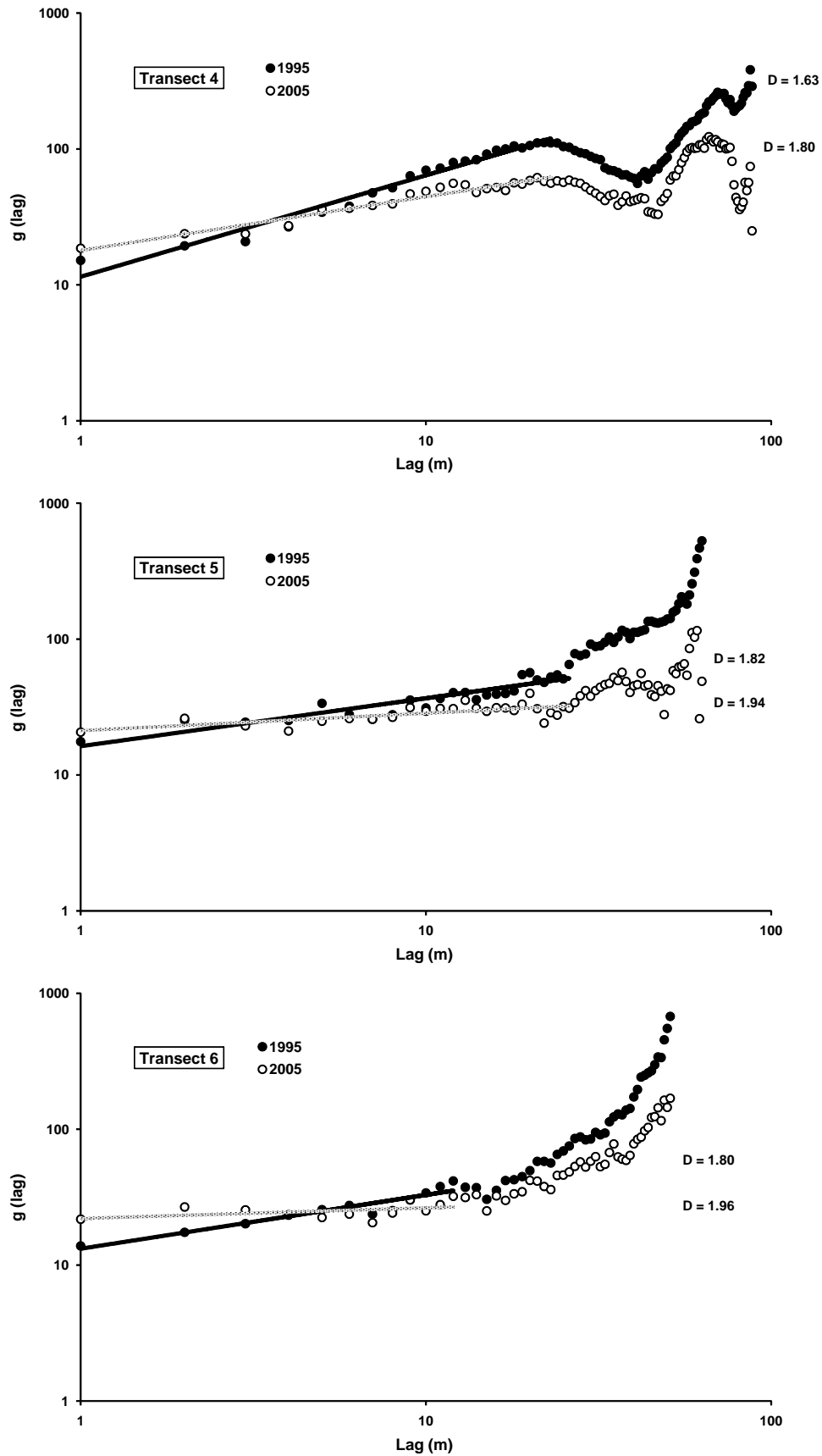


Fig. 5

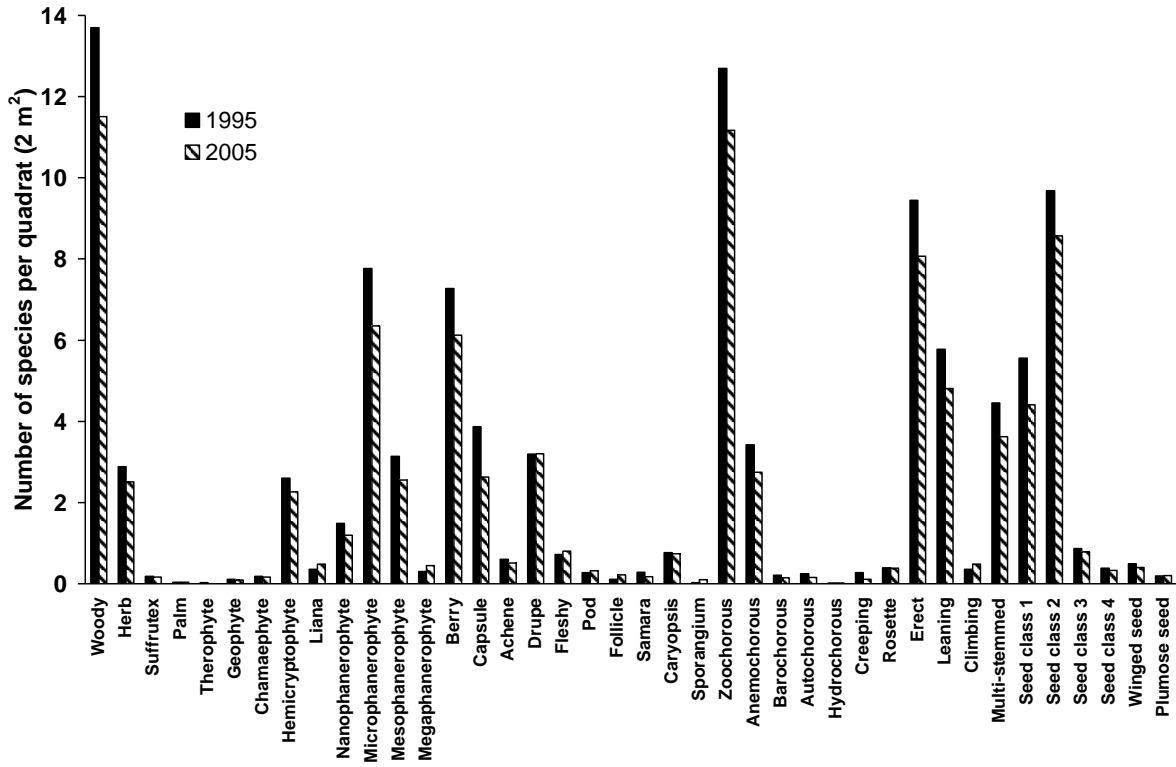
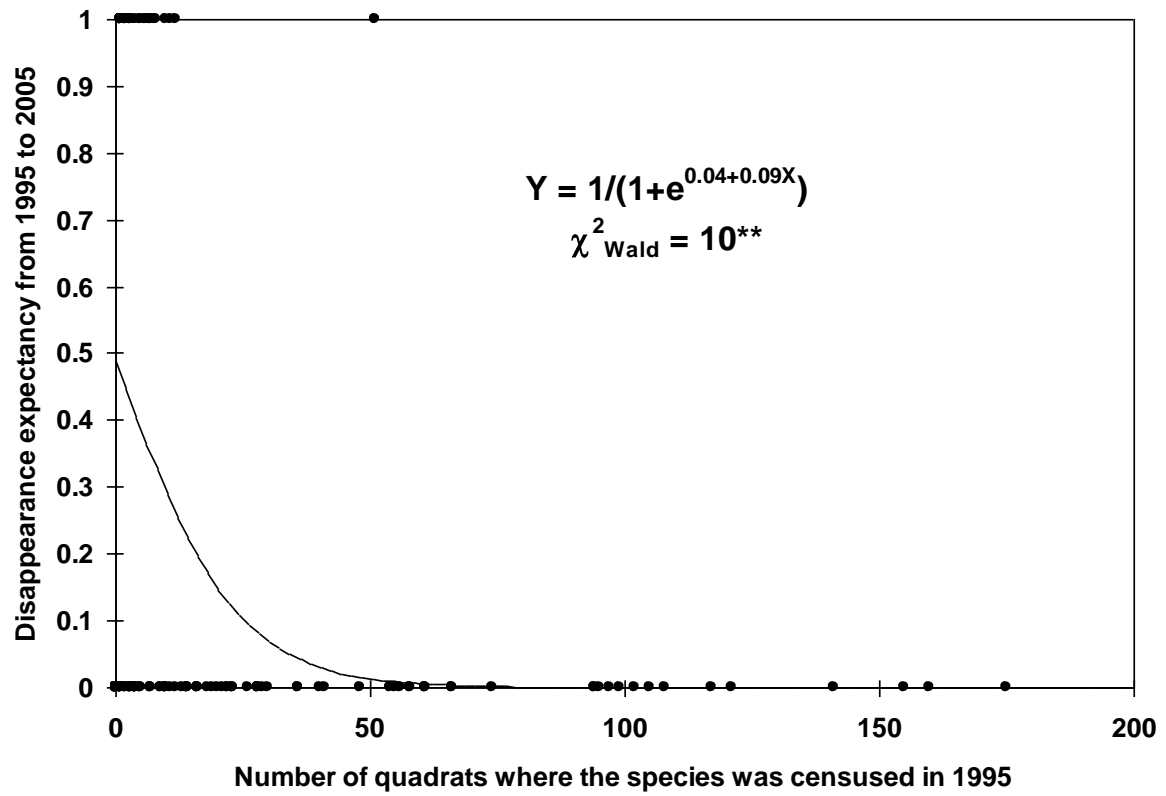


Fig. 6



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724 **Fig. 7**

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Appendix. List of latin names and traits of plant species found in the three studied transects. Species which totally disappeared in 2005 (compared to 1995) are indicated by (*)

Tree and shrubs	Family	Raunkiaer's life forms	Fruit types	Dispersion modes	Seed size
<i>Albertia myricifolia</i>	Rubiaceae	microphanerophyte	berry	zoochory	0.5-1 cm
<i>Antonia ovata</i> (*)	Loganiaceae	mesophanerophyte	capsule	anemochory	unknown (winged)
<i>Apocynaceae</i> sp. (*)	Apocynaceae	unknown	unknown	unknown	unknown
<i>Asclepiadaceae</i> sp.	Asclepiadaceae	liana	foliice	anemochory	unknown
<i>Aspidosperma cruentum</i>	Apocynaceae	megaphanerophyte	foliice	anemochory	>2 cm (winged)
<i>Aspidosperma mangraviana</i>	Apocynaceae	megaphanerophyte	foliice	anemochory	>2 cm (winged)
<i>Aspidosperma</i> sp.	Apocynaceae	mesophanerophyte	foliice	anemochory	unknown
<i>Bignoniaceae</i> sp. (*)	Bignoniaceae	liana	capsule	anemochory	unknown
<i>Brosimum guianense</i>	Moraceae	megaphanerophyte	fleshy	endozoochory	0.5-1 cm
<i>Burseraceae</i> sp. 1 (*)	Burseraceae	mesophanerophyte	dupe	endozoochory	unknown
<i>Burseraceae</i> sp. 2 (*)	Burseraceae	mesophanerophyte	dupe	endozoochory	unknown
<i>Calyptanthus lepidus</i>	Myrtaceae	mesophanerophyte	berry	zoochory	<0.5 cm
<i>Cassia</i> sp.	Faboaceae	mesophanerophyte	capsule	zoochory	0.5-1 cm
<i>Cassipourea guianensis</i>	Rhizophoraceae	mesophanerophyte	capsule	zoochory	0.5-1 cm
<i>Chrysobalanaceae</i> sp. (*)	Chrysobalanaceae	phanerophyte	dupe	endo/synzoochory	unknown
<i>Clusia grandiflora</i>	Cusciaceae	mesophanerophyte	capsule	zoochory	0.5-1 cm 1-2 cm
<i>Clusia minor</i>	Cusciaceae	microphanerophyte	capsule	zoochory	<0.5 cm
<i>Clusia nemosa</i>	Cusciaceae	microphanerophyte	capsule	zoochory	0.5-1 cm
<i>Coccoloba</i> sp.	Polygonaceae	liana	fleshy	zoochory/hydrochory	0.5-1 cm
<i>Cordia</i> sp.	Boraginaceae	microphanerophyte	dupe	zoochory	0.5-1 cm
<i>Croton falcifolius</i>	Euphorbiaceae	microphanerophyte	capsule	auto/banochory	<0.5 cm
<i>Croton</i> sp. (*)	Euphorbiaceae	microphanerophyte	capsule	auto/banochory	<0.5 cm
<i>Cupira diphyle</i>	Sapotaceae	mesophanerophyte	capsule	endozoochory	0.5-1 cm
<i>Cybanthus guianensis</i>	Myrsinaceae	microphanerophyte	dupe	zoochory	0.5-1 cm
<i>Daphnopsis granitica</i>	Thymelaeaceae	microphanerophyte	dupe	zoochory	0.5-1 cm
<i>Dialanthea</i> sp. (*)	Dianellaceae	liana	unknown	zoochory	unknown (arilied)
<i>Dunlia</i> sp.	Rubiaceae	phanerophyte	berry	zoochory	0.5-1 cm
<i>Eriofeca surinamensis</i>	Bombacaceae	microphanerophyte	capsule	anemochory	0.5-1 cm
<i>Ernestia granulifera</i>	Melastomataceae	nanophanerophyte	capsule-like	barochory or anemochory	<0.5 cm
<i>Erythroxylum caribaeum</i>	Erythroxylaceae	microphanerophyte	dupe	zoochory	0.5-1 cm
<i>Erythroxylum ligustrinum</i>	Erythroxylaceae	mesophanerophyte	dupe	zoochory	0.5-1 cm
<i>Erythroxylum squamatum</i>	Erythroxylaceae	mesophanerophyte	dupe	zoochory	0.5-1 cm
<i>Eugenia albicans</i>	Myrsinaceae	microphanerophyte	berry	zoochory	0.5-1 cm
<i>Eugenia florida</i>	Myrtaceae	microphanerophyte	berry	zoochory	0.5-1 cm 1-2 cm
<i>Eugenia marianensis</i>	Myrtaceae	mesophanerophyte	berry	zoochory	1-2 cm
<i>Eugenia ramiflora</i>	Myrtaceae	mesophanerophyte	berry	zoochory	0.5-1 cm
<i>Eugenia</i> sp. 1 (*)	Myrtaceae	mesophanerophyte	berry	zoochory	0.5-1 cm
<i>Eugenia</i> sp. 2 (*)	Myrtaceae	microphanerophyte	berry	zoochory	0.5-1 cm
<i>Euphorbia pinnata</i>	Euphorbiaceae	mesophanerophyte	dupe	zoochory	1-2 cm
<i>Guzmania oppositifolia</i>	Nyctaginaceae	microphanerophyte	dupe	zoochory	0.5-1 cm
<i>Hebeptalium</i> sp.	Linaceae	mesophanerophyte	dupe	zoochory	0.5-1 cm
<i>Hemipetala</i> sp. (*)	Melastomataceae	mesophanerophyte	berry	zoochory	<0.5 cm
<i>Hesperotis</i> sp.	Malpighiaceae	liana	samaras	anemochory	>2 cm (winged)
<i>Himatanthus bracteatus</i> (*)	Apocynaceae	mesophanerophyte	capsule	anemochory	unknown
<i>Hippocrateae</i> sp. (*)	Hippocrateae	liana or microphanerophyte	unknown	zoochory or anemochory	unknown
<i>Hirtella racemosa</i>	Chrysobalanaceae	mesophanerophyte	dupe	zoochory	0.5-1 cm 1-2 cm
<i>Humiria balsamifera</i> (*)	Humiriaceae	microphanerophyte	dupe	zoochory	0.5-1 cm 1-2 cm
<i>Inga latifolia</i> (*)	Mimosaceae	mesophanerophyte	pod	endozoochory	1-2 cm
<i>Inga stipitata</i>	Mimosaceae	mesophanerophyte	pod	endozoochory	1-2 cm
<i>Inga umbellifera</i>	Mimosaceae	microphanerophyte	pod	endozoochory	1-2 cm
<i>Inga virgultosa</i>	Mimosaceae	mesophanerophyte	pod	endozoochory	0.5-1 cm 1-2 cm
<i>Inga</i> sp. (*)	Mimosaceae	mesophanerophyte	pod	endozoochory	1-2 cm
<i>Licania maritima</i>	Chrysobalanaceae	microphanerophyte	dupe	zoochory	>2 cm
<i>Marikara bidentata</i>	Sapotaceae	megaphanerophyte	berry	zoochory	>2 cm
<i>Maytenus myrsinoides</i>	Celastraceae	mesophanerophyte	capsule	zoochory	1-2 cm
<i>Melastomataceae</i> sp. 1 (*)	Melastomataceae	liana	anemochory	autochory or zoochory	<0.5 cm
<i>Melastomataceae</i> sp. 2 (*)	Melastomataceae	phanerophyte	unknown	autochory or zoochory	<0.5 cm
<i>Miconia ciliata</i>	Melastomataceae	nanophanerophyte	berry	zoochory	<0.5 cm
<i>Miconia holosericea</i>	Melastomataceae	mesophanerophyte	berry	zoochory	<0.5 cm
<i>Miconia</i> sp.	Euphorbiaceae	mesophanerophyte	capsule	autochory or myrmecochochory	0.5-1 cm
<i>Mimosa</i> sp.	Rubiaceae	microphanerophyte	fleshy	zoochory	<0.5 cm 0.5-1 cm
<i>Myrcia caribaea</i>	Myrtaceae	mesophanerophyte	berry	zoochory	0.5-1 cm
<i>Myrcia fallax</i>	Myrtaceae	mesophanerophyte	berry	zoochory	0.5-1 cm
<i>Myrcia guianensis</i>	Myrtaceae	microphanerophyte	berry	zoochory	0.5-1 cm
<i>Myrcia guianensis</i>	Myrtaceae	mesophanerophyte	berry	zoochory	0.5-1 cm
<i>Myrcia saxatilis</i>	Myrtaceae	microphanerophyte	berry	zoochory	0.5-1 cm
<i>Myrcia sylvatica</i>	Myrtaceae	microphanerophyte	berry	zoochory	0.5-1 cm
<i>Myrciaria floribunda</i>	Myrtaceae	mesophanerophyte	berry	zoochory	0.5-1 cm 1-2 cm
<i>Myrciaria</i> sp. 1	Myrtaceae	phanerophyte	berry	zoochory	0.5-1 cm
<i>Myrciaria</i> sp. 2	Myrtaceae	phanerophyte	berry	zoochory	0.5-1 cm
<i>Myrtaceae</i> sp. 1 (*)	Myrtaceae	phanerophyte	fleshy	zoochory	0.5-1 cm or 1-2 cm
<i>Myrtaceae</i> sp. 2	Myrtaceae	phanerophyte	fleshy	zoochory	0.5-1 cm or 1-2 cm
<i>Myrtaceae</i> sp. 3 (*)	Myrtaceae	phanerophyte	fleshy	zoochory	0.5-1 cm or 1-2 cm
<i>Myrtaceae</i> sp. 4	Myrtaceae	phanerophyte	fleshy	zoochory	0.5-1 cm or 1-2 cm
<i>Myrtaceae</i> sp. 5	Myrtaceae	phanerophyte	fleshy	zoochory	0.5-1 cm or 1-2 cm
<i>Myrtaceae</i> sp. 6	Myrtaceae	phanerophyte	fleshy	zoochory	0.5-1 cm or 1-2 cm
<i>Neea ovalifolia</i>	Nyctaginaceae	mesophanerophyte	dupe-like	zoochory	1-2 cm
<i>Nyctaginaceae</i> sp.	Nyctaginaceae	microphanerophyte	dupe-like	zoochory	unknown
<i>Ocotea</i> sp.	Myrtaceae	microphanerophyte	berry	zoochory	0.5-1 cm 1-2 cm
<i>Ouretea candollei</i> (*)	Ochnaceae	mesophanerophyte	dupelet	zoochory	0.5-1 cm
<i>Ouretea lehmanni</i>	Ochnaceae	mesophanerophyte	dupelet	zoochory	1-2 cm
<i>Oreandra adscendens</i>	Aroniaceae	mesophanerophyte	fleshy	zoochory	>2 cm
<i>Parrisia excelsa</i>	Chrysobalanaceae	megaphanerophyte	dupe	zoochory	>2 cm
<i>Parkia</i> sp.	Mimosaceae	megaphanerophyte	pod	zoochory	1-2 cm
<i>Peltogyne paniculata</i>	Caesalpiniaceae	megaphanerophyte	pod	zoochory	>2 cm
<i>Petrea volubilis</i>	Verbenaceae	liana	wing-like calyx lobes	anemochory	0.5-1 cm
<i>Phyllanthus attenuatus</i>	Euphorbiaceae	microphanerophyte	capsule	probable autochory	<0.5 cm
<i>Picramnia guianensis</i>	Simarubaceae	microphanerophyte	berry	zoochory	0.5-1 cm 1-2 cm
<i>Piptocarpha schomburgkii</i>	Asteraceae	microphanerophyte	achene	anemochory	<0.5 cm
<i>Pogonophora schomburgkiana</i>	Euphorbiaceae	mesophanerophyte	capsule	autochory	<0.5 cm
<i>Polygala spectabilis</i>	Polygalaceae	nanophanerophyte	capsule	anemochory or myrmecochochory	0.5-1 cm
<i>Pouzourea</i> sp.	Oecropiaceae	microphanerophyte	dupe-like	zoochory	0.5-1 cm
<i>Protilum heptaphyllum</i>	Burseraceae	mesophanerophyte	dupe	zoochory	0.5-1 cm 1-2 cm
<i>Psychotria cineriflora</i>	Rubiaceae	microphanerophyte	berry	zoochory	0.5-1 cm
<i>Psychotria cupulifera</i>	Rubiaceae	microphanerophyte	dupe	zoochory	<0.5 cm 0.5-1 cm
<i>Psychotria hoffmannsengiana</i>	Rubiaceae	nanophanerophyte	dupe	zoochory	<0.5 cm
<i>Psychotria morioidea</i>	Rubiaceae	microphanerophyte	dupe	zoochory	<0.5 cm 0.5-1 cm
<i>Roupala montana</i>	Protaceae	mesophanerophyte	foliice	anemochory	0.5-1 cm
<i>Rubiaceae</i> sp. 1 (*)	Rubiaceae	phanerophyte	unknown	zoochory or anemochory	unknown
<i>Rubiaceae</i> sp. 2 (*)	Rubiaceae	phanerophyte	unknown	zoochory or anemochory	unknown
<i>Rudaea crassifolia</i>	Rubiaceae	microphanerophyte	dupe	zoochory	0.5-1 cm
<i>Sapota racemosa</i>	Sapotaceae	mesophanerophyte	capsule	autochory	0.5-1 cm
<i>Sapum montanum</i>	Euphorbiaceae	microphanerophyte	capsule	zoochory	<0.5 cm 0.5-1 cm
<i>Schefflera decaphylla</i> (*)	Araliaceae	megaphanerophyte	dupe	zoochory	0.5-1 cm
<i>Scolobolium albidiflorum</i>	Caesalpiniaceae	megaphanerophyte	pod	anemochory	>2 cm (winged)
<i>Securidaca uniflora</i> (*)	Polygalaceae	liana	samaras	anemochory	0.5-1 cm (winged)
<i>Smilax</i> sp.	Smilacaceae	liana	berry	zoochory	0.5-1 cm
<i>Souroubea guianensis</i>	Mangroveaceae	liana	berry	zoochory	<0.5 cm
<i>Tabebuia capitata</i>	Bignoniaceae	microphanerophyte	capsule	anemochory	>2 cm
<i>Tapirina guianensis</i>	Anacardiaceae	mesophanerophyte	dupe	zoochory	0.5-1 cm
<i>Terminalia amazonia</i>	Combretaceae	mesophanerophyte	dupe	anemochory	0.5-1 cm (winged)
<i>Terminalia dentata</i>	Theaceae	mesophanerophyte	berry	zoochory	1-2 cm
<i>Thrysochloa guianense</i> (*)	Anacardiaceae	mesophanerophyte	dupe	endozoochory	1-2 cm
<i>Zygia integrans</i>	Mimosaceae	mesophanerophyte	pod	endozoochory	1-2 cm
Undetermined 1 (*)		phanerophyte	unknown	unknown	unknown
Undetermined 2 (*)		phanerophyte	unknown	unknown	unknown
Undetermined 3 (*)		phanerophyte	unknown	unknown	unknown
Undetermined 4 (*)		phanerophyte	unknown	unknown	unknown
Undetermined 5 (*)		unknown	unknown	unknown	unknown

Herbs and suffrutescent plants	Family	Raunkiaer's life forms	Fruit types	Dispersion modes	Seed size
<i>Aechmea melinonii</i>	Bromeliaceae	hemicyptophyte	berry	zoochory	<0.5 cm 0.5-1 cm
<i>Aganisia pulchella</i> (*)	Orchidaceae	hemicyptophyte	capsule	anemochory	<0.5 cm
<i>Anthurium jernianii</i>	Araceae	hemicyptophyte	berry	zoochory	<0.5 cm
<i>Axonopus ramosus</i>	Poaceae	hemicyptophyte	caryopsis	anemochory	<0.5 cm
<i>Bromelia</i> sp.	Bromeliaceae	hemicyptophyte	berry	zoochory	<0.5 cm 0.5-1 cm
<i>Calathea squarrosa</i>	Marantaceae	geophyte	berry	zoochory or myrmecochochory	0.5-1 cm 1-2 cm
<i>Chamaecrista desousii</i>	Faboaceae	chamaephyte	pod	anemochory	<0.5 cm
<i>Chelonanthus alatus</i>	Gentianaceae	hemicyptophyte	capsule	anemochory	<0.5 cm
<i>Chelonanthus purpurascens</i>	Gentianaceae	hemicyptophyte	capsule	anemochory	<0.5 cm
<i>Cleistanthus rosea</i> (*)	Orchidaceae	therophyte	capsule	anemochory	<0.5 cm
<i>Cuphea blackii</i>	Lythraceae	chamaephyte	capsule	anemochory	<0.5 cm
<i>Cyperaceae</i> sp.	Cyperaceae	hemicyptophyte	achene	autochory or anemochory	<0.5 cm
<i>Dietegenthus lateralis</i>	Bromeliaceae	hemicyptophyte	capsule	anemochory	<0.5 cm
<i>Ellenanthus brasiliensis</i> (*)	Orchidaceae	hemicyptophyte	capsule	anemochory	<0.5 cm
<i>Eryodora onosma</i>	Orchidaceae	hemicyptophyte	capsule	anemochory	<0.5 cm
<i>Epilasia spheleia</i> (*)	Gesneriaceae	hemicyptophyte	capsule	autochory	<0.5 cm
<i>Guzmania fragilis</i>	Bromeliaceae	hemicyptophyte	capsule	anemochory	<0.5 cm
<i>Ichmanthus nemoralis</i>	Poaceae	hemicyptophyte	caryopsis	anemochory	<0.5 cm
<i>Jessenia batava</i>	Araceae	microphanerophyte	dupe	barochory or zoochory	>2 cm
<i>Lindaea</i> sp. (*)	Devonstefiaceae	hemicyptophyte	sporangium	anemochory	<0.5 cm
<i>Ludovia lancifolia</i>	Cyclanthaceae	hemicyptophyte	berry	zoochory	<0.5 cm
<i>Macrocerium cristatum</i>	Melastomataceae	chamaephyte	capsule	anemochory	<0.5 cm
<i>Olyra oligophylla</i>	Poaceae	hemicyptophyte	caryopsis	anemochory	<0.5 cm
<i>Paradyrmonia campocypa</i> (*)	Gesneriaceae	liana	capsule	autochory	<0.5 cm
<i>Paradyrmonia densa</i>	Gesneriaceae	liana	capsule	autochory	<0.5 cm
<i>Pariana campocypa</i>	Poaceae	hemicyptophyte	caryopsis	anemochory	<0.5 cm
<i>Phragmidium indigyanum</i> (*)	Orchidaceae	hemicyptophyte	capsule	anemochory	<0.5 cm
<i>Pitcairnia grysseii</i>	Bromeliaceae	hemicyptophyte	capsule	anemochory	<0.5 cm (winged)
<i>Poaceae</i> sp. 1	Poaceae	hemicyptophyte	caryopsis	anemochory	<0.5 cm
<i>Poaceae</i> sp. 2 (*)	Poaceae	hemicyptophyte	caryopsis	anemochory	<0.5 cm
<i>Poaceae</i> sp. 3 (*)	Poaceae	hemicyptophyte	caryopsis	anemochory	<0.5 cm
<i>Poaceae</i> sp. 4	Poaceae	hemicyptophyte	caryopsis	anemochory	<0.5 cm
<i>Poaceae</i> sp. 5 (*)	Poaceae	hemicyptophyte	caryopsis	anemochory	<0.5 cm
<i>Poaceae</i> sp. 6	Poaceae	hemicyptophyte	caryopsis	anemochory	<0.5 cm
<i>Sauvagesia alifolia</i>	Ochnaceae	chamaephyte	capsule	anemochory	<0.5 cm
<i>Schizaea peruviana</i>	Schizaceae	hemicyptophyte	sporangium	anemochory	<0.5 cm
<i>Scleria cypripina</i>	Cyperaceae	hemicyptophyte	achene	anemochory	<0.5 cm
<i>Scleria secans</i>	Cyperaceae	liana	achene	anemochory	<0.5 cm
<i>Selaginella</i> sp.	Selaginellaceae	hemicyptophyte	sporangium	anemochory	<0.5 cm
<i>Stelephylla surinamensis</i>	Cyclanthaceae	hemicyptophyte	berry	zoochory	<0.5 cm
<i>Stylasanthus guianensis</i>	Fabaceae	chamaephyte	pod	anemochory	<0.5 cm
<i>Syngnathus stratiolita</i>	Araceae	micro-mesophanerophyte	dupe	zoochory	>2 cm
<i>Vanilla ovata</i> (*)	Orchidaceae	liana	capsule	anemochory	<0.5 cm
<i>Vriesia gladiolifera</i>	Bromeliaceae	hemicyptophyte	capsule	anemochory	<0.5 cm 0.5-1 cm (plumose)
<i>Vriesia pleocarpa</i> (*)	Bromeliaceae	hemicyptophyte	capsule	anemochory	<0.5 cm 0.5-1 cm (plumose)
<i>Vriesia splendens</i>	Bromeliaceae	hemicyptophyte	capsule	anemochory	<0.5 cm 0.5-1 cm (plumose)