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

3

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6

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13

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15

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18

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19 Abstract

20

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

31

32 Introduction

33

34 Threats to biodiversity in tropical forests have largely been attributed to deforestation and
35 associated events such as habitat loss (Soares-Filho *et al.*, 2006) and climate drift (Wright,
36 2005). Fires attributed to El Niño Southern Oscillation (ENSO) dry climate anomalies have
37 also been invoked as a cause of present-day losses of biodiversity (Barlow *et al.* 2003),
38 similarly to fires involved in past extinctions (Charles-Dominique *et al.*, 2001; Anderson *et*
39 *al.*, 2007). In unmanaged tropical forests, major changes are expected to stem from global
40 warming as a chief result of the anthropogenic greenhouse effect (Rosenzweig *et al.*, 2008),
41 but recent observations show divergences between continents, Africa being most and South
42 America least threatened by associated aridity (Malhi & Wright, 2004). However, recent
43 climate studies established that northern South America, which is still more or less preserved

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

49

50 Forest fringes in the tropics ('low forests') are more prone to shifts in biodiversity than
51 adjoining environments such as savannas and tall-tree rain forests (Favier *et al.*, 2004), even
52 without any marked advance of ecotone limits (Noble, 1993). Our aim was to compare across
53 a ten-year interval (1995-2005), encompassing a severe ENSO dry event in 1997-98
54 (Laurance, 2000; Paine & Trimble, 2004; Wright & Calderon, 2006), the botanical
55 composition of a neotropical forest fringe, free of human activity for centuries, embracing a
56 wide floristic and environmental gradient (Sarhou *et al.*, submitted). Our main expectation
57 was that, as predicted by Jump & Peñuelas (2005), present-day global warming in the wet
58 neotropics is too fast for the long-term maintenance of species-rich communities at the forest
59 limit, as this has been shown to occur in more temperate zones of South America (Villalba &
60 Veblen, 1998). Juvenile forms of plants are expected to suffer more than reproductive stages
61 from severe El Niño years (Engelbrecht *et al.*, 2002), resulting in a deficit of recruitment
62 directly related to scarcity of the species. If this hypothesis is verified, then threats to
63 biodiversity due to global warming itself (Thomas *et al.*, 2004) should add to those stemming
64 from fragmentation and shrinkage of tropical forested areas (Curran *et al.*, 1999; Laurance,
65 2000).

66

67 **Materials and methods**

68

69 *Study site*

70

71 The study site is included in a forest reserve located in French Guiana (northern South
72 America, 4°5'N, 52°41'W) around the Nouragues inselberg, a granitic whaleback dome
73 (altitude 410 m) protruding from the untouched rain forest which covers the Guianas plateau
74 (Poncy *et al.*, 1998). The climate is perhumid (4000 mm annual rainfall) and warm (mean
75 temperature 27°C). Climate data were recorded over fifty years in a nearby meteorological
76 station (Regina) and show seasonal changes in monthly precipitation, with a long rainy season
77 from December to June (more than 300 mm per month) and a short dry season from July to
78 November (Fig. 1). A regular increase in temperature was observed over the last 50 years
79 amounting to 1.6°C, corresponding to a mean increase of 0.32°C per ten-year period. No
80 decrease in annual precipitation was observed over the same period, but four years (1958,
81 1976, 1997 and 2005) experienced a severe water deficit during the dry season, as exhibited
82 by the Aridity Index which reached a value of 2 or more during the dry season (Fig. 1). The
83 year 1997 was in the range of our botanical record (1995-2005), but the strong drought
84 recorded in 2005 occurred several months after the completion of our study. The same
85 warming trend was depicted by other meteorological stations in French Guiana, including
86 coastal (open) as well as widely forested areas (Table 1), thus it could not be ascribed to
87 potential effects of deforestation upon local climate (Marland *et al.*, 2003).

88

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

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

99

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

109

110 The tall-tree rain forest is comprised of a variety of late- and early-successional tree
111 species growing isolated or in small clumps (Poncy *et al.*, 2001), mostly disseminated by
112 rodents (Dubost & Henry, 2006), monkeys (Julliot, 1997) and bats (Lobova & Mori, 2004).
113 Due to the absence of hurricanes, a peculiarity of the ITCZ (Liebmann *et al.*, 2004), single
114 tree-fall gaps, rapidly invaded by pioneer plant species, are mainly responsible for the renewal
115 of the rain forest (Riéra, 1995; Van der Meer & Bongers, 2001). Dry periods, accompanied by
116 forest fires and severe erosion, occurred in the past three millenaries (Granville, 1982) and
117 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

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

158

159 Fractal dimensions were calculated for each transect using the slope of log-log curves
160 relating the semi-variance $\gamma(h)$ of the series to the lag (h) of autocorrelated data (Burrough,
161 1983; Gonzato *et al.*, 2000; Dale *et al.*, 2002). We used the linear portion of the log-log curve
162 to compute the fractal (Hausdorff) dimension according to the formula $D = 2 - m/2$, D being
163 the fractal dimension of the series and m the slope of the log-log curve.

164

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

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

171

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

174

175 Species accumulation or rarefaction curves (Simberloff, 1978; Colwell & Coddington,
176 1994) were calculated for the whole set of quadrats, in order to check for the
177 representativeness of our sampling effort, using EstimateS version 8.0 for Windows
178 (<http://viceroy.eeb.uconn.edu/estimates>). The expected number of species was calculated
179 using the first-order jackknife richness estimator JACK1, which is considered as the most
180 precise estimator for large sample sizes (Palmer, 1990).

181

182 **Results**

183

184 Species accumulation curves of woody plant species for the years 1995 and 2005 show that (i)
185 threshold values were nearly reached in both years, (ii) woody species total richness
186 (inselberg scale) was lower in 2005 compared to 1995 (Fig. 2). Over the three transects, 205
187 quadrats (2 m² each, totalling 410 m²) harboured a total of 19,591 individuals belonging to
188 102 species in 1995, compared to 14,871 individuals and 80 species in 2005, representing a
189 decrease of 24% for individuals and 22% for species. The expected species richness (JACK1
190 estimator) was 116.9 species in 1995 and 89.95 in 2005, thus not much higher than the
191 cumulative species richness.

192

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

199

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

205

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

213

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

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

219

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

224

225 **Discussion**

226

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

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

245

246 Other hypotheses for the observed collapse in plant species richness could be
247 proposed, but none is satisfactory. From the last dry period with wildfire events, which ended
248 600 years ago, the forest ecosystem could be in a phase of development, still far from
249 equilibrium (Odum, 1969). A decrease in plant species richness is commonly advocated in
250 late stages of ecosystem development, following competition for light and nutrients by a few
251 dominant species (Connell, 1979). In this case, development of the forest ecosystem
252 following a major disturbance is accompanied by an increase in basal area (Chazdon *et al.*,
253 2007), which was not supported by our data. It would also be accompanied by a change in the
254 distribution of species traits, in particular shade-tolerant tall tree species, with big seeds and
255 autochory, should be increasingly represented (Swaine & Whitmore, 1988; Whitmore, 1989;
256 Ter Steege & Hammond, 2001), which was not the case. The effects of CO² fertilization
257 issued from fossil fuel combustion would be similar, by stimulating the growth of dominant
258 species and increasing the basal area (Laurance, 2000). This hypothesis can be discarded too,
259 for the same reasons. Interestingly, recent results by Wardle *et al.* (2008) showed that
260 retrogression of forest ecosystems could occur in the absence of disturbance, displaying a
261 pronounced decrease in basal area, accompanied, or not, by concomitant changes in plant
262 species richness. Such a decrease in basal area was not observed, thus retrogression is not
263 supported by our data either.

264

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

267 Rosenberg & Ben-Haim, 2002; Mouritsen *et al.*, 2005). This can be thought to affect juvenile
268 stages of all plant species, a number of which currently die from damping-off (Hood *et al.*,
269 2004). Such an explanation cannot be considered as antagonist to the hypothesis of a severe
270 moisture deficit affecting all plant species. Rather, it should be considered as an additional
271 cause of mortality, affecting indiscriminately the whole array of plant species living in the
272 low forest.

273

274 Dramatic declines in plant species diversity were observed in temperate, boreal and
275 mountain areas, following forced or actual climate warming (Klein *et al.*, 2004; Walker *et al.*,
276 2006), but such trends had not been demonstrated in species-rich neotropical forests yet,
277 where most changes in tree growth, mortality and recruitment were attributed to rising CO²
278 (Laurance *et al.*, 2004) and only more recently to global warming (Feeley *et al.*, 2007).
279 Studies done at Barro Colorado, Panama, concluded that seedlings of common tree species
280 were not affected by the severe 1997-98 ENSO dry event (Engelbrecht *et al.*, 2002), although
281 previous studies on the same sites demonstrated long-term effects of severe El Niño years on
282 drought-sensitive species (Condit *et al.*, 1995). However, the same 1997-1998 ENSO event
283 was shown to be a main cause of biodiversity loss in tropical rain forests of Southeast Asia
284 (Harrison, 2001), and decelerating growth rates of tropical trees are now recorded worldwide
285 (Feeley *et al.*, 2007). Experimental studies showed that warming trends could result in
286 changes in species trait distribution, by privileging species better adapted to warmer climate
287 (Post *et al.*, 2008) or reaching dominance through increased growth (Harte & Shaw, 1995),
288 and it is now admitted that the rapidity of present-day climate warming is likely to affect the
289 capacity of adaptation of most plant communities (Walther, 2003; Jump & Peñuelas, 2005). In
290 American and African rain forests lianas have been shown to increase in species trait
291 representation (Phillips *et al.*, 2002; Wright & Calderón, 2005; Swaine & Grace, 2007; but

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

307

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309

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314

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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 R²
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**

666

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	
Liana	9.5	7	$\chi^2 = 2.18$
Nanophanerophyte	5	5	P = 0.98
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	

668

669

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

670

671

672 **Figure legends**

673

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

679

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

683

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

688

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

692

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

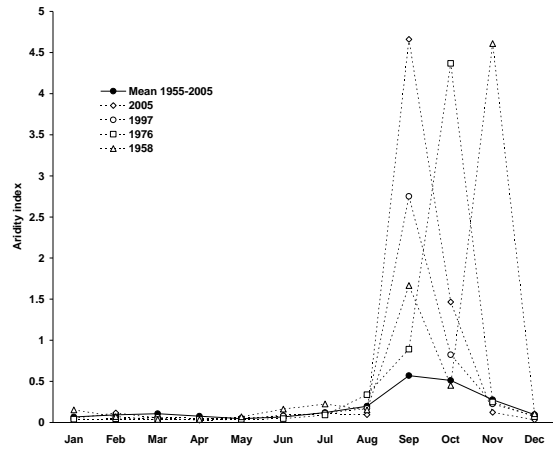
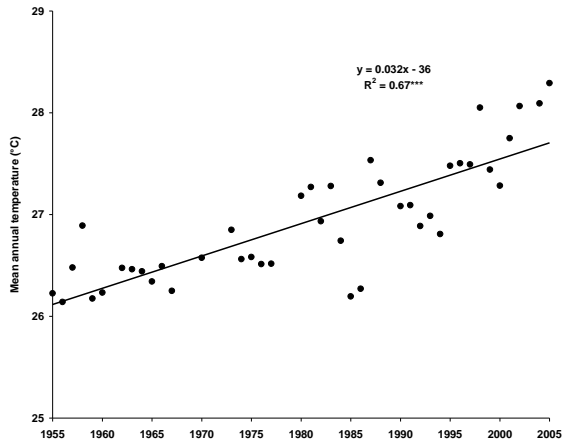
696

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

699

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

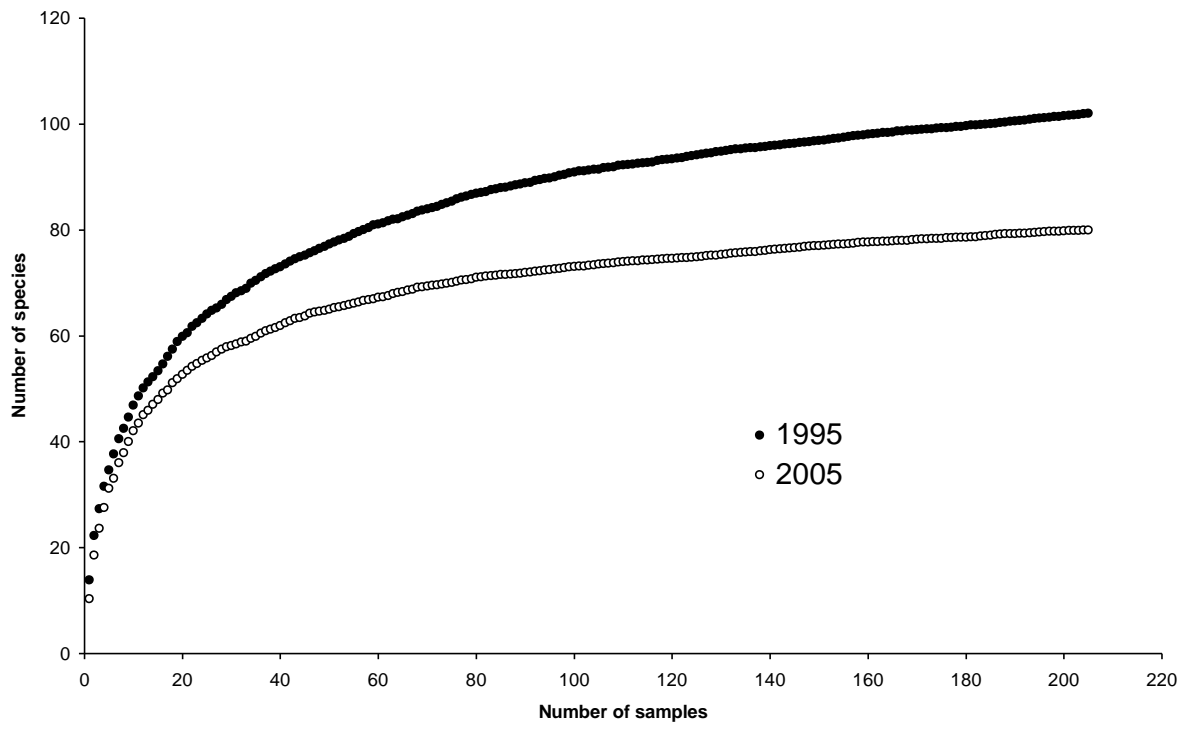
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706 **Fig. 1**

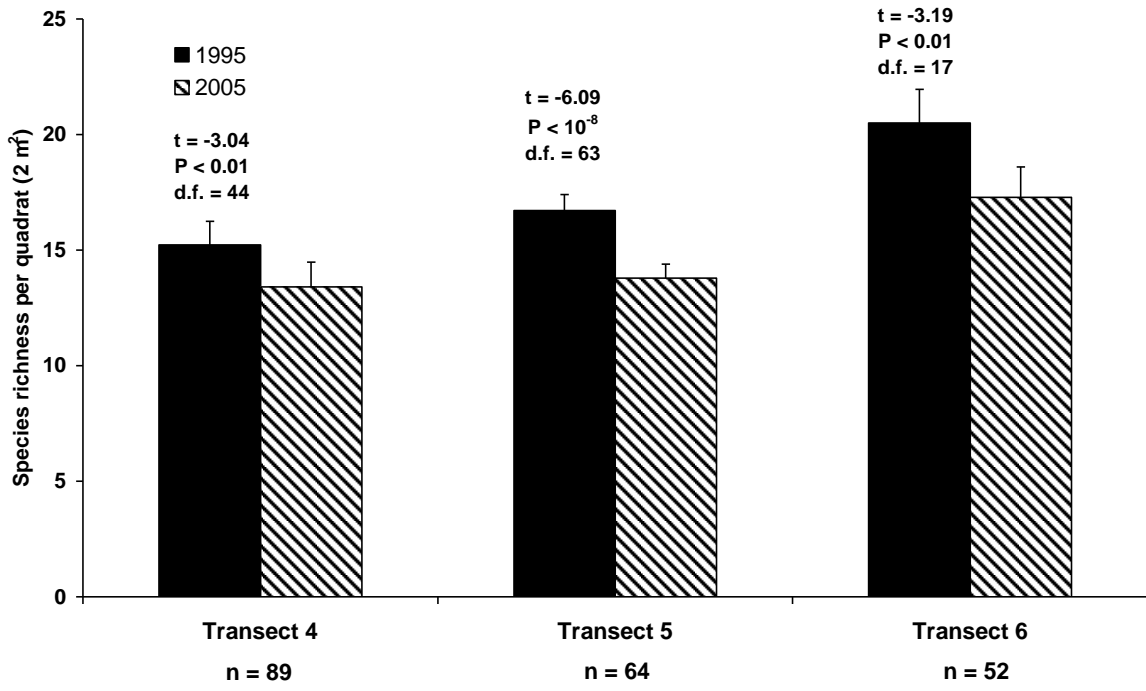
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709 **Fig. 2**

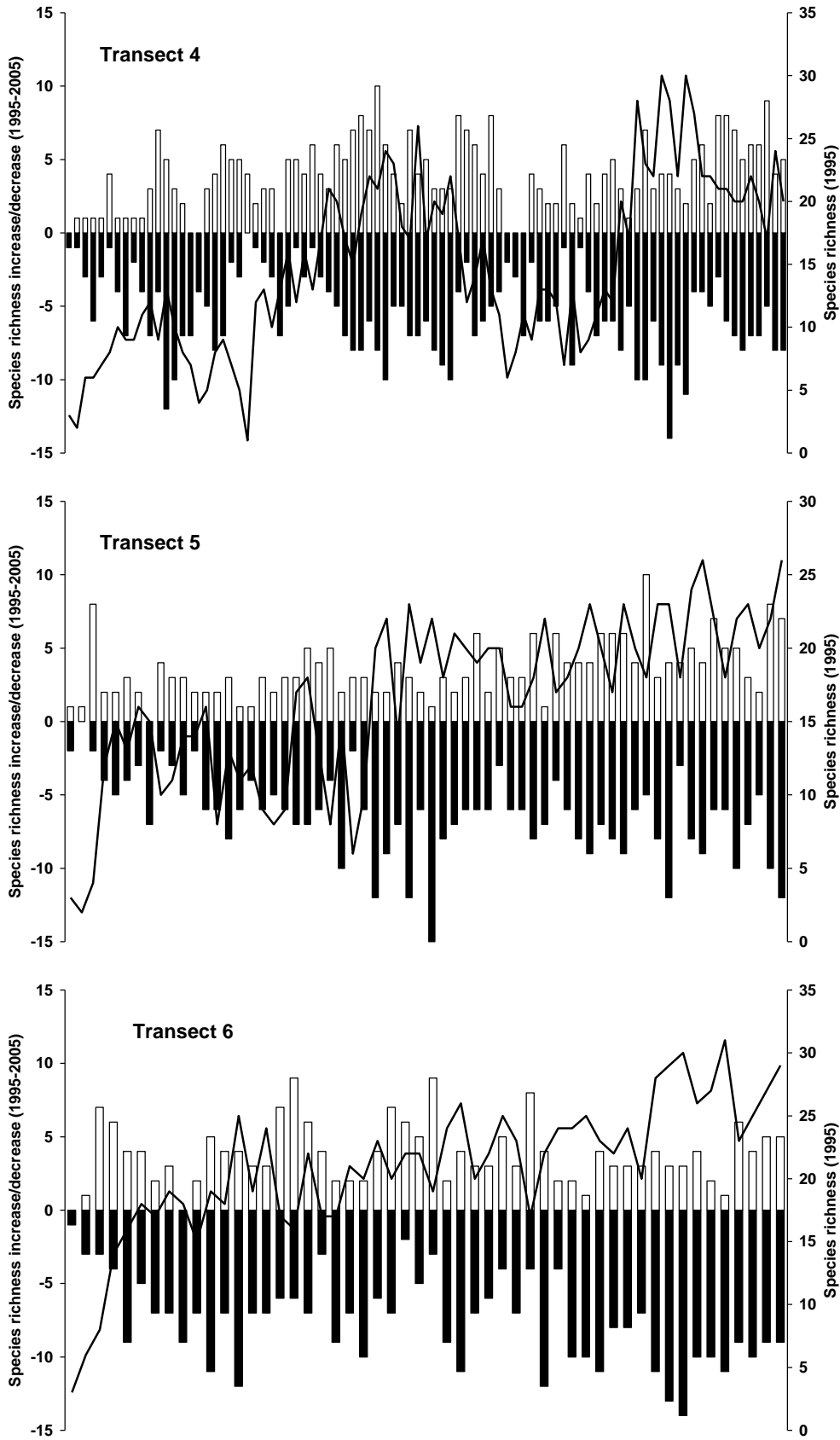
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712 **Fig. 3**

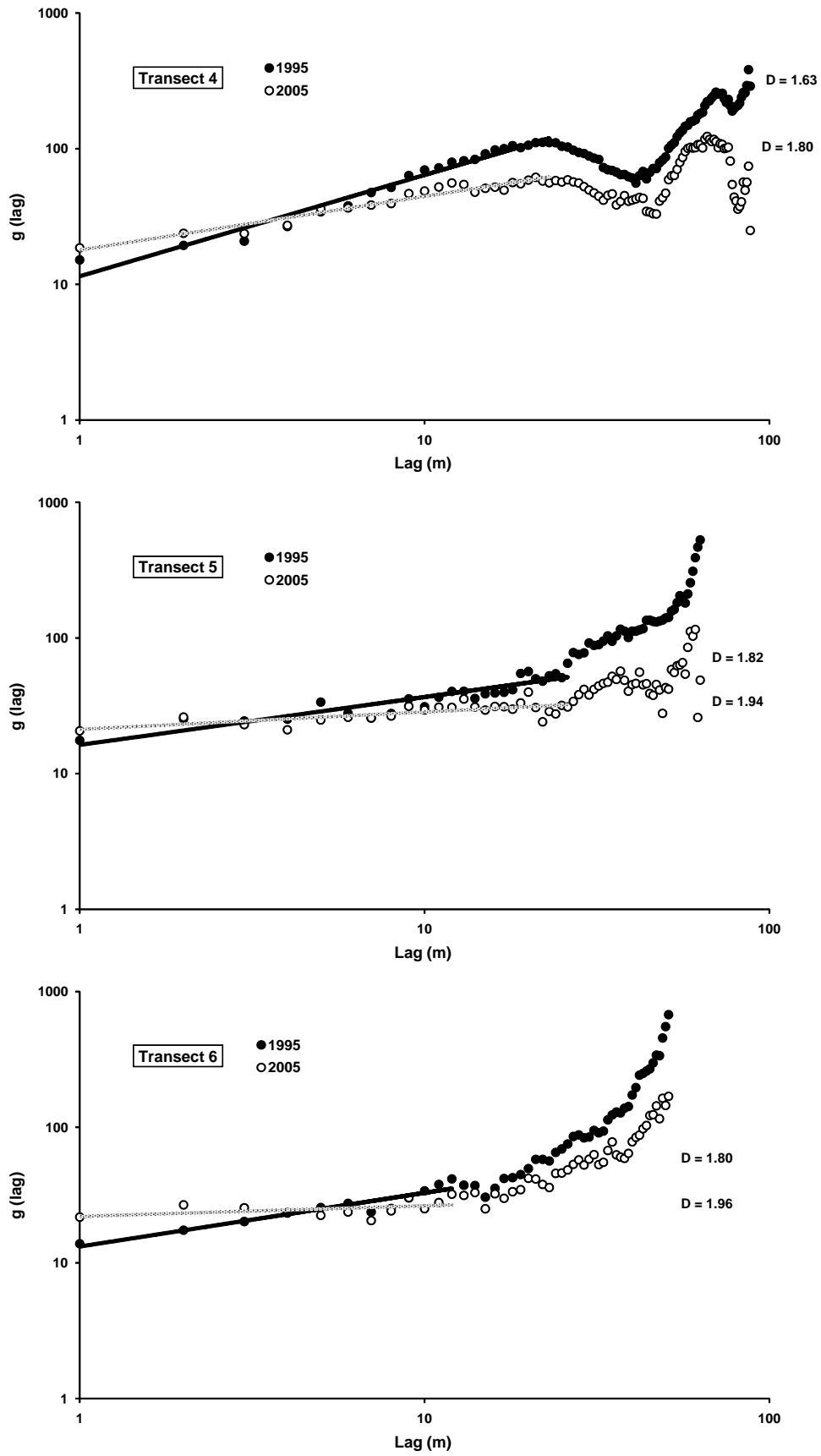
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715 Fig. 4

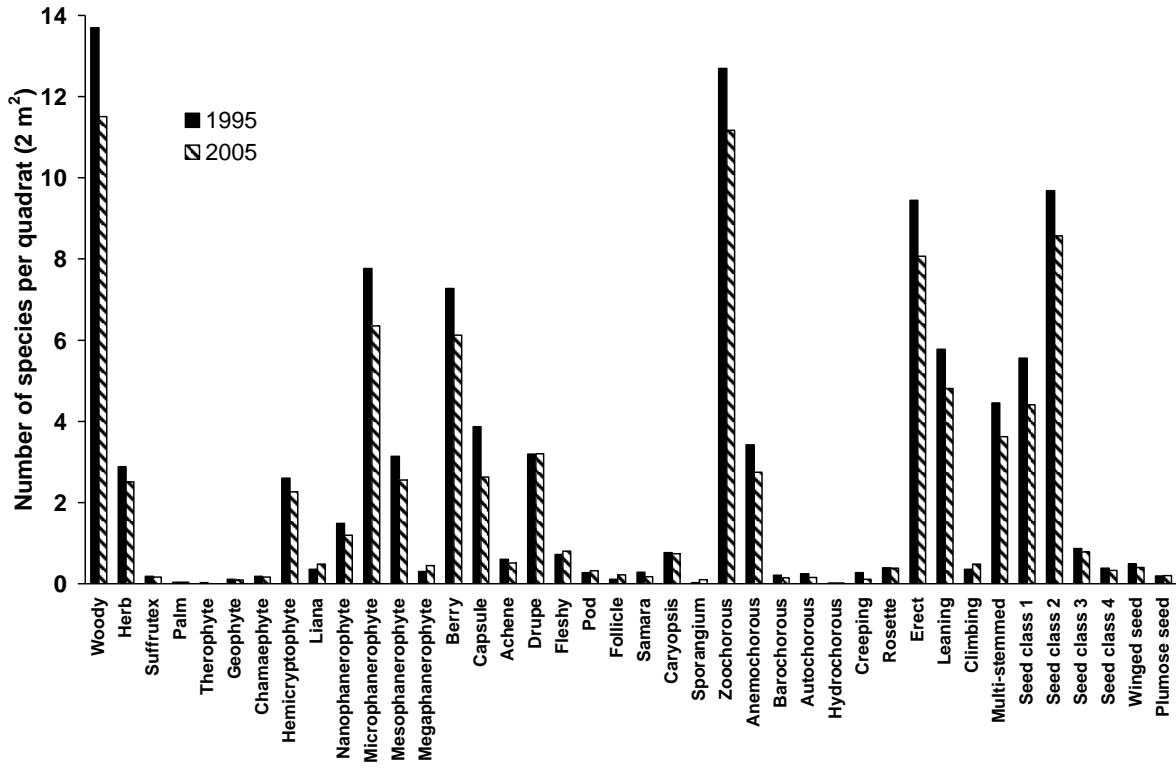
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718 Fig. 5

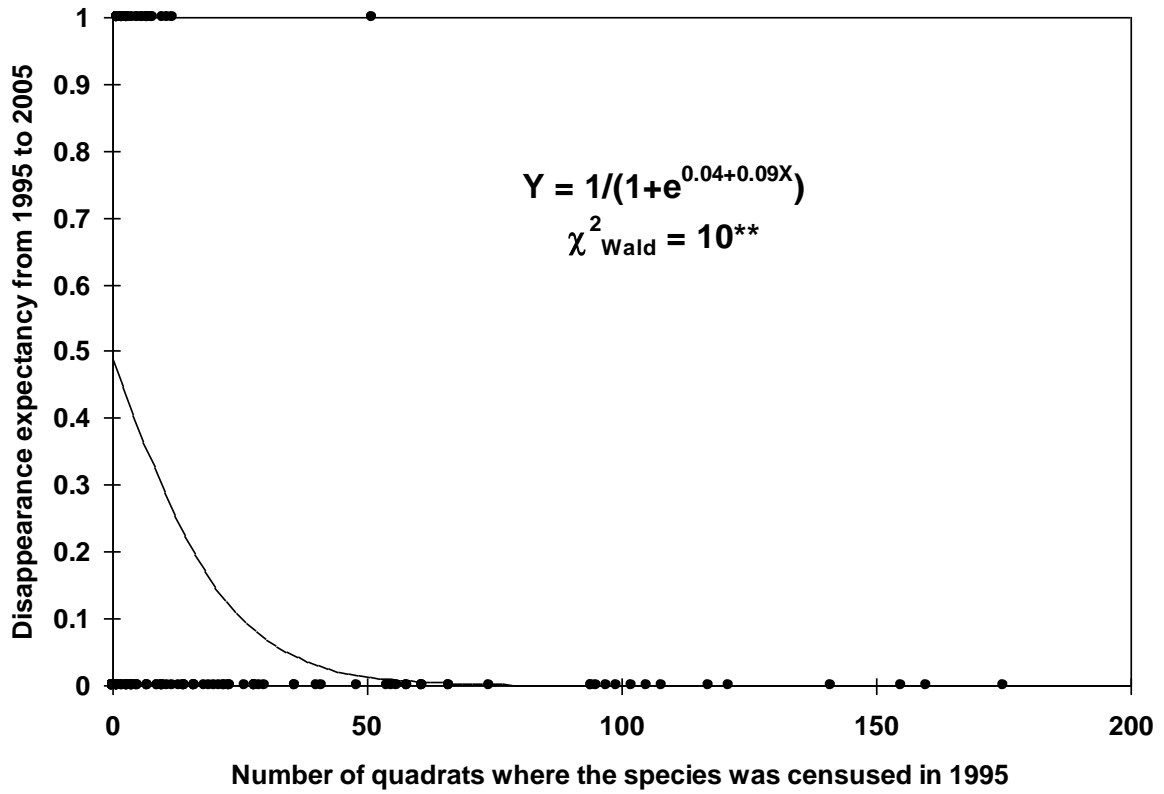
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720

721 **Fig. 6**

722



723

724 **Fig. 7**

725

