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24 **Abstract**

25

26 The combined effects of isolation within an unfavourable matrix and vegetation
27 development were studied in patches of scrub vegetation on a tropical inselberg (Nouragues,
28 French Guiana). Three thickets ~10 m² area were sampled, located at ~30 m distance from
29 each other, in which the same vegetation types were present at less than 3 m distance:
30 canopies of *Clusia minor* (Clusiaceae) and *Myrcia saxatilis* (Myrtaceae), two stages of thicket
31 development, and zones of destruction by fire. The shallow organic soil was sampled over ~2
32 dm² and down to 10 cm. The matrix was comprised of granite without any soil development.
33 Arthropods were classified into morphospecies and their food diets were characterized by
34 optical methods. The effect of isolation (between-thicket variation) on morphospecies
35 composition was negligible, while that of vegetation type and fire (within-thicket variation)
36 was prominent, as ascertained by principal component analysis and tested by partial
37 redundancy analysis. The importance of keystone structures (stages of vegetation
38 development) was stressed, and interpreted to the light of taxonomic and foodweb knowledge.

39

40 *Keywords:* arthropod communities, tropical inselbergs, keystone structures, isolation,
41 vegetation types, food diets

42

43 **1. Introduction**

44

45 The joint development of soil and vegetation exerts a profound influence on the
46 composition of soil animal communities (Parr, 1978). Trends in the abundance and diversity
47 of arthropod assemblages have been observed in primary as well as secondary successions,
48 and were interpreted as a response to changes in the amount and diversity of habitats and

49 resources (Shure and Ragsdale, 1977; Scheu and Schulz, 1996; Paquin and Coderre, 1997). In
50 fragmented landscapes, fragments may differ from each other due to dispersal limits for
51 wingless arthropods (Hopkins and Webb, 1984; De Vries and Den Boer, 1990; but see
52 Rantalainen et al., 2004). Dispersal barriers may impede soil invertebrates to colonize newly
53 created favourable habitats, thereby putting limits to the seral (successional) development of
54 their communities (Weigmann, 1982; Ojala and Huhta, 2001; Ponge et al., 2006).

55

56 Rocky outcrops, known in tropical rain forests under the name of inselbergs (Bremer
57 and Sander, 2000) are good models for studying the combined influence of isolation and
58 vegetation development. Habitats favourable to soil invertebrates are patches of vegetation
59 isolated within an unfavourable environment (matrix) made of granite covered with a thin
60 cyanobacterial biofilm (Sarhou et al., 1995; Sarhou and Villiers, 1998; Büdel et al., 2002). In
61 the absence of a continuous plant cover, soil is confined to vegetation clumps and rock pools
62 where organic matter (plant litter) or sand particles (granitic arena) accumulate, respectively
63 (Sarhou and Grimaldi, 1992; Porembski et al., 2000; Sarhou, 2001). Local disturbances,
64 such as lightning, create small gaps within shrub thickets and are the origin of micro-scale
65 successional processes which contribute to the renewal of the plant community (Ibisch et al.,
66 1995; Kounda-Kiki et al., 2008).

67

68 In a previous study on the Nouragues inselberg (French Guiana, South America) we
69 showed that soil arthropod communities differed between vegetation patches at varying stages
70 of development (Kounda-Kiki et al., 2004), but the influence of isolation has so far been
71 neglected. We expect that patches of invertebrate fauna will differ in their composition due to
72 the simultaneous influence of isolation and vegetation type. The question is which of these
73 factors prevails. We suggest that the vegetation type (including fire effects) is prevailing as it

74 dictates assembly rules, through (i) cascade effects within soil foodwebs (Hansen, 2000;
75 Wardle et al., 2004; Hedlund et al., 2004), and (ii) habitat cues to soil invertebrates (Evans,
76 1983; Salmon and Ponge, 2001; Coulson et al., 2003). For testing this hypothesis we selected
77 patches of shrub vegetation of similar area which were (i) isolated by vegetation-free granitic
78 terrain, (ii) were at the same stage of thicket development, (iii) showed distinct signs of
79 within-patch successional development. The influence of vegetation type and fire (within-
80 patch variation) will be compared to that of isolation (between-patch variation).

81

82 **2. Material and methods**

83

84 *2.1. Study sites*

85

86 The Nouragues inselberg (4°3'N, 52°42'W, alt. 410 m) is located in French Guiana
87 (South America), 100 km south of the Atlantic Coast, in the Nouragues Biological Reserve. It
88 is dome-shaped, of the so-called whaleback type (Bremer and Sander, 2000).
89 Geomorphological features of the Precambrian granitic substrate include flat surfaces, steep
90 slopes, depressions and gullies, with smooth pellicular erosion (exfoliation) due to high
91 thermic contrasts and chemical dissolution of plagioclases and potassic feldspars (Sarhou and
92 Grimaldi, 1992). Mean annual precipitation reaches 3250 mm, with a dry season from August
93 to November and a wet season from December to July, interrupted by a very short dry season
94 in March (Sarhou and Villiers, 1998). The air temperature varies daily from 18 to 55°C and
95 the air moisture varies from 20 to 100% (Sarhou, unpublished PhD thesis). The temperature
96 of the bare rock may reach 75°C in the dry season. Most of the surface is covered by
97 cyanobacteria (Sarhou et al., 1995), which take part in mineral weathering and fix carbon and
98 nitrogen (Sarhou and Grimaldi, 1992).

99

100 Vascular vegetation, locally called ‘rock savanna’ (English translation of ‘savane-
101 roche’), is made of scattered patches of herb and shrub communities (Fig. 1), but steep slopes
102 are covered only with cryptogamic vegetation. Organic soils (10-50 cm depth), acidic (pH
103 4.0-5.5), with a high faunal and microbial activity, are formed under patches of woody
104 vegetation where humified organic matter is prevented from flushing by a dense root network
105 (Sarhou and Grimaldi, 1992; Kounda-Kiki et al., 2006). The joint development of soil and
106 vegetation has been studied by Sarhou and Grimaldi (1992), Vaçulik et al. (2004), Kounda-
107 Kiki et al. (2006) and Sarhou et al. (2009). Two successional stages were determined within
108 shrub thickets, *Clusia minor* only (an epilithic Clusiaceae able to establish within
109 bromeliacean mats) as an earlier stage then a mixture of *C. minor* and several Myrtaceae such
110 as *Myrcia saxatilis*. The analytical study of humus profiles led to the conclusion that fire,
111 followed by fungal and termite activity, exerted a prominent role in the passage from the
112 *Clusia* stage to the *Clusia-Myrcia* stage (Kounda-Kiki et al., 2008; Sarhou et al., 2009).

113

114 2.2. Sampling and extraction of arthropods

115

116 In March 2006 we selected three shrub thickets (A, B, C) of quite similar area (~10
117 m²) on the lower terrace called ‘Les Terrasses’, south-west of a cliff, on slopes averaging
118 20%. They were located approximately at a distance of ~30 m from each other, forming a
119 triangle. They were separated by an undulating surface of granite without any vegetation
120 clumps inbetween. Inside each shrub thicket we selected three areas, each representing a stage
121 of the internal cyclic succession (Sarhou et al., 2009), (i) *Clusia* (Clu), a zone under the
122 canopy of *C. minor* only, (ii) a zone of destruction (Zd), with branch litter and accumulated
123 humus but without any woody canopy nor leaf litter, (iii) *Myrcia* (Myr), a zone under the

124 canopy of *M. saxatilis*. Samples taken within the same thicket were not at more than 3 m
125 distance from each other.

126

127 At the centre of each plot litter and soil were collected by forcing down an stainless
128 steel cylindrical frame with cutting edge (15 cm diameter, 10 cm height, 1.8 dm³). Care was
129 taken that litter, when present, was kept intact. Litter/humus samples were immediately put in
130 plastic bags then transported to the laboratory within three days. Extraction of arthropods
131 started immediately after arrival, by putting the samples into Berlese funnels (5 mm mesh
132 size, 15W bulb lights). Duration of extraction was 10 days, after checking for the absence of
133 last-minute fall of specimens. In order to keep enough free space around drying litter and
134 humus, each sample was halved then extracted in two distinct funnels. Specimens were
135 collected and preserved in 95% (v/v) ethyl alcohol until identification. In the absence of
136 taxonomic knowledge on most Guianan arthropods we classified specimens on the basis of
137 morphological characters which were visible at 40x magnification, i.e. we identified
138 morphospecies sensu Oliver and Beattie (1996). Morphospecies were further classified at a
139 supra-species level, mostly order.

140

141 The size of each morphospecies was measured to the nearest 10 µm by examining
142 bigger specimens with a micrometer in the eye piece of a dissecting microscope. Several
143 specimens of each morphospecies (10 when possible, less in other cases) were mounted in
144 chloral-lactophenol, and their gut contents were observed by transparency of after dissection.
145 Sizes of arthropods were classified in three classes: Size Class 1 (<0.4 mm), Size Class 2 (0.4-
146 1 mm) and Size Class 3 (>1 mm). Gut contents were classified into 9 categories and their
147 contribution to the mean diet of the morphospecies was visually estimated to the nearest 5%.

148 Empty guts mean that the animals either had not ingested anything at the time of extraction or
149 had a fluid food diet (sap, blood or prey externally digested).

150

151 *2.3. Data analysis*

152

153 The distribution of morphospecies was analysed by Principal Components Analysis
154 (Legendre and Legendre, 1998). Morphospecies were projected in a distance bi-plot diagram,
155 together with thickets (A, B, C) and vegetation types (Zd, Clu, Myr) as supplementary
156 (explanatory) variables. Other bi-plots were used to show the projection of community
157 descriptors (number of morphospecies, number of individuals, size classes, food items,
158 taxonomic groups), which were added as supplementary variables (calculated as %
159 individuals or morphospecies in each sample). Partial redundancy analysis, followed by
160 Monte-Carlo procedure, was used to test alternatively for residual effects of isolation (thicket)
161 or successional stage (vegetation type) after controlling for the other factor (Legendre and
162 Legendre, 1998). All these calculations were performed using XLSTAT[®] version 2008.2.01
163 (Addinsoft[®] software company).

164

165 Total species richness was estimated by functional extrapolation using the asymptotic
166 Michaelis-Menten function (Colwell and Coddington, 1994). The Jaccard index of similarity
167 was calculated between all pairs of samples. Calculations were performed using the free
168 software application EstimateS version 8.0 (<http://purl.oclc.org/estimates>).

169

170 **3. Results**

171

172 The Michaelis-Menten estimator for species richness, computed for the Mao Tau
173 species accumulation curve, was 263.5, thus our samples covered ~78% of the predicted total
174 species richness. Most specimens were mites (Acarida), encompassing 124 (60%) out of a
175 total of 205 morphospecies and 3472 (51%) out of a total of 6845 individuals. Collembola
176 were the second most abundant group in individuals (42%) but they represented only 7% of
177 the total number of morphospecies. There was an important pool of arthropods (35 to 60% of
178 morphospecies, 75 to 94% of individuals) common to all three vegetation types (Table 1) and
179 all three thickets (Table 2). They form the basic component of the inselberg arthropod
180 community, seemingly unaffected by either isolation or within-thicket vegetation dynamics. It
181 can be observed that the pool of species common to Clu and Myr was more important than
182 that common to either Zd and Clu or Zd and Myr (Table 1). The number of morphospecies
183 increased in the order Zd < Myr < Clu, while the number of individuals increased in the order
184 Myr < Clu < Zd.

185

186 Factor 1 of PCA (eigen value 35.7, 17.6% of total inertia) separated species associated
187 with destruction zones (Zd) from those associated with either *Clusia* (Clu) or *Myrcia* (Myr)
188 stages, while Factor 2 (eigen value 34.1, 16.9% of total inertia) separated Clu from Myr. The
189 three vegetation types (Zd, Clu, Myr) were projected far from the origin, while the three
190 thickets (A, B, C) were projected near the origin, thereby indicating that species composition
191 (as depicted by the two components with highest eigen values) was better explained by
192 within-thicket than by between-thicket variation (Fig. 2). This was verified by partial RDA
193 followed by Monte-Carlo permutation tests (500 permutations). When between-thicket
194 variation (isolation) was eliminated, within-thicket variation (vegetation type, successional
195 stage) explained a significant part of the residual variation ($P < 0.05$), while isolation did not
196 explain any residual variation when the effect of vegetation type was discarded ($P = 0.29$).

197

198 The bi-plot projection of community descriptors (Fig. 2) showed that Factor 1 opposed
199 morphospecies to individuals, depicting an opposite trend between Zd (many individuals but
200 few species) to Clu and Myr (more species but fewer individuals). The numerical abundance
201 of fauna in Zd was mainly due to microarthropods, i.e. mites (Acarida) and springtails
202 (Collembola). All taxonomic groups except Acarida and Collembola exhibited positive values
203 for Factor 1, both when counted as morphospecies and individuals. Acarida and Collembola
204 were more abundant in Zd (negative values for individuals) but more diversified in the other
205 two environments (positive values for morphospecies). The mean size of arthropods increased
206 with Factor 1, which was mainly due to an opposition between Size Class 1 (<0.4 mm) and
207 Size Class 2 (0.4-1 mm).

208

209 The bi-plot projection of food diets contributed by both individuals and morphospecies
210 (Fig. 3) showed that morphospecies feeding on bacterial and those with empty guts were
211 mainly found in Zd while those feeding on plant material were mainly found in Clu and Myr.
212 At the individual level, similar results were depicted, except that, in addition to discrepancies
213 mentioned above, more individuals consumed fungal spores and humified organic matter in
214 Zd.

215

216 Factor 2 of PCA opposed arthropod morphospecies living in Clu and Myr. There were
217 more morphospecies in Clu than in Myr (Table 1). Diptera, Crustacea and Pseudoscorpionida
218 were abundant in Myr, both as morphospecies and individuals, while Acarida exhibited a high
219 number of morphospecies (but not of individuals, which were higher in Zd) in Clu (Fig. 2).
220 Size classes differed also between Clu and Myr, with biggest arthropods (Size Class 3, >1
221 mm) associated with Myr. Concerning food diets, pollen and fungal hyphae were associated

222 with Clu, while individuals with empty guts, and morphospecies with animal prey (both
223 typical of predatory behaviour) were associated with Myr (Fig. 3).

224

225 **4. Discussion**

226

227 *4.1. The combined effects of isolation and vegetation type on arthropod communities*

228

229 Despite a low level of replication (3 thickets, 3 vegetation types in each), sampling
230 allowed to record 78% of the predicted total species richness. This can be explained by a high
231 degree of similarity among samples (mean Jaccard index 0.33 ± 0.06 mean \pm SD). Despite the
232 presence of a pool of species common to all thickets and all vegetation types, we showed that
233 the internal cycle of change within shrub thickets of the rock savanna controlled the
234 composition of arthropod communities both at the taxonomic and at the foodweb level and
235 that the effect of isolation was negligible compared to that of short-distance vegetation
236 change. Although distance separating thickets (30 m) was at least ten times that separating
237 samples inside a thicket (≤ 3 m), communities living in separate thickets differed less than
238 those living under different vegetation types within the same thicket. Can we apply to soil
239 animal communities the famous microbiologist's tenet that 'everything is everywhere, *but*, the
240 environment select' (De Wit and Bouvier, 2006) or is there another plausible explanation? We
241 can rule out that *Clusia* thickets were not isolated at all and that emigration and immigration
242 could take place in the absence of dispersal or ecological barriers. A thorough examination of
243 the granite substrate, either covered by cyanobacterial biofilms or not, did not reveal any
244 surface movement of animals, except termites (not found in our samples) and some
245 trombidids (only 4, belonging to the same morphospecies, among 6845 specimens found in
246 our samples). However, it should be considered that during the rainy season the granite

247 surface was regularly flushed down with precipitation water thus possibly transporting
248 invertebrates and their propagules (eggs, cocoons, pupae). This might explain passive
249 dispersal along gullies but not the existence of a widespread common population. Note that, if
250 dispersal of arthropods was effective on the inselberg, this cannot explain how nearby
251 communities might differ more than remote ones.

252

253 Further studies embracing a wide array of distances and topographical relationships
254 are awaited in order to measure the exchanges of species and of genotypes within species
255 which may occur between vegetation clumps. To the present state of our knowledge, we
256 cannot say whether vegetation clumps are issued from the fragmentation of a forest ecosystem
257 or from the colonization of vegetation 'islands'. However, the most plausible explanation for
258 the presence of a widespread pool of species in an otherwise harsh environment is that
259 present-day shrub thickets are remnants of a more complete cover by woody vegetation and
260 their associated organic soils.

261

262 Changes in soil arthropod communities are known to occur, in response to changes in
263 vegetation composition (Decaëns et al., 1998; David et al., 1999; Vohland and Schroth,
264 1999), age of trees (Baguette and Gérard, 1993; Loranger et al., 2001), amount of litter (Gill,
265 1969; Garay and Hafidi, 1990; David et al., 1991), soil/humus type (Van der Drift, 1962;
266 Chagnon et al., 2000; Loranger-Merciris et al., 2007), micro-climate changes (Majer, 1984;
267 Shure and Phillips, 1991) or these factors combined (Barclay-Estrup, 1974; Scheu and Schulz,
268 1996; Salmon et al., 2006). Considering the environment at the scale of a soil arthropod, each
269 shrub thicket of the rock savanna should be considered as a landscape in itself (Chust et al.,
270 2003), into which invertebrate communities are spatially organized in patches according to
271 small-scale environmental heterogeneity (Hamilton and Sillman, 1989; Torgersen et al., 1995;

272 Cannavacciuolo et al., 1998). Movements of animals within such landscapes will allow them
273 to select places favourable for foraging and reproduction and, of paramount importance in
274 harsh environments, refuges during unfavourable periods (Fairhurst, 1969; Joosse, 1981;
275 Huhta, 1996), thus without any depressive effect of habitat loss (Stanton and Tepedino, 1977;
276 Fahrig, 2003; Matlack and Leu, 2007). Competition and assembly rule mechanics (Drake,
277 1990) would reduce species richness at a much finer scale than that of the thicket, thus
278 without any strong and durable effect on the community as a whole (Ricklefs, 1987;
279 Bengtsson, 2002). The nested arrangement of scales of variation in the rock savanna of the
280 Nouragues inselberg seems quite different from that reported to occur in landscapes featured
281 by human activity and commonly studied in landscape ecology (Forman and Godron, 1981;
282 Harrison, 1991; Hanski, 1994), pointing on the importance of keystone structures, whatever
283 the scale at which they are distributed, in the determinism of soil arthropod assemblages
284 (Coulson et al., 2003; Tews et al., 2004). The heterogeneity observed at the inside of shrub
285 thickets of the rock savanna, governed by cycles of destruction by fire and shrub renewal, is
286 probably a decisive factor in the maintenance of a high level of biodiversity (Whittaker and
287 Levin, 1977; Niemelä et al., 1996; Hansen, 2000).

288

289 *4.2. The impact of fire*

290

291 The main effect of vegetation types on soil arthropod communities was the contrast
292 between zones of destruction by fire and *Clusia* or *Myrcia* canopies (Factor 1 of PCA, Figs. 2-
293 4). Most arthropods present in the organic matter accumulated in zones destroyed by fire were
294 microarthropods (<0.4 mm), mostly mites and springtails (Fig. 2). This size effect can be
295 explained by the absence of litter, which forces fauna to live in a network of small
296 interconnected pores (Kounda-Kiki et al., 2008) and by more unstable environmental

297 conditions which select for organisms with a shorter duration of life (Bazzaz, 1983; Bongers,
298 1990; Prinzing et al., 2002). The depressive effect on macroarthropods of gaps opened by fire,
299 windthrow or silvicultural practices has been registered (Huhta, 1976; Majer, 1984; Greenberg
300 and Forrest, 2003), although to the exception of the very short term (Siira-Pietikäinen et al.,
301 2003), as well as its counterpart, i.e. the development of a rich and diversified macroarthropod
302 population during the establishment and growth of woody vegetation (Shure and Ragsdale,
303 1977; Hutson, 1980; Scheu and Schulz, 1996). The role of litter in the maintenance of
304 macroarthropod populations has been verified experimentally (Pearse, 1943; David et al.,
305 1991).

306

307 From the examination of animal guts, it appeared that the number of arthropods
308 feeding on bacteria dominated in zones of destruction, opposed to those feeding on plant
309 material under *Clusia* and *Myrcia* canopies (Fig. 3). This indicated opposing trends between
310 foodwebs based on short-lived bacterial communities, associated with a high level of
311 disturbance (zones of destruction), and those based on plant litter and fungal decomposition,
312 associated with more stable environments (*Clusia* and *Myrcia* canopies), following the
313 scheme developed by Hedlund et al. (2004). In that sense, arthropod communities living in
314 zones of destruction resembled those living in cyanobacterial crusts, associated with pioneer
315 stages of vegetation and soil development (Vačulík et al., 2004), pointing on a temporary
316 return to early stages of plant succession after fire events.

317

318 4.3. *The impact of Clusia and Myrcia canopies*

319

320 Although secondary in importance, differences between *Clusia* and *Myrcia* canopies
321 were clearly expressed in the composition of arthropod communities (Fig. 2). The increase in

322 the size of arthropods under *Myrcia* canopies, already seen in a previous study done on shrub
323 thickets of varying plant composition (Kounda-Kiki et al., 2004), could be attributed to the
324 increased accumulation of litter under Myrtaceae (Kounda-Kiki et al., 2006), known for their
325 litter recalcitrance due to a high terpenic content (Haagen-Smit, 1953). More morphospecies,
326 although at a lower level of arthropod density, were living under *Clusia* than under *Myrcia*
327 canopies (Table 1), as shown in a previous study (Kounda-Kiki et al., 2004). This could be
328 due to an earthworm effect under *Clusia* (Kounda-Kiki et al., 2006): litter is buried more
329 efficiently, then spread in underlying horizons, thus offering a variety of niches with a limited
330 amount of resources in each to the other invertebrates (Szlavec, 1985; Marinissen and Bok,
331 1988; Hamilton and Sillman, 1989).

332

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334

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339

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613 **Figure captions**

614

615 **Figure 1.** Vegetation clumps on south-western slope of the Nouragues inselberg.
616 Bromeliacean carpets (*Pitcairnia geyskesii*) and shrub thickets (*Clusia minor*) are
617 separated by naked granite more or less covered with a cyanobacterial biofilm.

618

619 **Figure 2.** Principal component analysis. Projection of additional variables in the plane of the
620 first two components: taxonomic groups, size classes (Class 1 = <0.4 mm, Class 2 =
621 0.4-1 mm, Class 3 = >1 mm) and number of arthropods per sample, counted as
622 numbers of individuals (in italic type) or of morphospecies (in roman type), vegetation
623 types and thickets (A, B, C). Clu = *Clusia*; Myr = *Myrcia*; Zd = zones of destruction
624 by fire

625

626 **Figure 3.** Principal component analysis. Projection of additional variables in the plane of the
627 first two components: gut content categories, vegetation types and thickets (A, B, C).
628 Clu = *Clusia*; Myr = *Myrcia*; Zd = zones of destruction by fire

629

Table 1. Numbers of morphospecies per vegetation type and mean numbers of individuals per square metre, distributed according to their occurrence in one, two or three vegetation types. Zd = Zones of destruction. Clu = Clusia. Myr = Myrcia

	Zones of destruction	Clusia	Myrcia
Morphospecies			
Zd	22	0	0
Clu	0	44	0
Myr	0	0	30
Zd+Clu	17	17	0
Zd+Myr	14	0	14
Clu+Myr	0	28	28
Zd+Clu+Myr	48	48	48
Total	101	137	120
Individuals			
Zd	3989	0	0
Clu	0	5432	0
Myr	0	0	2546
Zd+Clu	5220	2165	0
Zd+Myr	1485	0	1358
Clu+Myr	0	14770	11077
Zd+Clu+Myr	121297	66972	50632
Total	131992	89339	65614

630

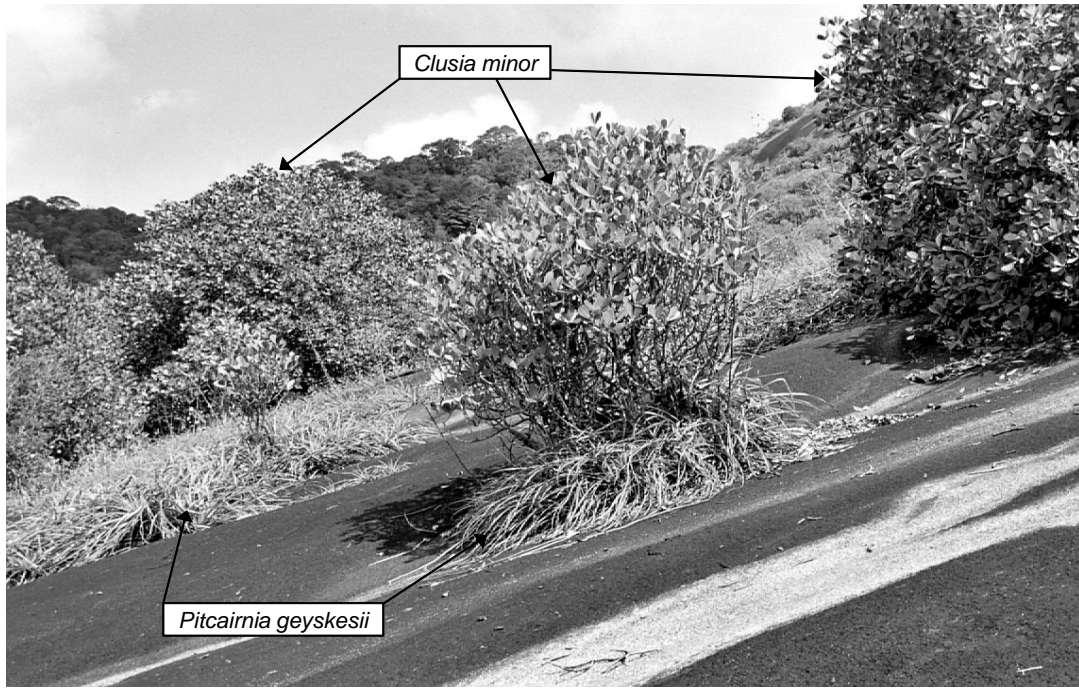
631

Table 2. Numbers of morphospecies per shrub thicket and mean numbers of individuals per square metre, distributed according to their occurrence in one, two or three shrub thickets (A, B, C)

	A	B	C
Morphospecies			
A	43	0	0
B	0	17	0
C	0	0	32
A+B	20	20	0
A+C	21	0	21
B+C	0	7	7
A+B+C	65	65	65
Total	149	109	125
Individuals			
A	6791	0	0
B	0	2801	0
C	0	0	3438
A+B	3226	3141	0
A+C	4117	0	3395
B+C	0	976	1188
A+B+C	80766	102453	78219
Total	94899	109371	86241

632

633



634

635 Fig. 1

636



637

638 Fig. 2

639

