Nested variation of soil arthropod communities in isolated patches of vegetation on a rocky outcrop

Charlotte Kounda-Kiki, Léonide Célini, Jean-François Ponge, Philippe Mora, Corinne Sarthou

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Names of authors: C. Kounda-Kiki, L. Celini, J.F. Ponge^{*}, P. Mora, C. Sarthou

Complete postal addresses or affiliations:

C. Kounda-Kiki, J.F. Ponge, C. Sarthou: Muséum National d'Histoire Naturelle, CNRS UMR 7179, 4 avenue du Petit-Château, 91800 Brunoy, France

L. Celini, P. Mora: Université Paris 12, UMR 137 BioSol, Laboratoire d'Écologie des Sols Tropicaux, 61 avenue Henri-Varagnat, 94010 Créteil Cedex, France

Full telephone, Fax number and E-mail address of the corresponding author:

Tel. +33 1 60479213

Fax +33 1 60465009

E-mail: ponge@mnhn.fr

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^{*} Complete correspondence address to which the proofs should be sent: Jean-François Ponge, Muséum National d'Histoire Naturelle, CNRS UMR 7179, 4 avenue du Petit-Château, 91800 Brunoy, France

Abstract

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

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

1. Introduction

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

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

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

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

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

2. Material and methods

2.1. Study sites

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

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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), Vačulik 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).

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114 2.2. Sampling and extraction of arthropods

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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

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

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

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

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

2.3. Data analysis

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

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

3. Results

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

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

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

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

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

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

4. Discussion

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

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

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

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

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

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

4.2. *The impact of fire*

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

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

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

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

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

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

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Figure captions

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

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

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

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

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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

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635 Fig. 1

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Fig. 2