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Distribution of soil and litter arthropods on Aldabra Atoll

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Data from a general survey of the soil and litter arthropods of Aldabra have been analysed in an attempt to reveal patterns in the distribution of the species. Analysis by means of a similarity index suggests that their distribution within 14 sites that were sampled quantitatively is to a large extent independent of vegetation type. This is supported by the results of a correspondence analysis of the faunal content of a total of 70 sites representing a variety of vegetation types from several localities around the atoll. It is suggested that this apparent lack of any clear association between vegetation type and fauna may be due to niche expansion by the immigrant species.

Introduction

There have been a number of publications dealing with the soil and litter invertebrates of Aldabra. Most of these have been taxonomic studies or records of occurrence (see Westoll & Stoddart (orgs) 1971 for references), but Spaull (1976) described certain aspects of the biology of a millipede on Aldabra, and Peake (1971) discussed the species–area curve of terrestrial Mollusca on the atoll compared with other islands in the western Indian Ocean. None have described the overall distribution of the soil and litter fauna on Aldabra. By using data collected over a period of 18 months, an attempt was made to correlate the distribution of selected groups of arthropods with the litter associated with different species of plants. The results are described in this paper.

The vegetation on Aldabra forms a complex of evergreen and semideciduous scrub and scrub forest together with a variety of grasses, sedges and ephemeral herbs. Apart from areas dominated by a single species it is difficult to recognize distinct habitat types, as delimited by the presence of recurring constant associations of plant species. Consequently, for the present study, the litter below one particular plant species was considered to be one type of habitat. An exception to this was the 'mixed scrub' litter. Here the plant species were often growing so close together that the litter below one species frequently included that produced by neighbouring, different species. In selecting the sample sites an effort was made to include examples of all the more common litter habitats on Aldabra.

Sample sites and extraction of the arthropods

Replicated quantitative samples of soil and litter were taken from the following habitats, the primary sample sites. (The location of place names used in this paper can be found in Stoddart 1971.) (1) *Casuarina equisetifolia* woodland near the old settlement, Ile Picard and (2) at Anse Cèdres, Ile Grand Terre; (3) *Calophyllum inophyllum* woodland, Takamaka Grove, Ile Grande Terre; (4) *Pandanus tectorius* scrub near Pointe Hodoul, Ile Grande Terre; (5) mixed scrub near

Croix Blanc, Ile Grande Terre – plant species included *Ochna ciliata*, *Polysphaeria multiflora* and *Ficus nautarum*; (6) mixed scrub near the Royal Society's research station, Ile Picard – plant species included *Acalypha claoxyloides*, *Azima tetracantha*, *C. equisetifolia*, *Dracaena reflexa*, *Clerodendrum glabrum*, *Erythroxylon acranthum*, *Euphorbia pyrifolia*, *Gouania scandens*, *Ipomoea macrantha*, *Maytenus senegalensis*, *O. ciliata* and *Tarenna supra-axillaris*; (7) *Pemphis acidula* scrub near Middle Camp, Ile Malabar, (8) at Anse Porche, Ile Malabar, (9) northeast of Anse Polymnie, Ile Polymnie and (10) north of Dune d'Messe, Ile Grande Terre; (11) *Fimbristylis* cf. *cymosa* turf growing beneath *C. equisetifolia* near Middle Camp, Ile Malabar; (12) *Cyperus niveus* turf amongst coconut trees (*Cocos nucifera*); (13) *Cyperus ligularis* turf at Anse Malabar, Ile Malabar; (14) *Sporobolus virginicus* turf inland of Dune Patates, Ile Grande Terre.

The arthopods were extracted from the samples over a 9 day period using Tullgren funnels similar to those described by Macfadyen (1961, fig. 2) except that there was no air conditioning. Species counts were made within the Isopoda, Diplopoda, Pseudoscorpiones, Chilopoda, Coleoptera, Diplura, Symphyla, Pauropoda, Embioptera, Psocoptera, Dictyoptera, Thysanoptera, Hemiptera, and Thysanura. Only a few of the species have been identified to a binomial but the others were recognized as distinct taxa. Representatives of all the species collected on Aldabra have been deposited at the British Museum (Natural History). In addition to the quantitative samples from the 14 primary sites, other samples of soil and litter were collected by hand from 56 secondary sites representing a variety of different vegetation types around the atoll. A list of these sample sites and their location on Aldabra are given in appendix 1. The soil and litter from these secondary sites were sorted by hand and a record kept of the species present.

Correlation of the arthropod fauna with different vegetation types

In order to reveal patterns in the distribution of the arthropod fauna and to characterize the different vegetation types, three methods were used to analyse the data from the sample sites: (*a*) the similarity method of Renkonen (1938); (*b*) the reciprocal averaging method of Hill (1973, 1974); (*c*) the rarefaction technique of Sanders (1968).

(*a*) *Renkonen's index of similarity*

The fauna of the 14 primary sites were compared by using the similarity method of Renkonen (1938). The degree of similarity is calculated for any pair of sites by selecting and summing the lower relative abundance value for each of the species present in both sites. Species absent from one site are ignored. This calculation was made for all the possible pairs of sites and the hierarchial relation of the sites, based on their degree of similarity, was then determined by using the method of Mountford (1962) (figure 1). It is clear from the figure that in several instances different vegetation types possess a more comparable fauna than similar vegetation types (compare the four *Pemphis* sites, the two *Casuarina* sites and the two mixed scrub sites). This was unexpected since it was assumed at the outset that major differences in the vegetation would result in marked differences in the type of habitat within the litter and that the fauna would be a reflexion of these differences.

(*b*) *Reciprocal averaging*

Data from both the primary sample sites and the non-quantitative secondary sample sites were analysed by means of a type of correspondence analysis known as reciprocal averaging

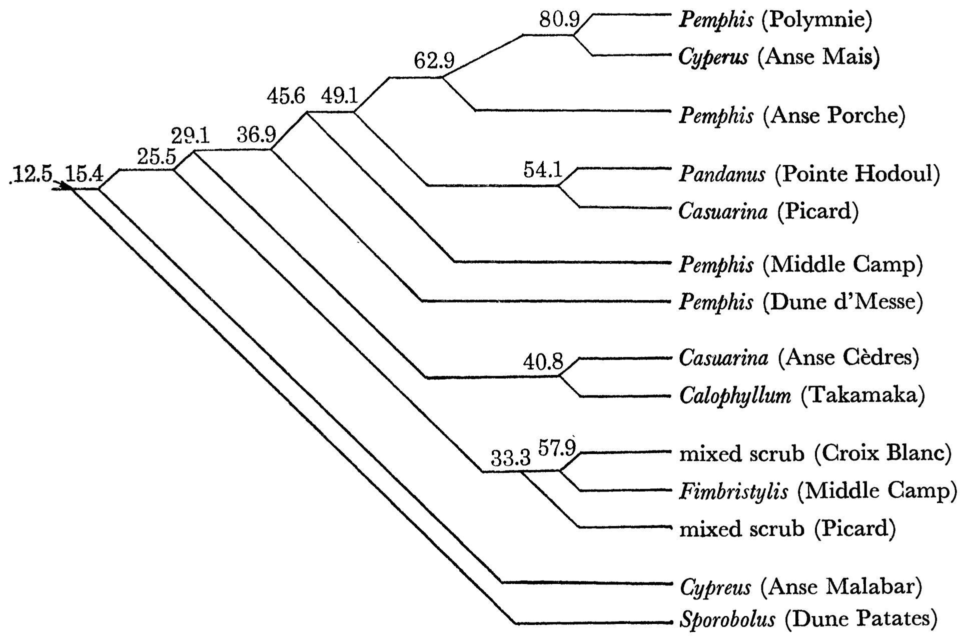

FIGURE 1. Hierarchial relation of the primary sample sites based on their degree of similarity. Derived from the Renkonen numbers of the sites by using 49 species of the selected arthropod groups.

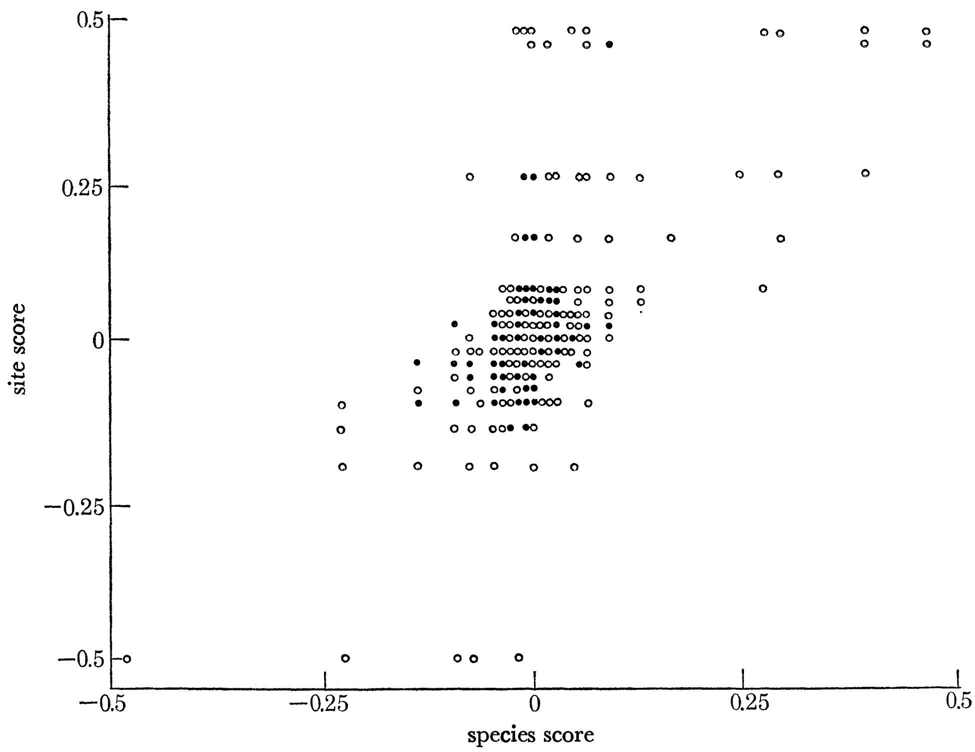

FIGURE 2. Computer print-out of the reciprocal averaging scores of arthropod species plotted against the scores of the sample sites in which they occur. See appendices 1 and 2 for a list of the scores of sites and species. Full circles represent multiple points.

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(Hill 1973, 1974). The data consisted of 60 species (belonging to 12 groups of arthropods) distributed through the 56 secondary sites and the 14 primary sites. Briefly, the analysis was carried out as follows: arbitrary weighting was given to the species by scoring each species in sequence from 1–60. The site scores were then obtained by averaging the scores of the species within the

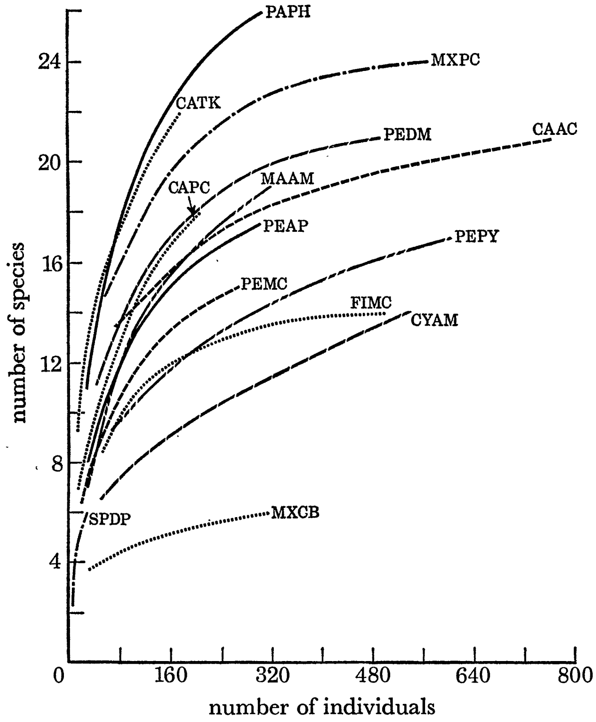

FIGURE 3. Species diversity curves for the 14 primary sites. Sample site abbreviations as follows: CAPC, *Casuarina*, Ile Picard; CAAC, *Casuarina*, Anse Cèdres; CATK, *Calophyllum*, Takamaka; PAPH, *Pandanus*, Pointe Hodoul; MXCB, mixed scrub, Croix Blanc; MXPC, mixed scrub, Ile Picard; PEMC, *Pemphis*, Middle Camp; PEAP, Pemphis, Anse Porche; PEPY, *Pemphis*, Ile Polymnie; PEDM, *Pemphis*, Dune d'Messe; FIMC, *Fimbristylis*, Middle Camp; CYAM, *Cyperus niveus*, Anse Mais; MAAM, *C. ligularis*, Anse Malabar; SPDP, *Sporobolus*, Dune Patates.

sites. The site scores were then rescaled such that the sum of the scores corresponded to zero and the sum of squares of the scores corresponded to one. This recalibration prevented convergence to trivial solutions. Improved calibrations for the species were obtained from these rescaled site scores by averaging the scores of the sites in which the species occurred. These species scores were then recalibrated and used to calculate new site scores. The process was repeated until the scores stablized, at which point they were considered to be the final ordination. This method of reciprocal averaging maximizes the correlation between site scores and species scores and thus gives the most meaningful characterization of the sites and species. The greater the similarity between the species content of two or more sites, the more comparable are the site scores, and the greater the number of occasions that two or more species occur together in the same sites, the more comparable their scores.

Together the 60 species were recorded on 687 occasions in the 70 sites. The scores of each of the sites and species are given in appendixes 1 and 2 respectively. Figure 2 shows the species scores plotted against the scores of the sites in which the species occur. Most of the site and species scores are concentrated around the zero point. In fact the scores of 62 of the 70 sites and

50 of the 60 species fall within the range −0.1 to +0.1. This indicates that the species composition of most of the sites is broadly similar. It therefore appears that, for the most part, vegetation type does not limit the distribution of soil and litter arthropods on Aldabra.

(*c*) *Rarefaction*

There is further evidence that, based on faunal composition, different vegetation types on Aldabra cannot be separated into distinct groups. Applying the rarefaction technique developed by Sanders (1968) and modified by Simberloff (1972) to the (selected) species composition of the 14 primary sample sites the relative species diversity of the sites can be illustrated as shown in figure 3. Rarefaction is a method whereby, from an analysis of the relative frequency of specimens within species, an estimate can be made of the number of species that would have been present had the sample size been smaller (the size of the sample here being the number of specimens extracted from the litter). Thus it is possible to compare estimated diversities at a constant sample size. It should be noted that such comparisons can only be made if the curves do not cross. It is clear from figure 3 that the species diversity curves for the primary sample sites form a series of increasing diversity but that there is no clear separation of dissimilar sites or grouping of similar sites. By definition, habitats of similar complexity have broadly similar species diversities and diversity reflects the number of available niches within one habitat, or at least the number of occupied niches. Thus it is concluded from the diversity curves that the number of niches available or occupied in the primary sample sites is not sufficiently different to allow distinct habitat groups to be recognized.

Discussion

During the present survey, samples were taken from the soil and litter below 12 species of broad leafed scrub plants belonging to ten families, 1 species of narrow leafed tree, 2 species of two families of broad leafed trees, 4 species of sedges, 1 species of grass, 1 species of orchid as well as from beach debris. Such a variety of sample sites might be expected to include a number of contrasting invertebrate habitats each containing a recognizably distinct fauna. For example, the litter below *Calophyllum* (broad leaves, constant shade, relatively moist conditions and overlying a deep organic soil) appears to be very different from that below *Pemphis* (small leaves, never completely shaded, relatively dry and overlying a shallow organic soil), and both contrast with the litter below *Casuarina* (needle-like minutely leaved twigs, partly shaded and overlying a deep sandy soil). However, analysis by the Renkonen method and reciprocal averaging indicates that, with a few exceptions, the distribution of the selected soil and litter arthropods on Aldabra is largely independent of vegetation type.

This apparent lack of any clear association between vegetation type and fauna may, possibly, be due to niche expansion by the immigrant species. Such ecological expansion is a common feature of island faunas and is explained by the ability of colonizing species to occupy a more diverse niche if competitors are absent (see MacArthur 1972; MacArthur & Wilson 1967). On Aldabra, competition is likely to be small since the species: family and species: genus ratios of the soil and litter arthropods, for which data are available, are very low (table 1, see also Cogan, Hutson & Schaffer 1971).

Data given by Stoddart & Walsh (1979, this volume) indicate that there have probably been long term fluctuations in rainfall on Aldabra, ranging from periods of drought to periods of

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relatively high rainfall in successive years. Such a climate might be expected to select those species that can survive arid conditions and cause the extinction of less tolerant species. It would thereby reduce the number of potential competitors and thus compound the ecological expansion of the successful species. This expansion may also be increased by the short-term or localized fluctuations in rainfall that have been recorded on Aldabra (Hnatiuk 1979, this volume). Relating birthrate, death rate and maximum population size attainable on an island with the probability of survival of propagules and the average duration of populations, MacArthur & Wilson (1967) showed that populations that cannot exceed some very small size are likely to become extinct much faster than those that can reach a very large size. Thus recent immigrants that can not multiply rapidly due to an unfavourable climate are likely to become extinct before they can compete with older more successful colonists. If the fluctuations in rainfall, both temporal and local, are sufficient to cause repeated extinctions of the fauna then at any one time opportunist species that have a high dispersal and reproductive potential and can tolerate new conditions, but are not necessarily good competitors, are likely to form a large proportion of the fauna on Aldabra. Conversely, more specialized species which are better competitors but which have a slower rate of colonization are likely to form a small proportion of the fauna.

TABLE 1. NUMBERS OF FAMILIES, GENERA AND SPECIES OF SELECTED GROUPS OF SOIL AND LITTER INVERTEBRATES ON ALDABRA

group	no. of families	no. of genera	no. of species	species/ family	species/ genus
Coleoptera	16	22†	27	1.7	1.2‡
Hemiptera	8	8†	9	1.1	1.1‡
Hymenoptera	1	6	7	7.0	1.2
Embioptera	1	1	1	1.0	1.0
Dermaptera	1	1	1	1.0	1.0
Dictyoptera	1	2	2	2.0	1.0
Collembola	4	9	10	2.5	1.1
Diplura	2	2	2	1.0	1.0
Isopoda	5	7†	8	1.6	1.1‡
Pseudoscorpiones	5	6	6	1.2	1.0
Scorpiones	1	1	1	1.0	1.0
Schizopeltida	1	1	1	1.0	1.0
Diplopoda	4	4	4	1.0	1.0
Chilopoda	3	3†	6	2.0	2.0‡
Symphyla	1	1	1	1.0	1.0
Pauropoda	1	1	1	1.0	1.0

† Minimum number. ‡ Maximum ratio.

As a result of reciprocal averaging, the exceptional site scores reflect the restricted distribution of some of the species within the sites. Such a distribution may be due to the special habitat requirements of these species. For example the pseudoscorpion *Anagarypus oceanus-indicus* (score +0.3889) and the isopod *Tylos minor* (score +0.4613) are both restricted to similar coastal habitats, namely beneath driftwood and other dry vegetation cast up onto the beach crest. *A. oceanus-indicus* was also found among the basal shoots of *Cyperus ligularis* growing a short distance inland from the beach crest. It should be noted, however, that neither the isopod nor the pseudoscorpion were present in a sample taken from *C. ligularis* growing in a similar situation near Dune Jean-Louis. This is reflected in the less extreme site score of −0.004. Other species with a limited distribution appear to be restricted to a particular locality rather than to a particular habitat. For example, the tenebrionid beetle. *Opatrinus attenvatus* (score −0.2271) was only found in four apparently dissimilar sites in the Cinq Cases–Bassin Flamant area at the southeastern corner of the atoll, namely litter below *Mystroxylon*, *Pandanus*, *Thespesia* and *Lumnitzera*. In the same way an unidentified ptiliid beetle (score −0.0932) was only recorded at the eastern end of Ile Grande Terre. Here it occurred in samples taken from ten sites of seven different vegetation types. Of several samples taken from three of these vegetation types from other parts of the atoll, none were found to contain this beetle.

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Appendix 1. Reciprocal averaging scores and location of the sample sites on Aldabra

+0.4860, Beach debris between Dune Jean-Louis and Anse Du Bois, Jan. 75; +0.4685, beach debris between Dune d'Messe and Anse Imagination, Jan. 75; +0.2525, *Mariscus ligularis* inland of beach crest, Cinq Cases, Mar. 74; +0.1680, *Cyperus niveus* below *Ochna ciliata*, west of Dune d'Messe, Jan 75; +0.0888, *C. ligularis*, Dune Au Pic, Jun. 74; +0.0770, *Casuarina* *equisetifolia* with *Suriana maritima*, Ile Esprit, Jul. 74; +0.0730†, *C. ligularis*, Anse Malabar, Feb. 75; +0.0637†, *Fimbristylis* cf. *cymosa* below *Casuarina*, east end of Ile Malabar, Jun. 74; +0.0575†, *Pemphis acidula*, north coast of Ile Polymnie, Dec. 74; +0.0573, *C. equisetifolia* and *Cocos nucifera*, Ile Esprit, Dec. 74; +0,0572†, *Sporobolus virginicus*, Dune Patates, Jan. 75; +0.0472†, *P. acidula*, east end of Ile Malabar, Nov. 74; +0.0470, *Sideroxylon inerme* among *Pemphis*, Anse Porche, Dec. 74; +0.0456, *Maytenus senegalensis* between Cinq Cases and Bassin Flamant, Mar. 74; +0.0437†, *C. equisetifolia*, northwest coast of Ile Picard, Dec. 74; +0.0393†, *P. acidula*, north of Dune d'Messe, Jan. 75; +0.0337, *Calophyllum inophyllum*, Takamaka, Dec. 73; +0.0306†, *P. acidula*, Anse Porche, Dec. 74; +0.0283, *Mystroxylon aethiopicum* and *Tarenna supra-axillaris*, Ile Esprit, Dec. 74; +0.0261†, *C. inophyllum*, Takamaka, Jan. 75; +0.0266, *M. aethiopicum*, near Anse Coco, Dec. 74; +0.0235, *S. inerme*, Dune d'Messe, Jan. 75; +0.0189, mixed scrub, south end of Ile Picard, Nov. 74; +0.0182†, *Pandanus tectorius*, southwest of Pointe Hodoul, Mar. 74; +0.0158, *C. equisetifolia*, south end of Ile Picard, Dec. 74; +0.0121†, *C. niveus* among *C. nucifera*, Anse Mais, Oct. 74; +0.0112, *Dracaena reflexa*, northwest of Anse Polymnie, Nov. 73; +0.0094, *S. inerme* between Anse Coco and Anse Porche, Dec. 74; +0.0061†, mixed scrub, south end of Ile Picard, Feb. 75; +0.0049, fallen *C. nucifera*, west coast of Ile Picard, Oct. 74; +0.0030, *S. inerme* between Cinq Cases and Bassin Flamant, Mar. 74; +0.0026, *M. senegalensis*, south end of Ile Picard, Oct. 73; −0.0043, *C. ligularis*, inland of beach crest, Dune Jean-Louis, Jan. 75; −0.0098, mixed scrub, Anse Tambalico, Oct. 74; −0.0117, mixed scrub, south end of Ile Picard, Dec. 74; −0.0120†, mixed scrub, Croix Blanc, Nov. 74; −0.0142†, *C. equisetifolia*, Anse Cèdres, Feb. 75; −0.0143, *C. ligularis*, just south of Pointe Hodoul, Mar. 74; −0.0203, *C. ligularis*, among low scrub, Dune Jean-Louis, Jun. 74; −0.0213, *S. inerme*, between Cinq Cases and Bassin Flamant, Mar. 74; −0.0225, *D. reflexa*, between Anse Coco and Anse Porche, Dec. 74; −0.0229, *S. inerme*, among *Pemphis*, Au Parc, Feb. 75; −0.0314, *Tricalysia sonderana*, west end of Ile Polymnie, Nov. 73; −0.0351, *S. inerme*, near Cinq Cases, Nov. 73; −0.0352, *M. aethiopicum* and *D. reflexa*, Anse Coco, Dec. 74; −0.0353, *M. senegalensis*, between Cinq Cases and Bassin Flamant, Mar. 74; −0.0362, 'three-leaf plant', west end of Ile Polymnie, Nov. 73; −0.0363, *C. ligularis* beneath *Ochna*, Dune Jean-Louis, Jan. 75; −0.0377, *S. inerme*, between Cinq Cases and Bassin Flamant, Mar. 74; −0.0378, *C. ligularis*, Anse Cèdres, Feb. 75; −0.0395, Gramineae sp. beneath *Casuarina*, Anse Coco, Dec. 74; −0.0429, *P. acidula*, southwest of Pointe Hodoul, Mar. 74; −0.0431, *S. inerme*, Anse Cèdres, Feb. 75; −0.0472, *S. inerme*, between Cinq Cases and Bassin Flamant, Mar. 74; −0.0474, *Guettarda speciosa*, Dune d'Messe, Jan. 75; −0.0494, *S. inerme*, Ile Michel, Mar. 75; −0.0498, *S. inerme*, between Cinq Cases and Bassin Flamant, Mar. 74; −0.0526, *M. senegalensis*, between Cinq Cases and Bassin Flamant, Mar. 74; −0.0530, *O. ciliata*, Bassin Flamant, Mar. 74; −0.0644, mixed scrub, south end of Ile Picard, Jul. 74; −0.0688, *C. equisetifolia*, Ile Michel, Mar. 75; −0.0754, *Fimbristylis ferruginea*, between Cinq Cases and Bassin Flamant, Mar. 74; −0.0856, *F.* cf. *cymosa* below *Casuarina*, east end of Ile Malabar, Jun. 74; −0.0970, *Acampe rigida*, lagoon islet near Bras des Cèdres, Feb. 74; −0.0975, *S. inerme*, just inland of Cinq Cases, Mar. 74; −0.0985, *P. tectorius*, just inland of Cinq Cases. Mar. 74; −0.1047, *S. maritima*, south of Pointe Hodoul, Mar. 74; −0.1359, *M. aethiopicum* just inland of Cinq Cases, Mar. 74; −0.2098, *Thespesia* sp., west of Cinq Cases, Nov. 74; −0.4965, *Lumnitzera racemosa* between Cinq Cases and Bassin Flamant, Mar. 74.

† Primary sample sites.

Appendix 2. Reciprocal averaging scores of arthropod species collected from the sample sites

+0.4613, *Tylos minor* Dollfus, Isopoda; +0.3889, *Anagarypus oceanus-indicus* Chamberlin, Pseudoscorpiones; +0.2921, Nitidulidae sp. 1, Coleoptera; +0.2701, *Phaleria* sp., Coleoptera; +0.2441, unidentified arthropod sp. 1; +0.1624, Staphylinidae sp. 1, Coleoptera; +0.1302, *Astenus* sp., Coleoptera; +0.0952, unidentified Coleoptera sp. 1; +0.0933, Elateridae sp. 1, Coleoptera; +0.0666, Porcellionidae sp., Isopoda; +0.0518, Curculionidae sp. 1, Coleoptera; +0.0444, *Scolopendra amazonica* (Bucherl), Chilopoda; +0.0422, unidentified arthropod sp. 2; +0.0422, Curculionidae sp. 2, Coleoptera; +0.0338, Elateridae sp. 2; Coleoptera; +0.0311, unidentified Symphyla sp.; +0.0294, Staphylinidae sp. 2, Coleoptera; +0.0278, Nitidulidae sp. 2, Coleoptera; +0.0265, unidentified Pauropoda sp.; +0.0266, Pselaphidae sp., Coleoptera; +0.0255, *Plesioderes* sp., Coleoptera; +0.0252, Dytiscidae sp., Coleoptera; +0.0226, unidentified Coleoptera sp. 2; +0.0225, Geophilomorpha sp. 1, Chilopoda; +0.0214, Cossonidae sp., Coleoptera; +0.0195, *Carpelinus* sp., Coleoptera; +0.0177, Polyxenidae sp., Diplopoda; +0.0170, *Oligotoma saundersii* Westwood, Embioptera; +0.0139, *Tyrannochthonius contractus* (Tullgren), Pseudoscorpiones; +0.0123, Scarabaeidae sp., Coleoptera; +0.0121, Japygidae sp., Diplura; +0.0026, *Spirobolus bivirgatus* Karsch, Diplopoda; −0.0005, *Allowithius congicus* Beier, Pseudoscorpiones; −0.0008, *Geogarypus impressus* Tullgren, Pseudoscorpiones; −0.0019, Geophilomorpha sp. 2, Chilopoda; −0.0028, *Xenolpium madagascariensis* (Beier), Pseudoscorpiones; −0.0040, *Pseudochiridium africanum* (Beier), Pseudoscorpiones; −0.0082, Armadillidae sp. 1, Isopoda; −0.0105, *Alphitobius crenatus* Klub. Coleoptera; −0.0121, Armidillidae sp. 2, Isopoda; −0.0142, Scolopendromorpha sp. 1, Chilopoda; −0.0152, Hydrophilidae sp., Coleoptera; −0.0191, Oniscidae sp. 1, Isopoda; −0.0227, Chrysomelidae sp., Coleoptera; −0.0248, *Temnopteryx dimidiatipes* Bolivar, Dictyoptera; −0.0291, Lygaeidae sp., Hemiptera; −0.0320, Lithobiomorpha sp., Chilopoda; −0.0339, Gelastocoridae sp., Hemiptera; −0.0360, *Stenus* sp., Coleoptera; −0.0402, Anthocoridae sp., Hemiptera; −0.0418, Carabidae sp. 1, Coleoptera; −0.0434, *Margattea* sp., Dictyoptera; −0.0458, unidentified arthropod sp. 3; −0.0464, *Tachys* sp., Coleoptera; −0.0615, Geophilomorpha sp. 3, Chilopoda; −0.0772, *Euborellia plebeja* (Dohrn), Dermaptera; −0.0932, Ptiliidae sp., Coleoptera; −0.1373, Oniscidae sp. 2, Isopoda; −0.2271, *Opatrinus attenuatus* Klug., Coleoptera; −0.4799, unidentified Coleoptera sp. 3.