Arthropod diversity associated with fallen logs and woody litter on the forest floor on a small Seychelles Island

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PREFACE

This study was carried out on Cousine Island, Seychelles, from the 14 February 1998 to 10 April 1998, under the supervision of Prof M.J. Samways.

This study represents original work of the author and has not been submitted in any other form to another university, other than the University of Natal. Where the work of others was referred to, it has been duly acknowledged in the text. Figures and tables have been inserted in appropriate places within the text.

This document is submitted as per requirements for the Master of Science degree

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ABSTACT

Cousine Island, Seychelles, is of major conservation significance as it is relatively pristine, and apparently the only tropical island over 20 ha with no alien invasive mammals. Such mammals, especially rodents, can impact substantially on arthropod faunas. This study focuses on the arthropods of the island that live in fallen logs and litter. The dominant log species are *Pisonia grandis* (Summerhayes, 1932), *Ficus* spp. and *Cocos nucifera* (Linnaeus, 1952). Stage of decomposition and forest type in which the logs occurred significantly influenced the composition and structure of the assemblages. Young logs were significantly richer in species than older logs, possibly due to the greater resources and more varied microhabitats in the younger logs. Log type was also important for arthropod species richness and abundance. Although *P. grandis* and *Ficus* spp. logs did not differ significantly, these two log types did differ greatly from *C. nucifera* which had a higher arthropod species richness, composition and abundance. However, these differences were only significant for recently fallen logs. As the logs decayed, their arthropod assemblages converged. Nevertheless, each log type had some arthropod species not present in another log type. This is important in terms of conservation, especially in the case of *C. nucifera*, which, according to one school of thought, should be removed from some Seychelles islands as it is considered an alien invasive. Arthropod assemblages in woody litter differed in composition depending on forest type in which they occurred. These woody litter assemblages were generally dissimilar to those in logs in the same forest type. Leaf litter was extremely poor in arthropod species. Species richness, both in logs and litter, was comparable to figures from temperate lands, possibly because the rich, topical fauna was ameliorated by small island size. As the logs are home to several Seychelles endemic species, their conservation is essential. Furthermore, as they are also the food base of certain threatened Seychelles vertebrates, their conservation is about conservation of a food chain on this unique tropical island.

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INTRODUCTION AND THESIS RATIONALE

Tropical forests are immensely rich in biological diversity (Stork 1999, Damodaran 1994, Huse 1994, Myers 1990, Stork 1988, FAO-UNEP 1982, Young 1982), and provide a wide variety of specialist (MacArthur 1972, Karr 1971, Lack 1971, Cain 1969, Levins 1968, MacArthur *et al.* 1966) and generalist habitats (Hawkins *et al.* 1992, Price 1980, Beaver 1979). Erwin (1982), extrapolating from data on canopy insects collected by fogging, together with estimates of tropical plant host specificity, suggested that one hectare of forest in Panama may have in excess of 41 000 species of arthropods. From this, Erwin (1982) estimated that arthropods may number as many as 30 million extant species globally. However, this figure, is now considered inflated (Hammond 1992, Ødegaard *et al.* 2000), and 10 – 15 million is more probable (Stork 1999). Hammond (1992) estimates arthropods to be 72 % of all organisms, while insects are an estimated 89% of these. It is this sheer diversity of forest insects that presents an enormous challenge to conservation (Bignell & Bignell 1997, Stork 1991, Hammond 1990, Palm 1959). Forest insects, as well as some other arthropods, being dominant in species richness and abundance, are linked to critical ecological processes and ecosystem functioning (McGeoch 1998, Simmonds *et al.* 1994). Yet, little is known of their ecology (Speight *et al.* 1999) and many appear to be going extinct without us having any knowledge of their biology (Mawdsley & Stork 1995).

Species extinction may be a result of habitat destruction and fragmentation, introduced species (alien invasives), chain extinctions and overkill (over-collecting) (Mawdsley & Stork 1995). These have not yet impacted on some dense tropical forests and they have had their biological diversity preserved simply due to their inaccessibility (Damodaran 1994). However, tropical forests overall are the most threatened habitat type (FAO-UNEP 1982, Huse 1994). These habitats cover only about 6 per cent of the earth's land area (FAO-UNEP 1982). Out of the 1.5 to 1.6 billion ha that existed in the recent past, tropical forests now only cover approximately 900 million ha. There is a general agreement that between 78 000 and 96 200 square kilometers (about 1%) of these habitats is eliminated through human activity every year (FAO-UNEP 1982, Balakrishnan 1994).

The introduction of an alien species can affect forest communities directly through species interactions such as predation, or indirectly, by altering resource availability (Sandlund *et al.* 1999, Mooney & Hobbs 2000). Furthermore, it appears that island species are more susceptible to decline and extinction as a result of an introduced (alien) species, than are the mainland species (D'Antonio & Dudley 1995). The invasive species *Rattus rattus* (Linnaeus, 1758) (common rat) and *Mus musculus* (Linnaeus, 1758) (brown mouse), have had a devastating impact on the indigenous fauna on many islands, including those in the Seychelles (Racey & Nicoll 1984).

Cousine Island, in the Seychelles archipelago, is exceptional. It has not been invaded by either the common rat or the brown mouse, and is a relatively undisturbed tropical forest ecosystem (Samways 2000). Because little is known about tropical forest-floor arthropods, Cousine provides an opportunity to study these organisms in a relatively pristine environment.

Forest-floor inhabiting arthropods are poorly understood because of their small sizes and cryptic habits. Yet they are of great importance in understanding complex processes of nutrient recycling, and contribute to studies of comparative biological diversity, forest management, and conservation (Coddington *et al.* 1997, Hoekstra *et al.* 1995, Kremen *et al.* 1993, Stork 1988). Furthermore, arthropods in the tropics are a major link in food webs (Anderson 2000, Young 1982, Orians 1969).

Within a tropical forest, there are several vertical layers or levels that are biologically distinct (Speight & Wainhouse 1989). However, it is becoming clear that the forest floor supports species numbers approaching that of the canopy, and overall, the arthropod abundance in these ground habitats may be greater (André *et al.* 1994, Purvis & Hammond 1990, Stork 1988). The composition and patterns of these arthropods is still poorly known, even in areas that have been thoroughly collected e.g. North America (Carton & Robinson 1998). The arthropods found on the forest floor include saproxylic species, which depend mostly on dead wood for some part of their life cycle (Key 1993, Speight 1989, Hickin 1975). Saproxylic arthropods include not only those that feed on the wood itself, but also predatory and parasitic species, and species that feed on fungi, both within and outside the dead wood (Grove & Stork 1999, Lomholdt 1975). Some species feed on the sap that exudes from trees, while others use empty insect emergence holes for nesting. The adult stages of many insects that inhabit logs as larvae do not live in dead wood but are either pollen or nectar feeders on flowers, or are predatory on other invertebrates (Key 1993). There are at least three feeding guilds among saproxylic insects, i) bast- and wood-feeders, ii) fungivores, and iii) predators (Howden & Vogt 1951). They contain representatives from all major insect orders. Saproxylic insect assemblages are functionally dominant (Elton 1966), and speciose (Siitonen 1994), and include many naturally rare species (Stork & Hammond 1997). Some are particularly vulnerable, as their highly specialised niches may be present on only tiny proportion of trees at a site at any one time, or they may have poor powers of dispersal and so do not easily colonise new sites, or new trees (Key 1993). Many saproxylic arthropods are confined to forest relics with the highest continuity of suitable conditions (often reflecting a long-term absence of intensive management). The consequent significance of saproxylic insects as habitat continuity indicators has come to be widely recognised in the last few years (Harding 1995, Harding & Alexander 1994, Speight 1989), and the group as a whole has been adopted for use in ecological assessments (e.g. Fowles 1997, Good 1997, Grove 1990).

Some saproxylic species are threatened with extinction and gazetted in national red data books (Berg *et al.* 1995, Shirt 1987). Throughout Europe, saproxylic species have been identified as the most threatened community of invertebrates (Key 1993). Of the red-listed insects in Swedish forests, 69% are saproxylic (Berg *et al.* 1994). In Scandinavia and the UK, many red-listed species are confined to decaying wood (Mawdsley & Stork 1995, Mikkola 1991). In Sweden, 80% of the red listed forest insects are saproxylic and dependent on specific habitat elements, mainly old trees, logs and snags (Berg *et al.* 1994).

As regards forest-floor arthropods, Cousine Island is significant from another point of view. The island has a large population of two endemic skinks, *Mabuya seychellensis* (Seychelles skink) (Dumeril & Bibron, 1836) and *Mabuya wrighii* (Wrights skink) (Boulanger, 1911) and resident birds (most notably *Gallinula chloropus* (Common moorhen) (Linnaeus, 1758), *Copsychus sechellarum* (Seychelles magpie robin) (Newton, 1867), *Foudia seychellarum* (Seychelles fody) (Newton, 1867). During the sea/migrant bird breeding season, thousands of birds (the lesser noddies (*Anous temirostris*) (Howard & Moore, 1984) estimated to be 70 000 to 75 000 breeding pairs) provide food in the form of dropped fish, seaweed, eggs etc., which is used by the resident island vertebrates and arthropods. However, when the seabirds leave the island, the resident vertebrates survive by feeding on the arthropods (LeMaitre 1999), which largely seek refuge and food in fallen logs and in the leaf litter.

This study explores various aspects of the habitat that may influence the distribution and assemblage structure of forest-floor arthropods, particularly those associated with fallen logs and woody litter. It is speculated here that decomposition stage of logs, type of log, and forest type in which the logs and litter occur, are important for determining arthropod assemblage composition and structure. A knowledge of such log characteristics is then used to enhance meaningful conservation efforts on forest-floor arthropod assemblages.

STUDY AREA

The Seychelles archipelago comprises about 45 islands (exclusive of islets and atolls), 1000 km northeast of Madagascar (Roth 1995), and has a total land area about 388 km^2. Formerly, it was heavily forested, but most of the forest has now been cut (Darlington 1957).

This study was undertaken on Cousine Island (Figure 1.1) which is a small granitic island within the Seychelles Inner Island group (Figure 1.2) (4°20' S and 44°40' E) (Braithwaite 1984). It is one of the smallest islands of the Inner Island group, being just over 1 km long and 400 m at its widest point, and an area of 27 ha (Bourquin 1997). The island has a humid tropical climate with mean monthly temperature of 25.7 °C - 27.8 °C and with the diurnal ranges of 3 °C - 4.2 °C. The relative humidity varies little, usually between 75 % r.h.- 80 % r.h. (Bourquin 1997, Iyer & Francis 1941). Cousine also experiences southeasterly trade winds from May to October, and lighter more variable northwesterly monsoon winds from December to March (Bourquin 1997). The average annual rainfall from 1993 to 1996 was 1742 mm with a range of 1466 to 2196 mm (Bourquin 1997). The average minimum and maximum temperature for the duration of this study (February to April 1998) were 28.5 ± 0.18 °C and 32 ± 0.13 °C respectively. The humidity ranged from 74.5 % to 98.5 % r.h. with a mean of 81.2 % r.h.. The total rainfall over these three months was 212 mm.

The most significant features of Cousine Island, and the main reasons why it was chosen for this study are:

- The isolation of the Seychelles islands makes them biologically important as they support a large number of endemic species (Stoddart 1984a, 1984b)
- Cousine's forests are largely intact. Most of the island's forest remains, and there are very few impacts that detract from its original, natural state.
- The invader species, *Rattus rattus* and *Mus musculus*, two rodents that have had a considerable impact on the fauna of other Seychelles islands (Racey & Nicoll 1984) do not occur on Cousine.

- It is one of the few islands that supports highly threatened bird species and many endemic Seychelles species (Bourquin 1997).

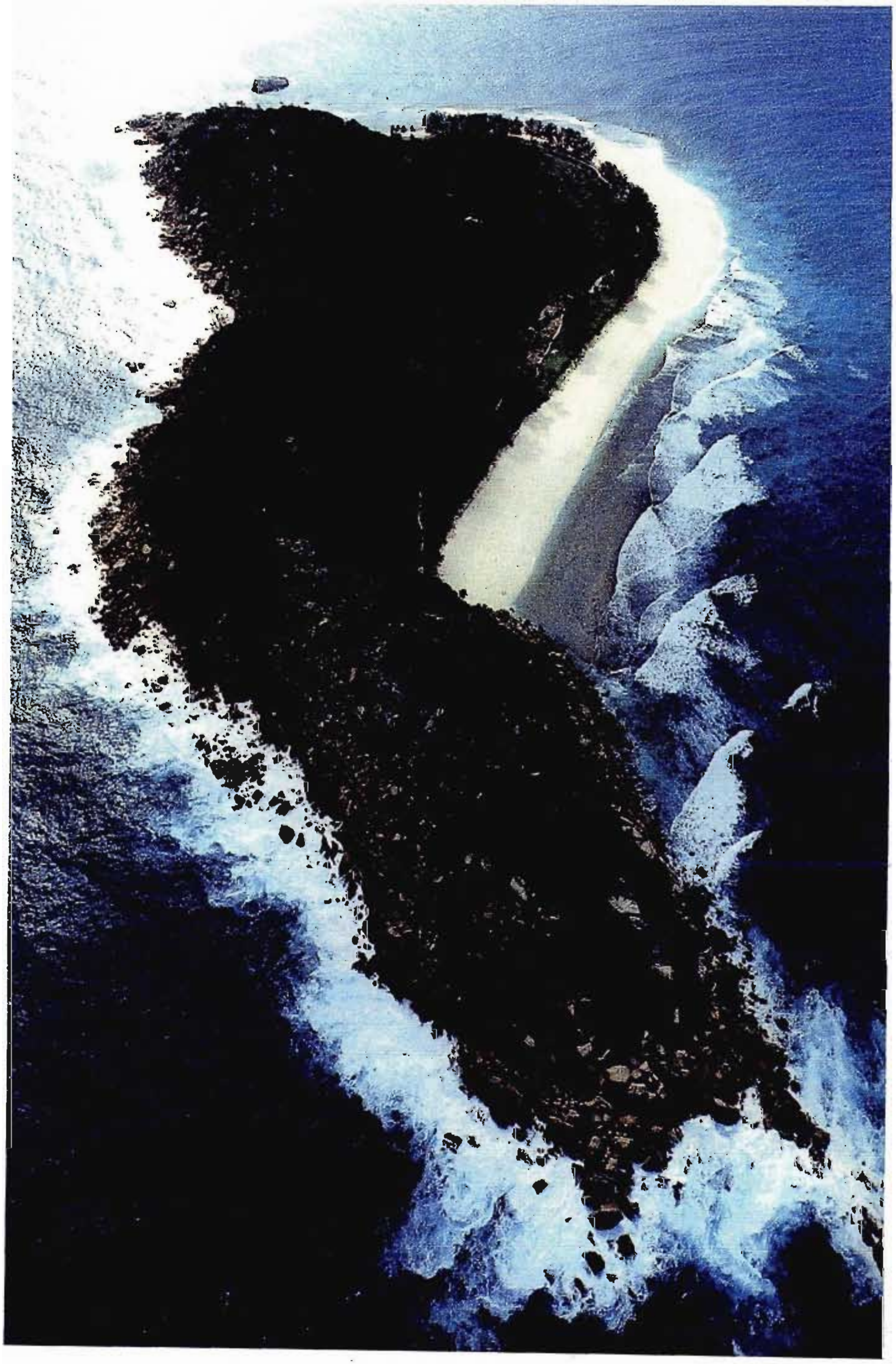

Figure 1.1 Cousine Island (from Amin 1991)

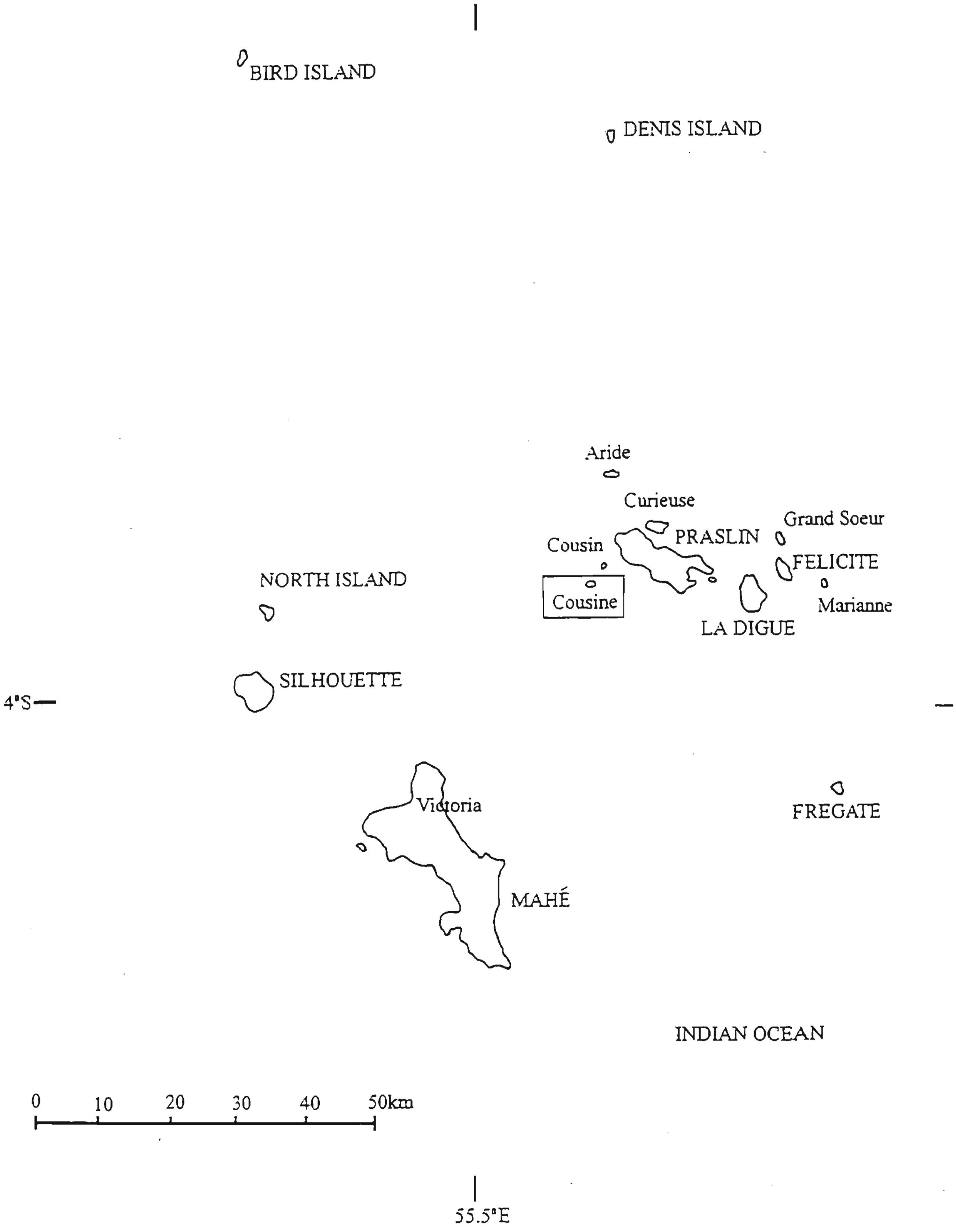

Figure 1.2 Position of Cousine Island within Seychelles Inner Island group (adapted from Amin & Willetts 1994)

Bourquin (1997) described 26 vegetation types on Cousine Island. Many of these vegetation types are very small or consist of grasslands, herblands or shrublands. Only the indigenous forests were considered for this study, as the other areas were without logs. Thus the study area consisted of five forest types covering 34 % of the island area (Figure 2). These were *Pisonia grandis* (Summerhayes, 1932) forest (Figure 2.1), *P. grandis / Ficus* spp. forest type 1 and 2 (Figure 2.2), *Ficus* spp. forest (Figure 2.3) and the *Euphorbia pyrifolia* (Summerhayes, 1932) / *Ficus* spp. forest (Figure 2.4). These forest types were very distinctive, each with its own unique composition of flora, except *P. grandis / Ficus* spp. forest types 1 and 2, which were very similar to each other.

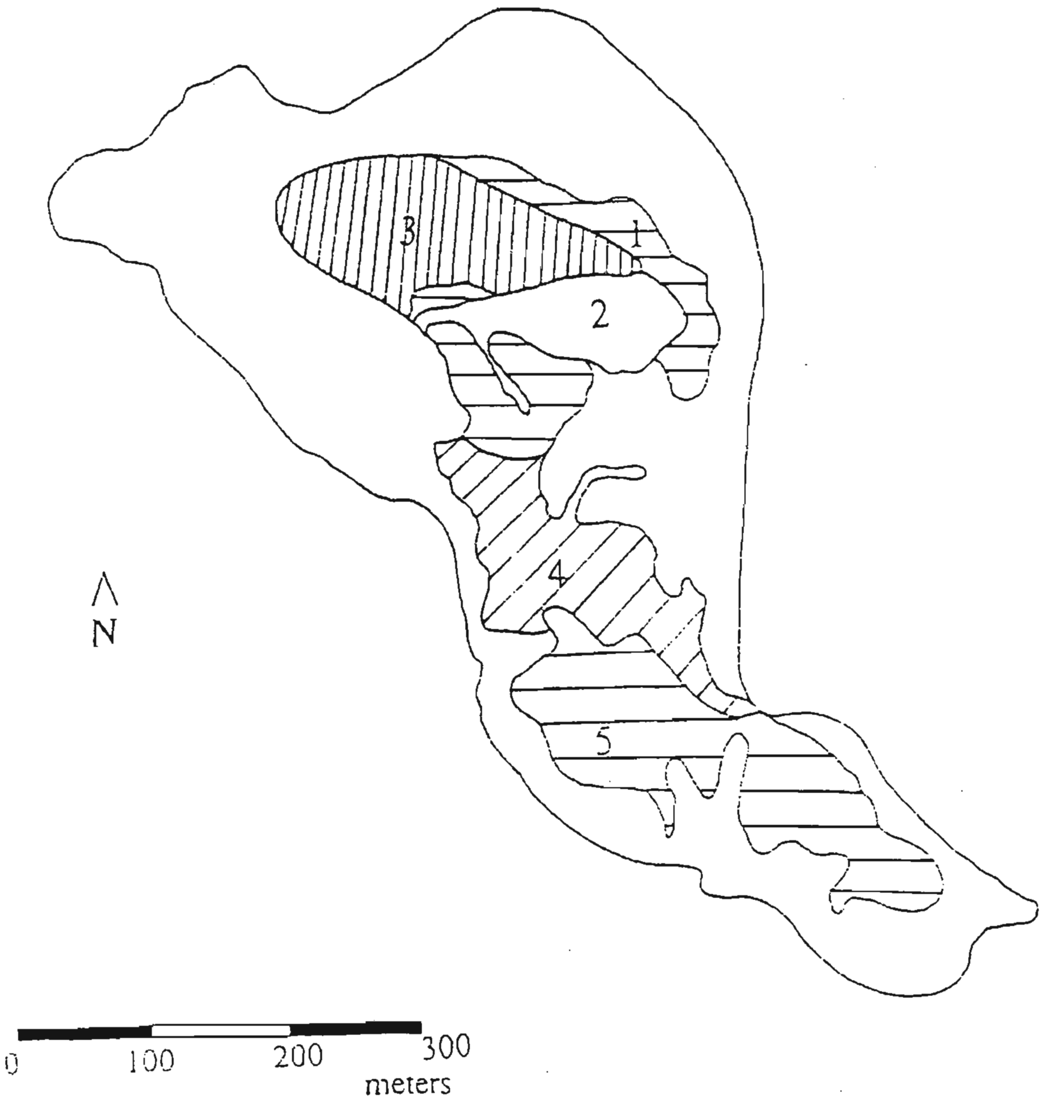

Figure 2 Forest types of Cousine Island (adapted from Bourquin 1997). 4 = *P. grandis,* 1 = *P. grandis / Ficus* spp., 5 = *P. grandis / Ficus* spp., 2= *Ficus* spp., 3= *E. pryifolia / Ficus* spp., (the forests are listed in the order they were sampled)

1) *P.grandis* forest type

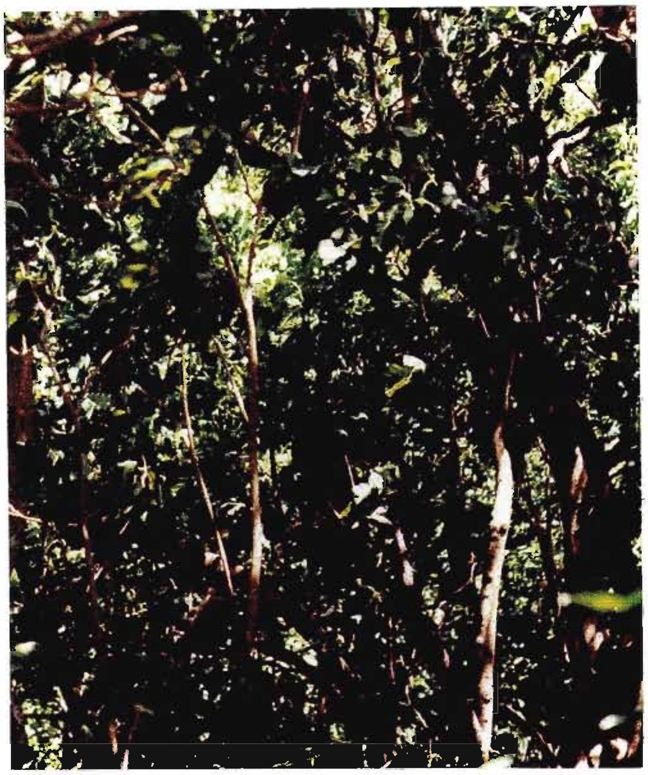

Figure 2.1 *Pisonia grandis* forest type

The *P.grandis* forest type is an indigenous area dominated by *P. grandis*. Other plant species present included *Cocos nucifera* (Linnaeus, 1952), *Ipomoea pescaprae* (Summerhayes, 1932), *Canavalia cathartica* (Fridemann, 1994) and *Datura metel* (Friedmann, 1994) (Figure 2.1).

2) *P. grandis* / *Ficus* spp. forest type 1 and 2

Figure 2.2 *Pisonia grandis / Ficus* spp. forest type

The *P. grandis / Ficus* spp. forest type is an indigenous area dominated by *P.grandis, Ficus* spp., *Morinda citrifolia* (Robertson, 1989), *E. pyrifolia, Calophyllum* sp. and *C. nucifera. Nephrolepis biserrata* (Christensen, 1912) was a common ground cover plant (Figure 2.2).

3) *Ficus* spp. forest type

Figure 2.3 *Ficus* spp. forest type

The *Ficus* spp. forest type is an indigenous area where *Ficus reflexa* (Summerhayes 1932) and *Ficus lutea* (Summerhayes 1932) made up about 60% of the canopy, with *P. grandis* and *C. nucifera* present at low percentages. Ground cover was dominated by *N. biserrata* (Figure 2.3).

4) *E. pyrifolia* / *Ficus* spp. forest type

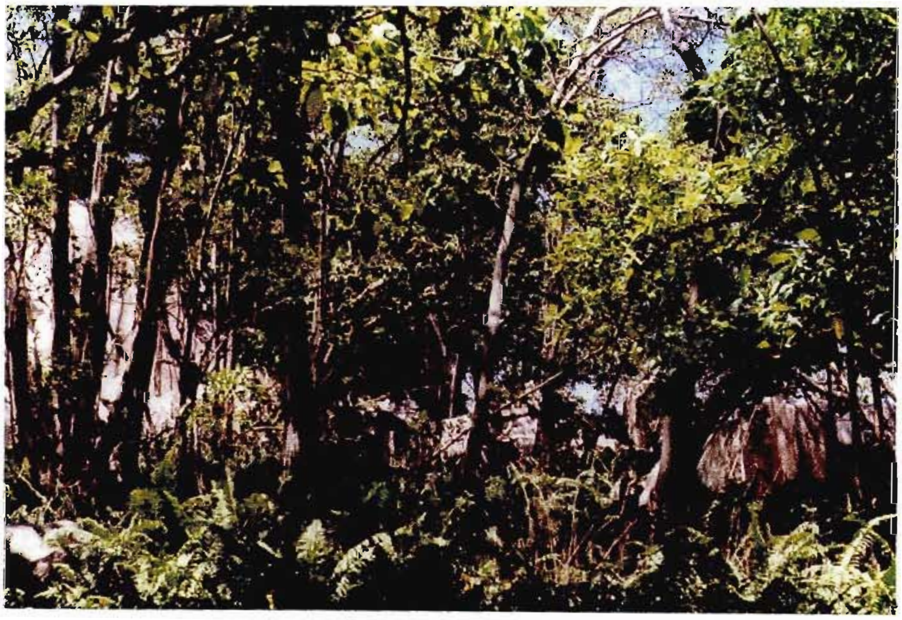

Figure 2.4 *Euphorbia pyrifolia / Ficus* spp. forest type

The *E. pryifolia / Ficus* spp. forest types is an indigenous open woodland community where *F. reflexa* and *E. pyrifolia* were the prominent trees. Other herb species present were *N. biserrata, Asystasia gangetica* (Fleishmann, 1995) and *Panicum brevifolium* (Robertson, 1989) (Figure 2.4).

MATERIALS AND METHODS

STUDY SITE ENVIROMENTAL ATTRIBUTES

Estimating the total study area and percentage rock cover

The total study area was calculated using graph paper with 2 mm X 2 mm squares over a map (scale 1: 4000) (Lawrence 2000). Very little leaf and woody material remained on the rock surface, therefore subtracting the percentage of the rock cover in each study site from the total area of each study site gave good estimates of the total litter area.

The rock cover was determined by using five sets of 20, randomly selected, line transects of 10 m each, in each forest type. The random sampling was decided by using equal-sized pieces of paper with a compass direction and a distance number. These were drawn from separate plastic bags. The numbers represented the direction and the distance (in meters) to the sample site or start of each transect. This method was used for all random transect sampling in this study. A rock that influenced distribution of woody or leaf material was defined as larger than 0.5 m x 0.5 m. The length of the rocks were measured and totaled for each transect. The mean percentage ±1 S.E., and the area that was not covered by rocks was calculated. These results were later used in the calculations of the density and biomass of leaf and woody materials. The rock cover did not affect the calculations of the log density and biomass, as the logs were not naturally cleared of the rock surface as was the leaf and woody material.

Estimating tree density

The arthropod communities in this study are dependent on a continued supply, as well as current availability, of logs. The density of trees was therefore estimated as they were potentially the future natural source of the logs. Over 95 % of the forest trees were mature (greater than 10 cm diameter stem), being at plagioclimax, with the occasional seedling taking advantage of the sunlit gaps. Each habitat type was sampled using 25 random strip-transects. The number and species composition of trees were estimated using 2 m x 10 m strip transects. The transects were randomly placed as described above. The mean number of each tree species ±1 S.E. per transect and the total number of trees was calculated for the study area.

Estimating log, woody and leaf litter composition and biomass

Logs in this study were defined by their diameters being more than 10 cm and having a length more than 50 cm. Woody litter in this study includes a wide variety of types and sizes of materials. Types of woody litter included snags, logs, chunks of wood (which resulted from disintegration of larger snags and logs), large branches, and coarse roots. However, a recommended minimum diameter of greater than 2.5 cm was used for all woody litter types (Harmon *et al.* 1985), as some ecologists (e.g. Christensen 1977) make no distinction between coarse and fine woody litter.

a) Log, woody and leaf litter composition

Log type composition was estimated using 25, 2 m x 10 m strip transects in each forest type. The woody and leaf litter composition measurements were estimated by using 0.5 m x 0.5 m quadrats. Twenty quadrats were placed randomly in each of the study sites. At each quadrat site, all organic material was removed from the soil surface. The leaf litter and woody litter were separated. The logs, woody litter and leaf litter were identified easily, as the wood, bark or leaf shape for the dominant species is very distinctive. Using the area calculations, the mean number ±1 S.E., for each type of log, pieces of woody litter and leaves per transect or per quadrat was calculated. The composition was then expressed as percentages for the whole study area.

b) Log, woody and leaf litter biomass

The term 'biomass' sometimes refers to dry weight, sometimes to fresh weight (Peterson & Luxton 1982). In this study, it refers to dry weight. The forest floor litter can be divided into three components: logs, woody and leaf litter. The biomass of each component was calculated as follows:

i) Log biomass

25 log samples of each of the three dominant tree species were collected and air-dried. Anderson & Ingram (1989) suggest that all samples are air-dried followed by oven drying before being weighed. However, owing to lack of facilities on Cousine Island to handle the large number of samples and the continued threat of rain, alternate approach had to be used. Each sample was placed in an open bucket, in a room housing a large electricity generator, which produced a considerable amount of heat. A bucket was used, due to space constraints and air movement on the ground caused by the generator. They were left for a standard comparative period of three days before being weighed. Trial testing showed that log material did not lose significant weight after this period. The mean ±1 S.E. minimum and maximum air temperatures in the generator room, for the duration of the study period, were 30.7 ± 0.2°C and 46.0 ± 0.4°C. The larger logs were carefully broken up to ensure even drying. The samples of each log type were then weighed to the nearest 0.2 g, using portable Pisola scales. The log volume was calculated ($V= pi^2$ sum of $d^2/8L$, where V is the volume, d is the diameter of a piece, and L is the log length (Harmon *et al.* 1985) based on the assumption that the logs were cylindrical in shape). This gave a working weight-to-volume ratio for each log type.

Each forest type was sampled using 25, 2 m x 10 m random strip transects. All the logs were identified on bark appearance, and texture and colour of wood. Diameters and lengths were also measured. The volumes were calculated, and the weight-to-volume ratio was applied. The mean mass ±1 S.E. for each log type per transect was calculated to determine the total mass of the log material for each forest type and the overall study area.

ii) Woody and leaf litter biomass

Leaf and woody litter biomass measurements were calculated by using 20, 0.5 m x 0.5 m quadrats randomly placed in each of the study sites. At each quadrat site, all loose litter material was removed from the soil surface and leaf litter and woody litter separated. The litter was then sifted using a 2 mm mesh to remove as much loose soil as possible. The woody litter was sorted and carefully broken up to ensure even drying. The woody and leaf litter was then air dried (as above). The samples were then weighed to the nearest 0.2 g. The mean ±1 S.E. of woody and leaf mass per quadrat was calculated to determine the total biomass of the leaf and woody litter.

Estimating forest types and their log, woody and leaf litter biomass

a) Forest type flora

The site flora in each forest type are summarised by Bourquin (1997). These observations were confirmed by a visual survey and identification of the floral species.

b) Total area of each forest type and percentage rock cover

Each forest type area was sampled using 20 random transects. The mean percentage ±1 S.E. of the area and rock cover were calculated.

c) Composition and biomass of logs, woody and leaf litter in each forest type.

The biomass of the logs, woody and leaf litter was calculated for each forest type using the same methods that were used for estimating the biomass for the whole study area.

SAMPLING OF ARTHROPODS FROM LOGS

Logs had first to be categorised and sampled before arthropods were sampled. The logs collected for the arthropod assemblage comparisons were classified by four ecological variables, decomposition stage, log type, forest type and the combination of forest type and log type. The logs in each of these categories were collected randomly. Each log was assigned a random number from a random number table (Abramowitz & Segun 1968) to determine the order in which they were collected. In all cases, the entire log was sampled. The results from the previous section clearly indicated the species, *P. grandis*, *Ficus* spp. and *C. nucifera* to be the most dominant and they were selected to be sampled for the arthropod community comparison.

Estimation of log decomposition

Measuring rates of decay in wood is difficult, principally because decay is slow and heterogeneous (Graham & Cromack 1982). The logs were thus collected from all the forest types in the study area and were classed according to guidelines provided by Torres (1994), which involves criteria such as elevation above the ground, presence of bark and twigs, and finally, physical properties of the heartwood and sapwood. These guidelines were modified for the logs on Cousine, which did not have twigs or distinctive sapwood and heartwood. In the case of *P. grandis* and *Ficus* spp. logs, once a log had fallen, the bark disintegrates and fell off the bole rapidly. This situation meant that the logs fell into two categories: one with the bark just beginning to disintegrate and the other with the bark largely or completely absent (Table 1). The bark around the *C. nucifera* logs is very hard and robust. This resulted in the breaking of the bark to assess the log's class of decomposition. Therefore, this log type was not sampled for decomposition, although it was for other characteristics. Twenty *P. grandis* and *Ficus* spp. logs from each decomposition class were collected.

Table 1: The decomposition classes of the logs found in the forested area of Cousine Island.

Class	Elevation class	Bark (% remaining)
Class 1	Elevated from the ground	Partly removed (> 80%)
Class 2	Elevated from the ground	Completely or largely absent (< 2%)
Class 3	Partially on the ground / base on the ground	Partly removed (> 80 %)
Class 4	Partially on the ground / base on the ground	Completely or largely absent (< 2%)

Estimating environmental characteristics of log types and influence of log type

One of the important factors affecting arthropods in logs is temperature and moisture (Graham 1925). Temperature within the log has an important influence in determining the part of the log attacked by the different taxa (Graham 1925, Speight & Wainhouse 1989).

Temperature and humidity of the log's upper surface, the area between the ground and the log, the log's core, and the surrounding leaf litter, was measured, *in situ,* using a portable hygrothermometer. The ambient shade air temperature and humidity adjacent to the log was recorded as a control.

5 logs of each species present in a forest type were collected. This resulted in 20 *P. grandis*, 20 *Ficus* spp. and 10 *C. nucifera* logs being sampled, for arthropod extraction.

Influence of forest type

10 logs of each type were collected in each forest type to determine the influence of forest type on the arthropod assemblages. Thus number of logs sampled were:

- 10 *P. grandis* logs in *P. grandis* forest type

- 10 *P. grandis* logs and 10 *Ficus* spp. logs in *P. grandis / Ficus* spp. forest types 1 and 2
- 10 *Ficus* spp. logs in *Ficus* spp. forest
- 10 *P. grandis* and 10 *Ficus* spp. logs in *E. pryifolia / Ficus* spp. forest.

Woody litter arthropod communities

The litter samples were collected from the 0.5 m x 0.5 m quadrats. 10 quadrats were collected from each forest type. All the litter was collected (down to the soil surface) and the arthropod extraction followed the same techniques as those applied to the log specimens.

Extraction and sampling of arthropods

The log and litter samples selected were placed directly into a large plastic bag. The log material was examined while still contained in the plastic bag, and the larger conspicuous arthropods were collected by hand as they emerged. There were problems with collection of small, often fast-moving arthropods, as fumigation is not permitted on the island. Therefore the sample was placed in a plastic bucket. The bottom of a plastic bucket was removed and a 1 cm^2 wire mesh substituted. This was joined to a large funnel. A collection jar filled with 70 % ethyl alcohol was placed beneath the funnel. The arthropods were driven from the broken-up wood material by light and heat supplied by a 60W bulb. Each sample was carefully broken-up and sub-divided into two buckets. These were left for 72 hr with the light on for two periods of 8 hr each (as and when electricity was available). The sample was then further examined after removal from the buckets to check for remaining specimens. The specimens were bottled in 70 % ethyl alcohol and brought back to the laboratory for sorting. The bottles were sorted at random to ensure that fatigue and familiarity were evenly distributed across all samples. Owing to inadequate taxonomy and life history knowledge of tropical soil arthropods, there are only a few reliable keys for identification of adults, and none for the early stages (Lawton *et al.* 1998, Niemela & Baur 1998, Wheeler & Cracraft 1997, Samways 1994, McLean & Speight 1993, Kremen *et al.* 1993, Kremen 1992, Pearson & Cassola 1992). Therefore, the arthropods in this study were sorted into morphospecies (see below) of higher taxa using various guides (Roth 1995, Scholtz & Holm 1994, Golovatch & Korsos 1992, Wanless 1983, Lewis 1981, Ferrara & Taiti 1972, Kaston 1972, Sutton 1972, Hughes 1959, Cloudsley-Thompson 1958, Imms 1957, Baker & Wharton 1952, Carpenter 1916). Nevertheless, an attempt was made, where possible, to identify some of the specimens (Appendix 1). M.I. Saaristo (Zoological Museum, Centre for Biodiversity, University of Turku, FIN-20014, Turku, Finland) assisted with the Arachnida and J. Gerlach (The Nature Protection Trust of Seychelles, 133 Cherry Hinton Road, Cambridge, CB1 7BX, United Kingdom) with the arthropods in general. Taxonomic difficulties have so far prevented species-level identification of Diplura, Thysanoptera, Collembola, Diptera and Acari. Each specimen was counted and recorded. A reference collection was established. Many of the specimens are housed on Cousine Island, while others are at The Nature Protection Trust of Seychelles, United Kingdom (all taxa), and the University of Turku, Finland (spiders).

As less than 20 % of all insect species have been described (Stork 1997, Hammond 1995, Stork 1993, Erwin 1982) it becomes obligatory to sample morphospecies i.e. physically recognisable taxonomic units (RTUs) (Oliver & Beattie 1992). Morphospecies however, have shown to be very valuable for comparative studies between sites (Oliver & Beattie 1992). The intensive collection of arthropods, classified as morphospecies in a multiple-taxa inventory are restricted by the taxonomic scope of the taxa involved (Heywood & Baste 1995). The method could result in many species with similar gross morphological structure being incorrectly classified in one unit (resulting in an underestimation of species richness), or species with different castes, being separated (resulting in an overestimation of species richness) (Slotow & Hamer 2000). However where the collection of the arthropods is intensive and the overall aim of the project is to make immediate conservation recommendations, the use of morphospecies becomes necessary (Heywood & Baste 1995). Indeed, at least for comparative purposes, the use of morphospecies is relatively accurate with only a 14.4 % error on the part of a relatively untrained biologist (Oliver & Beattie 1992).

STATISTICAL ANALYSIS

Arthropod community statistical analysis

The arthropod data were classified according to four ecological variables:

- Decomposition stage
- Log type
- Forest type
- Log type and forest type.

Firstly, the arthropod species richness was plotted for a visual comparison between the means, quartiles and ranges of each group. The comparisons between species number were then tested for any significant difference using Analysis of Variance (ANOVA) for multiple samples, and Student's t-test for two samples with unequal variances (Freund 1992). ANOVA is a powerful and versatile tool and is well suited to identifying interactive processes. The assumptions stipulated by the ANOVA were met by the data set (independence and homogeneity of data). Also ANOVA is relatively robust to non-normality. 'In other words, its outcome and interpretation are not affected by the data being non-normal' particularly when the sample size and number of replicates is large (Underwood 1997). The data were also tested for trends in the arthropod community assemblage using Correspondence Analysis (COA) (Ludwig & Reynolds 1988), using Canonical Community Ordination – CANOCO version 4 package. Because the data are distributed across the morphospecies gradient in a non-linear way, i.e. some of the arthropods are present in some samples but absent in others, the use of COA is appropriate (Ter Braack 1985, Ludwig & Reynolds 1988, Craig Morris pers. comm.). The use of COA, also allows the eigenvalues of the data set to be extracted in descending order of magnitude. Thus, the eigenvalues given represent the largest percentage of the total variation in the data set (Ludwig & Reynolds 1988) The data were $\log_{10}$ transformed to avoid bias of the very high or very low individuals number in some of the species (Ter Braak 1985, Craig Morris pers. com.). These results were plotted as scatterplots. The data were also tested using the Bray-Curtis index (Faith *et al.* 1987) to illustrate the similarities between the arthropod communities and allow these to be represented visually in the form of dendrograms.

Classification of arthropod communities

The data were classified according to the same four ecological variables as mentioned above. The arthropod assemblages were classified in terms of:

- The percentage of species relative to the total number of species in the survey.
- The percentage of species unique to each group relative to the total number of species for that group.
- The percentage of endemic species in a grouping relative to the total number of endemic species in this study.

The results of this classification were analysed to find the recommendations for conservation strategies.

RESULTS

OVERALL STUDY SITE ENVIROMENTAL ATTRIBUTES

The *P.grandis / Ficus* spp. forest 1 and 2 results were combined for this section, as they were almost identical.

Study area and percentage rock cover

The study area was 7.85 ha, 35 % of the whole island. The area that was free from significant rocks was only 4.42 ha (18 % of the island). The forest types were variable in size, the smallest being *Ficus* spp. (0.98 ha), while the largest was *P. grandis / Ficus* spp. (2.47 ha). This order did not change when the rock cover factor was considered (Table 2).

Table 2 Area (ha), mean percentage rock cover ± 1 S.E. (n=20) and the area of the site with no rock cover for each forest type.

Forest type	Area (ha)	% rock cover	Area with no rock cover (ha)
P. grandis	2.06	51.91 ± 16.65	0.99
P. grandis / Ficus spp.	2.47	38.05 ± 11.97	1.53
Ficus spp.	0.98	36.16 ± 12.43	0.63
E. pyrifolia /- Ficus spp.	2.34	45.94 ± 12.09	1.27

Tree density

The forest tree species composition in the overall study area was dominated by *P. grandis* (48.2 %) and *Ficus* spp. (43.2 %) (Figure 3). There were an estimated 6500 *P. grandis*, 5840 *Ficus* spp. and 757 *C. nucifera* trees on the island.

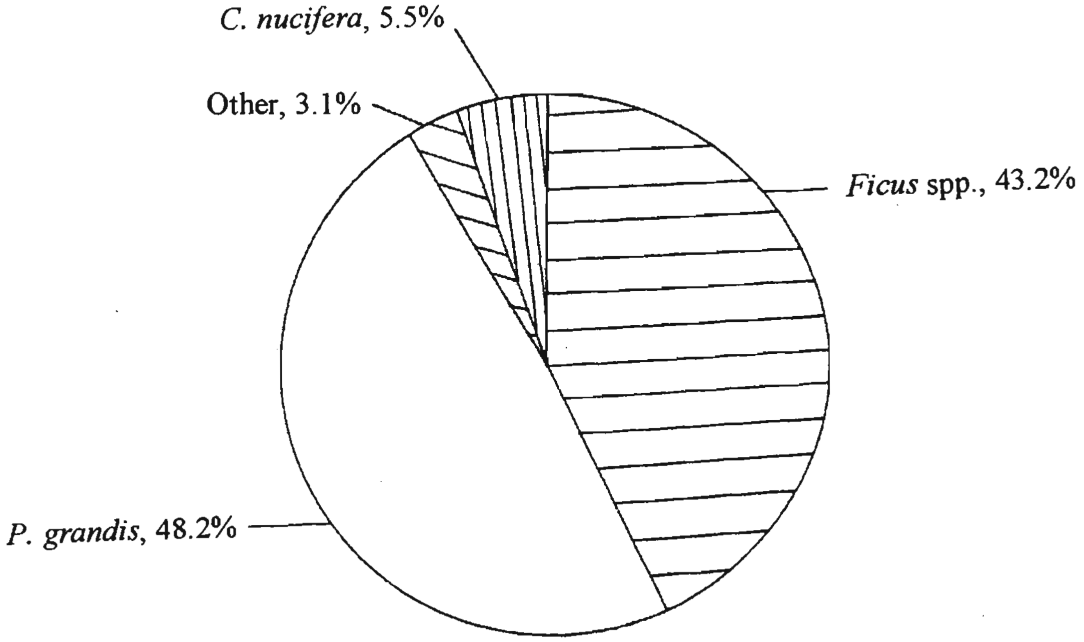

Figure 3 Percentage of tree species in all forest types combined

Composition and biomass of forest floor litter

The log material comprised 65.5 % of the forest floor organic material (= 429.22 t.ha^{-1}). The woody litter contributed 27.8 % (= 6.80 t.ha^{-1}). All leaf litter made up 6.7 % (= 1.07 t.ha^{-1}) (Figure 4).

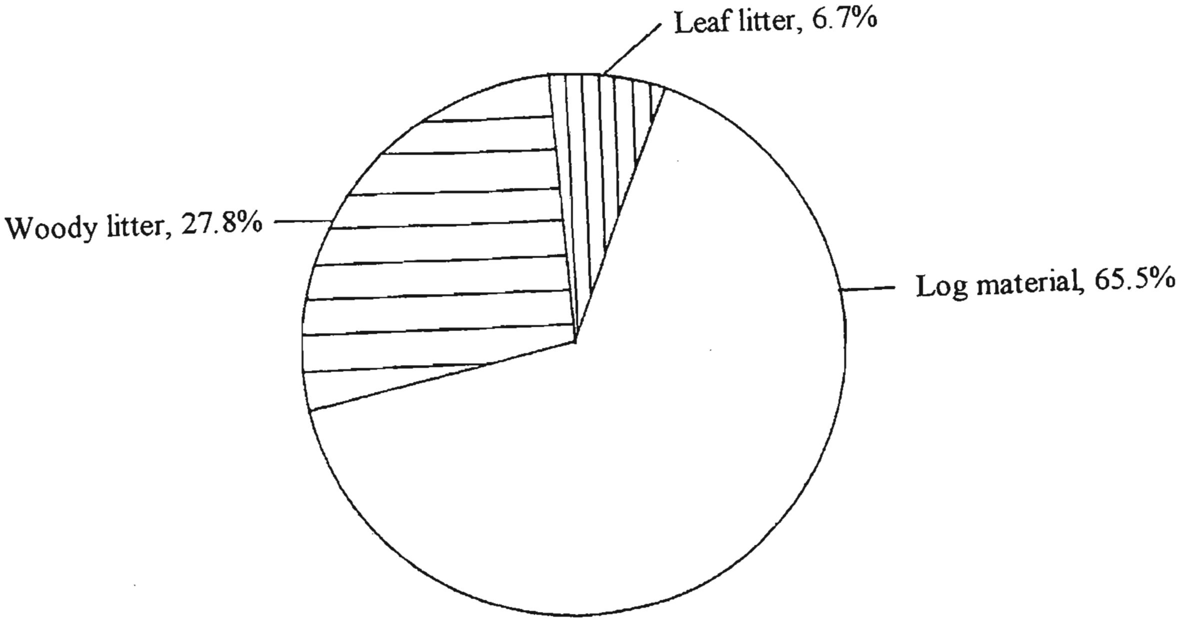

Figure 4 Percentage of forest floor organic litter biomass (for all forest types)

a) Log type composition and biomass estimates

Log abundance was dominated by *P. grandis* (48.7 % of all logs) and *Ficus* spp. (43.8 %) (Figure 5). This trend closely followed the tree species composition (*P. grandis* (48.2 %), *Ficus* spp. (43.2 %) and *C. nucifera* (5.5 %)) (Figure 3). Thus the weight to volume ratio for each log species was calculated to be: *P. grandis* $\overline{x} = 0.2 \pm 0.02$ g.cm^{-3} (n= 25), *Ficus* spp. $\overline{x} = 0.34 \pm 0.03$ g.cm^{-3} (n= 25) and *C. nucifera* $\overline{x} = 0.14 \pm$ g.cm^{-3} (n= 25). Log biomass was dominated by *P. grandis* (76.3 %) (Figure 6), indicating that this log type is larger in size than the *Ficus* spp., bearing in mind that log type numbers were similar.

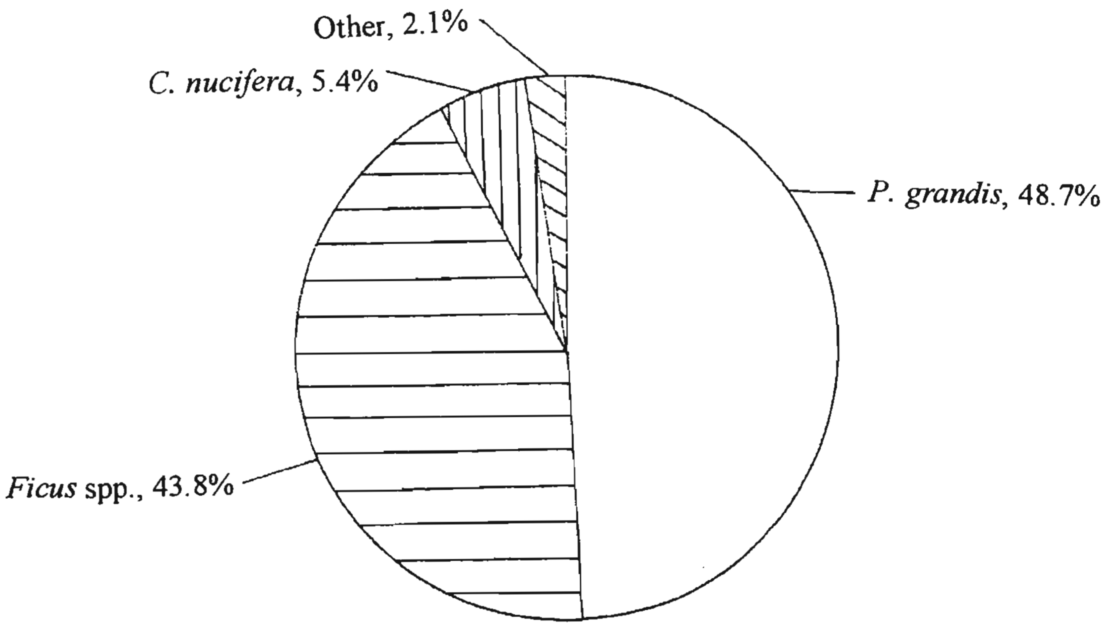

Figure 5 Percentage of the number of logs for each log type (for all forest types)

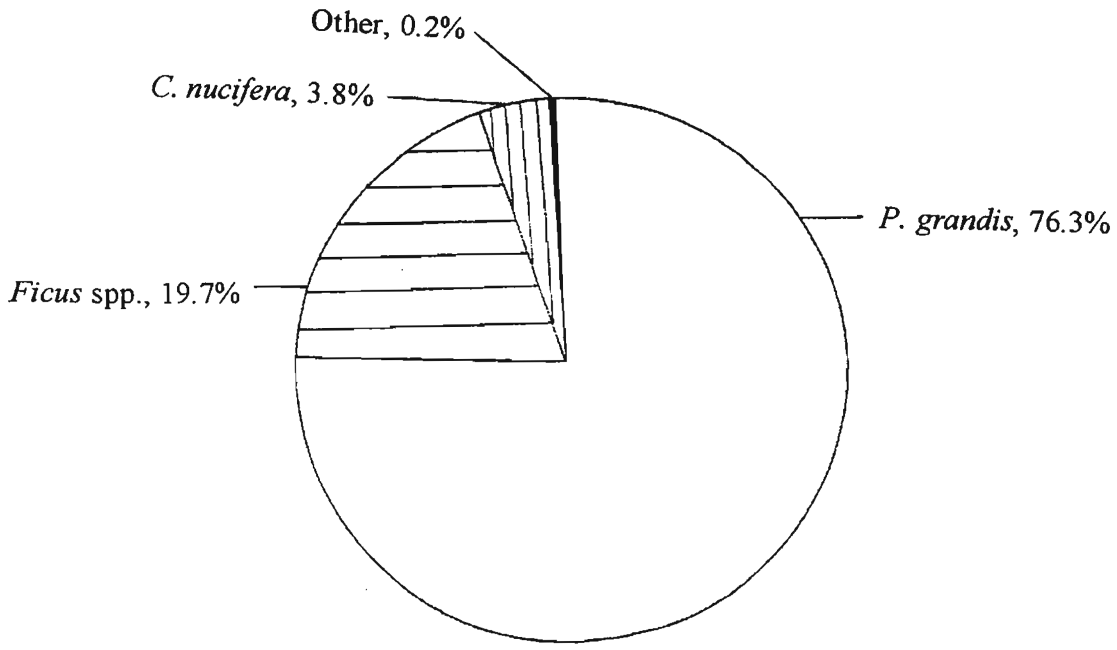

Figure 6 Log type biomass percentage in all forest types combined.

b) Woody litter biomass and composition estimates

P. grandis (76.4 %) dominated the woody litter on the forest floor (Figure 5). Overall, *P. grandis*, *Ficus* spp. and *C. nucifera* dominated the woody litter, with very little woody litter from any other species (0.05 %) (Figure 7).

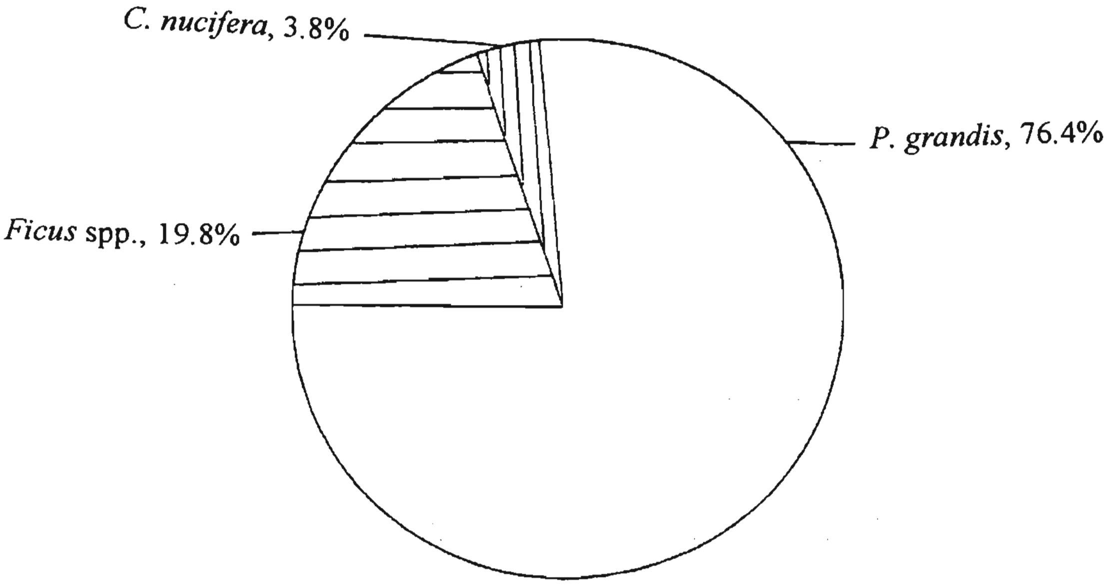

Figure 7 Percentage of woody litter types biomass (for all forest types)

FOREST TYPE ENVIROMENTAL ATTRIBUTES

The biomass of the logs was highest in the *P. grandis* forest type (= 399 780 kg), being up to 36 times the log biomass in other forest types, and the highest biomass of woody litter (= 4031.2 kg), despite it being the second smallest forest type. The *E. pryifolia / Ficus* forest had the lowest biomass of organic forest floor litter (Table 3).

Table 3 Estimated biomass (kg) of the logs, woody and leaf litter in each of the forest types.

Forest type	Log biomass (kg)	Woody litter (kg)	Leaf litter (kg)
P. grandis	399 780	4031.2	375.2
P. grandis – Ficus spp.	39 800	1590.1	385.5
Ficus spp.	18 770	750.8	243.2
E. pyrifolia – Ficus spp.	10 850	428.1	72.4

a) Log type number and biomass estimates in each forest type

The *P. grandis* forest type, although dominated by *P. grandis* logs (97), had some *Ficus* spp. and *C. nucifera* logs (Table 4), and the biomass estimates in this forest type were for the *P. grandis* log type were significantly higher than those of the *Ficus* spp. (394 468 and 3 094 kg 20 m^{-2}, respectively) (Table 5). In the *P. grandis / Ficus* spp. forest type there were more *P. grandis* logs than in the *P. grandis* forest type, while the *P. grandis / Ficus* spp. forest type had the highest number of logs (Table 4).

Table 4 Mean number of logs per transect ± 1 S.E. (n=25) and total number of logs in each forest type.

Site	*P. grandis*	Total	*Ficus* spp.	Total	*C. nucifera*	Total
P. grandis	1.4 ± 0.27	97	0.33 ± 0.16	23	0	0
P. grandis / *Ficus* spp.	1.6 ± 0.67	133	1 ± 0.34	83	0.2 ± 0.11	17
Ficus spp.	1.07 ± 0.43	35	1.33 ± 0.51	44	0.66 ± 0.66	22
E. pyrifolia / *Ficus* spp.	0.67 ± 0.23	52	1.27 ± 0.42	99	0	0

Table 5 Mean ± 1 S.E. biomass (kg.20 m^{-2}) of the logs per transect (n=25) and the total mass (kg) of logs in the forest types.

Forest type	*P. grandis*	Total	*Ficus* spp.	Total	*C. nucifera*	Total
P. grandis	196.9 ± 46.8	394 465	6.25 ± 3.98	3 093.7	4.5 ± 2.68	2 227.5
P. grandis - *Ficus* spp.	20.33 ± 6.72	15 552	27.25 ± 6.95	20 846.2	4.45 ± 2.63	3 404.2
Ficus spp.	33.3 ± 5.89	10 489	16.9 ± 8.51	5 323.5	9.4 ± 6.27	2 961
E. pyrifolia - *Ficus* spp.	10.3 ± 4.31	6 540.5	6.8 ± 2.5	4 318	0	0

b) Woody litter biomass estimates in each forest type

The *P. grandis* forest type supported a higher *P. grandis* woody litter density (169.9 ± 46.7 kg per quadrat) than the other forest types (Table 6). The biomass estimates for the logs and woody litter show that one average sized *P. grandis* log has the equivalent biomass of 1360 average quadrats of woody litter. Also, one average sized *Ficus* spp. or *C. nucifera* log has the equivalent biomass of 134 and 220 quadrats of woody litter respectively.

Table 6 Mean ± 1 S.E. biomass (kg.0.5 m^{-2}) of the woody litter per quadrat (n=25) and the total mass (kg) for each forest type.

Forest type	*P. grandis*	Total	*Ficus* spp.	Total	*C. nucifera*	Total
P. grandis	169.9 ± 46.7	3898.6	6.25 ± 3.9	123.7	4.5 ± 2.6	8.9
P. grandis / Ficus spp.	20.3 ± 6.7	621.1	27.2 ± 6.9	832.3	4.4 ± 2.6	136.7
Ficus spp.	33.3 ± 5.8	419.5	16.9 ± 8.5	212.9	9.4 ± 6.2	118.4
E. pyrifolia / Ficus spp.	10.3 ± 4.3	255.4	6.8 ± 2.4	172.7	0	0

c) Leaf litter biomass estimates in each forest type

The leaf litter biomass per quadrat was the highest in the *Ficus* spp. forest type (Table 7), which is the smallest forest type (Table 2).

Table 7 Mean ± 1 S.E. leaf litter biomass (g.0.5 m^{-2}) per quadrat (n=25) and total mass (kg) of the leaf litter for each forest type.

Forest type	Mean litter wt per quadrat (g)	Total mass (kg)
P. grandis	1.95 ± 5.05	375.2
P. grandis – Ficus spp.	12.6 ± 7.54	385.5
Ficus spp.	19.3 ± 9.19	243.2
E. pyrifolia - Ficus spp.	2.85 ± 0.73	72.4

ARTHROPOD COMMUNITIES IN DIFFERENT HABITATS

The log environment

The dominant logs had distinctly different appearances. A brief description of each follows:

a) *P. grandis*

P. grandis log texture is soft and flake-like without a hard core (heart wood). *P. grandis* bark is papery and is easily lost early in the decomposition process, except on the smaller branches and twigs. The woody material retains moisture so that the logs tend to become waterlogged (Figure 8.1).

Figure 8.1 *P. grandis* log (scale ruler = 30 cm)

b) *Ficus* spp.

Ficus spp. refers to *F. reflexa* and *F. lutea,* the logs of which are similar in all respects and virtually impossible to distinguish. The *Ficus* spp. log texture is harder than that of *P. grandis* and more cork-like. Throughout the decomposition process, the logs have a tunnelled, honeycomb appearance. The bark is hard and not usually thicker than 5 mm, often broken, with only small sections remaining attached to the log (Figure 8.2).

Figure 8.2 *Ficus* spp. log (scale ruler = 30 cm)

c) *C. nucifera*

C. nucifera logs tend to remain intact, through having a very hard bark, which surrounds the inner woody material. This bark is often present as a whole, even after the inner wood has completely decomposed. The inner material consists of long, string-like fibres that run in parallel. Late in the decomposition process, the inner material becomes soft but remains fibrous. The inner material retains moisture and tends to become waterlogged (Figure 8.3).

Figure 8.3 *C. nucifera* log (scale ruler = 30 cm)

The highest temperature difference was between the ambient air temperature and the log core temperature (these differences were: *P. grandis* 2.2°C, *Ficus* spp 2.1°C and *C. nucifera* 2.2°C lower than the ambient air temperature). Overall, the *C. nucifera* logs had the greatest temperature difference between 1) the core and under the logs, 2) the core and on the log surface, and 3) the inner core and the surrounding leaf litter (Table 8).

Table 8 Decrease in mean (±1 S.E.) temperature compared with the higher ambient air temperature (°C) for the three log types, *P.grandis* (n=20), *Ficus* spp. (n=20) and *C. nucifera* (n=10).

Log type	1	2	3	4	5
P. grandis	2.2 ± 0.3	1.7 ± 0.3	1.4 ± 0.3	0.04 ± 0.02	0.8 ± 0.2
Ficus spp.	2.1 ± 0.2	1.7 ± 0.3	0.87 ± 0.2	0.1 ± 0.1	0.8 ± 0.2
C. nucifera	2.2 ± 0.4	2.5 ± 0.5	1.6 ± 05	1.1 ± 0.2	2.2 ± 0.4

1 – Ambient air temperature versus log core temperature

2 - Log surface temperature versus temperature under the log

3 - Log core temperature versus log surface temperature

4 - Log core temperature versus temperature under the log

5 - Log core temperature versus surrounding litter temperature

P. grandis logs had the highest humidity difference between the ambient air compared with the log core (15 % r.h.), and the surface of the log compared with the log core (14.2 % r.h.). Also, *Ficus* spp. logs had the highest humidity difference between the log core and the log surface (13.4 % r.h.) (Table 9).

Table 9 Increase in mean (±1 S.E.) humidity compared with the ambient air humidity (% r.h.) for the three log types, *P. grandis* (n=20), *Ficus* spp. (n=20) and *C. nucifera* (n=10).

Log type	1	2	3	4	5
P. grandis	15 ± 1.9	9.4 ± 1.7	10.9 ± 1.5	1.5 ± 1.3	4 ± 2.1
Ficus spp.	12.6 ± 2	5.7 ± 1.9	13.4 ± 5.5	1.8 ± 1.1	4.7 ± 2.3
C. nucifera	14.2 ± 3	8.7 ± 3.5	11.4 ± 2.9	3.2 ± 2	4.6 ± 4.1

1 - Surrounding air humidity versus log core humidity

2 - Surface of the log humidity versus the humidity under the log

3 - Log core humidity versus the log surface humidity

4 - Log core humidity versus the humidity under the log

5 - Log core humidity versus the humidity litter material

General arthropod composition of logs

A total of 17 504 specimens were sampled. The species, with partial identification, and abbreviations used in the analyses are given in the Appendix. A summary of number of morphospecies and where possible, identified species per major taxon, is given in Table 10. The reference to species from this point onwards refers to the combination of morphospecies and identified species.

Table 10 Arthropods found in logs and woody litter on Cousine Island (morphospecies and identified species)

Order / Taxon	Number of species
Diptera	61
Coleoptera	58
Lepidoptera	44
Acari	36
Hemiptera	30
Arachnida	26
Collembola	24
Hymenoptera	23
Chilopoda	8
Isopoda	6
Orthoptera	5
Dermaptera	4
Diplopoda	4
Apterygota	4
Isoptera	4
Pseudoscorpiones	3
Thysanoptera	3
Blattodea	1
TOTAL	**344**

A total of 344 species were collected in all the logs and woody litter combined. The dominant groups, in terms of species richness, were Diptera (18 %), Coleoptera (17 %), Lepidoptera (13 %) and Acari (10 %) (Table 10).

C. nucifera logs supported the highest mean number ($\bar{x} = 48$) of species and the lowest range and variation about the mean. The other two log types, *P. grandis* and *Ficus* spp. had very similar means ($\bar{x} = 34$ and $\bar{x} = 27$ respectively) and greatest range and most variation about the mean compared with the *C. nucifera* logs (Figure 9).

Using ANOVA, there was a significant difference ($p = 0.0003$, $F_2 = 3.15$) in arthropod species richness between the log types. Individual t-tests comparing pairs of log types showed that *C. nucifera* was significantly different from both *P. grandis* and *Ficus* spp. logs, and there was no significant difference ($p = 0.365$, $F_1 = 4.09$) in species richness between *P. grandis* and *Ficus* spp. (Table 11).

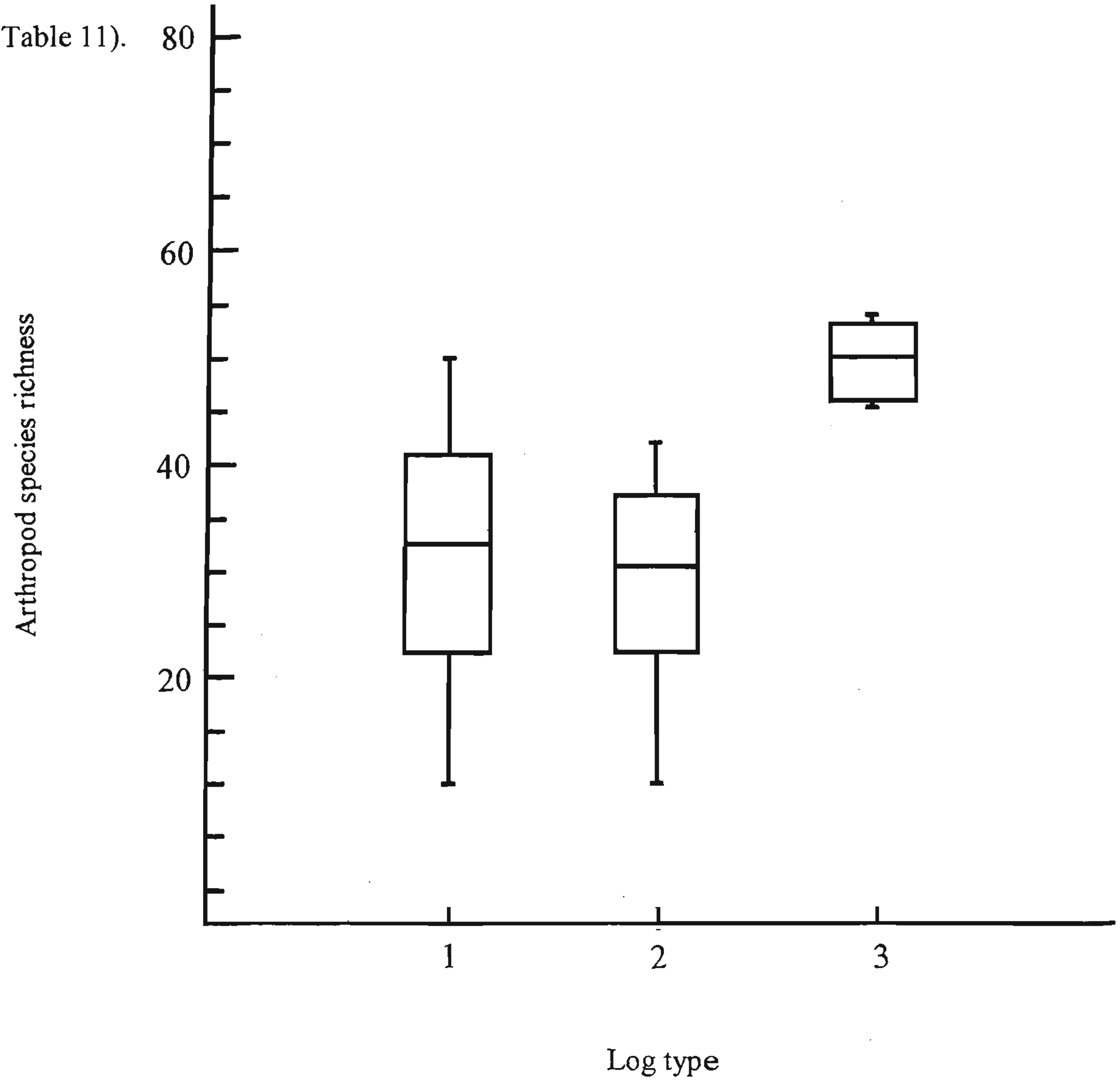

Figure 9 Comparison of arthropod species richness in the three different log types, 1= *P. grandis* (n=20), 2=*Ficus* spp. (n=20). 3= *C. nucifera* (n=10), showing the mean, 1st and 3rd quartiles and range of the data.

Table 11 Statistical comparison of arthropod richness in the three log types

Log type	t-test (95 % confidence level)
P. grandis and *Ficus* spp.	p = 0.365 not significant
P. grandis and *C. nucifera*	p = 0.024 significant
Ficus spp. and *C. nucifera*	p = 0.014 significant

Arthropod community structure for each log type

The log type scatterplot shows that the arthropod species assemblage differed widely in all three log types (Figure 10a). The arthropod species scatterplot showed *C. nucifera* logs to have a wide range of arthropod species, with a greater than 85 % cumulative fit (Figure 10b). These arthropod species include members from each taxon in the survey, except the Isopoda, Dermaptera and Thysanoptera. This log type also supports three endemic species, AHS12 – Arachnida, *Theridion clabrium*, CLS29 – Coleoptera, *Colobicones singularis* and HMDPS02 – Hemiptera, *Seychellesius niger* (Group 1). The *P. grandis* and *Ficus* spp. logs had unidentified species of Chilopoda (CHGPS04) and Thysanura (AHMNS04) respectively in great abundance. The Bray-Curtis dendrogram also shows that, in terms of the arthropod assemblages, the *P. grandis* and *Ficus* spp. logs were more closely related than either was to *C. nucifera* (Figure 11). However, the dendrogram distances for the three species differed by only 0.1 (Table 12).

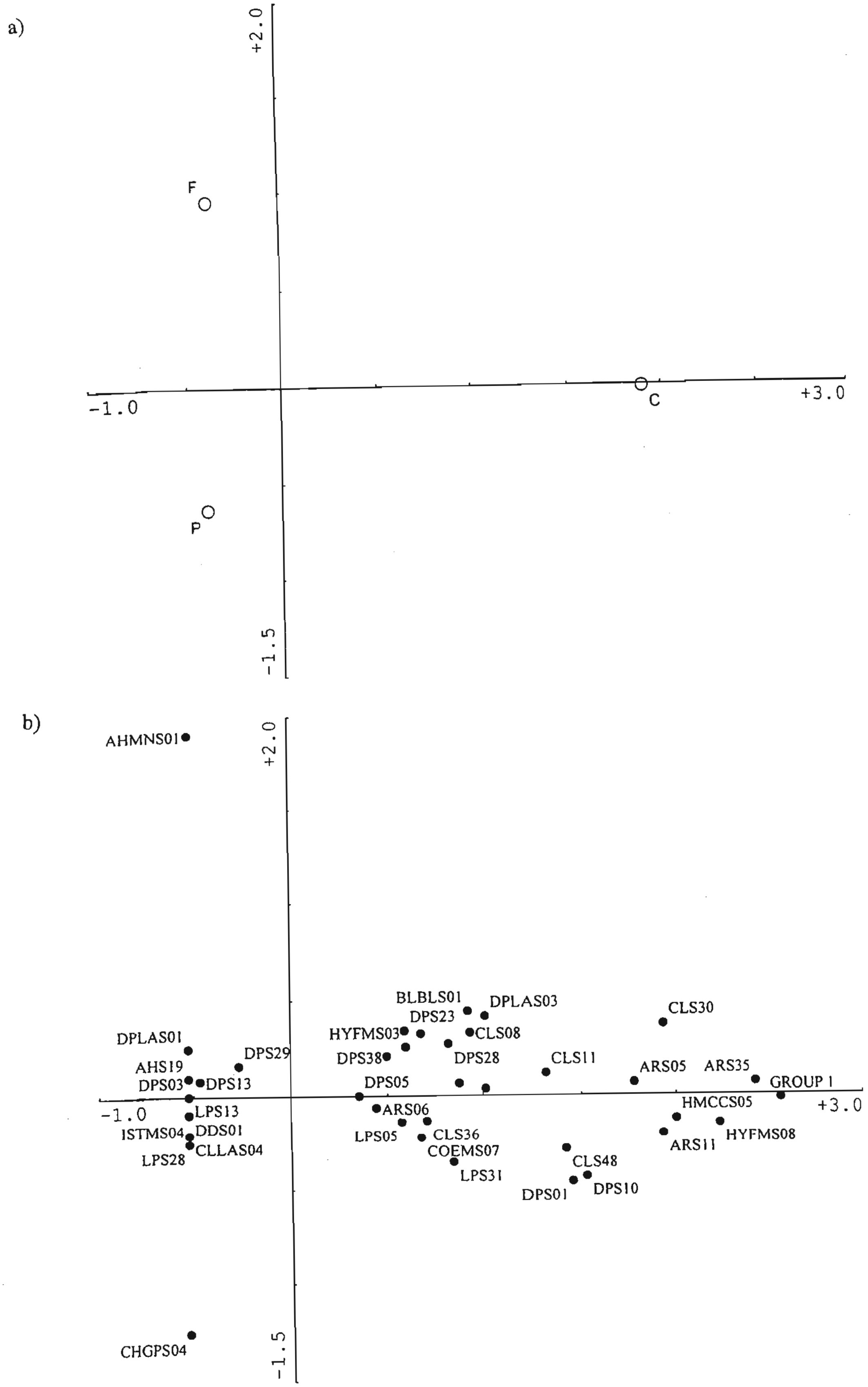

Figure 10 COA scatterplot of the arthropod community structure of the three log types.
a) Log type plot, b) Arthropod species plot (≥ 80 % cumulative fit shown for axis 1).
(P- *P. grandis*, F- *Ficus* spp., C- *C. nucifera*. Group 1 consists of: AHS01, AHS10, AHS12, AHS18, AHS22, AHS22, AHS25, CHSCS02, CLCUS01, CLS21, CLS28, CLS29, CLS43, DPLAS02, DPS15, DPS39, DPS41, HMDPS01, HMDPS02, LPS04, LPS10, LPS23, LPS36, ORGYS03, ORTHS01, PSS02, PSS04. Percentage variance of species values for axis 1 = 69.6 and axis 2 = 31.4. i.e. Total for both axes = 100. Eigenvalues for axis 1 = 0.555 and axis 2 = 0.254). Abbreviations for arthropod species are given in the Appendix. Note: AHS12, CLS29 and HMDPS02 are endemic to the Seychelles archipelago.

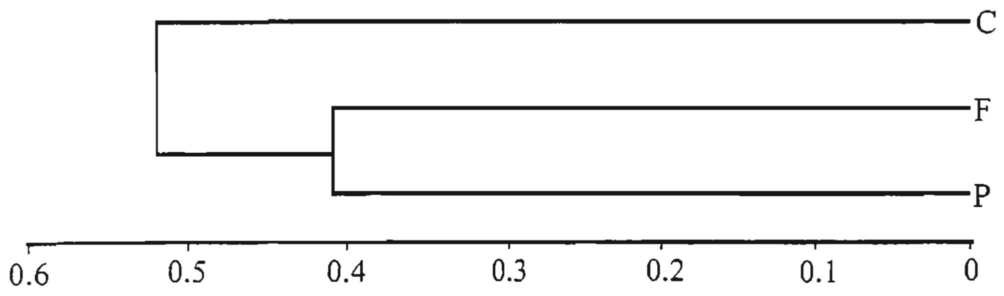

Figure 11 Bray-Curtis dendrogram of arthropod assemblages associated with the three log types P- *P. grandis*, F- *Ficus* spp., C- *C. nucifera*.

Table 12 Bray-Curtis dendrogram distance matrix for the log types

	P. grandis	*Ficus* spp.
Ficus spp.	0.410	
C. nucifera	0.538	0.502

Influence of rate of log decomposition on arthropod communities

The results show that decomposition class 1 (logs elevated from the ground and bark partly removed) had the highest mean number of arthropod species per log ($\overline{x} = 47.5$) yet the smallest range and variation about the mean. The other three groups i.e. class 2 - 4, had a similar means ($\overline{x} = 26.7$, 36, 30.9 respectively) as well as large ranges and variations about the means (Figure 12).

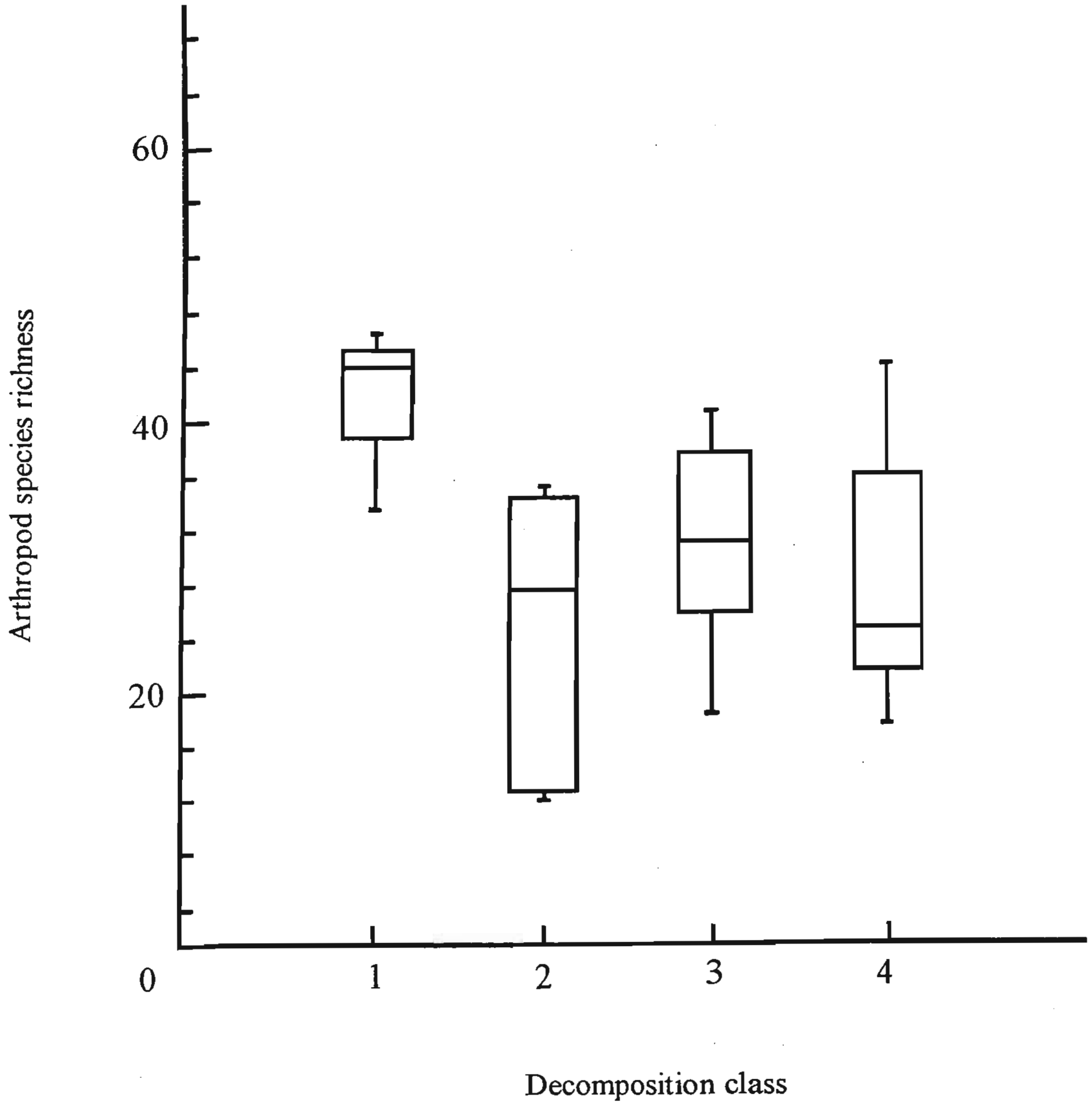

Figure 12 Comparison of arthropod species richness in the four decomposition classes, 1=least decomposed, 4=most decomposed (class 1 to 4, n=15), showing the mean, 1st and 3rd quartiles and range of the data.

The arthropod species number per log in the different decomposition classes were significantly different (p= 0.019, F_3= 2.76). The groups were tested separately using the student t-test and the results of this statistical analysis are given in Table 13. Decomposition class 1 was significantly different from the other three classes (p= 0.001 for class 2, 0.021 for class 3 and 0.003 for class 4). These other three class comparisons were not statistically significant (p = 0.529, F_2= 0.644).

Table 13 Statistical comparison of arthropod species richness in the four decomposition classes

Class combinations	t-test (95 % confidence level)
Class 1 and 2	p = 0.001 significant
Class 1 and 3	p = 0.021 significant
Class 1 and 4	p = 0.003 significant
Class 2 and 3	p = 0.064 not significant
Class 2 and 4	p = 0.170 not significant
Class 3 and 4	p = 0.125 not significant

The decomposition class scatterplot shows the arthropod assemblages in the four decomposition classes to be widely distributed, suggesting the classes to be very different in terms of their arthropod assemblage structure (Figure 13a). The arthropod species plot shows a wide distribution of the arthropod species abundance. However, the endemic species, *Nesogeophilus lepochilus* (Chilopoda) had a high abundance associated with decomposition class 3 (Figure 13b). The Bray-Curtis dendrogram shows classes 3 and 4 to be the most similar. Class 2 is most similar to classes 3 and 4, with class 1 the least similar to the other classes (Figure 14, Table 14).

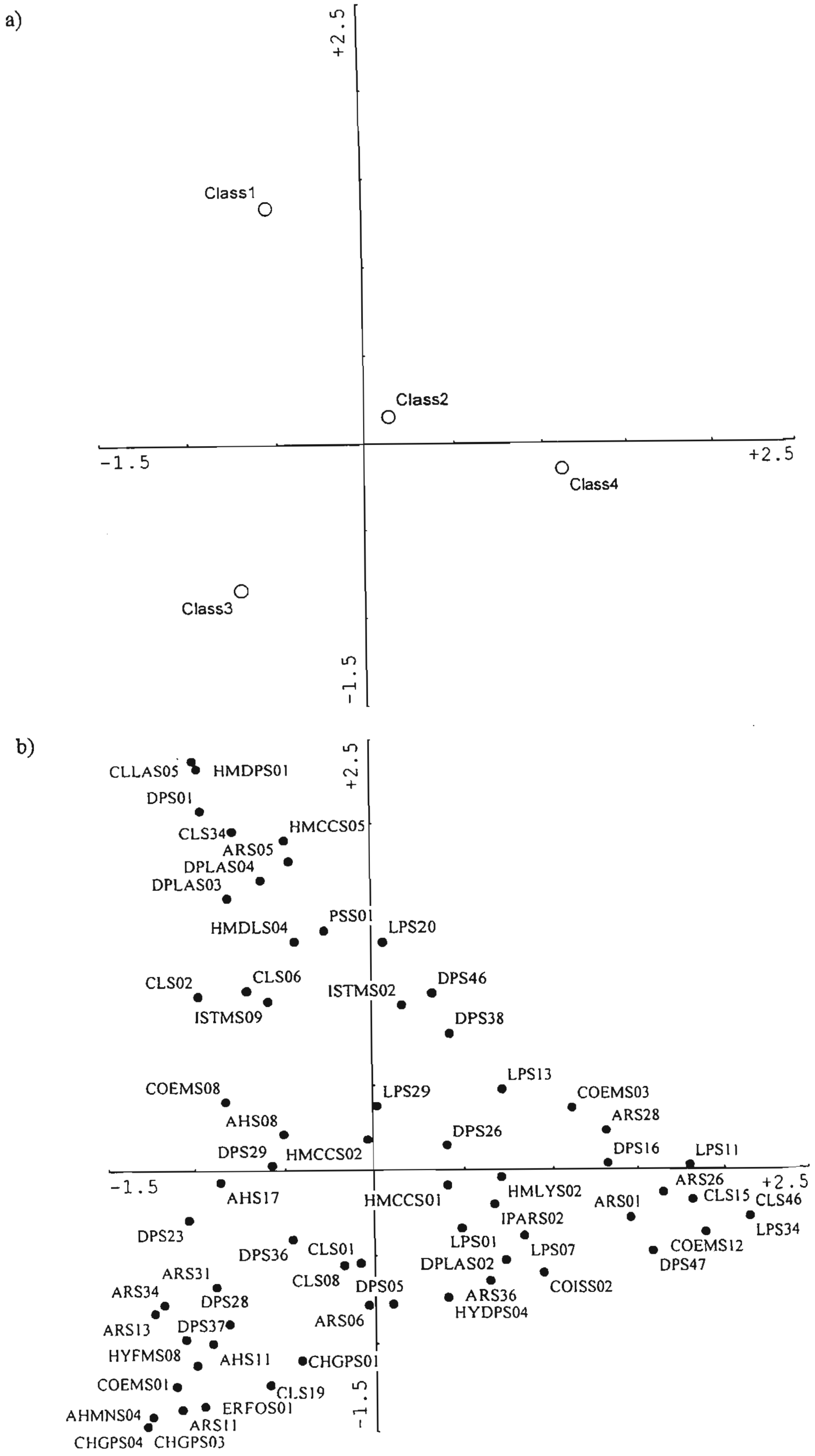

Figure 13 COA scatterplot of the arthropod community structure of the four decomposition classes
a) Decomposition class plot, b) Arthropod species plot (≥ 80 % cumulative fit shown)
(Percentage variance of species values for axis 1 = 34.3 and axis 2 = 38.8. i.e. Total for both axes = 73.1. Eigenvalues for axis 1 = 0.282 and axis 2 = 0.319). Abbreviations for the arthropod species are given in the Appendix. Note: CHGPS03 and HMCCS01 are endemic to the Seychelles archipelago.

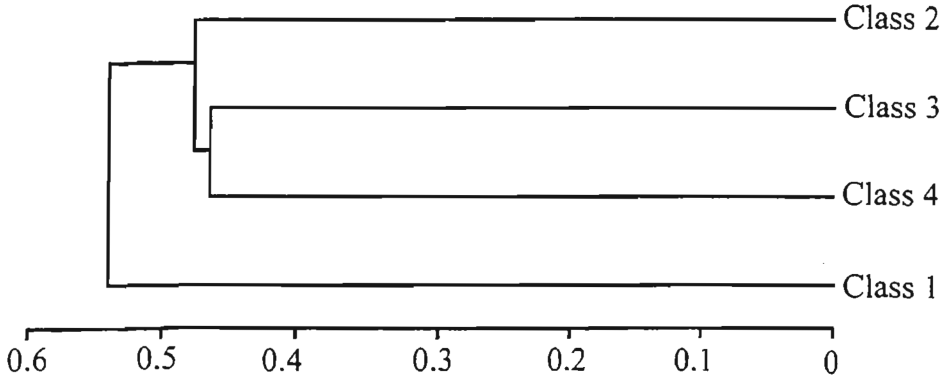

Figure 14 Bray-Curtis dendrogram of arthropod assemblages associated with the four decomposition classes.

Table 14 Bray-Curtis dendrogram distances matrix for each decomposition class

	Class 1	Class 2	Class 3
Class 2	0.563		
Class 3	0.56	0.421	
Class 4	0.488	0.506	0.469

Influence of forest type on arthropod communities

The differences in the mean number of arthropod species, per log for all log types, in each forest type are given in Figure 15. The *Ficus* spp. forest type has the lowest mean number of arthropods per log ($\overline{x} = 24.8$)

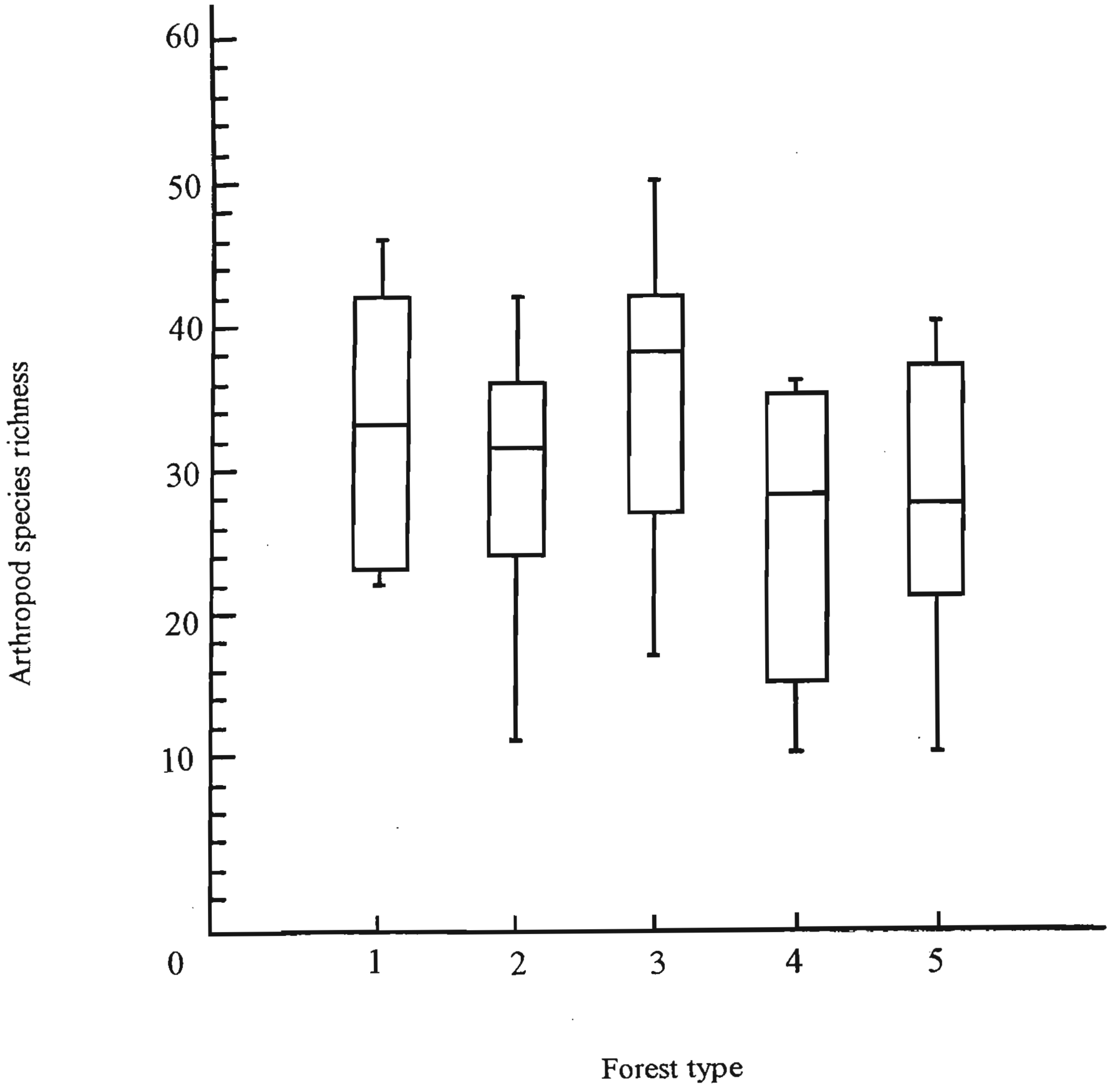

Figure 15 Comparison of arthropod species richness per log in the five forest types. 1= *P. grandis* (n=10), 2= *P. grandis / Ficus* spp. site 1 (n=20), 3= *P. grandis / Ficus* spp. site 2 (n=20), 4= *Ficus* spp. (n=10), 5= *E. pyrifolia / Ficus* spp. (n=20), showing the mean, 1st and 3rd quartiles and range of the data.

There was a significant difference (p =0.002, F_4= 4.939) in arthropod species richness per log in the different forest types. Further analysis using t-tests to compare pairs of forest types showed that there was a significant difference in the arthropod assemblage species richness between the *Ficus* spp. and *E. pyrifolia - Ficus* spp. (p = 0.04, Table 15).

Table 15 Statistical comparison of arthropod species richness in the logs of the five forest types

Forest type	t-test (95 % confidence level)
P. grandis and *P. grandis / Ficus* spp. site 1	p = 0.26 not significant
P. grandis and *P. grandis / Ficus* spp. site 2	p = 0.34 not significant
P. grandis and *Ficus* spp	p = 0.13 not significant
P. grandis and *E. pyrifolia / Ficus* spp.	p = 0.15 not significant
P. grandis / Ficus spp. site 1 and *P. grandis / Ficus* spp. site 2	p = 0.08 not significant
P. grandis / Ficus spp. site 1 and *E. pyrifolia / Ficus* spp.	p = 0.29 not significant
P. grandis / Ficus spp. site 2 and *Ficus* spp.	p = 0.23 not significant
P. grandis / Ficus spp. site 2 and *E. pyrifolia / Ficus* spp.	p = 0.06 not significant
Ficus spp. and *E. pyrifolia / Ficus* spp.	p = 0.04 significant

The forest type scatterplot shows little association of the arthropod species assemblages found in logs between the five vegetation types, with the exception of *P. grandis / Ficus* spp. site 2, being similar to the *E. pryifolia / Ficus* spp. forest type (Figure 16a). The arthropod species scatterplot shows a number of adult Diptera (DPS11, DPS02, DPS04, DPS17) associated with the *P. grandis / Ficus* spp. site 1 forest type (Figure 16b). The trends shown by the forest type scatterplot are contradicted by the Bray-Curtis dendrogram (Figure 17, Table 16) which shows the two *P. grandis / Ficus* spp. sites 1 and 2 log arthropod assemblages to be more closely related. However, these two sites are linked to the *E. pryifolia / Ficus* spp., while the *P. grandis* and *Ficus* spp. forest types stand alone.

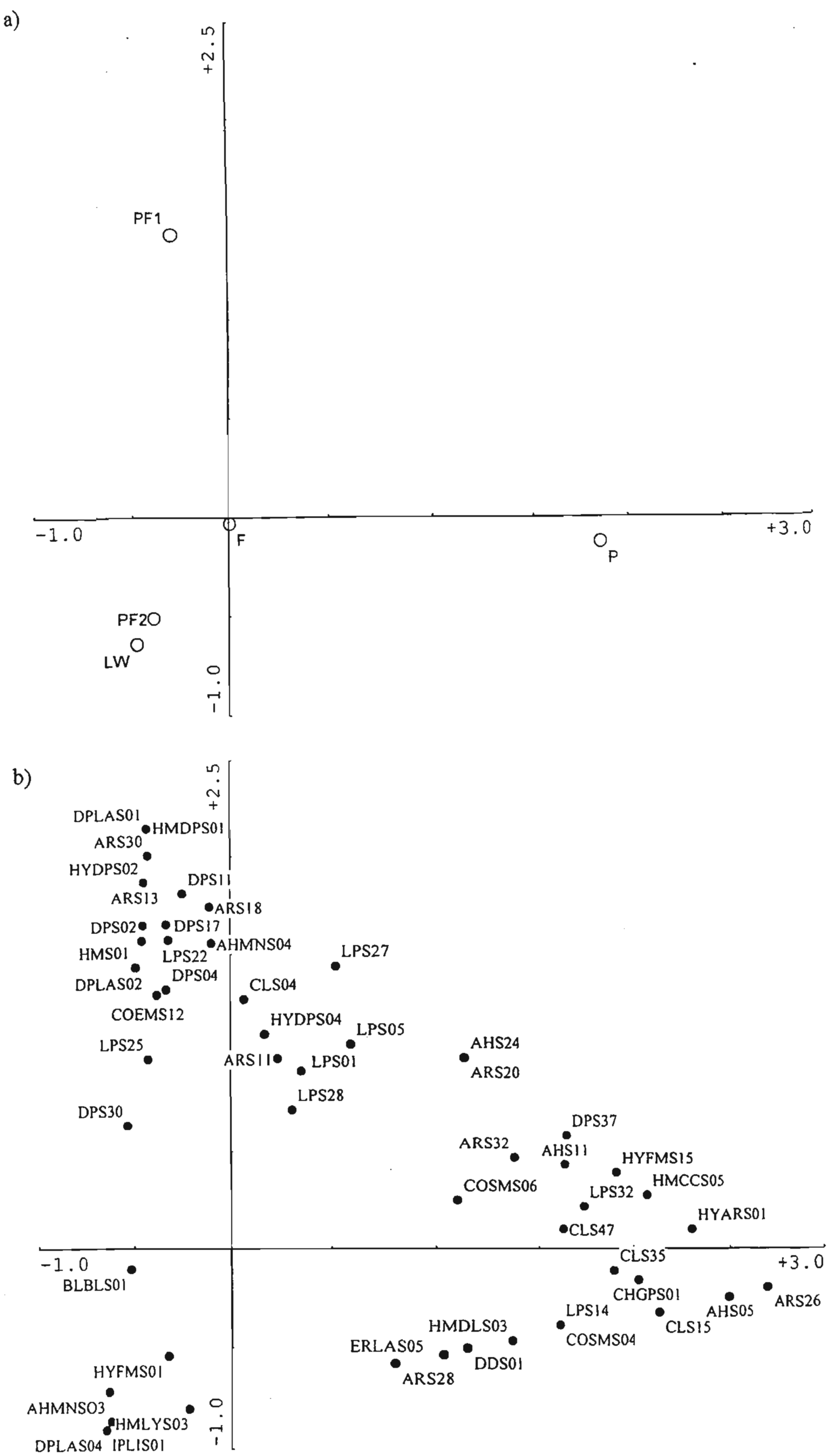

Figure 16 COA scatterplots of the arthropod community structure of logs in the five forest types.
a) Forest type plot, b) Arthropod species plot (≥ 80 % cumulative fit shown).
(P= *P. grandis*, PF1= *P.grandis / Ficus* spp. site 1, PF2= *P.grandis / Ficus* spp. site 2, F= *Ficus* spp., LW= *E. pryifolia / Ficus* spp. Percentage variance of species values for axis 1 = 33.4 and axis 2 = 30.6. i.e. Total for both axes = 64. Eigenvalues for axis 1 = 0.473 and axis 2 = 0.435). Abbreviations for arthropod species are given in the Appendix.

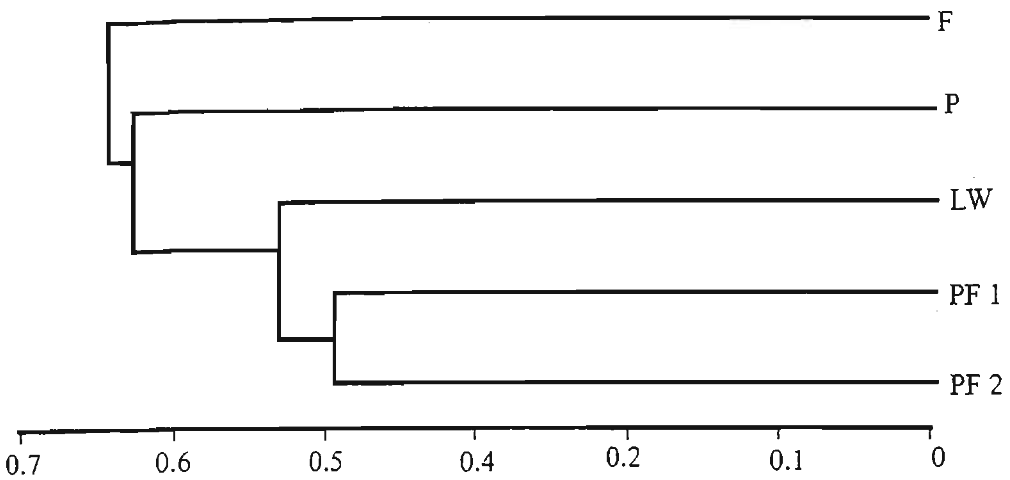

Figure 17 Bray-Curtis dendrogram of arthropod assemblages associated with the logs in the five forest types. P= *P. grandis*, PF1= *P.grandis / Ficus* spp. site 1, PF2= *P.grandis / Ficus* spp. site 2, F= *Ficus* spp., LW= *E. pryifolia / Ficus* spp.

Table 16 Bray-Curtis dendrogram distances matrix for the arthropod species assemblage associated with logs in each forest type.

	P. grandis	*P. grandis/ Ficus* spp. Site 1	*P. grandis / Ficus* spp. Site 2	*Ficus* spp.
P. grandis / Ficus spp. Site 1	0.609			
P. grandis / Ficus spp. Site 2	0.615	0.473		
Ficus spp.	0.645	0.638	0.638	
E. pryifolia / Ficus spp.	0.668	0.551	0.483	0.678

Influence of log type and forest type on arthropod communities

a) *P. grandis*

For *P.grandis* logs, although the means, of arthropod species per log, differed greatly (Figure 18), the differences, were not statistically significant ($p = 0.520$, $F_3= 2.24$). There was a similar situation with *Ficus* spp. logs (Figure 19) ($p = 0.122$, $F_3= 0.783$).

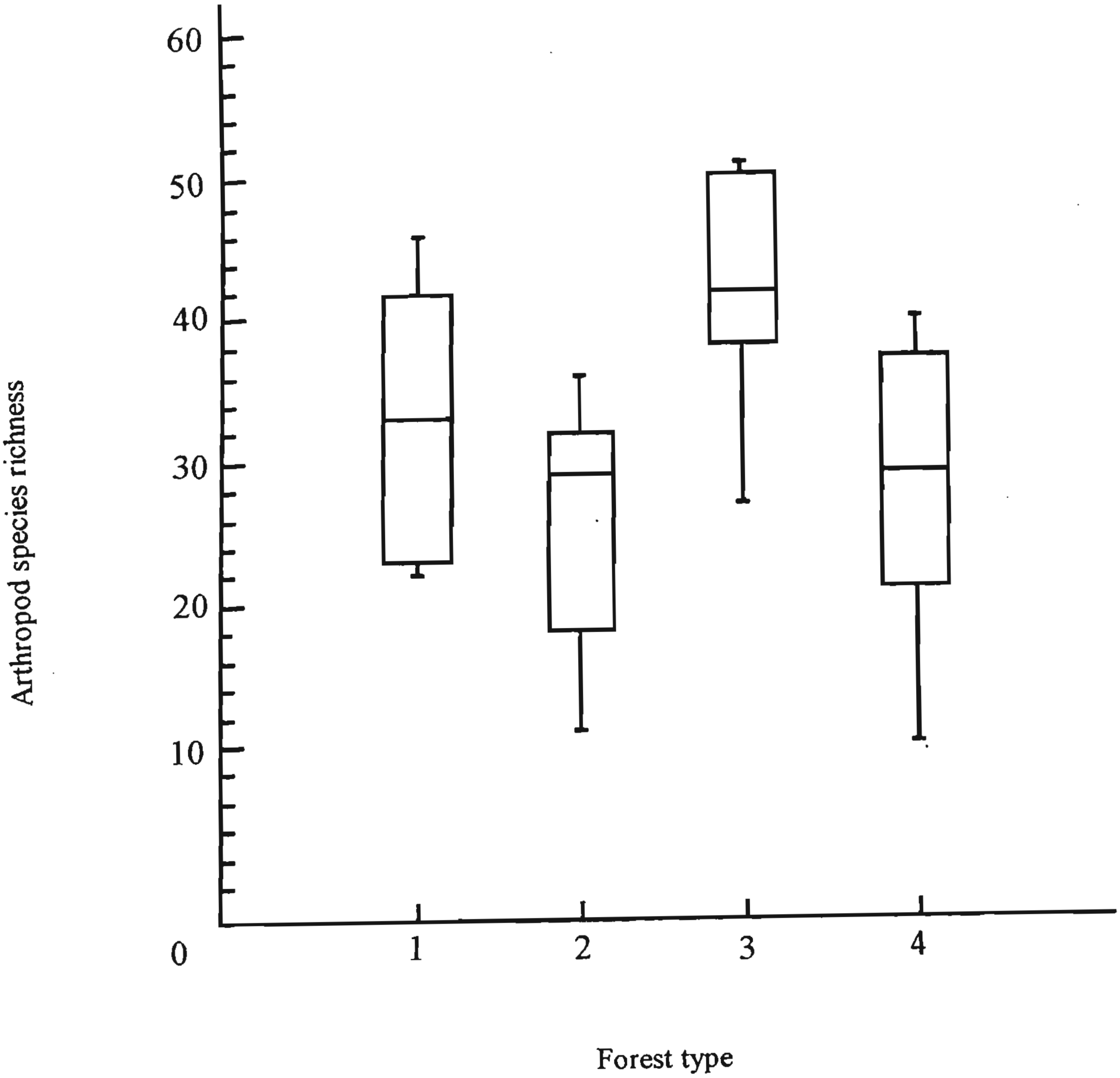

Figure 18 Comparison of arthropod species richness in the *P. grandis* logs in the forest types. 1= *P. grandis*, 2= *P. grandis* / *Ficus* spp. site 1, 3= *P. grandis* / *Ficus* spp. site 2, 4 = *E. pyrifolia* / *Ficus* spp. (n=10 for all forest types), showing the mean, 1st and 3rd quartiles and range of the data.

b) *Ficus* spp.

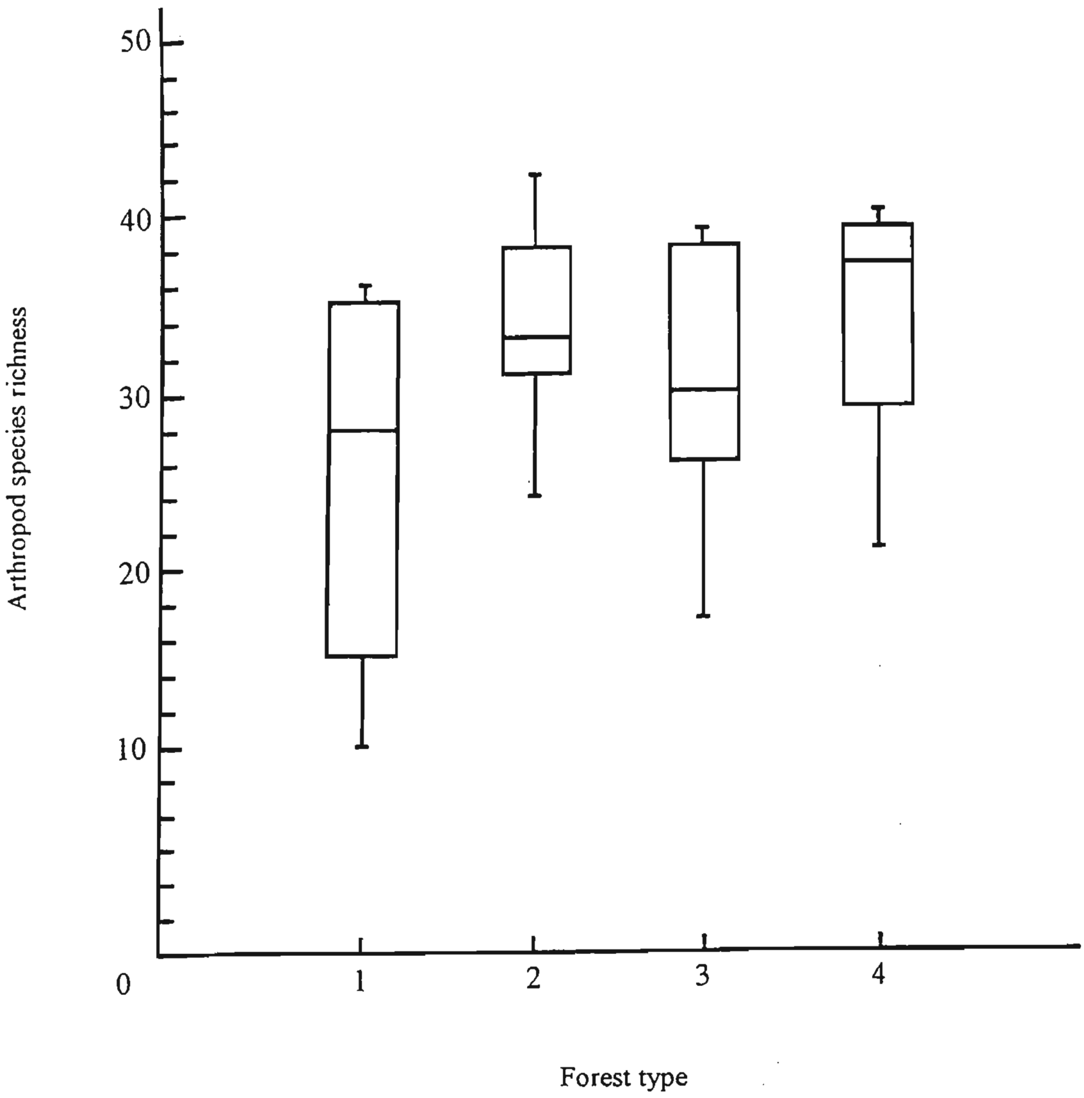

Figure 19 Comparison of arthropod species richness in the *Ficus* spp. log in the forest types. 1= *Ficus* spp., 2= *P. grandis* / *Ficus* spp site 1, 3= *P. grandis* / *Ficus* spp site 2, 4= *E. pyrifolia* / *Ficus* spp. (n=10 for all forest types), showing the mean, 1st and 3rd quartiles and range of the data.

The arthropod species composition results showed an association between the *P. grandis* and *Ficus* spp. logs from the same forest types. The *P. grandis* logs in the *P. grandis* forest type, and the *Ficus* spp. logs in the *Ficus* spp. forest types showed no association to any of the logs in the other forest types (Figure 20a, Figure 21, Table 17). The *P. grandis* logs in the *P. grandis* forest type, shows a number of arthropod species associated with it, including 2 members of the Chilopoda (CHSCS04 – not identified and CHSCS02 – *Otostigmus regulosus*) and Arachnida (AHS11 – not identified and AHS17 – *Schizomida* sp.) (Figure 20b).

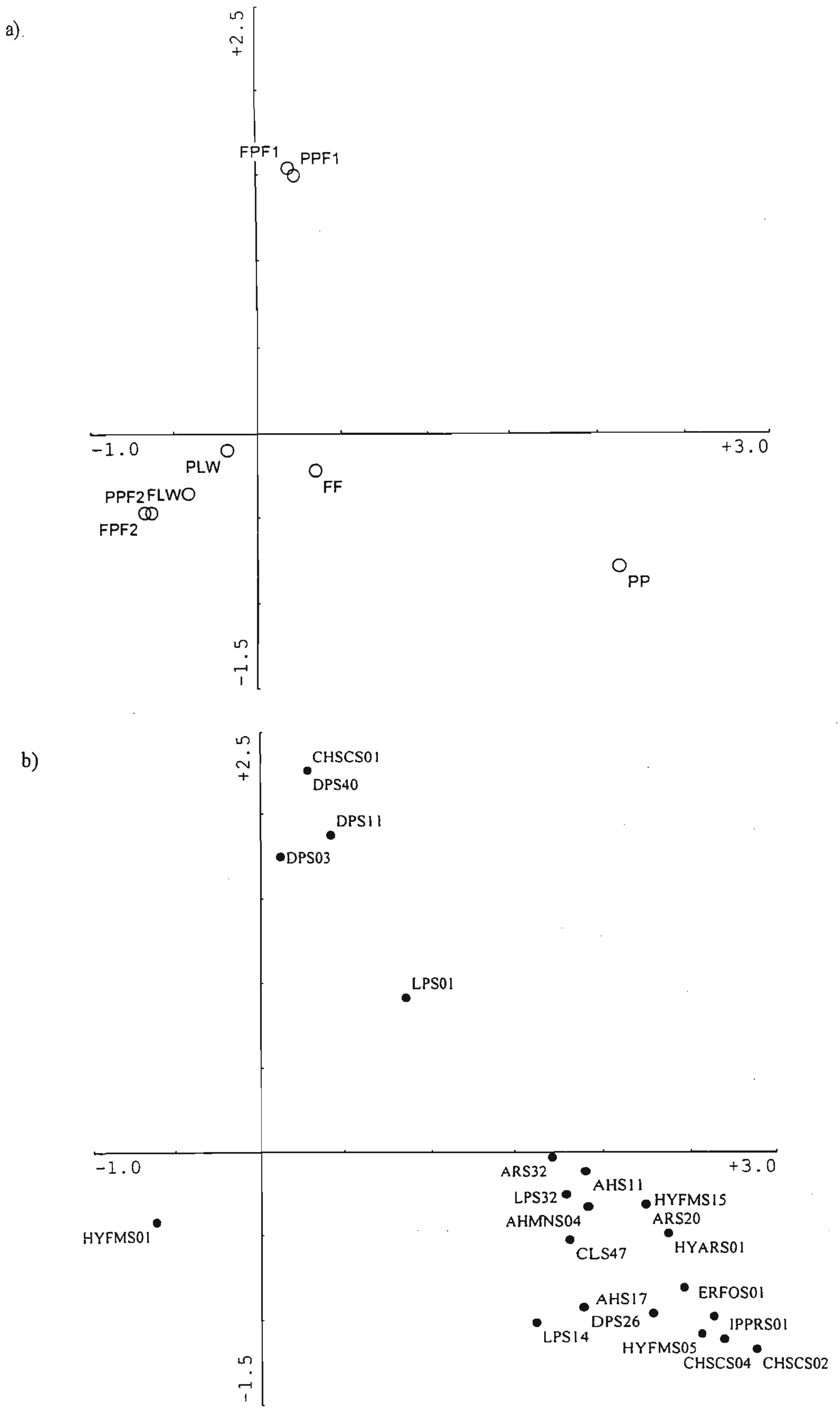

Figure 20 COA scatterplots of the arthropod community structure of log types in their respective forest types.
a) Log types in their respective forest type plot, b) Arthropod species plot (≥ 80 % cumulative fit shown).
(PP=*P. grandis* logs in *P. grandis* forest type, PPF1= *P. grandis* logs in the *P. grandis / Ficus* spp. site 1, FPF1= *Ficus* spp. logs in the *P. grandis / Ficus* spp. site 1, PPF2= *P. grandis* logs in the *P. grandis / Ficus* spp. site 2, FPF2= *Ficus* spp. logs in the *P. grandis / Ficus* spp. site 2, FF= *Ficus* spp. logs in the *Ficus* spp. forest type, PLW= *P. grandis* logs in the *E. pryifolia / Ficus* spp. forest type, FLW= *Ficus* spp. logs in the *E. pryifolia / Ficus* spp. forest type. Percentage variance of species values for axis 1 = 33.4 and axis 2 = 30.6. i.e. Total for both axes = 100. Eigenvalues for axis 1 = 0.473 and axis 2 = 0.435). Abbreviations for arthropod species are given in the Appendix. Note: CHSCS01 is endemic to the Seychelles archipelago.

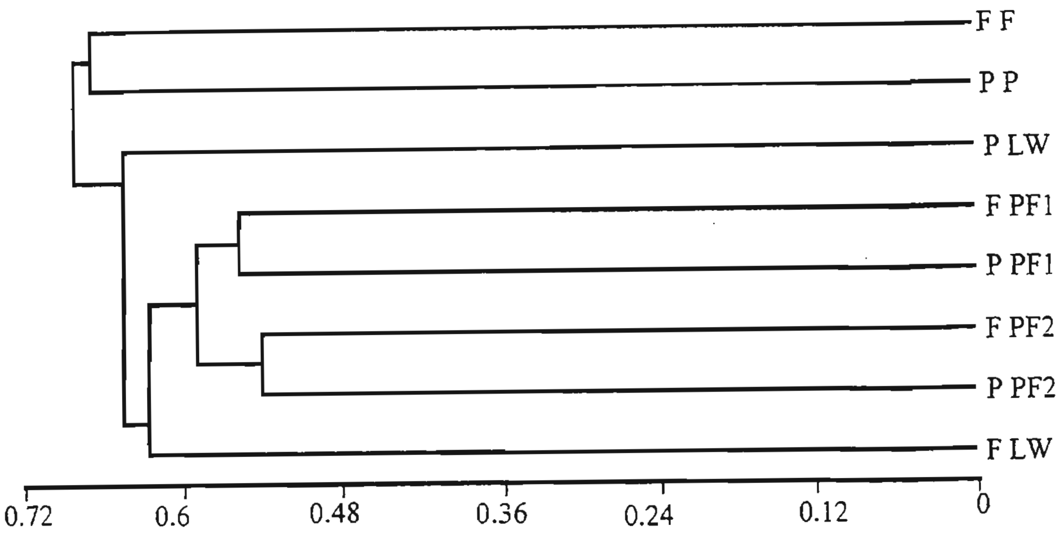

Figure 21 Bray-Curtis dendrogram of arthropod assemblages associated with the log types in each forest type. PP= *P. grandis* logs in *P. grandis* forest type, PPF1= *P. grandis* logs in the *P. grandis / Ficus* spp. site 1, FPF1= *Ficus* spp. logs in the *P. grandis / Ficus* spp. site 1, PPF2= *P. grandis* logs in the *P. grandis / Ficus* spp. site 2, FPF2= *Ficus* spp. logs in the *P. grandis / Ficus* spp. site 2, FF= *Ficus* spp. logs in the *Ficus* spp. forest type, PLW= *P. grandis* logs in the *E. pryifolia / Ficus* spp. forest type, FLW= *Ficus* spp. logs in the *E. pryifolia / Ficus* spp. forest type.

Table 17 Bray-Curtis dendrogram distances matrix for logs in each forest type. PP= *P. grandis* logs in *P. grandis* forest type, PPF1= *P. grandis* logs in the *P. grandis / Ficus* spp. site 1, FPF1= *Ficus* spp. logs in the *P. grandis / Ficus* spp. site 1, PPF2= *P. grandis* logs in the *P. grandis / Ficus* spp. site 2, FPF2= *Ficus* spp. logs in the *P. grandis / Ficus* spp. site 2, FF= *Ficus* spp. logs in the *Ficus* spp. forest type, PLW= *P. grandis* logs in the *E. pryifolia / Ficus* spp. forest type, FLW= *Ficus* spp. logs in the *E. pryifolia / Ficus* spp. forest type

	PP	PPF1	PPF2	PLW	FF	FPF1	FPF2
PPF1	0.636						
PPF2	0.677	0.583					
PLW	0.690	0.629	0.591				
FF	0.672	0.676	0.711	0.716			
FPF1	0.680	0.558	0.595	0.635	0.646		
FPF2	0.715	0.630	0.542	0.690	0.636	0.555	
FLW	0.723	0.690	0.644	0.688	0.709	0.629	0.548

Influence of woody litter on arthropod communities

Figure 22 Woody litter in a 0.5 m x 0.5 m quadrat

The highest mean number of arthropod species per quadrat in the woody litter was highest at *P. grandis* / *Ficus* spp. site 2. (x = 36), while the lowest was at *P. grandis* / *Ficus* spp. site 1 (x = 18) (Figure 24). There were no significant differences between arthropod species richness in woody litter in the different forest types (p = 0.383, F_4= 2.86).

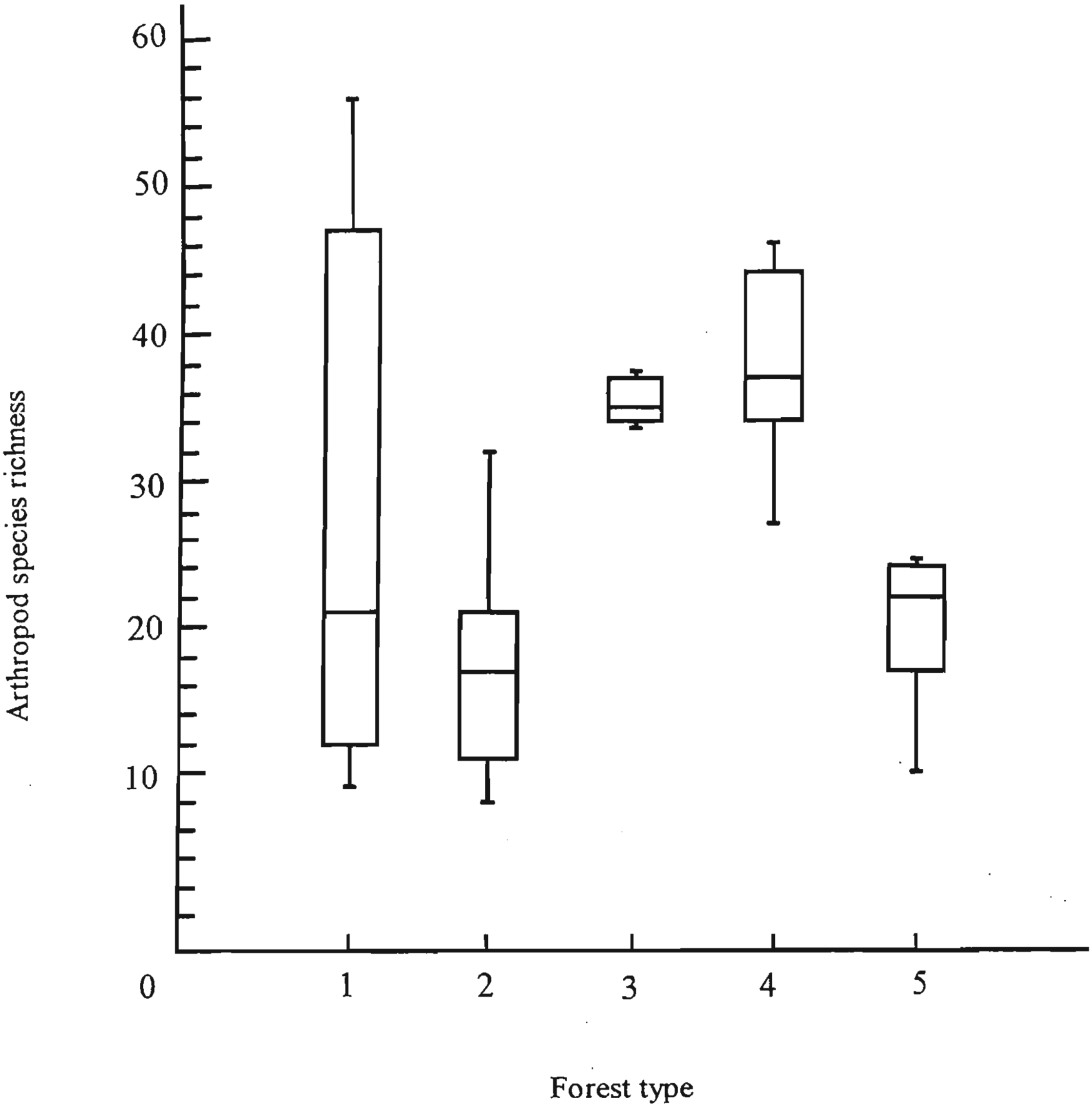

Figure 23 Comparison of arthropod species richness in the woody litter in the 5 forest types. 1= *P. grandis*, 2= *P. grandis / Ficus* spp. site 1, 3= *P. grandis / Ficus* spp. site 2, 4= *Ficus* spp., 5= *Ficus* spp. / *E. pryrifolia.*(n=10 for all forest types), showing the mean, 1st and 3rd quartiles and range of the data.

The scatterplot shows the arthropod assemblage in the woody litter in different forest types to be different in composition (Figure 24a) even though there was no significant difference in species richness (Figure 23). The arthropod species plot shows the woody litter in the *E. pryifolia / Ficus* spp. forest type supported a number of adult Diptera (DPS11, DPS31, DPS36, DPS47), seeking cover. The woody litter in the *P. grandis* forest type has the most arthropod individuals associated with it (Figure 24b).

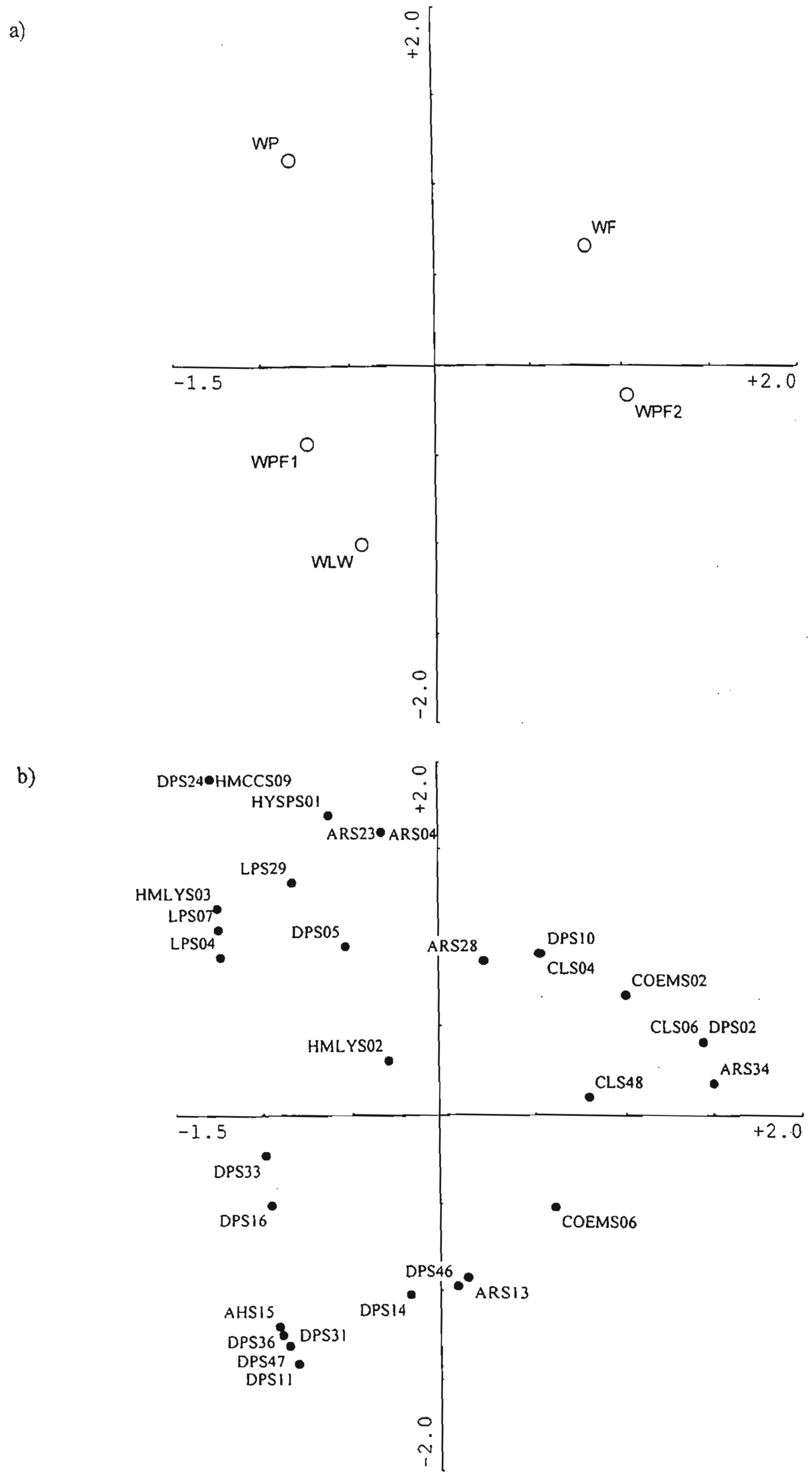

Figure 24 COA scatterplots of the arthropod community structure in the woody litter in the five forest types.
a) Woody litter in each forest type plot, b) Arthropod species plot (≥ 80 % cumulative fit shown)
(WP= *P. grandis*, WPF1= *P. grandis / Ficus* spp. site 1, WPF2 = *P. grandis / Ficus* spp. site 2, WF= *Ficus* spp., WLW= *E. pyrifolia / Ficus* spp. Percentage variance of species values for axis 1 = 29.1 and axis 2 = 25.7. i.e. Total for both axes = 54.8. Eigenvalues for axis 1 = 0.406 and axis 2 = 0.359). Abbreviations for arthropod species are given in the Appendix . Note: CLS05 is endemic to the Seychelles archipelago.

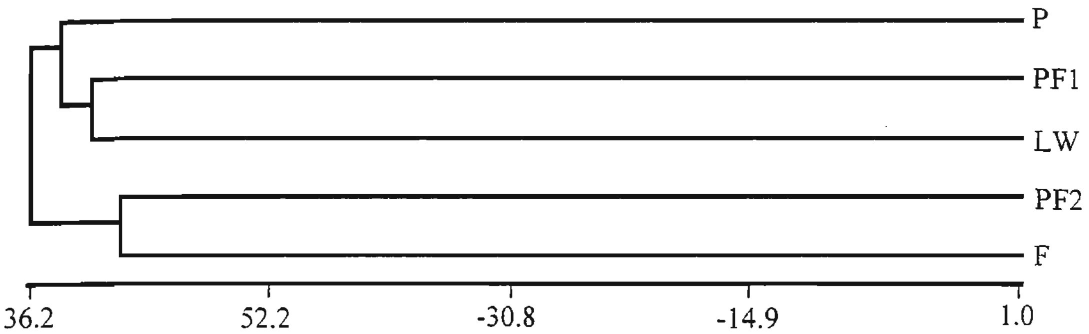

Figure 25 Bray-Curtis dendrogram of arthropod assemblages associated with the woody litter in each forest type. P= *P. grandis*, PF 1= *P. grandis / Ficus* spp. site 1, PF 2= *P. grandis / Ficus* spp. site 2, F= *Ficus* spp., LW= *Ficus* spp. / *E. pryrifolia.*

Table 18 Bray-Curtis dendrogram distances matrix for woody litter in each forest type. P= *P. grandis,* PF 1= *P. grandis / Ficus* spp. site 1, PF 2= *P. grandis / Ficus* spp. site 2, F= *Ficus* spp., LW= *Ficus* spp. / *E. pryrifolia.*

	P	PF1	PF2	F
PF1	0.402			
PF2	0.355	0.372		
F	0.361	0.339	0.425	
LW	0.385	0.413	0.409	0.339

b) Woody litter and logs from the same forest types

P. grandis- Ficus spp. site 2 logs had the highest mean number arthropod species richness per log ($\bar{x}$ = 48.1), while *P.grandis - Ficus* spp site 1, had the lowest mean ($\bar{x}$ = 17.8) per quadrat of woody litter (Figure 23). In all the forest types, the mean number of arthropods in the woody litter per quadrat was lower than the mean number of arthropods per log. The arthropod species number from the woody litter and the arthropod species richness found on the logs in the same forest type were not significant ($p = 0.001$, $F_9 = 3.41$).

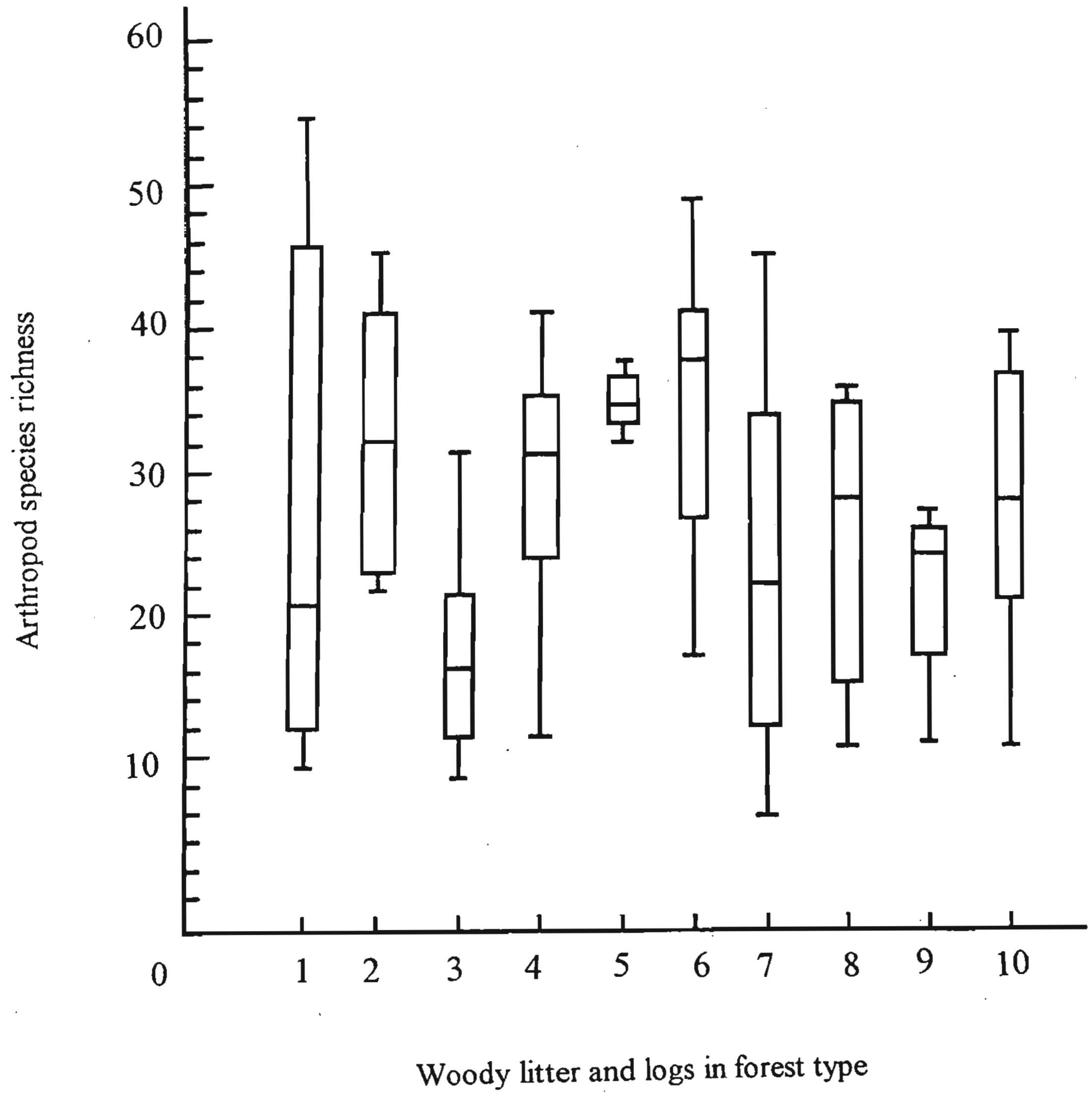

Figure 26 Comparison of arthropod species richness in the woody litter and logs in the 5 forest types. 1= *P. grandis*, woody litter (n= 10), 2= *P. grandis* logs (n=10), 3= *P. grandis / Ficus* spp. site 1 woody litter (n=10), 4= *P. grandis / Ficus* spp. site 1 logs (n=20), 5= *P. grandis / Ficus* spp. site 2 woody litter (n=10), 6= *P.grandis / Ficus* spp. site 2 logs (n=20), 7= *Ficus* spp. woody litter (n=10), 8= *Ficus* spp. logs (n=10), 9= *Ficus* spp. / *E. pryifolia*, woody litter (n=10), 10= *Ficus* spp. / *E. pryifolia* (n=20) logs, showing the mean, 1st and 3rd quartiles and range of the data.

The arthropod assemblage composition in the woody litter also did not show similarity to the logs of the same vegetation type. The arthropod assemblage in the woody litter show a closer similarity to each other (Figure 27a and 28). The arthropod species plot shows a large number of arthropods associated with logs in the *P. grandis* forest type (Figure 27b).

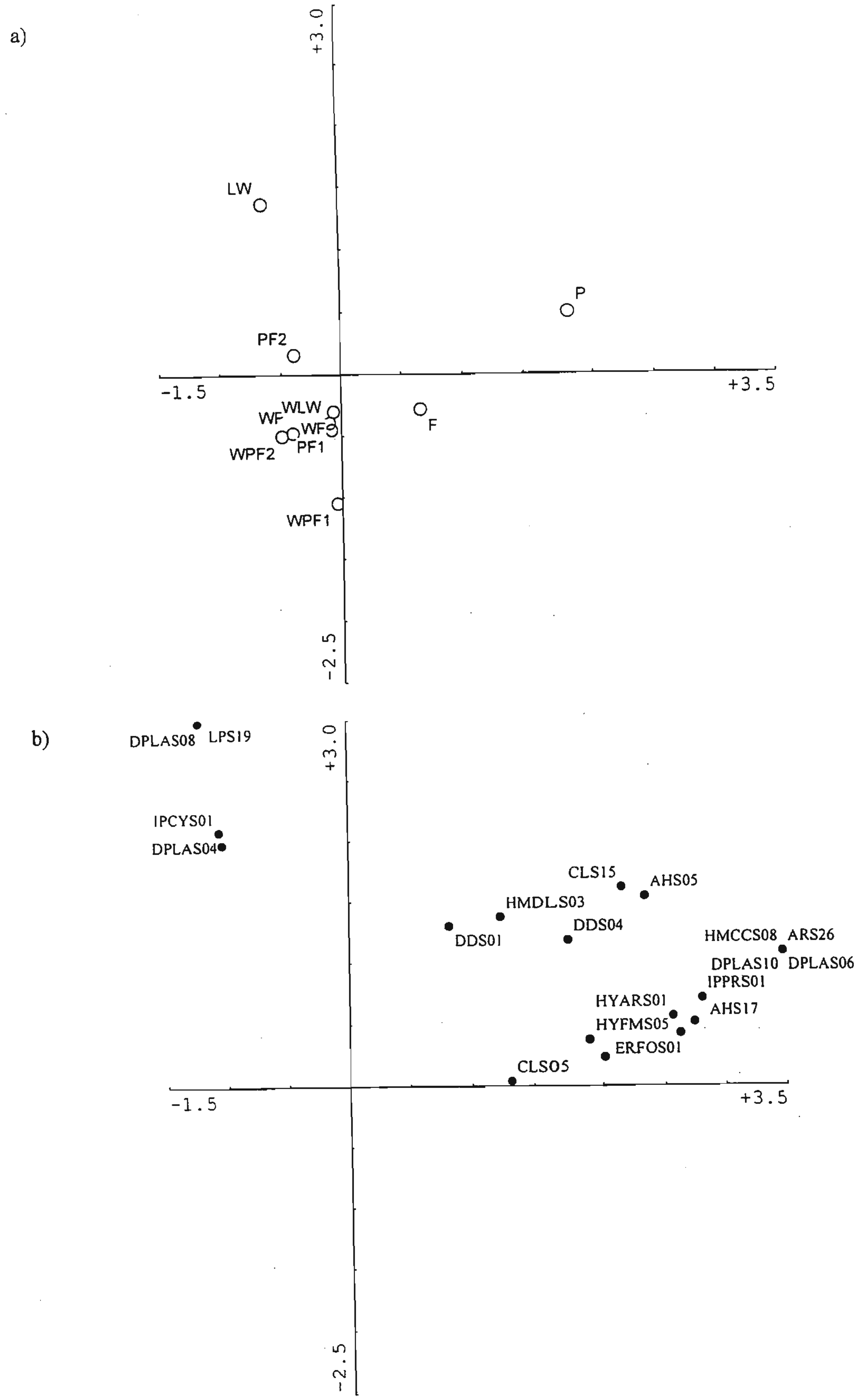

Figure 27 COA scatterplots of the logs and woody litter arthropod community structure their forest types.
a) Logs and woody litter in each forest type plot, b) Arthropod species plot (≥ 80 % cumulative fit shown)
(PW= *P. grandis*, woody litter, P= *P. grandis*, logs, WPF1= *P. grandis / Ficus* spp. site 1, woody litter, PF1= *P. grandis / Ficus* spp. site 1, logs, WPF2= *P. grandis / Ficus* spp. site 2, woody litter, PF2= *P.grandis / Ficus* spp. site 2, logs, WF= *Ficus* spp., woody litter, F= *Ficus* spp., logs, WLW= *Ficus* spp. / *E. pryifolia*, woody litter, LW= *Ficus* spp. / *E. pryifolia,* logs. Percentage variance of species values for axis 1 = 17.7 and axis 2 = 13.5 i.e. Total for both axes = 31.2. Eigenvalues for axis 1 = 0.273 and axis 2 = 0.208). Abbrevaiations for arthropod species are given in the Appendix.

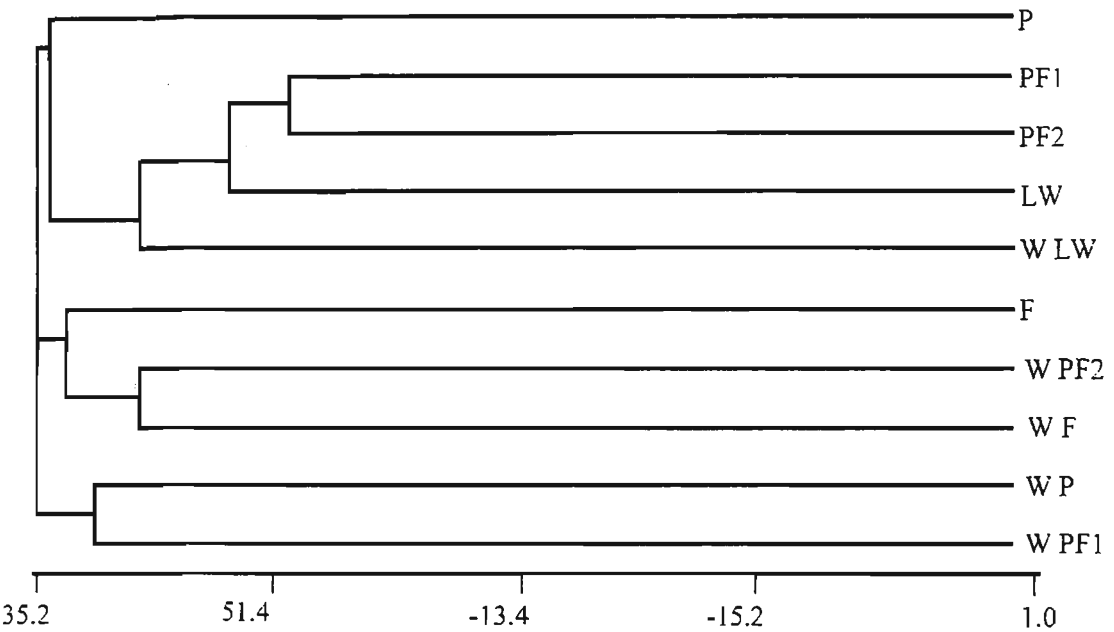

Figure 28 Bray-Curtis dendrogram of arthropod assemblages assoicated with woody litter and logs in each forest type. PW= *P. grandis*, woody litter, P= *P. grandis*, logs, WPF1= *P. grandis / Ficus* spp. site 1, woody litter, PF1= *P. grandis / Ficus* spp. site 1, logs, WPF2= *P. grandis / Ficus* spp. site 2, woody litter, PF2= *P.grandis / Ficus* spp. site 2, logs, WF= *Ficus* spp., woody litter, F= *Ficus* spp., logs, WLW= *Ficus* spp. / *E. pryifolia*, woody litter, LW= *Ficus* spp. / *E. pryifolia,* logs

Table 19 Bray-Curtis dendrogram distances matrix for woody litter and logs in each forest type. PW= *P. grandis*, woody litter, P= *P. grandis*, logs, WPF1= *P. grandis / Ficus* spp. site 1, woody litter, PF1= *P. grandis / Ficus* spp. site 1, logs, WPF2= *P. grandis / Ficus* spp. site 2, woody litter, PF2= *P.grandis / Ficus* spp. site 2, logs, WF= *Ficus* spp., woody litter, F= *Ficus* spp., logs, WLW= *Ficus* spp. / *E. pryifolia*, woody litter, LW= *Ficus* spp. / *E. pryifolia,* logs.

	P	PF1	PF2	F	LW	WP	WPF1	WPF2	WF
PF1	0.391								
PF2	0.385	0.527							
F	0.355	0.362	0.362						
LW	0.332	0.449	0.517	0.322					
WP	0.311	0.360	0.421	0.299	0.361				
WPF1	0.319	0.363	0.348	0.333	0.291	0.402			
WPF2	0.292	0.395	0.407	0.333	0.369	0.355	0.372		
WF	0.317	0.369	0.362	0.423	0.325	0.361	0.339	0.425	
WLW	0.367	0.454	0.435	0.383	0.393	0.385	0.413	0.409	0.339

Unique and endemic arthropod species

Table 20 summarizes the arthropod morphospecies relative to each ecological variable. The list of identified endemic species is given in the Appendix.

Table 20 Percentage importance in terms of species richness, uniqueness and endemism of the saproxylic arthropod communities.

Classification	Percentage of species out of the total number of species in the whole study	Percentage of species unique[1] to each group out of the total number of species in that group	Percentage of endemic[2] species in each group out of the total number of endemic species in the whole study
Log type			
P. grandis	81[3]	29[4]	79[5]
Ficus spp.	75	23	50
C. nucifera	51	18	57
Decomposition			
Class 1	42	10	43
Class 2	58	17	47
Class 3	66	22	43
Class 4	72	23	47
Forest type (logs)			
P. grandis	51	13	50
P. grandis/ Ficus spp. 1	53	20	66
P. grandis/ Ficus spp. 2	57	16	42
Ficus spp.	36	10	33
E. pryifolia/ Ficus spp.	57	18	42
Log type in forest type			
P. grandis logs in *P. grandis* forest type	34	21	50
P. grandis logs in *P. grandis / Ficus* spp. forest type 1	38	14	60
P. grandis logs in *P. grandis / Ficus* spp. forest type 2	40	15	25
P. grandis logs in *E. pyrifolia / Ficus* spp. forest type	31	17	33
Ficus spp logs in *Ficus* spp. forest type	30	15	33
Ficus spp. logs in *P. grandis / Ficus* spp. forest type 1	36	16	50
Ficus spp. logs in *P. grandis / Ficus* spp. forest type 2	32	14	25
Ficus spp. logs in *E. pyrifolia / Ficus* spp. forest type	29	19	25
Woody litter in forest type			
P. grandis	27	21	14
P. grandis/ Ficus spp. 1	28	22	21
P. grandis/ Ficus spp. 2	27	32	28
Ficus spp.	21	27	21
E. pryifolia/ Ficus spp.	25	17	28

[1] The term 'unique' refers to those arthropods that were confined to that particular environmental variable.
[2] The term 'endemic' refers to those arthropods endemic to the Seychelles archipelago.
[3] e.g. 81 % of all arthropod species recorded in the whole study occurred in *P. grandis* logs.
[4] e.g. 29 % of all arthropod species recorded in *P. grandis* logs only occurred in *P. grandis* logs and in no other log type.
[5] e.g. *P. grandis* log type had 79 % of all endemic species recorded in the whole survey.

The most important logs for maintaining the arthropod assemblage where the *P. grandis* and *Ficus* spp., while it did not matter in which forest type these logs were situated (Table 20).

DISCUSSION

Forest cover and log types on Cousine Island

In woodlands across the world, about 70 % of the annual primary production is shed as litter, although this varies greatly depending on forest type (Swift 1977). Bray & Gorham (1964) estimated that in temperate forests, branches and twigs constituted about 30 % of the average annual fall of litter to the forest floor. However, Swift (1977) believed this to be an underestimate and suggested that the input of twigs and branch wood to be closer to 40 % (additional inputs come from the occasional death of a whole tree).

On Cousine Island, the biomass of organic litter on the forest floor was dominated by the log and woody litter, amounting to 436 t ha^{-1} (Table 4). Rodin & Basilevic (1968) estimated that the biomass of woody litter in a tropical rain forest may be more than 500 t ha $^{-1}$. This is 100 t ha^{-1} more than in temperate deciduous woodland (400 t ha^{-1}) and 200 t ha^{-1} or more than in some other forests e.g. northern coniferous forest: 100-300 t ha^{-1} (Rodin & Basilevic 1968) Ghana: 150-172 t ha^{-1} (Greenland & Kowal 1960), Panama: 100-150 t ha^{-1} (Golley *et al.* 1975), New Guinea, lowland rain forest: 300-360 t ha^{-1} and New Guinea, lower montane forest: 225-399 t ha^{-1} (Edwards & Grubb 1977). The biomass of dead wood in the rain forests of Olympic National Park, Washington, USA (Graham & Cromack 1982) was 120 and 161 t ha^{-1} , which is lower than for other Pacific Northwest forests, and certainly lower than the log biomass estimates for Cousine Island. Franklin & Waring (1980) reported biomass of dead wood in ten middle elevation stands in the Cascade Range averaged 200 t ha^{-1}, with a maximum of 500 t ha^{-1}.

On Cousine, the woody litter was an estimated 6.8 t ha^{-1} (Table 6). The few reported values for the amount of woody litter (excluding logs), vary from 0.6 to more than 269 t ha^{-1} for intact temperate forests (Harmon *et al.* 1985). It appears that the moderate biomass values for Cousine may be due to the large number of granite domes and outcrops which limits trees to mostly only growing between these hard, soil-less features. Also, the trees on Cousine Island are rarely over 30 m tall (owing to susceptibility to tropical storms on this small, exposed island), thus limiting log production.

On Cousine the forest composition was dominated by *P. grandis* and *Ficus* spp. trees (*P. grandis* 48.2 %, *Ficus* spp. 43.2 %, *C. nucifera* 5.5 %) (Figure 3). The occurrence of logs is much the same as the tree populations, *P. grandis* (48.7 %) two *Ficus* spp. (*F. lutea* and *F. reflexa*) (43.8 %) and *C. nucifera* (5.4 %) (Figure 5). Other logs made up only 2.1 % of the total amount. However, in terms of total biomass, *P. grandis* logs were in the greatest proportion (76.3%), indicating that these, on average, were much larger than those of *Ficus* spp. Indeed, *P. grandis* logs generally had a diameter more than twice that of *Ficus* spp. However, *Ficus* spp. were often much longer than those of *P. grandis*. *C. nucifera* logs, although low in number, were thicker and longer compared to those of *P. grandis* and *Ficus* spp, and remained as an intact trunk. They contributed only 3.8 % of the overall log biomass (Table 5).

Arthropods associated with logs and woody litter on Cousine Island

A total of 344 arthropod species from 18 higher taxa were sampled (Table 10). Some of these were identified, although many could not be, especially as a large number have not been scientifically described. This total number of arthropod species found on Cousine, is similar to that found under Douglas Fir trees, which also had over 300 species (exact number not specified) (Deyrup 1981). In another study, Paviour-Smith & Elbourn (1993) found 368 invertebrate species (except the pseudoscorpions, harvestmen and spiders) in England at Wytham Woods, near Oxford. However their study included dead wood still attached to the trees.

Floater (1995) collected a total of 6682 individuals in ten insect orders from forest litter on Silhoutte Island, Seychelles. Adult beetles and ants were the most abundant groups, making 33% and 29 % of the total insects respectively. These are higher proportions than on Cousine (Coleoptera 17 % and Hymenoptera 6 %). Floater (1995) also showed that other abundant groups were the fly larvae, earwigs and lepidoperan larvae. These groups were also sampled on Cousine (Table 10), although the dipterans and lepidopterans were mostly adults, possibly owing to the Cousine study being from February to April, whereas Floater's (1995) study was July to September. Furthermore, Pfarr & Schrammel (1991) and Hilt & Ammer (1994) found that dipterans may constitute 80-90% of the insects reared from decaying wood, which was not the case on Cousine.

Gerlach (in press.) found that centipedes on the Seychelles islands of Mahé and Silhouette were widespread and abundant but not diverse. This was also the case on Cousine, with eight species so far being recorded (Table 10).

There may be a bias in the species richness and abundance estimates here for three possible reasons. The first is that some of the larger more active arthropods could have taken evasive action on hearing the approach to the log and during the handing of the log before it was placed in the collection apparatus. This problem is documented in Spence & Niemela (1994). Secondly, sorting morphospecies is likely to result in lumping of similar-appearing species. However, Oliver & Beattie (1992) noted that when sorting was performed by non-specialists (undergraduate students), these lumping events had minimal effect (only 14.4% error) on the overall outcome. Thirdly, the difficulty of finding many saproxylic arthropods within any reasonable time is the consequence of several factors, i.e. i) long periods of development (sometimes several years), ii) hidden within decaying timber as larvae or pupae, which are difficult (or impossible) to identify, iii)larvae or pupae cannot be found easily without disrupting, if not destroying, their fragile habitat, iv) characteristically found in only a portion of potentially suitable trees, which, in turn, are only a small fraction of the total tree population in most forests, v) often usually have only a short adult lifespan, when they are often difficult to find (McLean & Speight 1993).

Log type and associated arthropod communities

Arthropod assemblages in logs are partly determined by the physical composition and heterogeneity of the logs (Swift 1977). The log provides food, shelter and, in some cases, the opportunity to reproduce (Matthews 1976). Indeed, log-inhabiting organisms are as adapted to the specific conditions in which they live as are those organisms that live in any other environment (Graham 1925). On Cousine, the dominance and abundance of four principal tree species, *P. grandis*, *F. reflexa*, *F. lutea* and *C. nucifera* provided a situation for comparing arthropod assemblages associated with different log types (Figure 5).

C. nucifera logs were significantly richer in arthropod species than either of the other two log types, with an average of 48 species per log (Figure 9). This log type also supports a wide range of arthropod species (Figure 10b), including three endemic species: Arachnida – *Theridon clabruim*, Coleoptera – *Colobicones singularis* and Hemiptera – *Seychellesius niger*. The reason for this high richness may be that *C. nucifera* logs are much larger than those of either *P. grandis* or *Ficus* spp. *C. nucifera* also has a uniform tissue structure throughout its length, allowing easy movement of the arthropods within the log. Also *C. nucifera* logs differed from those of *P. grandis* and *Ficus* spp, in that they have a hard outer bark (even in the late stages of decomposition). This bark causes an insulating effect on the log's internal environment. The bark is a buffer medium, protecting the log from extreme fluctuations of temperature and moisture. Savely (1939), Griffin (1977) and Kaarik (1974) found that wood-inhabiting insects and microbes are influenced by temperature and humidity, and extremes in either of these conditions causes a decrease in organism activity or even mortality. *C. nucifera* had the greatest difference between the inner (core) temperature and the ambient temperature (Table 8), and it was also the least affected by changes in the ambient temperature, resulting in this type of log providing relative stable internal conditions. The bark also provides important protection for the arthropods which are under heavy predation from the resident skinks (*M.seychellensis* and *M. wrightii*), and to a lesser degree some birds e.g. Seychelles Magpie Robin (*C. sechellarum*) (LeMaitre 1999). Although hard bark may provide protection for the arthropods, it may also hinder their access to the log. Deyrup (1981) points out that an important factor for saproxylic insects is the portion of the tree available. The only entry points into *C. nucifera* are the open ends, or occasionally, breaks in the bark adjacent to the soil surface, having been opened up under the weight of the log. In contrast, *P. grandis* logs have a soft, papery bark, which is heavily pitted, thus allowing easy access along its whole length although providing little protection from predators. This means that on Cousine, *P. grandis* logs support an average of 34 arthropod species per log compared to 48 for *C. nucifera* (Figure 9).

Ficus spp. logs are intermediate in hardness and accessibility, and often have sections of bark remaining. Although the inner wood appears to be tough in texture, it easily decomposes and tunnels are always present. Although smaller than both *P. grandis* and *C. nucifera* logs, *Ficus* spp. logs are often long and offer various stages of decomposition within one log. Nevertheless, *Ficus* spp. supported an average of only 27 arthropod species per log (Figure 9), suggesting that the narrower structure of the log reduced opportunities for the arthropod assemblage.

In terms of the arthropod species assemblage, the results (Figures 10 and 11) from these logs both showed a widely scattered distribution with respect to the three species, indicating strong qualitative differences in arthropod assemblages in the different logs.

Decomposition and arthropod succession

The bulk of plant material that decomposes in a forest ecosystem is wood (Speight & Wainhouse 1989). During natural decomposition, wood on the forest floor may persist for longer than leaf and reproductive material (Swift 1977). In a mature forest, there is a steady state of equilibrium between input due to log and litter fall and output from decomposition, and there is a large standing crop of dead wood on the forest floor (Swift 1977). On Cousine, 93.3 % of the organic material on the forest floor consisted of log or coarse woody litter.

Under natural conditions, wood is decomposed by the interaction of a rich community of organisms and the dead wood provides a relatively constant habitat for a wide range of animals and micro-organisms (Swift 1977). Attack by wood-boring insects is an important factor in wood decay (Hickin 1975), although many different orders of animals feed on wood, either directly or indirectly. However, very few animal groups can digest cellulose unless assisted by bacteria, fungi or some other biota in a symbiotic relationship (Hickin 1975). Fager (1968) found 48 species of animals per log at Wytham Wood. On Cousine, the mean number of arthropods (all decomposition stages) was 32 species per log (Figure 11). Fager (1968) showed that most of the species were rare, many occurring only as single individuals. This was also the case on Cousine, with the exception of the ants. Groups of insects closely associated with the decomposition of wood are species of Isoptera, Diptera and Coleoptera, and a few species of Blattodea (Speight & Wainhouse 1989), all of which were well-represented on Cousine.

Changes in concentration of nutrients and arthropod assemblages of different stages in the decomposition process have been recorded by many authors with a distinct pattern of succession being recognized (Jonsell *et al.* 1999, Esseen *et al.* 1997, Esseen *et al.* 1992, Speight & Wainhouse 1989, Peterson & Luxton 1982, Deyrup 1981, Lambert *et al.* 1980, Grier 1978, Lang & Forman 1978, Swift 1977, Deyrup 1976, Matthews 1976, Deyrup 1975, Fager 1968, Madge 1958, Elton 1927, McNamara 1955, Howden & Vogt 1951, Hungate 1940, Savely 1939, Graham 1925, Blackman & Stage 1924, Blackman & Stage 1918, Saalas 1917, Adams 1915, Felt 1906, Packard 1890, Townsend 1886). However patterns of succession show considerable variation depending on the type and species of wood resource and the intervention of environmental factors (Swift 1977).

On Cousine, the arthropod assemblages inside logs varied considerably, depending on the decomposition stage (Figures 13a and 14), suggesting distinct succession. The arthropod species from all taxa show a wide distribution across all the decomposition classes (Figure 13b). The young logs (Class 1) were consistently different from the three older classes, both in terms of species richness per log (Figure 12) and in arthropod assemblage structure (Figures 13 and 14). These arthropods are the early colonizers and mechanically break down the wood. It appears that these pioneers are the displaced or succeeded by later-colonizing arthropods (Fager 1968). The Class 1 logs had most of their bark intact and were elevated from the ground (i.e. most of the log was resting either between large boulders or resting against a tree). Nevertheless, the logs had started to decompose. It has been suggested that these young logs have a variety of microhabitats which allow an increase in arthropod colonisation (Santos & Whitford 1981, Seastedt & Crossley 1981), i.e. gaps where the bark has started to pull away from the woody material. Although the woody material is consistent in structure, there were patches of softer and harder woody material present throughout the log. The older logs, in contrast, have less diversity of microhabitats, though the log material becoming soft very rapidly and collapsing (as in the case of *P. grandis*) or becoming very tunneled (as in the case of *Ficus* spp.). Although in some cases the bark may still be present, the inner woody material is usually no longer attached to it, and has less volume than before. This allows easier access for vertebrate and possibly large arthropod predators and does not provide adequate protection for the smaller arthropods. The different individual tolerances of the arthropods can be dependent on the density and biomass of the inner material (Schowalter 1985) leading to a change in the arthropod assemblage structure. Also, when wood decays, the tree species becomes less important for substrate selection by arthropod species, resulting in seral faunas becoming more similar in different types of old logs (Jonsell *et al.* 1999, Warren & Key 1989, Haack & Slansky 1987, Howden & Vogt 1951).

Added to this, arthropods, and insects in particular, can discriminate and exploit gradients or differences in the nutritional value of the host tissues. They are thus dependent on the quality and abundance of the host tissues (Schowalter 1985). It is suggested that the concentration of nutrients is higher in the younger logs. This is due to the continued leaching caused by the high humidity and continued condensation permeating logs on Cousine. The logs in Class 1 are protected by their bark, and although Class 3 logs also still have their bark, the woody material has pulled away from it, thus allowing moisture to condense inside the logs. The upshot is that whereas the younger logs are rich in resources and microhabitats, both these become reduced in the older logs leading to a gradual impoverishment of the arthropod assemblage with log age.

Influence of forest type on arthropod communities

The forests of the world are often categorized by the dominant tree species in the ecosystem. The animal assemblages associated with each forest type, including insect assemblages, are influenced by and have a major influence on tree species composition (Speight & Wainhouse 1989). On Cousine, the arthropod species richness per log in each forest type were uniform across all the forest types, with the exception of the *Ficus* spp. forest (Figure 15). This forest was significantly different to the *E. pryifolia / Ficus* spp. forest. The *E. pryifolia / Ficus* spp. forest had the lowest biomass of logs, woody and leaf litter, and did not contain *C. nucifera*. These differences do not explain why this forest type was significantly different in terms of arthropod species richness from the *Ficus* spp. forest, yet not significantly different from any of the other forests. The two forests *E. pryifolia / Ficus* spp. and *Ficus* spp. had the lowest arthropod species richness, and are adjacent to each other.

When the different logs in each forest type were compared, the arthropod species richness per log was not significantly different between forest types (Figure 18 and 19), although the *Ficus* spp. logs did have a consistently lower arthropod species richness per log, compared with *P. grandis* and *C. nucifera*, irrespective of forest type in which the logs occurred.

In *P. grandis / Ficus* spp. forest Site 2 and the *E. pyrifolia / Ficus* spp. forest, the arthropod assemblages were very similar (Figures 17 and 18). This may be partially explained by the fact that they were adjacent. Low dispersal capacity of log-inhabiting species can be a factor limiting distribution, density and the survival of many saproxylic species (Nilsson & Baranowski 1997). Speight & Wainhouse (1989) suggest that some insects are dependent on wind dispersal, and in a forest, most insects do not appear to travel very far. The similarity of the two *P. grandis / Ficus* spp. forests 1 and 2 in terms of the arthropod assemblage (Figures 16 and 17), may have been partly due to the vegetation composition of the two sites being almost identical. The difference shown by Figure 16a is shown by Figure 16b to be the distribution of adult Diptera, seeking refuge and / or resting in the logs. The arthropod assemblages of each log type found in each forest type show a closer association to each other than to logs of the same type in another forest (Figures 20 and 21). The *P.grandis* and *Ficus* spp. forest types showed little association with any of the other forest types, and both were characterized by almost complete dominance by either *P. grandis* or *Ficus* spp. logs (Figures 16a and 17), where the *P. grandis* logs in the *P. grandis* forest type support a wide variety of arthropods from different taxa.

Litter and its arthropod communities

Informed forest management decisions cannot be made without an understanding of the role of wood litter in tropical forests (Lang & Knight 1979, Harmon *et al.* 1985). Low in nutrient concentration (Merrill & Cowley 1966) and slow to decompose, these materials are ignored in many ecological studies, despite the large amounts of organic matter represented (Harmon *et al.* 1985, Bray & Gorham 1964). Also, the woody litter may be a major long-term source of both energy and nutrients in many ecosystems (Triska *et al.* 1984, Triska & Cromack 1980, Larsen *et al.* 1978, Cornaby & Waide 1973, Sharp & Millbank 1973, McFee & Stone 1966).

Woody material is a unique habitat for many species, both autotrophs and heterotrophs (Harmon *et al* 1985, Franklin *et al.* 1981, Elton 1966). Many arthropods of forests are heavily dependent on woody litter for habitats (Ausmus 1977, Maser *et al.* 1978). Elton (1966) estimated that as much as 20 % of extant fauna in a British woodland was dependent on decaying wood as a habitat.

As with the logs, terrestrial arthropods may also use woody litter as protection from environmental extremes. For example, Lloyd (1963), found that slugs, snails, terrestrial isopods, centipedes, and earthworms migrate into branches during warmer weather, but lived in the litter layer during colder weather.

Stanton (1979) compared the species richness and diversity of litter mites in three habitats in Costa Rica and Wyoming and found a greater species richness and diversity of mites in forest litter. A greater diversity of mites was found in the tropical forest habitat than any other of the habitats sampled, and a greater proportion of temperate zone mite species was classified as colonizers (Stanton 1979). This again provides support for Young's (1982) contention that decomposer assemblages contribute to the great diversity and species richness of organisms in tropical forests.

The high proportion of the *P. grandis* woody litter (76.4 %) (Figure 6) found on Cousine could be a result of the growth form of the *P. grandis* tree. Wind is an agent of tree mortality, at least in temperate forests, generating woody litter by uprooting, snapping trees and breaking branches (White 1979). Trees may also be crushed and broken by wind. Windstorms are common in both temperate and tropical regions (White 1979), and on Cousine, *P. grandis* branches are easily broken (Bourquin 1997, pers. observ.) resulting in very large inputs of woody litter. The soil in the forests on Cousine is very shallow (Bourquin 1997), which also makes the trees more susceptible to damage from wind (Alexander 1954, Gratkowski 1956, Ruth & Yoder 1953).

The arthropod assemblages found in the woody litter in each forest type showed little association which each other (Figures 25 and 26), supporting many species of adult Diptera. There is a difference between the arthropod assemblage in the woody litter and the logs of the same forest type, with those in the woody litter showing a stronger association to each other in different forest types than to those in logs of the same forest type (Figures 27 and 28). The *P. grandis* logs in the *P. grandis* forest supporting a number of arthropods from different taxa. This may be due to the substantially different physical structure and condition of woody litter compared to that of logs. The woody litter may also provide protection for arthropods moving between areas, especially with the high number of predators always present on the island.

Significance of the findings for the ecology of Cousine Island

The World Conservation Strategy (IUCN-UNEP-WWF 1980) has emphasized the need for conserving the genetic diversity of the world through sustainable maintenance and management of natural ecosystems. Tropical ecosystems have a prominent role to play in the conservation of genetic diversity, as these habitats contain the majority of the world's species (Balakrishnan 1994).

Studies by Kirby & Drake (1993), Hammond (1990) and Stork (1987) indicate that saproxylic species form a high proportion of the tropical forest insect fauna. Given the much higher numbers of insect species in the tropics compared to higher latitudes, it would seem likely that many more tropical than temperate saproxylic insects are potentially under threat from long-term logging. At the same time, there is an ever-increasing recognition that biodiversity conservation and tropical forestry can and should be compatible (Grove 1998).

Log invertebrates are particularly vulnerable, as their highly specialized habitats may be present on only tiny proportion of a log at a site at any one time (Key 1993, Graham 1925). Also they may have poor powers of dispersal and so are not able to easily colonise new sites (Key 1993). Therefore, the value of a given type of substrate is determined not simply by the number of species using it. A substrate with many specialists is more valuable, as the dependent species cannot survive elsewhere (Jonsell *et al.* 1999).

Conservation and management recommendations

It has been suggested that sites with a continuity of megatrees should get highest priority for preservation so as to maintain the diversity of saproxylic organisms (Martin 1989, Nilsson & Baranowski 1997). Such localities have decreased substantially in number, and regeneration takes many decades. Megatrees also contain many other microhabitats that are rare and required by saproxylic species, e.g. thick branches, course bark, and dead part of the stem (Jonsell *et al.* 1999). The results here on Cousine indicate that conservation of the saproxylic arthropods should include all the study sites dominated by *P. grandis* and *Ficus* spp. trees (Table 20). Because each of these forest types have different arthropod assemblages, to conserve the full complement of saproxylic arthropods it is necessary to conserve all the forest types. This is further emphasised by the fact that the total forest cover on Cousine is only a tiny area (7.8 ha). The threat to some species could be further compounded by their limited ability to colonize distant substrate patches (Nilsson & Ericson

1997). All inclusive, protectionist conservation strategy is supported by Jonsell *et al.* (1999) who concluded that a landscape should include a mixture of tree species, wood in different stages of decay, coarse wood, different types of stem (i.e. logs, snags and old living trees) to satisfy the requirement of different saproxylic insects (Jonsell *et al.* 1999).

In sites important for saproxylic invertebrates, as much large deadwood as possible should be left (Key & Ball 1993). Timber removal reduces the density of dead wood in different stages of decay (Linder & Ostlund 1992, Syrjanen *et al.*1994), and thereby the abundance and the species richness of wood-inhabiting fungi (Lindblad 1995, Okland 1995) and, in turn, the saproxylic arthropods dependent on those fungi (White & Tutin 1998, Plumptre & Reynolds 1994, Isabirye-Basuta & Kasenene 1987). Sometimes thinnings are made into habitat piles (e.g. Brooks 1980, Watkins 1990), although there is a lesser benefit for saproxylic fauna in having piles rather than leaving material scattered on the woodland floor in a more natural condition. Only opportunistic and ubiquitous saproxylic species, with relatively undemanding niche requirements are likely to take advantage of such habitat. While it is useful that an increase in these species may result from such efforts, leaving small-sized deadwood is no substitute for the retention and eventual replacement of living ancient trees (Key & Ball 1993).

Where dead material is retained, consideration should be given to its location. Most saproxylic species are unable to utilize dead timber in dry, open conditions in full sunlight. Such timbers sometimes become almost 'heat sterilized'. Timber falling in the open should be moved into moister, shadier areas. Although in theory, moving logs into the moister, shadier areas (if practical) would appear to be a positive conservation option for most saproxylic species, there are, however, some species of saproxylic beetles which need timber in just such hot dry conditions, while empty insect burrows in such conditions are important nest sites for specialized solitary wasps and bees. Not all dead material therefore should be moved out of the sunshine. Furthermore, there is no evidence that importing dead logs to boost the amount of deadwood on a site has any value for deadwood specialists (Key & Ball 1993).

Should the forests on Cousine Island come under threat due to development, there are some conservation management options to consider. The first of these is translocation of the saproxylic arthropods. However, translocation of arthropods to re-establish populations is likely only to be successful for species whose ecology is well known, whose popularity attracts sufficient resources to pay for the site management, and where habitat management can be maintained in the long term. For most insect species, these conditions are not met and their conservation depends on maintaining suitable management on sites where they still exist (Key & Ball 1993). Speight (1989) recommends the re-establishment of saproxylic species at their former sites as larvae in logs which are transferred between sites. This may seem a more attractive proposition, but it is fraught with difficulty and controversy because, along with the target species, other fauna and flora will be present but unrecorded, and even possibly harmful. Such inadvertent translocations make it difficult to determine the true status and biogeography of the species concerned. This problem is beginning to arise already in the case of other habitats, with the increasing use of 'habitat transfers' either between conservation sites or from threatened sites to 'safe' localities (Key & Ball 1993). In addition, while conditions in a translocated log may be suitable for the species within it for some time, in the absence of detailed knowledge of their ecology, there is no guarantee that suitable niches are available at the receptor site and the exercise may simply be a drain on the source population. Translocations are not automatically ruled out in every case by the above arguments, but certainly any proposed scheme should be approached with caution (Key & Ball 1993).

A second suggestion would be to encourage agreement among conservationists and foresters to emphasize that forestry and land management practices can cater for the requirements of many saproxylic species (Kaila *et al.* 1997, Reid & Kirby 1996, Stubbs 1972), often at low economic cost.

All forests are probably capable of supporting some saproxylic species. However, more species-rich assemblages, including those with the most specialized or restricted niches, are likely to develop on sites which have as close to the full range of saproxylic habitat features as exists (or would have existed), in regular and continuous supply, in natural old-growth forests. Chief among these are large diameter 'overmature' or 'veteran' trees. The snags and logs resulting from their natural death are also important (Okland *et al.* 1996, Hammond & Harding 1991) but represent a more short-lived and essentially non-renewable substrate for colonization, and thus tend to support fewer specialist species dependent on habitat continuity than over mature trees themselves (Speight 1989). Management prescriptions that favour the survival of such features, even if not throughout the whole forest stand, are likely to conserve a wider range of saproxylic species than those which only enable the survival of smaller diameter trees and dead wood. Indeed, a wide range of conditions provides small arthropod populations in natural communities with a more stable long-term habitat (Reichert & Lockley 1984).

Although the survival of saproxylic arthropods until now has been by chance, their future depends upon their distinctive needs becoming recognized more widely and their remaining sites receiving protection and where appropriate, positive management (Key & Ball 1993). Perhaps the best strategy for conserving tropical insects is to ensure that there is an adequate coverage of protected areas (nature reserves, national parks etc. (Groombridge 1992)). Speight (1989) emphasizes the need to draw attention to the plight of saproxylic arthropods. Such publicity should aim to increase sympathetic attention by demonstrating the colourful and attractive nature of many species, and indicate what is required for the survival of species and sites. Good colour photographs of saproxylic species in their natural environment are needed for publications and interpretive displays. The ancient trees themselves have considerable value for publicity and arousing public sympathy in their own right (Davies 1998), both as wildlife and their aesthetic appeal. Such approaches have the potential to capture the attention of many more people concerned about arthropod conservation than in the past. They therefore should be welcomed as ways of creating better understanding for this largely neglected area of wildlife conservation.

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APPENDIX

Table 21 Species list for Cousine Island

Key
P – *P. grandis* logs in *P. grandis* forest type
F – *Ficus* spp. logs in *Ficus* spp. forest type
PPF1 – *P. grandis* logs in *P.grandis / Ficus* spp. forest type 1
FPF1 – *Ficus* spp. logs in *P.grandis / Ficus* spp. forest type 1
PPF2 – *P.grandis* logs in *P.grandis / Ficus* spp. forest type 2
FPF2 – *Ficus* spp. logs in *P.grandis / Ficus* spp. forest type 2
PLW – *P.grandis* logs in *E.pryifolia / Ficus* spp forest type
FLW – *Ficus* spp. logs in *E.pryifolia / Ficus* spp. forest type
C – *C. nucifera* logs

P –Woody litter in *P. grandis* forest type
F – Woody litter in *Ficus* spp. forest type
PF1 – Woody litter in *P.grandis / Ficus* spp. forest type 1
PF2 – Woody litter in *P.grandis / Ficus* spp. forest type 2
LW – Woody litter in *E. pryifolia / Ficus* spp. forest type

* Endemic to the Seychelles

Taxon	Abbreviation	Species name (species marked with * = endemic to Seychelles)	Log type and forest type in which the species occurred.	Woody litter in forest type in which the species occurred.
Acari				
Unknown	ARS01- ARS36	36 species not identified	P – 10 species F – 9 species C – 18 species PPF1 – 18 species FPF1 – 10 species PPF2 – 14 species FPF2 – 10 species PLW – 11 species FLW – 10 species	P – 14 species F – 14 species PF1 – 7 species PF2 – 16 species LW – 9 species

Apterygota				
Japygidae	AMNS04	2 species not identified	P – 1 species C - 1 species PPF1 – 1 species PPF2 – 1 species PLW – 1 species	
Unknown	AHMNS03	2 species not identified	P, PPF2, PLW, FPF1, FPP2, FLW	LW
Arachnida				
Tetragnathidae		*Nesioneta benoiti* (van Helsdingen, 1978)	F	PF1
Scytotidae		*Scytodes fusca* (Walckenaer, 1837)	FPF1	
		1 species not identified	FPF1	
Theridiidae	AHS12	*Theridion clabnum* * Roberts, 1978	C	
	AHS25	2 species not identified	C – 2 species	
	AHS28		PPF1 – 1 species	
			FPF2 – 1 species	
Schizomidae		*Schizomida* species 1	C	F
		Schizomida species 2	P, F	
		Schizomida species 3	PPF1	
Corinnidae	AHS08	*Oedignatha scrobiculata* Thorell, 1881	P, PPF1, PLW	F
	AHS19	2 species not identified	P, F, PPF2	P
Oonopidae		*Opopaea deserticola* Simon, 1891	PPF1, PLW, F, FPF2	
	AHS05	*Oonopinus kilkus* Suman, 1965	P, PPF1, PPF2, PLW, F, FPF1, FPF2, PLW, FLW, C	
	AHS24	*Gamasomorpha trichinalis* * Benoit, 1979	PLW	
Pholcidae		*Hedypsilus culiculus* * (Simon, 1893)	PPF1	PF1, LW
		Mircopholcus fauroti (Simon, 1887)	F	P
Lexoscelidae		1 species not identified	C	PF1
Unknown	AHS11	6 species not identified	P, F, C, PF1	
Blattodea				
	BLBLS01	*Pycnoscelus indicus* (Fabricius, 1775)	PPF1, PPF2, PLW, F, PPF2, FPF2, FLW, C	PF1, PF2, LW, F
Unknown		2 species not identified	P – 2 species F – 2 species C – 2 species PPF1 – 1 species FPF1 – 1 species PPF2 – 2 species FPF2 – 1 species PLW – 1 species FLW – 2 species	

Chilopoda				
Geophilomorpha	CHGPS03	*Nesogeophilus leptochilus* * Demange, 1981	P, C	
	CHGPS01	*Mechistocephalus* sp.	P, PPF2, F, FPF1	LW
	CHGPS04	*Mechistocephalus* cf. *vanmoli* Demange, 1981	PPF1	
	CHSCS02	*Otostigmus rugulosus* Porat, 1887	P, C	
	CHSCS04	1 species not identified	C	
Scolopendridae		*Cryptops philammus* Demange, 1981	PPF1, FPF1	
Lithobiidae		1 species not identified	P	
Unknown		1 species not identified	C	
Symphyla				
		Symphyla sp.	F, C	
Coleoptera				
Platypodidae		*Platypus* sp.	P, F, C	
Elateridae		*Cardiophorus lutosus* Fleutiaux, 1923	PPF1, PPF2, PLW, F, FPF1, FPF2, FLW, C	P, PF1
		Cardiophorus gardineri Fleutiaux, 1922	FPF2 , C	FPF2
		Portmidius solitarius Fleutiaux, 1923	FLW	FLW
Carabidae		2 larva not identified	P – 1 species	P – 1 species
			PPF1 – 1 species	F – 1 species
			FPF1 – 1 species	
			PPF2 – 2 species	
			PLW – 1 species	
	CLS28	*Anilus* sp.	FPF1, C	
		Chlaenius bisignatus Dejean, 1826	PPF1, FPF1	
Tenebrionidae		1 larva not identified	PLW, FPF2	PF2
		Pseudhadrus sp.	F, C	
Scolytidae		*Xyleborus* cf. *ferrugineus* (Sampson, 1914)	PPF1, PPF2, PLW, F FPF1, FPF2, C	PF2, F
	CLS04	*Hypothenemus* cf. *birmanus* Eichhoff, 1879	P, PPF2, FPF1, C	P, PF2, F
		Xyleborus sp.	PPF1	F
		Xyleborus cf. *piceus* Jordan, 1913	PPF1, PPF2, PLW, F, FPF1	
		Cryphalus cf. *discretus* Eichhoff, 1871	PPF2	
Nitidulidae	CLS02	*Stelidota explanata* Grouvelle, 1913	PPF2, PLW, FPF1, FPF2, C	PF1, PF2, F
Rhizophagidae		*Rhizophagus* sp. 1	P, PPF1, PPF2, PLW, FPF1, FPF2, FLW, C	PF2
		Rhizophagus sp. 2	PPF1, PPF2	
	CLS19	1 species not identified	PPF2	
Ptilidae	CLS05	*Throscidium testaceusm* * Britten,, 1926	P, PPF1, PPF2, F, FPF1, FPF2, C	PF1, PF2, F
		Ptinus sp.	PPF2, PLW, F	PF2, F, LW, P
Cryptophagidae	CLS06	*Hapalips championi* Grouvelle, 1917	PLW, C	PF2
		Eleusis kraatzi Fauvel, 1878	PLW, FLW	F

Scarabidae	CLS08	*Oxyomus palmarum* Scott, 1912	PPF1, PPF2, FPF1, FPF2, C	P
		Perssosoma grande * Scott, 1912	PPF1, FPF1	
Pselaphidae		*Apheloplectus obesus* * Raffray, 1913	PPF2, PLW	LW
		Triomicrus seychellensis Raffray, 1913	P, F, C, PPF1, FPF1, PPF2, FPF2, PLW, FLW	P, PF1, PF2, F, LW
Coccinellidae		1 species not identified	F	F
Colydidae	CLS29	*Colobicones singularis* * Grouvelle, 1917	C	PF1
Staphylinidae		*Stenus* cf. *silvicola* Bernhauer, 1921	FPF1, PPF2	P
		Astenus neglectus Markel 1917	PPF2, FPF2	F
		Coproporus sp.	P, C	PF2
		Medon sp.	P, F, C, PPF1, FPF1, PLW, PPF2, FPF2	P, PF1. PF2, F
		Astenus depressipennis (Bernhauer, 1921)	PPF2. FPF2	P
		Cafinus sp.	PPF1	
		Medon debilicornis Bernhauer, 1921	PPF2, FPF2, FLW	
		Medon microthorax Fauvel, 1907	PPF1	LW
		1 species not identified	P, C, PPF1, F	P, F
Hydrophilidae		*Coelostoma* cf. *punctulatum* (Klug, 1833)	F	
Curculionidae	CLCUS01	*Cratops grisevestitus* (Champion, 1914)	C	
Unknown	CLLAS04 CLLAS05	2 larva not identified	P – 1 species F – 1 species C PPF1 – 2 species FPF1 – 1 species PLW – 1 species FLW – 1 species	
	CLS15 CLS30 CLS34 CLS35 CLS36 CLS46 CLS47 CLS43 CLS48	15 species not identified	P – 6 species F – 5 species C – 11 species PPF1 – 6 species FPF1 – 7 species PPF2 – 5 species FPF2 – 7 species PLW – 3 species FLW – 4 species	

Collembola	COEMS02 COEMS06 COEMS07 COEMS01 COEMS03 COEMS12 COISSO2 COSMS04 COSMS06	24 species not identified	P – 9 species F – 8 species C – 13 species PPF1 – 9 species FPF1 – 8 species PPF2 – 12 species FPF2 – 5 species PLW – 9 species FLW – 6 species	P – 2 species F – 7 species PF1 – 2 species PF2 – 10 species LW – 6 species
Dermaptera				
Carcinophoridae		*Gonolabris electra* (Floater, 1994)	PPF1, PF2, PLW	PF2
	ERLAS05	*Labia minor* (Burr, 1910)	P, PPF2, PLW	PF1, PF2
	ERFOS01	*Euborella annulipes* (Floater, 1994)	P, F, FPF1, C	F
Unknown		2 species not identified		P, PF1
Diplopoda				
	DDS01	*Trigoniulus naresi* (Pocock, 1893)	P, PPF2, F, FPF2, FLW	
	DDS04	*Pseudospirobolellus avernus* (Butler, 1876)	P, PPF2, FPF2	PF2
Unknown		2 species not identified	P – 1 species F – 2 species C – 1 species PF1 – 1 species FLW – 2 species	P – 1 species F – 1 species PF1 – 1 species PF2 – 1 species LW – 1 species
Diptera				
Micropeziidae	DPLAS03	*Nereius alluaudi* (Lamb, 1914) larvae	PLW, F, C, FPF1, FPF2	LW
Stratiomyiidae	DPLAS01	1 species not identified larvae	PPF1, PLW, FPF1	
Tipulidae		*Monogoma pennipes* Osten-Sacken, 1887 larvae	C	P
Drosphoidae		1 species not identified	FLW	
Muscidae		*Mydea compressipalpis* Stein, 1910	PPF1	
Chironomidae	DPLAS06	1 species not identified	P	
Unknown	DPLAS02 DPLAS04 DPLAS08	6 larvae not identified	P – 3 species F – 3 species C- 1 species PPF1 – 1 species FPF2 – 2 species PLW – 1 species	P – 3 species F – 2 species PF1 – 3 species PF2 – 2 species LW – 1 species

Unknown	DPS01- DPS55	55 species not identified	P – 15 species F – 16 species C – 26 species PPF1 – 22 species FPF1 – 27 species PPF2 – 19 species FPF2 – 12 species PLW – 16 species FLW – 14 species	P – 11 species F – 13 species PF1 – 19 species PF2 – 12 species LW – 22 species
Hemiptera				
Reduviidae	HMDPS01	*Oncocephalus* sp.	PPF1, FLW, C	
Capsidae		*Felisacus auritus* Distant, 1913	PPF2	
Anthocoridae		*Lasiochilus scotti* Distant, 1913	F, FPF1, FLW	
		Ostorodiasodes typicus Distant, 1913	P, PPF1, PPF2, FPF2, FLW	
		1 species not identified	PLW	P
Cicadellidae		*Paganalia virescens* * Distant, 1913	P, F, PPF1, FPF1, PPF2, FPF2, PLW, FLW, C	P, F, PF1, PF2, LW
		Jakellrella ineffectus * Distant, 1913	F, PPF1, PPF2, FPF2, PLW, FLW, C	P, PF1, F, LW
	HMCCS02	*Scaphoideus seychellensis* Distant, 1913	PPF1, PPF2, PLW, FPF1, FPF2, FLW	P, PF1, PF2, F, LW
	HMDLS03	2 species not identified	P – 1 species LW – 1 species	P, PF1, PF2, F, LW
Jassidae	HMCCS05	*Nehela bimaculicollis* Distant, 1913	P, C, FPF1	PF1, LW
		Nehela species 1	F, FPF2	P, PF2
		Nehela species 2	C	
Pentatomidae		*Chilocoristoides feliciatus* Distant, 1913	P, C, PPF1, PPF2, PLW, F, FPF1, FPF2, FLW	P, PF1, PF2, F, LW
Cercopidae	HMDLS04	*Ptyelus mahei* Distant, 1913	P, PPF2, PLW, FPF2, C	
Fulgoridae		*Osaka relata* Distant, 1913	P	P
		Armilustrum scotti Distant, 1916	P, F, PPF2, FLW, C	PF2
		Opiconsiva gloriosa Distant, 1916	P	
Miridae		*Seychellesius niger* * Distant, 1913	C, PLW	
Lygaeidae	HMLYS03	2 species not identified	P – 1 species C – 1 species PPF2 – 2 species FPF2 – 1 species PLW – 1 species FLW – 1 species	P – 1 species PF1 – 1 species

Unknown	HMLYS02 HMS01 HMCCS09	9 species not identified	P – 1 species F – 1 species C – 2 species PPF1 – 2 species PPF2 – 1 species FPF2 – 1 species PLW – 1 species FLW – 1 species	P – 1 species F – 1 species PF1 – 1 species PF2 – 2 species LW – 1 species
Hymenoptera				
Formicidae		*Strumigenys emmae* (Smith, 1860)	PPF1	
	HYFMS01	*Pheidole megacephala* (Fabricius, 1775)	P, F, C, PPF1, FPF1, PPF2, FPF2, PLW, FLW	P, PF1, PF2, F, LW
		Pheidole cf. *punctulata* (Forel, 1912)	PPF1, PPF2	
	HYFMS03	*Hypoponera ragusai* (Santschi, 1963)	P, C, PPF1, PLW, FPF1	P, PF1
		Technomyrmex albipes (Smith, 1861)	P, C, PPF1, FPF1, PPF2, FPF2, PLW, FLW	P, PF1, F, LW
	HYFMS05	*Odontomachus troglodytes* (Santschi, 1938)	P, F, C, FPF2	P
		Tetramorium similimum Mayr, 1855	PPF2	F
Unknown	HYFMS08 HYFMS15 HYDPS01 HYDPS02 HYDPS04 HYARS01 HYSPS01	16 species not identified	P – 4 species F – 2 species C – 4 species PPF1 – 5 species FPF1 – 4 species PPF2 – 2 species FPF2 – 6 species PLW – 1 species FLW – 2 species	P – 7 species F – 2 species PF1 – 3 species PF2 – 5 species LW – 2 species
Isopoda				
	IPCYS01	*Nagurus nanus* Budde-Lund, 1908	PPF1, PPF2, PLW, FPF2, FLW	PF2
	IPARS02	*Cubaris murina* (Budde-Lund, 1913)	PPF2, PLW, FPF2, FLW	PF2
		Venezillo parvus Budde-Lund, 1885	FLW	
		Reductoniscus costulatus (Ferrara & Taiti, 1983)	P, PPF1, PLW, F	F
Unknown	IPLIS01 IPPRS01	2 species not identified	P – 1 species F – 1 species C – 1 species PPF1 – 1 species FPF2 – 1 species PLW – 1 species	P – 1 species
Isoptera				
Termitidae	ISTMS02	*Calotermes scotti* Holmgren, 1910	P, F, C, PPF1, FPF1, PPF2, FPF2, PLW	PF1, PF2, F, LW
	ISTMS04	*Arrhinotermes calanifrons* Holmgren, 1910	PPF1, F, FPF1	LW
	ISTMS09	*Nasutitermes nigritus* Holmgren 1910	F, C, FPF2	F

Unknown		1 species not identified	P, F, C, PPF1, FPF1, PPF2, PLW, FLW	PF1, PF2, F, LW
Lepidoptera				
Lyonetidae		1 species not identified	FPF1	PF1
Lithocolletidae		1 species not identified	P, PPF1	
Geometridae		1 species not identified	PPF1	
Unknown		1 larva not identified	PPF2, PLW, FPF1	
Unknown	LPS01 – LPS40	40 species not identified	P – 10 species F – 4 species C – 13 species PPF1 – 13 species FPF1 – 19 species PPF2 – 13 species FPF2 – 10 species PLW – 5 species FLW – 13 species	P – 18 species F – 4 species PF1 – 15 species PF2 – 10 species LW – 15 species
Orthoptera				
Gryllidae		1 species not identified	P, FPF1, FPF2 FLW	P, F, PF1, LW
Unknown		4 species not identied	P – 2 species C – 2 species FPF1 – 1 species PPF2 – 1 species FLW – 2 species	P – 1 species
Pseudoscorpiones				
	PSS01	*Withius piger* Simon 1922	C, PPF1, PPF2, PLW	PF2
Unknown	PSS02 PSS04	2 species not identified	P – 1 species C – 2 species PPF1 – 1 species	
Thysanoptera				
Thripidae		*Brachyurothrips anomalus* Bagnall, 1921	PLW, F	PF2
		Thrips sp. Bagnall, 1921	P, F, PPF1, FPF1, PPF2, FPF2, PLW, FLW	P, F
Unknown	AHMNS01	1 species not identified	FLW	