A study of habitat structure and vegetation in Seychelles

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Abstract: A quantified study of the habitats of the granitic Seychelles islands is used to propose an objective habitat classification. Each defined habitat is described and data on temporal changes are discussed.

Keywords: habitat, forest structure

The granitic islands of Seychelles are well known for their unique flora. Interest in the evolution of these continental islands and their conservation has resulted in descriptions of the main habitats currently found in the islands (Jeffrey 1962; Procter 1984; Gerlach 1993). These have been based on subjective impressions of the boundaries between habitat types and there are no published habitat accounts based on quantitative data with the exception of the studies of 'inselberg' biogeography (Flieschmann *et al* 1996), forest regeneration (Flieshmann 1997) and invasion (Gerlach 1993b, 1996). The importance of recognising specific habitats and understanding the dynamics of vegetation change in the islands prompted the present study which represents the most exhaustive collection of quantitative habitat data for the islands.

Methods

36 sites were studied on the islands of Mahé, Silhouette, Praslin, Aride, Curieuse and La Digue (Fig. 1.). At each site 10 quadrats were used to record the number of each plant species over 2m high. The quadrats measured 5×5m and were centred on a randomly located point. Additional studies on herbaceous vegetation and canopy cover were carried out in these quadrats, but are not reported on here.

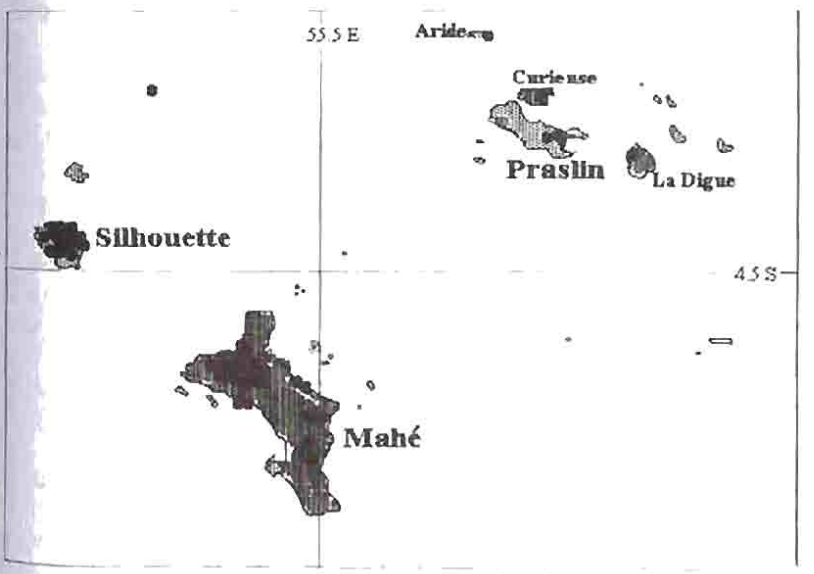
Most recent habitat classification studies have used cluster analysis methods to group similar habitats. These methods are appropriate to situations where habitats are well defined as a result of discrete external variables, such as geochemistry. In situations where external variables are effectively constant and the areas concerned are small (characteristics applying to Seychelles) cluster methods fail to provide robust classifications. The data from the 5×5m quadrats were analysed using the phylogenetic analysis program Hennig86 (Farris 1988). This detects phylogenetic groupings from character data and was used to provide a classification that reflects similarity in data sets and provides some indication of the most likely transitions.

Results

Data were coded using a geometrical series (0=0, 1 per quadrat =1, 2=2, 3-4=3, 5-8=4, 9-16=5, 17-32=6, 33-64-7, 65-128=8, 129-256=9). Data analysis using additive characters and a branch-and-bound algorithm produced 3 equally parsimonious patterns of relationships of 827 steps, consistency and retention indices of 0.53. A strict consensus of these groups the sites as shown in Fig. 2.

This provides a series of recognisable groupings with the exception of the group comprising the Vallée de Mai, Mare aux Cochons, Mont Dauban and Mon Plaisir (9-12). Four different habitats are found in this group, all dominated by plant species not found to any significant extent within the other habitat groups. If all Palmae are grouped together (thus stressing the structural similarity between *Lodoicea maldivica* and the more widespread *Phoenicophorium borsigianum, Nephrosperma vanhouetteana, Vershaffeltia splendida* and *Roscheria melanochaetes*) the Vallée de Mai site can be added into the palm derived habitats (44-47). The remainder of the group are united by the presence of *Clidemia hirta*, exclusion of this species retains the grouping but moves it to the high forest habitats. Two other sites appear to be anomalously placed. The *Eucalyptus* plantation (13) is grouped with the lowland habitats (14-19) due to its open structure, as is the suburban site (20) within the open high altitude (21-24) grouping. Neither of these are included on the basis of shared taxa and should be removed from their groupings.

Fig. 1. Islands studied with field sites marked.



Beoliere: *Dracaena* 360 (60%); *Canthium bibracteatum* 200 (33%). Diversity=1.53, native 1.57, alien 0.15

4. ***Casuarina* habitat** - *Casuarina equisetifolia* forming >50% of trees.
Casuarina plantations closely resemble natural *Casuarina* habitat on coastal sandy soil, although tree density is un-naturally high. This habitat is slowly invaded by other species, *Alstonia macrophylla* frequent on Mahé, *Calophyllum inophyllum* and *Terminalia catappa* are the most widespread colonists.
Coral mountain: *Casuarina* 2000 (100%). Diversity=0.
Pt. Ramasse Tout: *Casuarina* 1000 (99%). Diversity=0.29, native 0.29, alien 0.
Casuarina plantation: *Casuarina* 5000 (100%). Diversity=0

5. **Lowland habitats** - *Terminalia catappa* present at >500/ha
5a. Mangroves - >50% mangrove species.
Mangrove forests are stable in the short term, with very little invasion in the waterlogged muds. Mangrove roots trap sediments and lead to the formation of banks in the marshes. As these accumulate and dry they are colonised by other species. The commonest are *Calophyllum inophyllum* and *Terminalia catappa*. *Heritiera littoralis* is also abundant. The species composition of the mangroves varies with location.
Curieuse: *Avicennia* 2960 (39%); *Calophyllum* 2400 (30%); *Terminalia* 1580 (13%), *Cocos* 720 (9%); *Lumnitzera* 680 (8%). Diversity=0.42; native 0.42, alien 0
5b. *Calophyllum-Terminalia* forest - *Terminalia catappa* >50% & *Calophyllum inophyllum* >30%
This typical lowland forest type is developed from marshy ground (as in succession from mangroves) or in flood areas where seed is dispersed by flood waters. It is usually mixed with *Heritiera littoralis* being an important natural component. This habitat is present in the main areas of development and consequently have high invasion by alien species (planted and escapes). The characteristic *Calophyllum-Terminalia* forest found on La Digue is a secondary habitat and represents a low diversity transitional stage in the development of coastal mixed forest (5c). In drier areas *T. catappa* is rare or absent, the main species in this form at *C. inophyllum* with significant numbers of *Mimusops sechellarum*, *Deckenia nobilis* and *Pandanus* spp. Pristine areas of this habitat have been found at Coco dans Trou and La Reserve (Silhouette)
La Digue: *Terminalia* 1200 (59%); *Calophyllum* 800 (38%). Diversity=0.49, native 0.49, alien 0
5c. Mixed - no one species or combination forming more than 80% (with the exception of planted coconuts, *Cocos nucifera*), *Terminalia* & *Calophyllum* abundant (>500 & >300 per ha respectively). Includes rocky valleys with abundant *Barringtonia racemosa* and *Heritiera littoralis* (e.g. Anse Mondon and Riviere Machabee, Silhouette). Many areas heavily invaded or are secondary forest (characterised by alien species forming >25%).

Beau Vallon: *Terminalia* 1200 (40%), *Calophyllum* 400 (13%), *Heritiera* 500 (17%), *Cocos* 300 (10%). Diversity=0.67; native 0.47, alien 0.29.

Grande Barbe: *Terminalia catappa* 1000 (40%), *Calophyllum inophyllum* 750 (30%), *Cocos nucifera* 300 (12%), *Tabebuia pallida* 200 (8%). Diversity 0.52, native 0.50, alien 0.

Anse Mondon: *Barringtonia racemosa* 3000 (60%), *Heritiera littoralis* 800 (16%), *Terminalia catappa* 600 (12%), *Calophyllum inophyllum* 300 (6%), *Cocos nucifera* 800 (15%). Diversity 1.05; native 1.25, alien 0.17.

La Passe: *Cocos nucifera* 4000 (79%), *Terminalia catappa* 500 (9%), *Calophyllum inophyllum* 300 (5%), *Tabebuia pallida* 200 (5%). Diversity=1.11; native 1.01, alien 0.45.

6. **Suburb** - trees restricted to areas of garden, buildings <50m apart.

Suburb: *Cinnamomum verum* 1000 (67%), *Manguifera indica* 240 (8%). Diversity=0.28, native 0, alien 0.28.

7. **Open high altitude** - open canopy, vegetated, >400m above sea-level.

7a. Mixed (*Clidemia hirta* habitats) - heavy *C. hirta* invasion (200/ha.).

The changes in *Clidemia hirta* dominated mixed open high altitude habitat are discussed in full detail in Gerlach 1996. The coffee (*Coffea canephora*) plantation at Mare aux Cochons is a typical plantation habitat in its origins and total domination by one plant species. The very wet nature of the site results in the site being colonised by a small number of species characteristic of mixed open high altitude forest. Following abandonment of this site the trees have grown rapidly, seeding in profusion, resulting in very dense vegetation (increases from 0.25m^{-2} to 3.4m^{-2} have been recorded in a 5 year period).

Mare aux Cochons: *Coffea* 34000 (99%). Diversity=0.05; native 0, alien 0.

Mont Dauban: *Roscheria* 1200 (39%), *Northea* 1600 (35%), *Cinnamomum verum* 800 (14%), *Phoenicophorium* 400 (7%), *Clidemia* 400 (7%), *Dillenia ferruginea* 400 (7%), *Gltonettia* 800 (7%), *Pandanus seychellarum* 400 (7%). Diversity=1.11, native 1.01, alien 0.45.

Mon Plaisir: *Cinnamomum verum* 1200 (48%), *Psidium cattleianum* 1100 (44%), *Clidemia* 200 (8%). Diversity=0.10; native 0.02, alien 0.52.

7b. *Pisonia sechellarum* forest - characterised by *P. seychellarum* presence.

Species present: *Pisonia sechellarum* 400 (73%); *Dracaena* 66 (12%), *Cinnamomum verum* 27 (5%). Diversity=0.51; native 0.44, alien 0.30.

7c. *Cyathea* scrub - *Cyathea seychellarum* abundant (>4000/ha.).

Cyathea - Mt. Pot a Eau: *Cyathea* 6000 (60%), *Angiopteris* 4000 (40%). Diversity=0.11; native 0.11, alien 0.

Cyathea - Mt. Dauban: *Cyathea* 4500 (100%). Diversity=0.10; native 0.10, alien 0.

Cyathea - Morne Seychellois: *Cyathea* 4000 (98%). Diversity=0.10; native 0.10, alien 0.

8. **Dry scrub** - trees restricted to isolated pockets. <200m above sea level.

8a. Open - extensive areas of bare rock

Mt. Poules Marrons: *Anacardium* 160 (28%), *Phoenicophorium* 120 (20%), *Calophyllum* 120 (20%), *Intsia* 80 (13%), *Pandanus balfouri* 80 (13%), *Terminalia* 40 (6%). Diversity=0.30; native 0, alien 0

8b. Closed - *Memecylon floribundum* or *Tabebuia pallida* >2000/ha.

Memecylon floribundum: *Memecylon floribundum* 74750 (98%). Diversity=0.07; native 0, alien 0.06.

Tabebuia pallida forest: *Tabebuia pallida* 20000 (80%), *Cinnamomum verum* 1500 (6%). Diversity=0.30; native 0, alien 0.30.

9. **Invaded high altitude forest** - aliens forming >80%

9a. Old plantations - as 2. But with invasion by other species and regeneration of natives. At least one alien species other than *Cinnamomum verum* >40%.

Riviere Bois de Fer: *Sandoricum* 3000 (47%), *Cinnamomum verum* 1480 (23%), *Hevea* 560 (9%); *Pterocarpus* 400 (6%). Diversity=0.64; native0.18, alien0.58.

Hevea plantation: *Hevea* 1440 (67%); *Phoenicophorium*, 240 (11%); *Cocos* 240 (11%). Diversity=0.50; native 0.29, alien 0.39.

9b. *Cinnamomum verum* forest - old plantations or areas with heavy *C. verum* invasion (>40%).

Trois Freres: *Cinnamomum verum* 5360 (89%); *Paraserianthes* 400 (8%); *Cerbera* 280 (5%), *Memecylon floribundum* 280 (5%); *Chrysobalanus* 240 (5%) Diversity=0.50; native 0.29, alien 0.39

Morne Blanc: *Syzygium jambos* 20000 (47%); *Cinnamomum verum* 17600 (41%) Diversity=0.55; native 0.80, alien 0.36

Riverine: *Cinnamomum verum* 2000 (56%); *Dillenia ferruginea* 400 (22%), *Phoenicophorium* 400 (22%) Diversity=0.58; native 0.30, alien 0.47.

Le Niol: *Cinnamomum verum* 3085 (53%); *Chrysobalanus* 1028 (17%), *Phoenicophorium* 571 (10%), *Pentadesma* 457 (8%).

Diversity=0.70, native 0.29, alien 0.64.

9c. *Chrysobalanus icaco* scrubby forest - invaded by *C. icaco* (to 3600/ha.).

La Reserve mahogany: *Chrysobalanus* 8000 (50%), *Cinnamomum verum* 6000 (38%), *Swietina* 2000 (11%) Diversity=0.49; native 0, alien 0.49

Chrysobalanus - Le Niol: *Chrysobalanus* 16000 (98%). Diversity 0.02; native 0, alien 0.

Chrysobalanus - Beoliere: *Chrysobalanus* 10000 (95%), *Phoenicophorium* 500 (5%). Diversity=0.19, native 0.57, alien 0.09.

9d. Mixed forest - no one species forming more than 25%, aliens >50%.

Forest at Le Niol: *Cinnamomum verum* 1250 (25%), *Phoenicophorium* 1000 (20%), *Tabebuia pallida* 500 (10%), *Alstonia* 250 (5%) *Calophyllum* 1000 (20%), *Cocos* 250 (5%), *Memecylon floribundum* 250 (5%), *Nephrosperma* 250 (5%). Diversity=0.55, native 0.32, alien 0.47

Baie Cipailles: *Calophyllum* 1250 (25%), *Cocos* 1250 (25%), *Phoenicophorium* 1250 (25%), *Nephrosperma* 1000 (20%), *Cinnamomum verum* 750 (15%), *Tabebuia pallida* 750 (15%). Diversity=0.75, native 0.54, alien 0.51

10. High forest - >300m above seal level, aliens forming <60%.

10a. Dry high forest - formed on shallow soils or in soil pockets in glacis areas. This is a very dry habitat with a xerophytic flora. It may also form on eroded fire prone slopes where a natural successional process would lead to conversion to closed high forest. These areas are subject to frequent fires and remain dry. Includes forest patches within glacis areas and *Dicranopteris* invaded burnt slopes, both are colonised by high altitude xerophytic trees, leading to closed forest where soils are sufficient. Some pockets of dry high forest in burnt areas are isolated and relatively inaccessible, these may preserve easily overlooked rare species (e.g. *Bakerella clavata* above Grande Barbe on Silhouette, *pers. obs.*).

Copolia: *Cinnamomum verum* 740 (49%), *Dillenia ferruginea* 180 (12%). Diversity=0.87, native 0.52, alien 0.79

Mont Sebert glacis: *Nephrosperma* 2000 (33%), *Pandanus multispicatus* 2000 (33%), *Soulamea* 1600 (25%), *Erythroxylum* 400 (7%) Diversity=0.55, native 0.80, alien 0.36.

10b. Closed high forest - >350m, complete canopy

10bi. Mossy montane forest - *Roscheria melanochaetes* >480/ha

Species present Congo Rouge: *Cinnamomum verum* 1320 (32%), *Northea hornei* 920 (23%), *Roscheria* 480 (12%), *Phoenicophorium* 400 (10%), *Pandanus seychellarum* 280 (7%), *Psidium cattleianum* 280 (7%). Diversity=0.72, native 0.57, alien 0.20

Jardin Marron high: *Northea hornei* 1600 (33%), *Roscheria* 1200 (25%), *Cinnamomum verum* 800 (17%), *Dillenia ferruginea* 400 (8%), *Pandanus seychellarum* 400 (8%), *Phoenicophorium* 400 (8%). Diversity=0.90, native 0.41, alien 0.78.

10bii. Palm habitats - palms >30% and *Verschaffeltia splendida* >36/ha

Palm forest appear to be vulnerable to invasion by non-palm species. This is most apparent in small patches of palm forest ($50m^2$ of *Phoenicophorium borsigianum* at Congo Rogue was replaced *Psidium cattleianum* over a 5 year period). Replacement of larger areas by both invasive and native non-palm species can also be detected, suggesting that palm forest is a transitional stage retained by the its dry, fire-prone nature.

10biia. True palm forest - palms >50% of trees

Vallée de Mai: *Lodoicea* 945 (59%), *Phoenicophorium* 145 (9%), *Psidium cattleianum* 145 (9%); *Pandanus hornei* 109 (7%). Diversity=0.6; native 0.35, alien 0.

La Reserve: *Phoenicophorium* 930 (47%), *Deckenia* 530 (27%), *Nephrosperma* 270 (14%). Diversity=0.64; native 0.58, alien 0.

10biib. Palm rich forests - palms <50% of trees.

Source of Grande Riviere: *Phoenicophorium* 1400 (21%); *Cinnamomum verum* 1200 (18%), *Hevea* 1200 (18%); *Paraserianthes* 800 (12%), *Lodoicea* 400 (9%), *Cola* 400 (6%), *Verschaffeltia* 400 (6%). Diversity 0.80, native 0.42, alien 0.66.

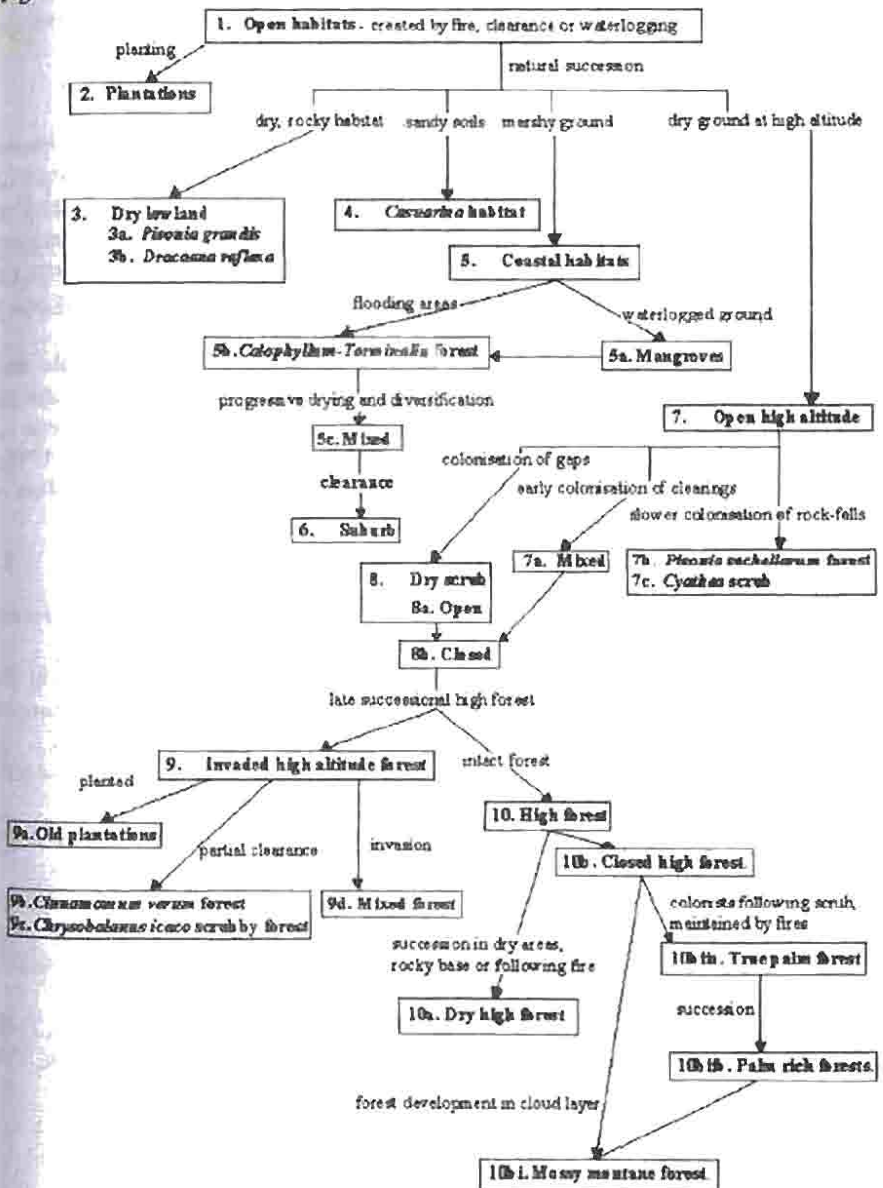
Jardin Marron: *Psidium cattleianum* 1400 (22%); *Artocarpus heterophyllus* 1200 (19%), *Cinnamomum verum* 1000 (16%); *Phoenicophorium* 800 (13%); *Verschaffeltia* 800 (13%); *Roscheria* 600 (9%). Diversity=0.90, native 0.41, alien 0.78.

Evolution of the habitats

The treatment of habitat data as phylogenetic data allows the habitat classification to be interpreted in the light of a hypothetical succession, analogous to an evolutionary process. This 'evolution' of the habitats starts with the open, low diversity habitats. A process of colonisation leads to increased diversity. In dry soils early colonisation is predominantly by *Casuarina equisetifolia* which grows on extremely poor soil where few other species can grow. A ground layer of sedges and *Phyla nodiflora* colonized and the habitat gradually accumulates a litter high in chemicals which appear to inhibit many other plants. Invasion of this habitat is slow until the *Casuarina* trees reach a height at which they become unstable, the gaps created by falling trees are then open to colonists of other species. On rocky slopes vegetation remains relatively low in diversity (with microclimatic exceptions, e.g. *Dracaena* forest). A greater tree density and diversity develops in the coastal habitats where more water is available and a continuing pattern of increased diversity is apparent until closed forest habitats are reached. Forest degradation tends to lead to a reduction in diversity, this is most apparent in suburban habitats where the diversity of ornamental shrubs may be high but very few tree species are retained.

The relationships between all the Seychelles habitats (with the possible exceptions of permanently waterlogged and rocky sites) are dynamic. The general increase in diversity in forest development follows a basic 'succession' but at each stage disturbances or changes are relatively frequent. Rock and tree falls are a frequent feature of the steep hillsides, these result in localised gaps which are colonised by the pioneer species characteristic of the open high altitude and dry scrub habitats. Fire has a similar effect and although less frequent than tree and rock falls affects larger areas. Repeated burning may account for the persistence of large areas of palm habitats on Praslin where-

Fig 3. Relationships between habitats



as such habitat is rapidly converted into closed high altitude forest on Mahé and Silhouette. Such dynamic changes require that large areas of high diversity habitat are preserved to provide the source of colonists for gaps or fire slopes.

Discussion

The habitat classification proposed above covers all the large areas of habitat found in the granitic islands of Seychelles. Coconut plantations are not listed as a separate group despite being an easily recognised habitat. While these plantations were maintained they represented a distinctive habitat that could be included in the plantation category (sharing the planted origin and the extremely low diversity). Few coconut plantations are now maintained in the granitic islands and most former plantations are now undergoing a transition from plantation to low mixed forest forms.

Studies of habitat change in Seychelles are too new to provide reliable data although the available data have previously been summarised for high forests on Silhouette (Gerlach *et al.* 1997). The only long term monitoring project has been on Aride where there are 20 years of data from *Pisonia grandis* woodland (Ayrton 1995), such studies are required for all other habitats. The habitat classification proposed here is intended as a first step in the quantification of habitat characteristics and dynamics.

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