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Population status of five Hawaiian endemic fern taxa within the genus *Diellia* (Aspleniaceae)

Ruth Aguraiuja

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The life-stage and size structure of 10 populations of five endemic fern taxa was studied (*Diellia erecta* Brack; *D. falcata* Brack; *D. pallida* W.H. Wagner; *D. unisora* W.H. Wagner and *D.* x *lauii* (*D. falcata* x *D. unisora*) W.H. Wagner), with the aim of assessing the overall condition of the populations. During the study, populations were defined as spatially distinct assemblages of plants at certain sites, with no consideration of the genetic structure of the populations. Spatial patchiness of habitat, clumped distribution patterns, life-stage specific survival and slow establishment of gametophytes are characteristic of all taxa of the genus *Diellia.* Data from field observations of *D. falcata* over three months lead to the assumption that *Diellia* ferns show a continuous growth pattern with irregular periods of dormancy and spore release with defined peaks. The proportion of vegetative premature and reproductively mature sporophytes could be one possible variable for use in the assessment of the population status of *Diellia* ferns in short-term studies. The single population of *D. pallida* in Mahanaloa Valley, Kauai, is in critical condition with only 31 individuals of different life stages found in heavily disturbed habitat. The process of hybridisation between *D. falcata* and *D. unisora* requires further study, which may contribute to our understanding of the hybridisation of rare species and/or speciation.

Ruth Aguraiuja, Tallinn Botanic Garden, Kloostrimetsa tee 52, Tallinn EE-11913, ESTONIA.
Fax: +372-6005529. E-mail: ruth@tba.ee

Diellia pallida

Diellia x *lauii*

Introduction

The fern genus *Diellia* Brack. (*Aspleniaceae*) is endemic to the Hawaiian Islands, comprising six species and a single hybrid (Wagner 1994): *Diellia erecta* Brack.; *D. falcata* Brack.; *D. leucostegioides* (Baker) W. H. Wagner; *D. mannii* (D.C. Eaton) W. Robinson; *D. pallida* W.H. Wagner; *D. unisora* W.H. Wagner and *D.* x *lauii* (*D. falcata* x *D. unisora*) W.H. Wagner.

Diellia ferns are small to medium-sized ferns found on steep slopes in dry and mesic lowland and montane forests (Wagner 1951). They differ from *Asplenium* species by their short or fused submarginal sori, which open outwards and the areolate venation pattern. One exception is *D. leucostegioides,* which shares most of its morphological features with the other *Diellia* species, but has free venation and medial linear sori along the veins which is typical of *Asplenium* species (Wagner 1953).

The taxonomy of the genus and its species has undergone many changes through its history, being related to various genera and families by different authorities (Brackenridge 1854, Hillebrand 1888, Christensen 1925, Wagner 1952). The fact that these ferns are so rare and variable has meant that there is still no clear agreement about the taxonomic status of the genus *Diellia.* Recently, it has been reduced to a synonym under the genus *Asplenium* L. by R. Viane (Kramer & Viane 1990, Viane & Reichstein 1992).

Diellia is a monophyletic genus evolved from *Asplenium* ancestory (Wagner 1952, Wagner 1953), which has radiated out over the Hawaiian Islands. In his monographic study, Wagner suggested an origin from the *Asplenium trichomanes* group. Later, he suggested a more specific prototype in the form of *Asplenium leucostegioides* Baker (Wagner 1953), now recognised as *Diellia leucostegioides* (Baker) W.H. Wagner comb. nov. (Wagner et al. 1995).

D. erecta, and its associated forms, is the only *Diellia* species which was originally found on all of the bigger islands, though it is now only found on Hawaii, Maui, Molokai and Oahu. The five other *Diellia* species are all single island endemics. The type specimens of *D. leucostegioides* were collected on East-Maui sometime before 1879 and identified as *Asplenium normale* Don, only being described as a separate species some years later (Wagner 1953). Since that time, this species has not been relocated. *D. mannii,* originally collected from Kauai, has also not been found for 100 years (Anon. 1999). *D. pallida* is endemic to Kauai, found only in the western part of the Kokee Mountains. Three taxa are then endemic to the island of Oahu. *D. falcata,* the only locally common species of the genus, occurs over the whole of the Waianae Mountains. *Diellia unisora* was discovered at Pohakea Pass in the Waianae Mountains on Oahu in 1932. It is now rare with a localised distribution (Wagner 1951). *Diellia* x *lauii* is a recently discovered endemic hybrid (Wagner et al. 1999). It was mentioned as locally common when found by J. Lau in 1991. All three endemic taxa occur together in the Pualii-Palawai region in the southern Waianae Mountains. According to Wagner (1999), the hybrid establishes dense colonies in the vicinity of parental species.

The restricted distribution of the *Diellia* species is mentioned in several published studies (Hillebrand 1888, Smith 1934, Degener 1950, Wagner 1952, Fosberg & Herbst 1975, Wagner 1952). All species have always been considered very rare and local, on the verge of extinction, or decreasing. According to Wagner, these species have always been rare and localised because of the restricted area of suitable habitat. The major threats to their survival are habitat degradation by feral ungulates and competition with naturalised, introduced plant species (Anon. 1995, Anon. 1996, Anon. 1998, Anon. 1999). The first assessment of the status of the populations was given by Fosberg & Herbst (1975). Their work was based mainly on their lengthy personal experiences of Hawaiian flora and almost without quantitative data and ecological information. The current status of the taxa is given in Table 1.

According to Menges and Gordon (1996), the status and trends of populations of rare plants may be studied on three levels: population distribution; quantitative monitoring (study) of population size/condition; and demo-

Table 1. Status and distribution of the *Diellia* taxa

Taxon	IUCN 1997*	USFWS 1999**	Distribution
Diellia erecta	Endangered	13 pop. 63 ind.	Hawaii, Maui, Molokai, Oahu. Extinct Lanai and Kauai.
Diellia falcata	Endangered	22 pop. > 6000 ind.	Oahu
Diellia x lauii	–	–	Oahu
Diellia leucostegioides	–	0	Maui, not found
Diellia mannii	Extinct/Endangered	0	Kauai, not found
Diellia pallida	Endangered	3 pop. 23 ind.	Kauai
Diellia unisora	Endangered	4 pop. 700 ind.	Oahu

* IUCN Red List of Threatened Plants 1997, IUCN The World Conservation Union:5
** U.S. Fish & Wildlife Service Species List.
– not listed

graphic study of the population. The first level, including an inventory, distribution mapping and presence/absence and spatial extent of the populations, has been the base for the present status assessment of the populations of *Diellia* (Anon. 1996).

Long-term studies of demography, together with life-cycle studies, give useful information for conservation management concerning critical stages and specific biological requirements of rare plants. Another method for describing population status/condition in a single census may be to study the population structure and determine the relative proportions of individuals in different life-cycle stages (van't Veer & den Nijs 1994). Monitoring the demographics of populations of rare plant species allows us to follow population trends and hypothesize about the demographic mechanisms driving them (Menges & Gordon 1996).

This paper describes the population size and life-stage structure of 10 populations of *D. erecta*, *D. pallida*, *D. falcata*, *D.* x *lauii* and *D. unisora.* For this study, populations were defined as spatially distinct assemblages of plants at certain sites, without considering the genetic structure of the populations. The aim of the study was to assess the status (condition) of the populations of the taxa within the endemic genus *Diellia*, on the basis of population structure and life cycle characteristics.

Methods

Over the period 13 February to 16 July 1999, field surveys were conducted to determine the current population status of four species and one hybrid within the genus *Diellia* at 13 sites on the islands of Kauai, Oahu, Molokai and Hawaii (Fig. 1). For all sites, general community and habitat descriptions were made and for all observed populations, the number of individuals and their life stage structure were assessed.

To describe the relevant plant communities, lists of associated species were compiled (Appendices 1 and 2). To describe the habitats at each locality, variables recorded included elevation (altitudinal range), aspect, slope, substrate, soil pH, soil moisture and canopy closure (Table 2).

Assessments of population size were derived mainly from direct counting of individuals, while sample estimates were made for the more abundant *Diellia falcata* at Kahanahaiki.

To record the stage structure of the populations, the following stages were differentiated: prothallium; sporeling; premature (pre-reproductive adult); mature (reproductive adult); dormant/dead (Figure 2). As prothalli were difficult to find and identify, during analyses of stage structure the prothalli and sporelings were pooled together. To identify the spore release period, the frond phases were described as follows: vegetative; sori developing; sori opened;

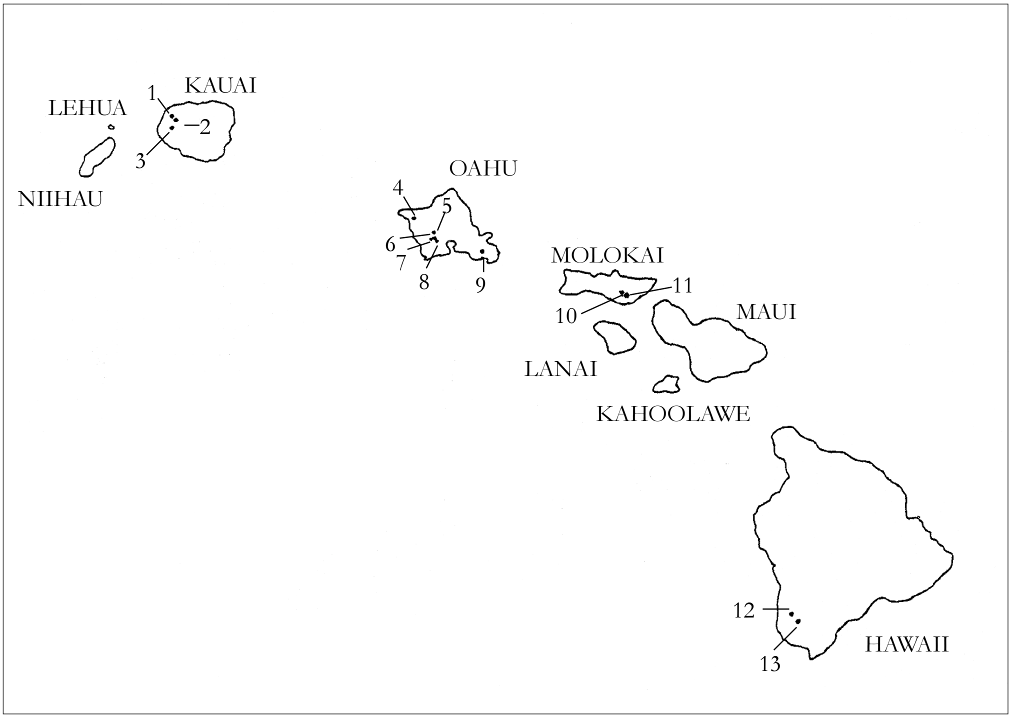

Figure 1. Study sites of the genus *Diellia* in Hawaii: 1– Mahanaloa (*D. pallida*); 2– Makaha (*D. pallida*); 3– Puu Ka Pele (*D. pallida*); 4 – Kahanahaiki (*D. falcata*); 5 – Pualii (*D. unisora*); 6 – South-Palawai (*D. unisora*); 7 – South-Palawai (*D.* x *lauii*); 8 – South-Palawai (*D. falcata*); 9 – Hawaii Loa (*D. erecta*); 10 – Onini Gulch (*D. erecta*); 11 – Puu Kolekole (*D. erecta*); 12 – Honomalino (*D. erecta*); 13 – Manuka (*D. erecta*).

sporangia dehisced. Where possible, the diameter and height of the plants and the length of the fronds were also measured. For each individual, the number of old stipes and vegetative and generative fronds was counted. At Kahanahaiki, a permanent plot of 6 x 10m was established and the population of *D. falcata* censused three times (March, April and June).

Voucher specimens (fronds and pinnae) are preserved in the herbarium at the National Tropical Botanical Gardens on Kauai. All statistical analyses were made using StatView for Windows, Version 5.0, SAS Institute Inc. 1992–1998.

Results

I found different taxa of the genus *Diellia* growing on nine sites (Table 2). For all observed populations, the number of individuals and their life stage structure was assessed. Measurements of individuals were made for four populations: at Hawaii Loa (*D. erecta*); Mahanaloa (*D. pallida*); Pualii (*D. unisora*) and Kahanahaiki (*D. falcata*).

Habitat and community

Diellia ferns are restricted to a particular spatially fragmented habitat type on the steep sides of gulches. Usually, they occur on northern slopes at an altitude of 300–1100 m a.s.l. Slope angle varied among sites from gentle to steep, nearly vertical, cliff faces. *D. falcata*, *D.* x *lauii*, *D. pallida* and *D. unisora* are usually terrestrial ferns, whilst *D. erecta* occurs on soil as well as on old lava blocks and cliffs. Sparse ground cover and a bare soil surface appear to be essential for the persistence of these populations. Typically, plants were found on soil that was rocky, granular and usually dry, with some leaf litter and mosses. Soil pH varied

Table 2. Checked sites with previous and current data.

Taxon	Island	Locality	Previous data (no. of ind.)	Source	Current data (1999) (no. of ind.)
D. erecta					
	Hawaii	Honomalino	20	Lau 1991	–
	Hawaii	Manuka	1	Lau 1992	205
	Oahu	Hawaii Loa	c. 40	Anon. 1998b	212
	Molokai	Onini Gulch	1	Wood 1997	1
	Molokai	Puu Kolekole	few	Anon. 1996	–
D. falcata					
	Oahu	Kahanahaiki	c. 40–2000	Anon. 1998b	c. 1000
	Oahu	S-Palawi	c. 10	Anon. 1998b	18
D. x lauii					
	Ohau	Pualii	few	Anon. 1998b	30
	Ohau	S-Palawii	hundreds	Lau 1991	141
D. pallida					
	Kauai	Puu Ka Pele	2	Flynn 1998	–
	Kauai	Makaha	6	Wood 1998	–
	Kauai	E-Mahanaloa	c. 10	Perlman 1991	4
	Kauai	W-Mahanaloa	c. 10	Wood 1996	31
D. unisora					
	Oahu	Pualii	c. 600	Anon. 1998b	153
	Oahu	S-Palawai	90	Anon. 1998b	112

– not found

from slightly acidic (sites on Oahu) to neutral and basic (Kauai, Mahanaloa) (Table 3).

The surrounding natural community was usually mesic lowland or mountain forest where *Metrosideros polymorpha* Gaud. is dominant. The communities at Pualii, South-Palawai in the Waianae Mts. and Hawaii Loa in the Koolau Mts. were dominated by naturalised *Psidium cattleianum* Sabine and *Schinus therebinthifolius* Raddi (Table 3).

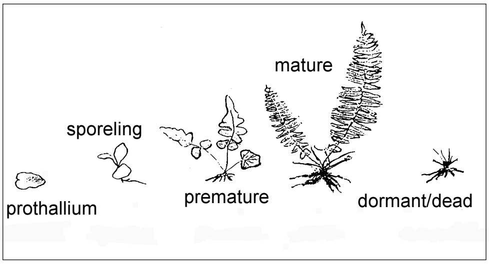

Figure 2. Schematic drawing of the life cycle stages of taxa in the genus *Diellia*: prothallium; sporeling; premature (pre-reproductive adult); mature (reproductive adult); dormant/dead.

Diellia erecta

A total of five sites on three islands were searched for populations of *D. erecta* (Table 2). On Molokai, only a single mature individual was found growing on a steep slope at Onini Gulch in mesic mixed forest. At the end of March, this individual plant had five fronds from its last growing period and one young generative frond. A few unopened sporangia were found between older, dehisced sporangia. This individual differed morphologically from ferns in other populations of *D. erecta* by its narrower pinnae, simple venation and distinct auricles, which diagonally overlapped the stipe and next pinna on the abaxial side of the frond.

In Manuka Natural Area Reserve, *D. erecta* was found growing along a loop trail in dry forest dominated by *Nestegis sandwicensis* (A. Gray)

Table 3. Habitat characteristics for the *Diellia* ferns

Taxa, site	Island	Alt (m)	Aspect	Slope	Moisture	Canopy
D. erecta						
Onini Gulch	Molokai	894	N	Steep, ca 45°	Mesic	Closed
Puu Kolekole	Molokai	920	N	Steep, ca 45°	Dry	Closed
Honomalino	Hawaii	586	S W	Gentle	Mesic	Closed
Manuka	Hawaii	625	S W	Moderate	Dry	Closed
Hawaii Loa	Oahu	360	S E	Steep, nearly vertical	Dry	Closed
D. falcata						
Kahanahaiki	Oahu	555–645	NW	Moderate	Mesic	Closed
S-Palawai	Ohau	670–730	N	Moderate	Mesic	Closed to semi-closed
D. x lauii	Ohau	670–730	N	Steep	Mesic	Closed to
S-Palawai	Kauai	670–730	N	Steep	Mesic	semi-closed
D. pallida						
Mahanaloa	Kauai	580–690	N	Steep	Mesic per. dry	Closed to semi-closed
Makaha	Kauai	915	N	Steep, nearly vertical	Dry	Closed to semi-closed
Puu Ka Pele	Kauai	1010	SE	Steep	Dry	Open to semi-closed
D. unisora						Open
Pualii	Oahu	670–750	N	Steep	Mesic	Closed to semi-closed
S-Palawai	Ohau	671–732	N	Steep	Mesic	Closed to semi-closed

Table 3. continues on next page

Degener, I. Degener & L. Johnson. Most of these individuals were found on moss covered lava blocks, with only a few growing on soil. Altogether, 151 individuals in various life cycle stages were recorded in this population (Figure 3). At the beginning of April, 61% of this population was in the reproductive stage. Fronds of all different phases were found on mature plants. The whole area was very dry and the ferns were wilting, with many of the wilted plants having young fronds with inconspicuous developing sori.

On Oahu, *D. erecta* was found on the southeastern slope of the Hawaii Loa Ridge. The slope was covered with non-native secondary forest, where *Psidium cattleianum* was dominant. All individuals were found on nearly vertical old lava cliffs. Altogether, 212 individuals in different life stages were recorded (Figure 3), with a single mature individual growing on a separate cliff 30m from the main population. In June, 13% of the population was in the reproductive phase and nearly half of the population (48.3%) consisted of prothallia and sporelings. Fronds of all phases were found on mature plants. Mean values of the measurements of individuals in different lifestages are given in Table 4.

Diellia falcata

Two sites with populations of *D. falcata* were visited in the Waianae Mts. on Oahu (Table 2). The entire population at Kahanahaiki Valley

Table 3. continued. Habitat characteristics for the *Diellia* ferns

Taxa, site	Substrate	Soil pH	Groundcover	Natural community	Dominant species
D. erecta					
Onini Gulch	Brown soil with moss and leaf litter	–	20%	Mixed mesic forest	*Metr poly*
Puu Kolekole	Brown soil with leaf litter	–	10%	Mixed mesic forest	*Metr poly*
Honomalino	Old aa lava blocks and clinker	–	20%	Mesic Metr. forest	*Metr poly,* *Nest sand*
Manuka	Soil, old aa lava blocks and clinker	–	10%	Nest dry forest	*Nest sand*
Hawaii Loa	Old pahoehoe cliff	–	5%	Sec. forest of alien trees	*Psid catt,* *Schi tereb*
D. falcata					
Kahanahaiki	Heavy granular soil	5.7	30%	Lowland mesic forest	*Diosp hilleb*
	Brown-black granular soil	–	60%	Lowland mesic forest	*Cenchr agri*
S-Palawai	Rocky soil	5.0	20%	Relic mesic forest with sec. succession of weeds	*Psid catt*
D. x lauii					
S-Palawai	Rocky soil	5.0	20%	Relic mesic forest with sec. succession of weeds	*Psid catt*
D. pallida					
Mahanaloa	Pure native soil with leaf litter	6.9–7.7	<10%	Kauai diverse mesic forest	*Metr poly,* *Ptera kaua*
Makaha	Brown granular rocky soil	–	75%	Aca-Metr montane mesic forest	*Metr poly,* *Aca koa*
Puu Ka Pele	Brown granular rocky soil	–	30%	Remnants of dry mixed mesophytic forest	*Crypt mannii*
D. unisora					
Pualii	Granular rocky soil	–	<10%	Relic mesic forest with sec. succession of weeds	*Psid catt,* *Schin tereb*
S-Palawai	Granular rocky soil	–	20%		*Psid catt,* *Schin tereb*

consisted of 1000 or more individuals, growing in small and large groups on the north-western side of moderately steep slopes above the gulch bottom. The natural community at this site was *Diospyros hillebrandii* (Seem.) Fosb. mesic lowland forest. This area is owned by the Army Ecosystem Management Region and is fenced for protection from trampling by feral animals.

The 60 m^2 sample plot of *D. falcata* at Kahanahaiki was censused on three occassions (in March, April and June). In this population, the mature stage of sporophytes was more prevalent than stages of prothallia and sporelings (Figure 4). The number of individuals varied between months (Table 5), mainly because of the establishment and death of individuals during

Figure 3. Life stage structure of populations of *Diellia* taxa. *Census in April.

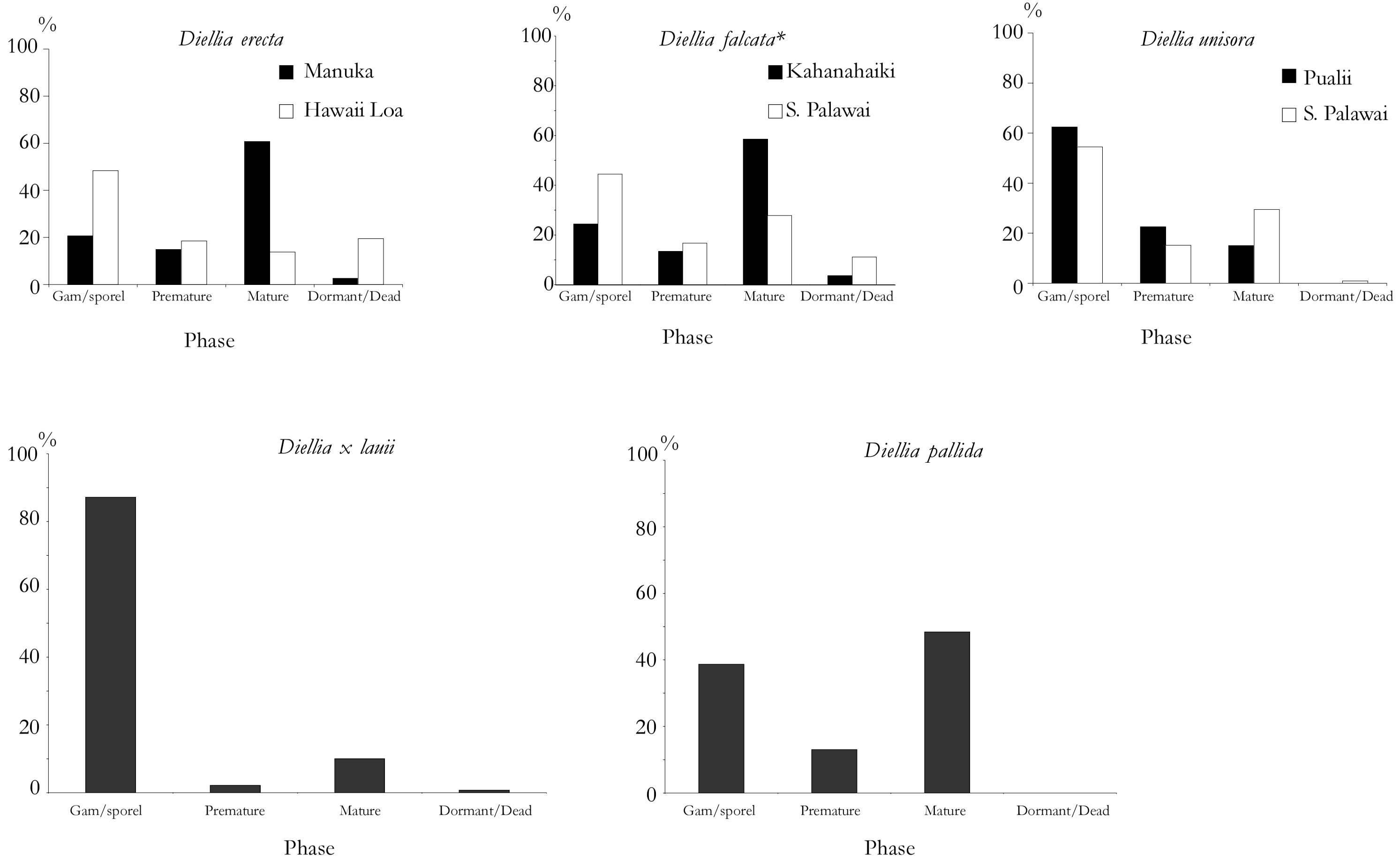

Table 4. Mean values (± SE) of measurements of the plants of *D.erecta*, *D. pallida*, *D. unisora* and *D. falcata* in different life stages.

Species	Site	Plant heigth (cm)	Frond length (cm)	Fronds per rhizome (no.)	Reproductive fronds per rhizome (no.)
Sporelings					
D. erecta	Hawaii Loa	0.5±0.1	0.7±0.1	2.7±0.2	–
D. pallida	Mahanaloa	0.4±0.1	0.5±0.1	2.0±0.3	–
D. unisora	Pualii	0.6±0.1	0.6±0.1	1.2±0.1	–
D. falcata M	Kahanahaiki	0.7±0.2	0.7±0.3	2.0±0.4	–
D. falcata A	Kahanahaiki	0.7±0.2	1.0±0.4	3.0±0.4	–
D. falcata J	Kahanahaiki	1.0±0.2	1.3±0.3	3.3±0.3	–
Premature					
D. erecta	Hawaii Loa	2.3±0.3	3.8±0.3	3.1±0.4	–
D. pallida	Mahanaloa	5.0±0.6	5.8±0.7	3.3±0.8	–
D. falcata	Pualii	3.4±0.7	4.2±0.9	4.0±0.4	–
D. falcata M	Khanakahaiki	5.5±0.5	7.2±0.8	3.8±0.5	–
D. falcata A	Khanakahaiki	4.7±0.5	7.0±0.8	3.2±0.4	–
D. falcata J	Kahanahaiki	5.1±0.9	7.8±0.9	3.0±0.3	–
Mature					
D. erecta	Hawaii Loa	6.0±0.7	9.2±0.8	3.4±0.5	1.8±0.3
D. pallida	Mahanaloa	14.0±1.2	19.6±2.8	2.1±0.2	1.4±0.2
D. unisora	Pualii	9.0±1.5	13.1±2.1	7.5±1.4	4.0±1.1
D. falcata M	Kahanahaiki	16.7±0.8	22.1±1.0	4.1±0.2	2.0±0.2
D. falcata A	Kahanahaiki	14.9±0.8	22.9±0.9	3.8±0.2	1.2±0.2
D. falcata J	Kahanahaiki	13.3±0.8	20.4±0.9	3.0±0.2	1.8±0.2

M– March
A – April
J– June

the prothallia and sporeling stages. The peak for gametophyte establishment and vegetative growth was in April. The formation and maturation of new reproductive fronds was also highest in April (Figure 5), whilst the total number of mature reproductive sporophytes was highest in June (52%). The total number of fronds (vegetative and reproductive) per individual differed significantly between March and June (ANOVA, F = 5,234, $p < 0.005$). The mean number of vegetative and reproductive fronds per rhizome was highest in March (Table 4).

During observations, the spread of an infestation of *D. falcata* by the greenhouse thrips *Heliothrips haemorrhoidalis* (Bouché) was discovered. Approximately 10% of the plants in the plot were damaged.

In the South-Palawai drainage, *D. falcata* occurred in small groups in the vicinity of *D. unisora* and *D.* x *lauii*. On the northern slope of the drainage, 18 individuals of different stages were observed (Figure 3). These ferns were growing in a mesic relic forest with a secondary succession of weeds, where *Psidium cattleianum* Sabine was dominant. Premature stages formed ca. 60% of the population.

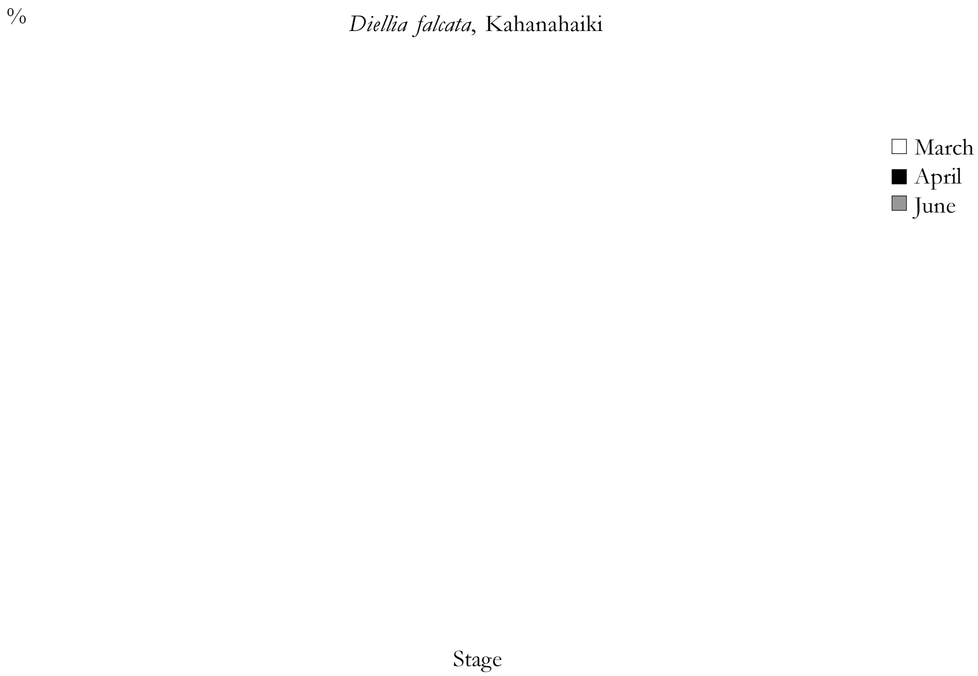

Figure 4. Life stage structure of *D. falcata* at Kahanahaiki.

Diellia x *lauii*

In South-Palawai, *D.* x *lauii* was found in scattered groups over an area of ca. 1000 m^2 at an elevation of 670–730 m. In total, 140 plants in various life-stages were recorded in April (Figure 3). In this population, the prothallia and sporelings stages were more prevalent than premature and mature sporophytes. The prothallia and sporelings around premature and mature plants of the hybrid were counted as individuals of *D.* x *lauii*. At these stages, it is impossible to identify the species without damaging them, and they may actually belong to the parental species, hybrids or backcrossings. All mature individuals had new fronds with developing or already opened sori.

Individuals of the hybrid *D.* x *lauii* were very variable, with some of the intermediates similar to *D. falcata* and others to *D. unisora*. Spores of the hybrids appeared to be normal, except for a few individuals that showed irregular and poorly developed sori.

Diellia pallida

All previously known localities, except Koaie Canyon, were searched for *D. pallida*. Individuals were only found in Mahanaloa Valley in the Kokee Mountains, where two groups were found growing. In the eastern part of the population, only four separate individuals were found, whilst in the western part, 31 individuals in different life stages were recorded (Figure 2). Of these, 15 were mature with only four in the premature stage. For *D. pallida*, the mean number of vegetative and reproductive fronds per rhizome was the lowest (Table 4).

The whole area was heavily influenced by ungulates and *D. pallida* was only found in sites protected by stones or tree roots. Disturbed patches of forest with an open canopy were densely covered with introduced species.

Diellia unisora

D. unisora was studied at two sites, Pualii and

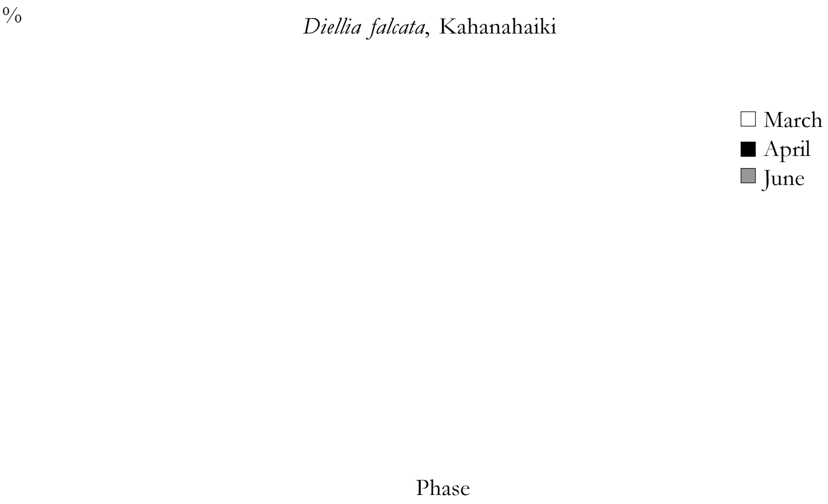

Figure 5. Phenology of *D. falcata* at Kahanahaiki during March, April and June. Proth – prothallium; veg – vegetative; dev– developing sori; deh– dehisced sori; dorm– dormant.

South-Palawai, in the Waianae Mts. (Table 2). At Pualii, *D. unisora* was growing in *Metrosideros-Acacia* lowland mesic relic forest with secondary succession of weeds. Dominant species found here were *Schinus terebinthifolius* and *Psidium cattleianum*.

This population held 183 plants growing in five groups (11, 20, 30, 40 and 82 individuals in each), with an approximate distance between groups of 60–100 m. The median-sized group of the population (30 individuals) proved to be hybrid *D.* x *lauii*. In March, two groups at the upper part of the population showed the prothallia and sporeling stages prevailing (Figure 3). Also, most of the mature plants had young generative leaves with developing or recently opened sori. The mean number of vegetative and reproductive fronds per rhizome was highest for *D. unisora* (Table 3). About 11% of the population were in the reproductive phase (Table 5).

In South-Palawai, *D. unisora* was only found in localized groups on very steep, rocky slopes in relic mesic forest with secondary succession of weeds. The dominant species here was *Psidium cattleianum*. In total, 112 plants in different life stages were counted (Figure 3). In April, 70% of this population were in the reproductive phase (Table 5).

Discussion

The populations of *Diellia* ferns are very localised and small, with plants usually growing in big or small clumps, or even solitary and scattered. Usually, *Diellia* ferns are very inconspicuous (except *D. falcata*) and their relative abundance can vary between years. In unfavourable years, or during long-lasting dry periods, the plants may not be apparent at all, and searching for these species may require more than one season to locate populations (Wood pers. comm.). At only four of 13 sites checked during this research were any plants found. The habitat at Puu Ka Pele on Kauai (*D. pallida*) seems to be irreversibly degraded, whilst the sites at Makaha on Kauai (*D. pallida*), Puu Kolekole on Molokai (*D. erecta*) and Honomalino on Hawaii (*D. erecta*) need repeated checking.

Diellia ferns seem to grow most vigorously in the shade, in areas of sparse ground cover and under a closed canopy. Occasional occurrences under shrubs or more open areas may be only

Table 5. Percentage of plants in different phenological phases at the time of observation of the populations of *Diellia.*

Taxa	Site	Time	Individuals (no.)	Veg (%)	Reprod (%)	Dormant/ dead (%)
D. erecta	H, Manuka	April	151	36	61	3
D. erecta	O, Hawaii Loa	June	212	68	13	19
D. falcata	O, S-Palawai	April	18	72	17	11
D. pallida	K, W-Mahanaloa	June	31	55	45	0
D. unisora	O, Pualii	March	93	89	11	0
D. unisora	O, S-Palawai	April	112	70	29	1
D. x lauii	O, S-Palawai	April	141	89	10	1
D. falcata	O, Kahanahaiki	March	128	47	48	5
D. falcata	O, Kahanahaiki	April	164	54	41	5
D. falcata	O, Kahanahaiki	June	140	37	52	11

temporary or due to the changes in the community. Furthermore, not all patches of suitable habitat are colonised.

According to Wagner (1952), the habitat of *Diellia* is transitory and depends to a certain degree on disturbance, which creates safe sites with bare soil for gametophyte establishement. However, all *Diellia* species have a short rhizome and very fragile stipes, which makes them particularly vulnerable to trampling, and during the present study, most of the sites visited were too heavily disturbed by feral ungulates. Most critical is that the single viable population of *D. pallida* at Mahanaloa, where prothallia, sporelings, premature sporophytes and mature individuals were found, only grows in places protected by stones or roots of the trees.

The occurrence of a natural spore bank of *Diellia* species and spore viability have not been studied. According to Dyer (1994), the regular turning of the upper layer of the soil may cause the depletion of a natural spore bank and prevent spontaneous re-establishment of a population. Considering that fern spore banks have been found in very different habitats at the study sites, experimental re-establishment of a population of *D. pallida* by natural soil spore bank could be possible at Makaha , where the habitat is overgrown with an introduced species (*Erigeron karvinskianus* DC).

The peculiarity of the pteridophytes is that the mature sporophyte, which is vascular, leafy and relatively large, is limited to establishment in a habitat that has proved to be suitable for the independent survival of its small thalloid non-vascular gametophyte. Environmental changes and periodic fluctuations in conditions must then be withstood through all following life cycle stages (Page 1979).

Water deficiency is the key limiting factor for pteridophytes in seasonally dry tropical areas, which determines their adaptations in relation to specific habitat use and seasonal periodicity of growth and dormancy (Kornaš 1985). As *Diellia* ferns grow in dry and mesic forests with occasional dry periods, they exhibit certain periodicity in their growth with alternate active and dormant periods. However, analyses of frond length and number of generative fronds over a three month period did not indicate any significant differences. It must then be assumed that *Diellia* ferns exhibit mainly continuous growth with only irregular dormant periods. Additional long-term studies could add more detailed information.

Observations made over the period of spore maturation and release indicate that most of the spores of the studied species are released during a peak period. For *D. falcata*, *D.* x *lauii* and *D. unisora* in Waianae Mts. on Oahu, this peak appears to be in April. As the growth of new fertile fronds, the development of sori on the fronds and the maturing of sporangia all take place gradually, the total period of spore dispersal is probably much longer, lasting for several months. Fronds from the last growing period had certain quantities of unopened sporangia together with older, dehisced sporangia. Unspread spores of *D. pallida*, collected from the fronds from the last growing period, were viable and germinated (Sugii 1999, pers. comm.).

The formation of new generations of ferns begins with the dispersal of spores to safe sites for germination and gametophyte establishment. Given the normal production of spores, it may be hypothesized that the occurrence of individual species of *Diellia* is limited only by the scarcity of safe sites rather than by spore dispersal.

The growth process from spore germination to establishment of prothallia and sporelings comprises two sensitive life stages. These stages are most vulnerable depending on microedaphic and microclimatic conditions (Peck et al. 1990), with mortality of individuals during these stages being the highest. Therefore, the proportion of individuals in the youngest and oldest life stages does not appear to adequately reflect the condition of the population. On the basis of life-stage structure analysis, the ratio of premature sporophytes to reproductively mature sporophytes appears to be one possible attribute for the assessment of the condition and status of populations of *Diellia* ferns in the short-term. The number of premature individuals, as an indicator of possible recruitment as reproductive individuals, appears to be a better indicator of the condition of the population than the most sensitive stages of prothallia and sporelings. Populations would seem to be in good condition where the number of premature individuals is equal to, or higher than, 2/3 of the number of mature individuals and sporelings (*D. erecta* in Hawaii Loa, *D. unisora* in South-Palawai). Populations where the number of premature individuals is significantly lower than the number of reproductive individuals may be experiencing population fluctuation or be disturbed by some other factor (*Diellia erecta* in Manuka, *Diellia falcata* in Kahanahaiki). In the case of a very small population combined with a low number of individuals in the premature stage, the population must be considered in critical condition (*Diellia pallida* in Mahanaloa). Further long-term demographic studies are required to check this hypothesis.

All the studied populations, except for *D. falcata* at Kahanahaiki and *D. erecta* at Manuka, had a higher proportion of plants in the gametophyte and sporeling stages than in more mature stages. The low proportion of these premature stages at Manuka may have been caused by a lengthy dry period and at Kahanahaiki by reduced shelter from a closed canopy. At Manuka, it was probable that in a lasting drought, the wilted fronds with very young sori would dry out and never reach the spore release phase. A consequent reduction in spore production, and thus establishment of new gametophytes and sporelings, may result in decreased recruitment in the population during the following years, allowing for fluctuations in population size.

For all *Diellia* species, there was a significant difference between the frond size of the plants at different life stages (Kruskal-Wallis, $H= 121.967$, $p< 0.001$). The number of fronds of *Diellia* ferns was not correlated with the life stage, and this is probably indicative of the soil and moisture conditions of the habitat. The significant difference between the number of fronds of *D. falcata* in March and June was probably caused by a dry period in May and June, which also increased the number of dormant and dead individuals.

Occasional reverting of mature plants to a vegetative stage (of only one or two short vegetative fronds) was observed at Kahanahaiki. This may have been as a result of ageing, or as a response to some unrecognised environmental stress in combination with a drought.

Though *Diellia* ferns have adequately adapted to tolerate drought, a peak in mortality for all stages possibly still occurs during the dry season. By comparing the species and populations at different sites on different islands, it was shown that there are seasonal variations in mortality depending on local differences in dry and wet periods. The periods of active growth, peak of spore release and germination timing are probably not only species specific, but also population specific. However, the limited period of observation made it difficult to evaluate the status of the different populations in relation to within-year climatic variation.

D. x *lauii* (*D. falcata* x *D. unisora*)

The actual distribution of these hybrids is not known, as observations from different sites on Pualii, South Palawai, inferred that these plants can represent many separate, independent parental hybridisations, rather than spreads from a single source. It is possible then, that the distribution of hybrids is wider than recorded in this study.

Hybrids are very variable, being intermediates between the parental species with mostly fertile fronds and normal spores. The normal appearance of the spores and the whole spectrum of intermediate forms suggests that the parent species and the intermediate forms are capable of interbreeding (Wagner et al. 1999). In hybrid swarms where one species predominates, the minor species often declines over time, whereas if both species contribute similarly to such a swarm, the integrity of both species may be lost. Thus, generations of hybridisation and backcrossing may erode the genetic integrity of a rare species (Levin et al. 1996).

Unfortunately, there is still insufficient information on the breeding systems, breeding barriers and hybridisation processes of *Diellia* species. For hybridisation to occur in the *Diellia*, there should be mixed populations of parental gametophytes, though such mixed populations of mature plants of different species were not found in this study. Hybrids and parental species did occur in a patchy pattern, but without direct contact between the parental species.

On the basis of current information, it is difficult to predict whether ongoing hybridisation, spreading of the hybrid, unstable hybrid formation or genetic assimilation of the rare parental species will prevail. Hybridisation of the rare and localized *D. unisora* with the locally common *D. falcata*, and possible growth of a hybrid population, may push *D. unisora* to extinction through genetic assimilation, while the process of natural hybridization may produce genotypes that establish new evolutionary lineages (Arnold & Hodges 1995). Further study is required to determine the actual distribution of hybrids and to monitor the status of the various species. Genetic studies of the populations, hybridisation experiments and an assessment of the fitness of hybrid classes and parental species could add a lot of relevant information.

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Appendix 1. Plant species commonly associated with *Diellia* taxa.

Site		Onini Gulch	Puu Kolekole	Honomalino	Manuka	Hawaii Loa	Kahanahaiki		S-Palawai		Mahanaloa	Makaha	Puu Ka Pele	Pualii
Diellia species		*D. erecta*						*D. f.*	*D.*x *l.*	*D. u.*	*D. pallida*			*D. u.*
1 *Acacia koa*	E									x		x	x	x
2 *Ageratina adenophora*	N	x	x					x	x	x				x
3 *Ageratina riparia*	N						x							x
4 *Aleurites moluccana*	Pol			x							x			
5 *Alphitonia ponderosa*	E		x	x								x		
6 *Alyxia oliviformis*	E						x	x	x	x	x			
7 *Antidesma p.* var. *platyphyllum*	E			x			x				x			
8 *Antidesma pulvinatum*	E			x										
9 *Bidens torta*	E								x	x				
10 *Broussaisia arguta*	E			x										
11 *Canthium odoratum*	I			x	x	x					x			
12 *Carex meniae*	E													x
13 *Carex meyenii*	I				x						x			
14 *Carex oahuensis*	E													x
15 *Carex wahuensis*	E										x			
16 *Cenchrus a.* ssp. *agrimonoides*	E						x							
17 *Chamaesyce multiformis*	E					x	x							
18 *Charpentiera elliptica*	E												x	
19 *Charpentiera tomentosa*	E						x							
20 *Clidemia hirta* var. *hirta*	N						x							
21 *Cocculus tribulus*	I				x									
22 *Coprosma foliosa*	E	x	x											
23 *Cordyline fruticosa*	Pol					x								
24 *Cryptocarya mannii*	E												x	
25 *Cyperus hillebrandii*	E													x
26 *Dianella sandwicensis*	I								x	x				
27 *Diospyros hillebrandii*	E						x				x			x
28 *Diospyros sandwicensis*	E			x	x						x			
29 *Dissochondrus biflorus*	E		x											
30 *Dodonea viscosa*	I	x	x								x	x		
31 *Dubautia linearis* ssp. *opposita*	E	x	x											
32 *Erigeron karvinskianus*	N											x		
33 *Fraxinus uhdei*	N	x	x											
34 *Hedyotis foggiana*	E										x			
35 *Hedyotis knudseni*	E										x			
36 *Hedyotis terminalis*	E						x							
37 *Hibiscus arnottianus*	E						x							
38 *Kalanchoe pinnata*	N										x	x	x	
39 *Lantana camara*	N												x	
40 *Lipochaeta rockii*	E		x											
41 *Luzula hawaiiensis*	E													x
42 *Melicope peduncularis*	E													x

Appendix 1. continued

Site		Onini Gulch	Puu Kolekole	Honomalino	Manuka	Hawaii Loa	Kahanahaiki		S-Palawai		Mahanaloa	Makaha	Puu Ka Pele	Pualii
Diellia species		*D. erecta*						*D. f.*	*D.* x *l.*	*D. u.*	*D. pallida*			*D. u.*
43 *Melinus minutiflora*	N	x	x											
44 *Metrosideros polymorpha*	E	x	x	x	x		x	x	x	x	x	x	x	x
45 *Morinda trimera*	E						x							
46 *Myrsine kauaiensis*	E												x	
47 *Myrsine lanaiensis*	E										x			
48 *Myrsine lessertiana*	E			x										
49 *Neraudia melastomifolia*	E													x
50 *Neraudia sericea*	E		x											
51 *Nestegis sandwicensis*	E	x		x	x		x				x			
52 *Ochrosia compta*	E	x	x											
53 *Oxalis corniculata*	N						x						x	
54 *Panicum nephelophilum*	E							x	x	x				
55 *Passiflora molissima*	N												x	
56 *Passiflora suberosa*	N							x	x	x				x
57 *Pisonia sandwicensis*	E			x	x	x								
58 *Pittosporum flocculosum*	E					x								
59 *Pleomele aurea*	E										x		x	
60 *Pouteria sandwicensis*	E		x				x							x
61 *Psidium cattleianum*	N					x	x	x	x	x				x
62 *Psychotria greenwelliae*	E												x	
63 *Psychotria hawaiiensis*	E				x									
64 *Psychotria mariniana*	E											x		
65 *Pteralyxia kauaiensis*	E										x			
66 *Ricinus communis*	N	x	x											
67 *Rubus argutus*	N											x		
68 *Rubus rosifolius*	N	x												
69 *Schinus terebinthifolius*	N			x		x	x	x	x	x				x
70 *Styphelia tameiameiae*	I	x	x									x		
71 *Tetraplasandra kavaiensis*	E											x		
72 *Wilkesia gymnoxiphium*	E											x		
73 *Xylosma hawaiiense*	E						x							
74 *Zanthoxylum dipetalum*	E											x		

Notes:
I – Indigenous
E – Endemic
Pol – Polynesian introduction
N– Naturalised

Appendix 2. Pteridophyte species commonly associated with the taxa of *Diellia.*

	Site		Onini Gulch	Puu Kolekole	Honomalino	Manuka	Hawaii Loa	Kahanahaiki		S-Palawai		Mahanaloa	Makaha	Puu Ka Pele	Pualii
	Diellia species		*D. erecta*						*D. f.*	*D.* x *l.*	*D. u.*	*D. pallida*			*D. u.*
1	*Adianthum hispidulum*	N			x							x		x	
2	*Asplenium kaulfussi*	E						x		x					
3	*Asplenium macraei*	E						x	x		x				x
4	*Asplenium nidus*	I			x		x								
5	*Blechnum occidentale*	N	x		x	x					x	x	x	x	x
6	*Cyrtomium falcatum*	N			x										
7	*Doodia kunthiana*	E	x	x					x	x	x	x	x	x	x
8	*Doryopteris decipiens*	E		x									x		
9	*Doryopteris decora*	E												x	
10	*Dryopteris fusco-atra*	E										x			
11	*Dryopteris hawaiiensis*	E												x	
12	*Dryopteris unidentata*	E			x			x							
13	*Lepisorus thunbergianus*	I								x					x
14	*Microlepia strigosa*	I	x	x			x	x				x		x	x
15	*Nephrolepis multiflora*	N		x	x	x									
16	*Odontosoria chinensis*	I								x					
17	*Phymatosorus scolopendria*	N					x								
18	*Psilotum nudum*	I			x				x	x				x	
19	*Pteridium decompositum*	E												x	
20	*Pteris cretica*	I												x	
21	*Pteris* x *hillebrandii*	E												x	
22	*Pteris irregularis*	E										x		x	
23	*Thelypteris dentata*	N										x			

Notes:
I – Indigenous
E – Endemic
N – Naturalised

CBM:s Skriftserie 3: 25–38 Uppsala 2001.

Utilisation of remnant dry-forest corridors by the native fauna in a pastural landscape in the Paraguayan Chaco

Veronika Areskoug

Areskoug, V. 2001. Utilisation of remnant dry-forest corridors by the native fauna in a pastural landscape in the Paraguayan Chaco. – CBM:s Skriftserie 3: 25–38.

In the agricultural landscape of the Chaco Central of Paraguay, remnant strips of primary forest separating pastures are used in cattle ranching to control erosion and to prevent the spread of disease and fire. As the cattle industry expands and the rate of land conversion, from natural forest and bushland to cattle pastures increases, the possible impact of habitat loss, fragmentation and decreased connectivity of the landscape raises concerns for the native animal populations.

I have inventoried remnant strips of forest present in the pastural landscape, cattle pastures and surrounding primary forest in an attempt to determine if the remnant vegetation also serves as wildlife corridors and partially alleviates possible impacts of fragmentation. I conducted track sampling, bird census, and drift trapping in three replicates sites, each consisting of core forest, remnant forest strips and pastural landscape components.

In all faunal groups studied (birds, small and large mammals, amphibians and reptiles), it was found that the remnant forest strips are highly utilized. Species composition and abundance ranking were remarkably similar between the three landscape elements, yet the rate of mammal observations in the corridor (remnant forest strip) was twice that of the other landscape elements. Although some degree of connectivity is provided by the pastures themselves for the majority of species in all studied faunal groups, the inclusion of remnant strips of forests in the pastural landscape appears to drastically increase movement of individuals and connectivity across pastures.

Veronika Areskoug, Swedish Biodiversity Centre, P.O. Box 7007, SE-750 07 Uppsala, SWEDEN.
E-mail: veronika.areskoug@cbm.slu.se

Introduction

The Gran Chaco is one of South America's most biodiverse and unique habitats (Taber et al. 1997). It is listed by the World Wildlife Fund as a global top 200 conservation priority habitat. Despite this, the region has received almost no conservation investment or research (Redford et al. 1990). The main vegetation type is dry thorn forest. Historically, the area has been sparsely populated by nomadic hunters and gatherers practicing limited agriculture. The Chaco Central was settled by agricultural Mennonites in 1927. Since then, large portions have been converted to pastural and agricultural fields at a rapidly increasing pace. Agriculture is now responsible for 80% of the gross income in the Paraguayan Chaco. Beef and dairy production constitute 90% of agricultural activities, making the cattle industry the major economic activity of the region (Janzen pers. comm.).

Within the Chaco, there are currently still vast tracts of natural primary forests and abundant wildlife. The current legislation regarding land-use practices specify the obligation of estancia owners to leave at least a 100 m wide strip of natural vegetation to separate fields (ley 422 art. 60) and a total of 25% of the property owned in natural state (ley 422 art. 42), to prevent erosion and the spread of disease and fire. The result is a landscape mosaic of forest fragments and structural corridors within the agricultural landscape. Remnant corridors are defined as strips of natural vegetation that result from the clearing of the surrounding matrix during landscape fragmentation (Forman 1983; Saunders and Hobb 1991). The utilisation of these various landscape components by the native fauna have yet to be studied in the Gran Chaco.

Habitat loss and fragmentation is the main cause of the modern-day extinction crisis (Wilcox and Murray 1985). Evaluating the effectiveness of current land-use practices at meeting the needs of wildlife in one of the world's top conservation prioritised habitats is essential as land conversion accelerates.

Corridors are often cited as the solution to the well-known and common problems of habitat fragmentation, including genetic isolation and local extinction. Globally, millions of dollars are being invested into corridor creation projects, often without any real scientific study into the actual effectiveness or consequences of corridor implementation (Nohlgren and Gustafsson 1995; Simberloff et al 1992). Corridors have been criticized for the lack of empirical evidence of their effectiveness. Nohlgren and Gustafsson (1995) warn that the use of corridors is a biological experiment based on weak scientific evidence and must be evaluated.

It is generally accepted, based on evidence provided by population viability modelling and demographic studies that landscape connectivity enhances a population's viability (Beier and Noss, 1998; Hobbs, 1997). The debate about corridors and landscape connectivity has moved beyond 'Is landscape connectivity needed?' to 'Do corridors effectively increase landscape connectivity?' (Simberloff et al. 1992). Most studies in the literature fail to present evidence that corridors function as conduits between patches (Nohlgren and Gustafsson 1995). To show that a corridor increases connectivity, a study must not only provide a measure of plant or animal movement within corridors but also of the movement through the matrix. Beier and Noss (1998) state that few studies provide a measure of the extra-corridor movement by animals for comparison and therefore do not demonstrate that the presence of a corridor adds connectivity beyond the level which may exist had the corridor not been present. I sampled equally in the core habitat (primary dry thorn forest), matrix (pasture) and corridor (remnant primary dry thorn forest) to allow a comparison of movement and species composition within all three landscape elements.

Corridor studies on species richness and community composition and on ecosystem level are greatly lacking in the literature (Beier and Noss 1998). Beier and Noss (1998) argue that observations of the natural movement of animals in a fragmented habitat better demonstrate the influence of conservation corridors on landscape connectivity than controlled experiments.

This method allows for detection of the real life benefits of corridors in the actual landscape and on the actual community that is targeted.

It has been suggested that corridor studies should be species specific, concentrating on animals that require landscape connectivity such as mammals with large home ranges (Beier and Noss 1998). I argue that the value of approaching a corridor's affects on the entire community in which it is intended to provide connectivity to, is greater than a species per species approach. Conservationists accept that no species is protected without protection of the health and quality of the habitat on which it depends. Therefore, studies on the continued functioning of a system during times of fragmentation are essential. The holistic ecosystem approach will provide broader and more long-term conservation benefits.

The aim of this study was to assess if remnant corridors passing through pastural land areas are utilised by the native fauna and thereby increase the connectivity of the landscape and may therefore be considered as an effective tool to mitigate the effects of forest fragmentation in the Chaco Central. This was accomplished by comparing the utilisation of the corridors and the pastural fields by the species present in the core forest habitat. Track sampling, bird census and drift trap setting were the techniques used to inventory the various landscape elements.

Study site and methods

Study site

The study took place at Gran Siete (located south-west of Filadelfia), dept. Boqueron, Chaco Central, Paraguay (22° 30.851' S, 060° 35.986'W). The area is a complex of 5 cattle ranches, surrounded by unbroken primary forest. The dominant vegetation type is dry thorn forest as described by Short (1975).

Cattle grazing was established in the area during the 1970's. Since then, a total of 172 53.5 ha have been cleared for cattle grazing, mainly in 200 ha blocks. The pastures are divided by remnant strips of primary thorn forest. These strips physically connect blocks of the original, primary forest across the pastures. They have been exposed to grazing. The pastures are seeded with a combination of Gatom panic (*Panicum maximum* var. gatom panic) and Buffalo (*Pennisetum ciliare*) grasses. Grazing density is 1-1.5 cows/ha. Shrubs and weeds are removed approximately every two years, using plowing or rolling. Burning has not been used as a management tool on the studied pastures (interview with estancia owner and employees). Hunting has been banned on the main estancia since its establishment, yet a local indigenous community carries out a subsistence level of hunting (per. observation).

The study took place during the dry season, from the 20th of May 1999 to the 17th of July 1999. The mean minimum and maximum temperature was 14°C and 24°C, respectively, with a range from -1°C to +35°C. A total of 20 mm of rain fell in the area during the period of data collection.

The core forest sites studied represent various locations in one continuous forest. Vegetation characteristics are very similar among the forest replications. Dense patches of bromeliads are the dominant groundcover interspersed with ground cacti and various herbs (80% total ground cover). Algarrobo (*Prosopis spp.)* and Acacia (*Acacia spp.*) create a dense canopy at 3 m height. A top canopy at 10 m height is constituted of sparsely spread Quebracho (*Aspidosperma quebracho-blanco and Schinopsis quebracho-colorado*), Palo Santo (*Bulnesia sarmientoi*), cactus tree (*Cereus stenogonus, C. coryne*), and bottle tree (*Chorisia insignis*) individuals. The corridors are remnant strips of primary thorn forest, left during land clearing for pastures. Exposure to grazing has reduced the density of the shrub and groundcover vegetation within the corridors. Both visibility and ease of movement are increased in the corridors relative to the intact forest. On the pastures, grass height and density varied considerably between replicates (40-120 cm height, 60-90% cover). Shrub cover on the pastures range from

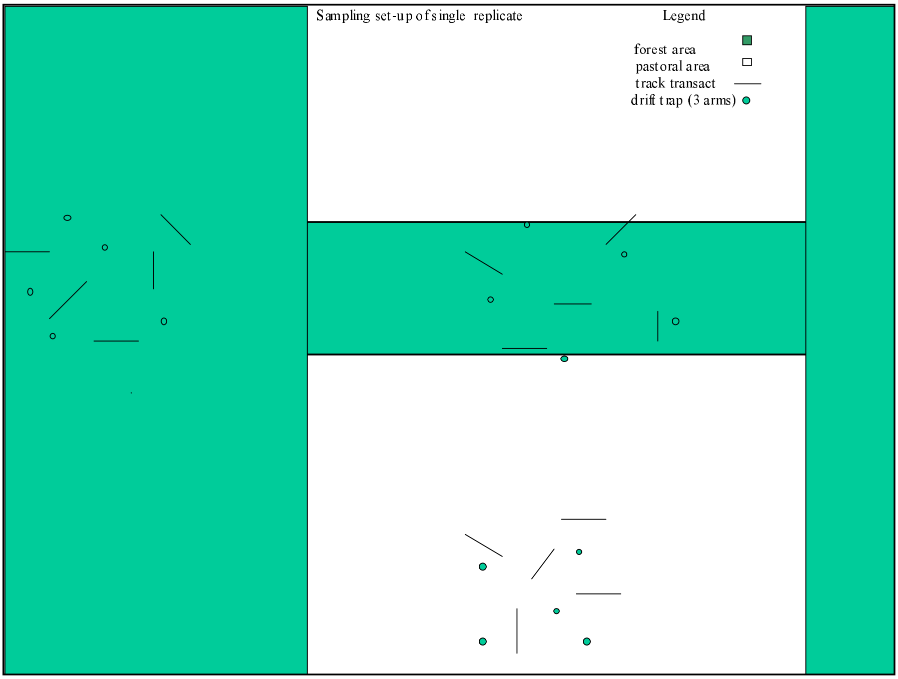

Figure 1. Sampling setup of single replicate

5-20% and a shrub height of 60-180 cm.

Sampling

I selected three replicate sites, consisting of remnant thorn forest corridor, which pass through cattle pasture. Each end of the corridors connects to unbroken primary thorn forest. I inventoried the corridor, core forest and adjacent pasture in each replicate with identical methodology. The corridors have a width of 208, 155, and 100 m, with equal lengths of 2 km. The large mammal fauna was identified using track identification; bird fauna, using visual and auditory census and; small vertebrate fauna, using drift trapping. Data for each faunal group was collected simultaneously in each of the landscape elements, over consecutive days, one replication at a time. Skin contact with vegetation and soil was avoided to reduce scent trails.

I conducted the large fauna census using track identification. Five, 20 x 1 m transects were established using a blocked random approach over a 4 ha area in the central region of each landscape element. Each transect was cleared of all ground vegetation and the soil sieved and swept for optimal track identification conditions. The canopy vegetation if present, was left intact. Each transect was randomly orientated in a South to North, East to West, Northeast to Southwest, or Southeast to Northwest direction. One to two days of data collecting was carried out with no bait present prior to commencement of baiting at each replicate. Each transect was baited and checked for tracks every 24 hours over 10 consecutive days as weather permitted. Each transect was randomly baited in the centre with one of: 10 g of ground maize, 1 canned sardine, half a banana, 100 g piece of pumpkin or 1 tbsp. of peanut butter. Tracks were photographed and preserved as a plaster of Paris mould for confirmation of identification.

In the same four ha areas, using blocked random distribution, I placed five drift trap stations for the small vertebrate census. Each station consisted of four smooth-walled, plastic buckets, 25 cm deep with a 25 cm diameter, buried at ground level, in a three-arm formation.

The buckets were connected by veneer wood, 450 cm in length and 30 cm in height, to guide animals into the buckets. I emptied each trap once every 24-hour period for 12-16 days/replicate. Voucher specimens are deposited at Museo Nacional de Paraguay, Asuncion.

An avian species census was conducted for a 20 min. timed interval at one randomly chosen track transect in each landscape element, on each day, during which all avian species present within visual and auditory range were recorded.

Analysis

I compared the species richness between the three landscape elements for each of the faunal group: large mammals, small mammals, reptiles and amphibians and avian species. The Friedman Two-way analysis of Variance by Ranks test was used to examine differences in species numbers and number of observations between the landscape elements. Sørensen Similarity Values were calculated using species presence data and species frequency of mammal track observation data, as described in (Magurran 1988) $C_s = 2j/a + b$ where j = the number of species found in both landscape components and a = the number of species found in landscape component a; and b = the number of species found in landscape component b. The total number of observations between the landscape elements were compared at a species level and at a guild level, using the Friedman Two-way analysis of Variance by Ranks test.

Two sightings of a canid were determined to be Maned wolf (*Chrysocyon brachyurus*) in highest probability and were analysed as such.

A single observation was considered to have occurred each time a species was identified on a transect. As a result several individuals of the same species which stepped on the same transect on the same day were recorded as only one observation, while a single individual who stepped on more than one transect in a day's period was recorded as an observation for each imprinted transect. Despite this lack of real abundance data, frequency of species observation was still used as a measure of relative abundance for between landscape element comparisons, as I judged it most probable that individual species behaviour in this regard remained constant from landscape element to landscape element.

Results

Species richness between landscape elements

The species richness was surprisingly uniform between the three landscape elements for all faunal groups studied with the exception of the avian community (Appendix 1 to 3). The communities of birds and large mammals contribute the most to faunal species richness in all of the studied landscape elements.

Large mammals

A total of 24 mammal species were identified from the track transects during the study period. No significant difference was detected in the number of mammal species identified between the three landscape elements (The Friedman Two-way Analysis of Variance by Ranks) (Fig. 2). No mammal species was found in the forest, which was not found in either the corridor or the pasture. The armadillo *Chaetophractus sp.* and the rodent *Ctenomys sp.* were observed exclusively in the pasture.

Small mammals

A total of three species of opossum mice and four species of rodents were captured in the drift traps. All of the opossum mice species occurred

Figure 2. Total number of large mammal species identified on baited track sampling transects (1 x 20 m) in various landscape components. Pooled data from 3 replicates containing 5 transects over 10 days in each landscape component.

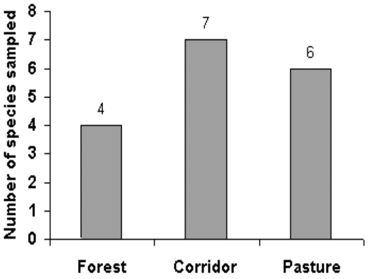

Figure 3. Total number of small mammal species captured in drift traps in various landscape components of the pastoral landscape of the Chaco Central of Paraguay.

in each of the studied landscape elements. All of the rodents species were represented in the corridor, while the pasture lacked representation of one species and only a single species was captured in the forest (Fig. 3). Species determination is still in progress at Museo Nacional de Paraguay. Morpho-species groups were used for the analysis.

Reptiles and Amphibians

A total of sixteen species of amphibians and five species of reptiles were captured in the drift traps. The corridor and pasture contained an equal number of twelve species captured, while only five of the species were captured in the forest (Fig. 4). Species determination is still in progress at Museum Nacional de Paraguay for some species (Appendix 3). Morpho-species groups were used for the analysis.

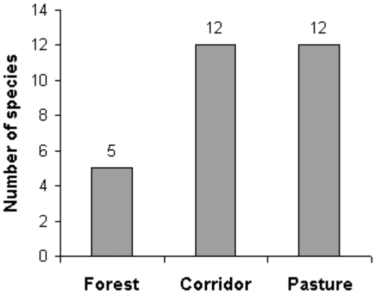

Figure 4. Total number of amphibian and reptile species captured in drift traps in various landscape components of the pastoral landscape of the Chaco Central of Paraguay.

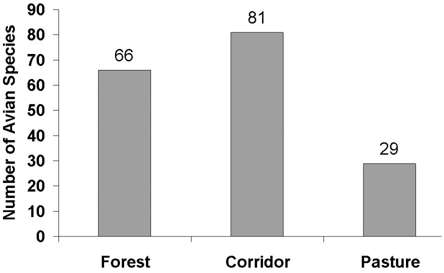

Figure 5. Number of avian species censused in various landscape elements

Avian Species

A total of 100 bird species were recorded during the timed avian species census. 80 of the species occurred in the corridor, 67 species in the forest and 29 species in the pasture (Fig. 5). The number of species in the pasture was significantly lower than the forest or corridor (The Friedman Two-way Analysis of Variance by Ranks, X_r^2 = 6, p = 0.028).

Frequency of observations

A total of 687 observations of track prints were identified. No significant difference was found between the total number of track observations per replicate between the three landscape elements (Table 1. Friedman Two-way Analysis of Variance by Ranks, X_r^2 = 4.67, p = 0.194). 46.6% of all track observations occurred in the corridor. Of all track observations encountered outside the

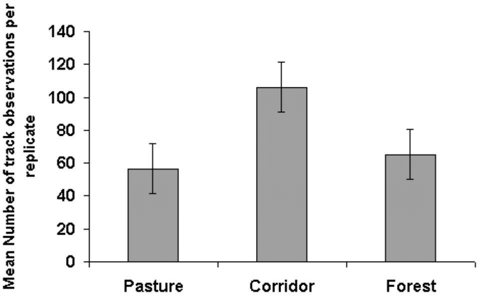

Figure 6. Mean total number of track observations of mammals per replicate (SD) in various landscape elements. One observation = one or more footprints of a species/transect/day.

Table 1. Friedman two-way analysis of variance for the number of track observations between landscape elements for large mammal guilds.

Guild	Significance		p =
Armadillos *Chaetophractus sp.* *Dasypus novemcinctus, Euphractus sexcinctus, Tolypeutes matacus*	Significant preference of pastures	6	0.028
Top Predators *Chrysocyon brachyurus, Oncifelis geoffroyi, Leopardus pardalis, Herpailurus yaguarondi, Panthera onca, Puma concolor*	Nonsignificant	4.67	0.194
Smaller Predators *Cerdocyon thous,* *Pseudalopex gymnocerus,Conepatus chinga, Galictis cuja,Galictis vittata, Procyon cancrivorus*	Nonsignificant	2.67	0.361
Herbivores *Catagonus wagneri,Ctenomys dorsalis* *Dolichotis salinicola, Mazama gouazoubira, Mazama rufina, Sylvilagus brasiliensis,Tapirus terrestris*	Significant preference of corridors	6	0.028

core forest habitat, 65.6% occurred inside the corridor, i.e. corridor passage occurred with nearly twice the frequency as did extra-corridor passage (Fig. 6). Both the species richness and the rates of capture of small mammals and reptiles and amphibians were higher in the corridor and pasture than in the forest (Table 2).

The number of track observations of the guilds armadillos, top predators, small predators and herbivores were also tested for significance between the landscape elements (Friedman two-way analysis of variance by ranks test). Armadillo tracks were significantly more often observed in pasture. Herbivore tracks were significantly more often observed in corridor. There was no significant difference in the number of observations of top nor smaller predator tracks between the landscape elements.

Table 2. The rates of capture of faunal groups between various landscape elements in drift traps (Captures/board/night).

Faunal group	Forest	Corridor	Pasture
Opossum mice	0.018	0.015	0.054
Rodents	0.002	0.021	0.034
Reptiles	0.002	0.008	0.021
Amphibians	0.015	0.1236	0.055

Community structure

I calculated Sørensen Similarity Values for each faunal group between the three landscape elements. The landscape elements are quite similar based on species presence (Table 3). The Sørenson Values describe even greater similarity when, the frequency of observation values are added as a measure of abundance (Table 4).

The total number of track observations per species when expressed as an abundance ranking does not differ markedly between landscape element versus total number of track observations per species for the complete landscape (fig. 7). Exceptions to this are *Dolichotis salinicola*, which was exclusive to the corridor with the exception of one track observation in the forest (fifth most

Table 3. Sørensen Similarity Values for species richness of faunal taxon groups between landscape elements, (value closer to 1 denotes greater similarity).

	Large mammal	Small mammal	Reptiles & Amphibians	Avian
Forest-corridor	0.581	0.615	0.580	0.767
Corridor-pasture	0.545	0.920	0.583	0.407
Pasture-forest	0.750	0.800	0.580	0.333

commonly observed track in the landscape, yet second most commonly observed track in the corridor) and *Sylvilagus brasiliensis* (fourth most commonly observed track, yet never encountered in the pasture).

Discussion

Community structure

The species composition and species richness for mammals are very similar between the three studied landscape elements. Natural grasslands occur in the dry thorn forest of the Chaco and the fauna appears to be quite savannah adapted behaviorly. Historically, the natural grassland has been the most desirable for conversion to agricultural land. As a result, large portions of the natural grasslands have disappeared in congruence with the appearance of grazing pastures. My results indicate that the native fauna has been able to adapt to this land conversion. It is highly probable that the populations are continuous across the various studied landscape elements.

An exception to this is the mara (*Dolichotis salinicola*), which seems to reside nearly exclusively at forest edges and open patches within forest. Furthermore, although common in both the forest and corridor, the forest rabbit (*Sylvilagus brasiliensis*) was also never encountered in the pasture habitat. These two important prey species likely have a greater dependency on the presence of corridors for movement than other species.

Table 4. Sørensen Quantitative Similarity Values for species diversity of large mammals between landscape elements based on frequency of observation values (value closer to 1 denotes greater similarity).

	Forest	Corridor
Forest	-	-
Corridor	0.6988	-
Pasture	0.8361	0.6270

My abundance ranking analysis as well as the Sørensen Similarity Values indicated that the community structure is extremely similar both in species composition and in relative species abundance. The greater frequency of track observations in the corridor as compared to the core forest and the pasture matrix is of interest. It is apparent that the corridor holds a special function in the landscape, as activity was more concentrated within the corridor.

My results on amphibian presence differed drastically from those of Stevens and Husband (1998) in Brazilian Atlantic forest fragments. They had zero captures in the matrix agricultural land and a very impoverished species diversity in edge areas, where as experienced highest rates of capture in the matrix and edge areas. Drift trap rates of capture were extremely low (0.12 captures/ board/night), as may be expected during the dry winter season. 83% of amphibian captures coincided with precipitation. As little as 1 mm of rain was sufficient to initiate amphibian movement. A possible explanation to the differing rates of capture between the landscape elements may be the difference in precipitation reaching ground level as the denser canopy vegetation of the forest may prevent the saturation of the soil.

Landscape Connectivity

The high level of species richness in the corridor indicates that it is indeed highly used by mammals and birds. Although this study did not

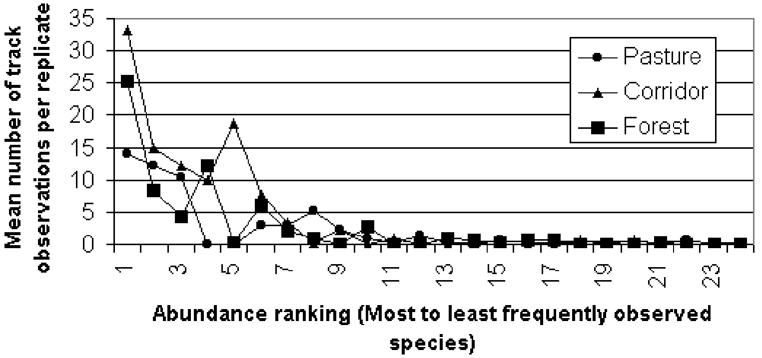

Figure 7. Mean number of track observations per species in various landscape elements vs. abundance ranking for mammalian fauna. Pooled data from 3 replicates containing 5 transects over 10 days in each landscape component. One observation = one or more footprints of a species/transect/day.

focus on the function of the corridor for each species, the patchiness in time of observations of several species (especially *Galictis cuja*, *Eira barbara, Puma concolor, Panthera onca, Myrmecophaga tridactyla,Tamandua tetradactyla*) suggests that the corridor is used on occasion to expand their territorial range. On several occasions *Herpailurus yaguarondi* tracks were observed leaving the pasture and entering the corridor or forest while dragging prey.

The repeated observation of species such as armadillos, mara, rabbit, and foxes day after day, suggests that they are residing within the corridor. The occurrence of such a resident population within a corridor suggests that the corridor will facilitate movement between habitat patches (Beier and Noss 1998). With this assumption, the repeated presence of a species in a corridor or in the matrix indicates that the population of that species is continuous from forest segment to forest segment.

Haas (1995) showed that although her studied avian species were capable of dispersing over matrix to unconnected patches, they showed a strong preference to disperse over connected habitat. My study made no observations of forest bird's movement over the matrix, where as nearly all species of forest birds were observed in the corridors.

Beier and Noss (1998) state that few studies provide a measure of the extra-corridor movement by animals for comparison and therefore do not demonstrate that the presence of a corridor adds connectivity beyond the level which, may exist had the corridor not been present. I found that nearly all species found in the core forest are also using the pasture, with the exception of avian species. The landscape connectivity in this landscape is high even across the matrix as the rates of encouter for most mammals and small vertebrates were not lower in the matrix pasture than in the core forest. Yet, it is clear by the high rate of animal encouters that the presence of the corridor are increasing movement in the landscape greatly. Beier (1993) simulated population dynamics of cougar (*Puma concolor*) in California over 100 years and found that even minimal immigration (1-4 ind.) increased the probability of population survival in fragmented areas markedly. Such a minimal level of immigration is likely facilitated by the matrix pastures in my study area.

Movement is important not only for genetic, demographic and population reasons but also for allowing access to the full range of resources needed by an individual through-out its life history (Merriam, 1991). For this reason, corridors may be of greater importance in the Chaco Central in the winter season when drought may pose greater need for passage to fresh water sources.

It is possible that the presence of the corridors are extending the ability of animals to enter the pasture matrix by providing a sense of safety and nearness to shelter and in so doing are expanding the real available habitat for some species. Yet it is too be remembered that as Rosenberg et al (1997) state, corridors do not fully compensate for habitat loss.

Conservation Implications

The study was performed on a property with a low level of human activity. The effectiveness of a corridor may vary with the level of human activity and disturbance in the area (Reijnen et al. 1997). Even the level of animal activity across the matrix may decrease with increased disturbance. In this situation it can be speculated that the importance of the corridor increases as disturbance to the area increases. A wider corridor breadth may be necessary in more disturbed areas.

Animal populations are at a greater risk to hunting by people in the corridor. This is of special concern as my frequency of observation data indicate the native fauna seem to be attracted to the corridors. Preliminary work on nest predation (Eriksson, manuscript), reveals high rates of predation in the corridor. The community dynamics and demographic consequences of the presence of the corridor in the landscape need serious attention from conservationists, wildlife managers and researchers. The high level of animal activity occurring in the corridor suggests it may be a sink in the meta-populations.

Future research should be performed to measure actual rates of migration and to determine how high the level of connectivity is and most importantly on the demographic and species interaction effects of the presence of the corridor. Further research comparing natural grasslands and pastures, and on the landscape processes such as succession and disturbance are needed to gain a better understanding of the changes occurring in the Chaco and their implications on animal populations.

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Appendix 1. Mammal Species Observed on track transects in various landscape elements in Central Paraguayan Chaco [+ denotes species identified on the track transect in that habitat during the course of the study, (+) denotes species found present in that habitat outside of the studied transects, - denotes species not found by the author in that habitat during the time of the study]

Scientific name	Common Name English	Common Name Paraguay	Forest	Corridor	Pasture
Chaetophractus sp.	Hairy armadillo	Peludo armadillo	–	–	+
Dasypus novemcinctus	9-banded armadillo	Tatu' hu'	+	–	+
Tolypeutes matacus	3-banded armadillo	Tatu' bolita	+	+	+
Euphractus sexcinctus	6-banded armadillo	Gualacate, tatu' poju'	+	+	+
Myrmecophaga tridactyla	Giant anteater	Oso hormiguero, jurumi'	+	+	–
Tamandua tetradactyla	Collared Anteater, Lessor Anteater	Kaguare'	–	+	+
Chrysocyon brachyurus	Maned Wolf	Aguara Guazu', zorro de crin	–	+	+
Cerdocyon thous,	Crab-eating fox	zorro de monte, aguara-I'	+	+	+
Pseudalopex gymnocercus	Azara's fox	zorro de pampa, aguara-I'	+	+	+
Herpailurus yaguarondi	Jaguarundi	Jaguarundi', Gato Eyra	(+)	+	+
Leopardus pardalis	Ocelot	Gato onza	+	–	+
Oncifelis geoffroyi	Geoffroy's cat	Gato montes	+	+	+
Puma concolor	Puma	Leon americano	+	(+)	+
Panthera onca	Jaguar	Tigre, jaguarete'	(+)	+	–
Conepatus chinga,	Skunk	zorrino comon, jaguane'	+	+	+
Eira barbara	Tayra	Eira'	–	+	–
Galictis cuja	Lessor grison	Eira'	+	(+)	+
Procyon cancrivorus	Crab-eating Raccoon	Osito lavador, mapache, aguara' pope'	–	+	–
Tapirus terrestris	Brazilian tapir	Tapir, mborevi'	(+)	+	–
Catagonus wagneri	Giant peccary, Chacoan peccary	Tagua'	+	–	+
Tayassu tajacu	Collared peccary	Kurei'	(+)		
Tayassu pecari	White-lipped peccary	Tanikati'	(+)	(+)	(+)
Mazama gouazoupira	Grey Brocket deer	Guasuvira'	+	(+)	+
Mazama rufina	Red brocket Deer	Guasu'-pyta'	(+)		
Dolichotis salinicola	Mara	Tapiti' boli'	+	+	–
Ctenomy dorsalis	Tuco Tuco	Tuco tuco	–	–	+
Sylvilagus brasiliensis	Forest Rabbit	Tapiti	+	+	–

Appendix 2. List of avian species present in various landscape elements of Gran Siete, Chaco Central, Paraguay [+ denotes species identified on the track transect in that habitat during the course of the study, (+) denotes species found present in that habitat outside of the studied transects, - denotes species not found by the author in that habitat during the time of the study]

Scientific name	English name	Forest	Corridor	Pasture
Rhea americana	Greater Rhea	–	+	+
Nothoprocta cinerascens	Brushland Tinamo	–	+	–
Crypturellus tataupa	Tataupa Tinamou	–	+	–
Eudromia formosa	Quebracho crested tinamo	–	+	–
Syrigma sibilatrix	Whistling Heron	–	+	–
Theristicus caudatus	Buff-necked Ibis	–	+	–
Coragyps atratus	Black Vulture	+	+	+
Cathartes aura	Turkey Vulture	+	+	+
Elanus leucurus	White-tailed kite	–	–	+
Accipiter erythronemius	Rufous-thighed Hawk	–	+	–
Heterospizias meridionalis	Savannah Hawk	–	(+)	(+)
Geranoaetus melanoleucus	Black-chested Buzzard-eagle	–	–	(+)
Harpyhaliaetus solitarius	Crowned Eagle	–	–	(+)
Buteo magnirostris	Road-side Hawk	+	+	+
Buteo albicaudatus	White-tailed Hawk	–	–	+
Polyborus plancus	Crested Caracara	(+)	+	+
Herpetotheres cachinnans	Laughing Falcon	–	+	–
Micrastur ruficollis	Barred Forest falcon	+	+	–
Falco sparverius	American Kestrel	–	–	+
Falco femoralis	Aplomado Falcon	–	+	+
Ortalis canicollis	Chaco Chachalaca	+	+	–
Cariama cristata	Red-legged Seriema	+	(+)	(+)
Chunga burmeisteri	Black-legged Seriema	+	+	–
Columbina picui	Picui Ground-Dove	+	+	+
Columba picazuro	Picazuro Pigeon	+	+	+
Zenaida auriculata	Eared Dove	+	+	+
Leptotila verreauxi	White-tipped Dove	–	+	–
Nandayus nenday	Black-hooded Parakeet	+	+	+
Aratinga acuticaudata	Blue-crowned Parakeet	+	+	+
Amazona aestiva	Turquoise-fronted Parrot	+	+	+
Myiopsitta monachus	Monk Parakeet	+	+	+
Guira guira	Guira Cuckoo	–	+	+
Tapera naevia	Striped Cuckoo	–	–	(+)
Tyto alba	Barn Owl	–	(+)	–
Strix rufipes	Rufous-legged Owl	–	(+)	–
Glaucidium brasilianum	Ferruginous Pygmy-Owl	+	–	–
Caprimulgus parvulus	Little Nightjar	+	–	–
Hydropsalis brasiliana	Scissor-tailed Nightjar	+	–	–
Chlorostilbon aureoventris	Glittering-bellied Emerald	+	+	–
Nystalus maculatus	Spot-backed Puffbird	+	+	–
Picumnus cirratus	White-barred Piculet	+	+	–
Melanerpes candidus	White Woodpecker	–	+	–
Melanerpes cactorum	White-fronted Woodpecker	+	+	–
Picoides (Dendrocopos) mixtus	Checkered Woodpecker	+	+	–

Appendix 2. continued

Scientific name	English name	Forest	Corridor	Pasture
Piculus chrysochlorus	Golden-green Woodpecker	+	+	–
Dryocopus schulzi	Black-bodied Woodpecker	+	–	–
Campehpilus (Phloeoceastes) leucopogon	Cream-backed Woodpecker	+	–	–
Campylorhamphus trochilirostris	Red-billed Scythebill	+	–	–
Sittasomus griseicapillus	Olivaceous Woodcreeper	+	+	–
Drymornis bridgesii	Scimitar-billed Woodcreeper	+	+	–
Xiphocolaptes major	Great Rufous Woodcreeper	+	+	–
Lepidocolaptes angustirostris	Narrow-billed Woodcreeper	+	+	–
dummy	Site-billed woodcreeper	+	+	–
Upucerthia certhiodes	Chaco Earthcreeper	+	–	–
Furnarius cristatus	Crested Hornero	+	+	–
Furnarius rufus	Rufous Hornero	+	+	–
Furnarius cristatus	Crested Hornero	+	+	–
Cranioleuca pyrrhophia	Stripe-crowned Spinetail	+	+	–
Synallaxis albescens	Pale-breasted spinetail	+	–	–
Schoeniophylax phryganophila	Chotoy Spinetail	–	+	+
Pseudoseisura lophotes	Brown Cacholote	+	–	–
Phacellodomus sibilatrix	Little Thornbird	+	+	–
Phacellodomus ruber	Greater thornbird	–	+	–
Coryphistera alaudina	Lark-like Brush-runner	+	+	+
Taraba major	Great Antshrike	+	+	–
Thamnophilus doliatus	Barred Antshrike	–	+	–
Thamnophilus caerulescens	Variable Antshrike	+	+	–
Thamnophilus punctatus	Slaty Antshrike	+	+	–
Mymorchilus strigilatus	Stripe-backed Antbird	+	+	–
Rhinocrypta lanceolata	Crested Gallito	+	+	–
Melanopareia maximiliani	Olive-crowned crescent-chest	–	–	+
Suiriri suiriri	Suiriri Flycatcher	+	+	–
Elaenia sp.	Elaenia sp.	+	+	–
Camptostoma obsoletum	Southern Beardless Tyrannulet	+	+	–
Sublegatus modestus	Scrub Flycatcher	+	–	–
Griseotyrannus aurantioatrocristatus	Crowned-slaty flycatcher	–	+	–
Stigmatura budytoides	Greater Wagtail-Tyrant	+	+	–
Hemitricus margaritaceiventer	Pearly-vented Tody-Tyrant	+	+	–
Pyrocephalus rubinus	Vermilion Flycatcher	–	–	(+)
Myiophobus fasciatus	Bran-coloured flycatcher	+	+	–
Xolmis irupero	White Monjita	–	–	(+)
Kniplegus striaticeps	Cinereous Tyrant	+	+	–
Myiarchus tyrannulus	Brown-crested Flycatcher	+	+	–
Pitangus sulphuratus	Great Kiskadee	–	+	–
Machetornis rixosus	Cattle Tyrant	–	–	(+)
Casiornis rufa	Rufous Casiornis	+	–	–
Cyanocorax chrysops	Plush-crested Jay	+	+	–
Polioptila dumicola	Masked Gnatcatcher	+	+	–
Troglodytes aedon	House Wren	+	+	+
Mimus triurus	White-banded Mockingbird	+	+	+
Cychlariss gujanensis	Rufous-browed Peppershrike	+	+	–

Appendix 2. continued

Scientific name	English name	Forest	Corridor	Pasture
Parula pitiayumi	Tropical Parula	+	+	–
Piranga flava	Hepatic Tanager	+	+	–
Paroaria coronata	Red-crested Cardinal	–	+	–
Coryphospingus cucullatus	Red-crested Finch	+	+	+
Saltator aurantiirostris	Golden-billed Saltator	+	+	–
Saltatricula multicolor	Many-coloured Chaco-Finch	–	+	+
Sicalis luteola	Grassland Yellow-Finch	–	+	(+)
Poospiza torquata	Ringed warbling finch	–	+	–
Poospiza cinerea	Black-capped Warbling-Finch	+	+	+
Lophospingus pusillus	Black-crested Finch	–	(+)	–
Myiospiza humeralis	Grassland sparrow	–	+	+
Zonotrichia capensis	Rufous-collared sparrow	+	+	+
Molothrus bonariensis	Shiny Cowbird	–	+	–
Molothrus badius	Bay-winged Cowbird	–	+	(+)
Cacicus solitarius	Solitary Black Cacique	+	+	–
Syurnellas superciliaris	White-browed Blackbird	–	–	+

Appendix 3. Amphibian and reptile species observed in various landscape elements in Gran Siete, Chaco Central, Paraguay. [+ denotes species identified on the track transect in that habitat during the course of the study, (+) denotes species found present in that habitat outside of the studied transects, - denotes species not found by the author in that habitat during the time of the study]

Scientific Name	English Name	Paraguayan Name	Forest	Corridor	Pasture
Leptodactylus bufonius	Shovel-nosed chamber frog	Rana hocico de pala	–	+	–
Leptodactylus chaquensis	Chaco frog	Rana chaqueña	–	–	+
Physalaemus biligonigerus	False-eyed frog	Jui vaca ra'y	+	+	+
Bufo granulosus	Granulated toad	Kururu, sapo	+	+	+
Bufo paracnemis	Rococo toad	Kururu, sapo	–	+	–
Phyllomedusa sauvagei	Chaco leaf frog		+	+	+
Physalaemus albonotatus	Frog		+	+	+
Dermatonotus muelleri	Mueller's narrow-mouthed frog		–	+	+
Elachistocleis ovalis	Orange thigh		–	+	–
Elachistocleis sp.	Blue		–	–	+
Homonota horrida	Chacoan straight-toed gecko		+	+	+
Tropidurus sp.	Spine lizard		–	+	–
Proctotretus doellojuradoi			–	+	–
Mabuya frenata	Bridled skink	Ambere'	–	+	+
Mabuya sp. guaporicola?	Brindled skink		–	–	+
Leptotyphlops melanotermus	Blind snake		–	–	+
Leptotyphlops sp.	Blind snake		–	–	+

CBM:s skriftserie 3: 39–52. Uppsala 2001.

Nest-predation at the edge: an experimental study contrasting two types of edges in the dry Chaco, Paraguay

Lena M. Eriksson

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Forest fragmentation leads to the creation of isolated forest patches with subsequent impact on forest-interior flora and fauna. Forested corridors have been suggested to alleviate some of the impact by increasing the connectivity between remnant forest patches. However, both fragmentation and corridors increase the ratio of edge to core habitat. We studied nest predation of artificial nests at edges between 1) contiguous forests and pastures and 2) forested corridors and pastures, in a forest-dominated landscape in the dry Chaco, Paraguay. The aim was to determine if nest predation was higher near habitat edges compared to within forests and pastures, with special emphasis on edges at forested corridors. We found that predation rates were similar at edges and in interior habitats. Nest predation was higher for both ground and shrub nests in forested areas than in pastures. Predation rates were also higher for both ground and shrub nests at edges along forested corridors compared to edges neighbouring contiguous forests. Forested corridors connecting contiguous forests may thus act as an ecological sink for some species breeding here. Analysis of predator categories revealed that ground nests in pastures were relatively more depredated by mammals and less by birds, compared to both shrub nests in pastures and ground nests in forests.

Lena M. Eriksson, Swedish Institute for Ecological Sustainability, P. O. Box 7980, SE-907 19 Umeå, SWEDEN. E-mail: Lena.Eriksson@ieh.se

Introduction

As fregmentation of natural habitats continues at an accelerating rate, there is a growing concern for its documented and presumed negative impact on native flora and fauna (Estrada et al. 1993, Robinson et al. 1995, Keyser et al. 1998, Harrison and Bruna 1999). The increased ratio of edge to core area that follows fragmentation may benefit generalist predators at the expense of their prey species and species with narrower niches (Wilcove 1985, Noss and Csuti 1997). Furthermore, the increased isolation of populations might increase risks of extinction (Noss and Csuti 1997). Corridors with natural vegetation have been suggested to alleviate the negative impact of fragmentation to some extent by increasing the connectivity in the landscape and providing shelter, habitat and dispersal routes between patches of natural habitat (Simberloff and Cox 1987, Noss 1987, Saunders and Hobbs 1991). However, corridors may also have negative effects by increasing the ratio of edge to core habitat and by facilitating the spread of invasive alien species, fire and diseases (Noss 1987). Corridors may in addition turn out to be ecological sink habitats for some species, if these suffer higher mortality rates in the corridors than they would in their native habitats (Simberloff and Cox 1987, Saunders and Hobbs 1991). Nicholls and Margules (1991) argue that explicit evidence for the conservation value of corridors is still scarce and in need of scientific verification, if limited economic resources should be diverted from securing the protection and management of large areas of natural habitats.

Nest predation is suggested to be a major cause for the reproductive failure of passerine birds, especially in landscapes fragmented by humans (Wilcove 1985, Robinson et al. 1995). However, natural nests are sometimes difficult to locate and their fates troublesome to determine. They are also not always placed in accordance with required experimental designs. Predation on artificial bird nests has therefore been used as a convenient tool to evaluate the effects of fragmentation and habitat edges (Wilcove 1985, Andrén 1992, see Paton 1994). Even though predation on artificial nests may not mimic natural predation rates (Storaas 1988, Willebrand and Marcström 1988, King et al 1999), the method is suggested to be suitable when comparisons of relative predation rates are made between local habitats (Reitsma 1992, Roper 1992, but see Martin 1987). We are therefore chosen this approach although we are aware of the ambiguities involved when using artificial nests. The dry Chaco is not well studied ecologically and the use of artificial nests presents a first indication of ecological interactions in the area, that could be followed up with additional studies. Many studies of nest predation in forests adjacent to forest-farmland edges suggest that bird nest predation increases near edges (see Paton 1994, Andrén 1995), but the opposite result has also been found (Nour et al. 1993, Marini et al. 1995, Bayne and Hobson 1997).

We performed a nest-predation study in a forest-dominated landscape in the dry Chaco, Paraguay, that has been exposed to clear-cuttings during the last 20 - 25 years following the establishment of cattle-ranches. The legislation of Paraguay states that buffer zones of natural vegetation (henceforth forested corridors), at least 100 m wide, must be left between pastures in order to prevent soil erosion and spread of pests and fire (Anon. 1986). Corridor use as habitat and dispersal routes for the native fauna has just recently begun to be studied (Areskoug, unpubl.). By carrying out the study in a forest-dominated landscape, the effects of edges and corridors may not be confounded by differences in forest patch-size and in differential isolation of these.

We used artificial nests to experimentally evaluate the relative level of nest predation at forest-pasture edges and forested corridors in this landscape. We addressed three connected aspects: 1) Does the level of predation differ between forest and pasture, the two major habitats at this study-site? 2) Does the level of predation differ between edges at forested corridors and edges neighbouring contiguous forest? 3) Does an edge effect exist, i.e. increased pre-

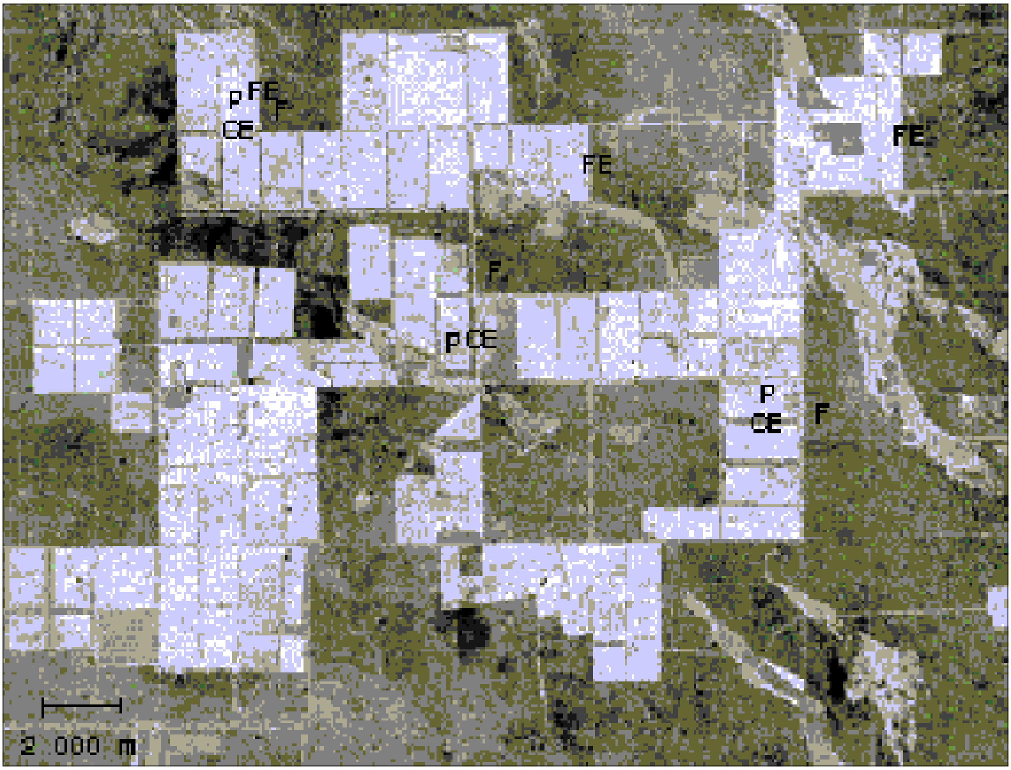

Fig. 1. Satellite image of the study area. FE = Forest edges, CE = Corridor edges, F = Interior forests, P = Interior pastures.

dation near edges, and if so, how far from the edge does it extend? In addition we aimed at identifying categories of predators in forests and pastures by marks left in clay-eggs.

Nomenclature for birds follow Hayes (1995), for mammals Wilson and Reeder (1993) and for trees Lopez et al. (1987).

Methods

Study Site

The study was carried out at Gran Siete in the dry Chaco, Paraguay (S 22(31', W 060(36'). Gran Siete encompasses five cattle-ranches that cover a total of 35 000 ha of which 17 000 ha have been cleared for pastures since the 1970's (Fig. 1). Mean annual temperature is around 24(C, reaching above 40(C during the austral summer months (November to Januari), and occasionally dropping below freezing during winter nights (Hayes 1995). Precipitation is low, reaching around 800 mm per year, and is highly seasonal and concentrated to the summer months (Hayes 1995). No precipitation was recorded during this study (July and August 1999), but drinking water for animals is available at human-made water holes.

The dominant natural vegetation in the area is dry thorn scrub forest with a 3-4 m high canopy. Dominating species are *Ruprechtia triflora*, *Acacia* spp. and *Prosopis* spp., together with some *Cereus stenogonus* and *Cereus coryne*. The canopy is interspersed with 10-12 m high trees of predominantly *Aspidosperma quebracho-blanco*, *Schinopsis quebracho-colorado*, *Bulnesia sarmientoi*, *Chorisia insignis*, and in lower areas also *Calycophyllum multiflorum*. Bromeliaceae and Cactaceae are major components of the ground vegetation. Vegetation composition in natural habitats has been described in detail by Short (1975). Almost all of the natural grasslands have been turned into pastu-

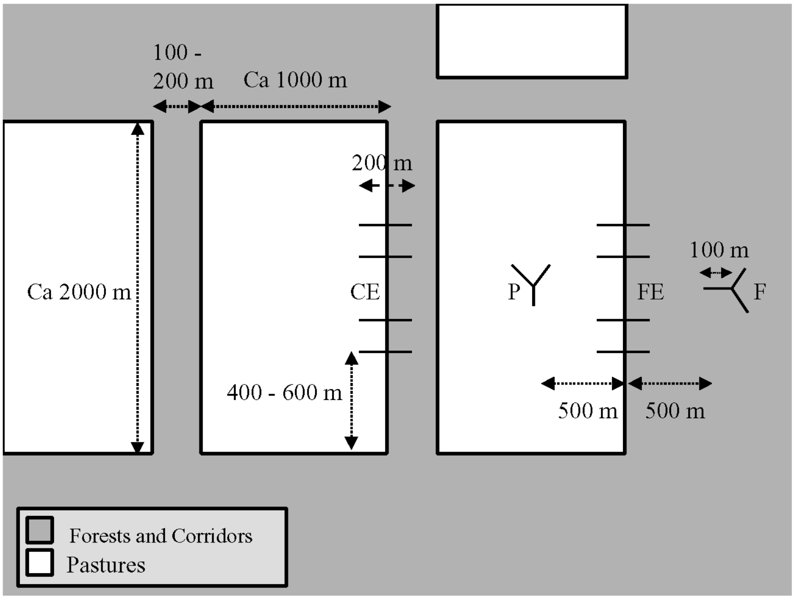

Fig. 2. A schematic view showing an approximate set-up for a forest edge (FE), a corridor edge (CE), an interior forest (F) and an interior pasture (P).

res or cultivated fields and planted with introduced, more palatable, grasses or crops.

The pastures at Gran Siete are normally around 200 ha (1000 x 2000 m) with forested corridors 70 - 200 m wide in between, connecting areas of contiguous forests (Fig. 1). The pastures are planted with Buffalo grass Pennisetum ciliare and Gatom panic Panicum maximum var. gatom panic, and varies much in grass height, shrub height and in percentage cover of grass, shrub and bare ground, depending on their management history. Acacia spp. and Ruprechtia triflora dominate among shrubs.

The edges between forests and pastures are straight and sharp, at most creating a limited visual edge-zone with denser vegetation, although effects of abiotic factors such as wind, light and temperature are likely to extend some distance into the forests. Wire-fencing separates different pastures and are located in the middle of corridors and 35 - 50 m into the forest at edges between contiguous forests and pastures. Grazing has therefore had an impact on ground vegetation to a varied extent at edges. The fences are not a hinder for the passage of the native fauna.

Some open cup nesters in this region are cinereous tyrant *Knipolegus striaticeps*, red-crested finch *Coryphospingus cucullatus*, greater wagtail-tyrant *Stigmatura budytoides*, many-coloured chaco-finch *Saltatricula multicolor* and grassland sparrow *Ammodramus humeralis*; see de la Peña (1988, 1989). Of 65 species of the Order Passeriformes mist netted or seen at Gran Siete during the course of this study, 16 species are open cup nesters; 26 are closed cup; 8 are cavity nesters; 5 use hanging cups; 2 utilise mud or dirt; there is 1 platform and 1 ground depression nester, and there is 1 brood parasite. Five species have nest types which are unknown/not described (de la Peña 1988, 1989, Isler and Isler 1999, Sick 1993). Potential mammal nest predators in the area are Azara's fox *Pseudalopex gymnocercus*, crab-eating fox *Cerdocyon thous*, Geoffroy's cat *Oncifelis geoffroyi*, tayra *Eira barbara*, lesser grison *Galictis cuja*, white-eared opossum *Didelphis albiventris* and several rodents. Potential nest predators among birds are great antshrike *Taraba major*, rufous-browed peppershrike *Cyclarhis gujanensis*, plush-crested jay *Cyanocorax chrysops*, golden-billed saltator *Saltator aurantiirostris*, white-banded mockingbird *Mimus triurus*, red-legged seriema *Cariama cristata* and crested caracara *Polyborus plancus*. The dry Chaco also has a prolific reptile fauna where some species could be potential nest predators.

Nest Predation

The study was carried out in August 1999, just before the onset of the main breeding season for birds. We selected edges between contiguous forest and pasture (FE) and edges between forested corridors (100 - 200 m wide) and pasture (CE) (Fig. 1). Edges were for some analysis further divided into a forested part (FE-F and CE-F respectively) and a pasture part (FE-P and CE-P respectively). We used interior forests (F) and interior pastures (P) as controls and these were located at least 400 m from the nearest edge (Fig. 1). Three replicates of each type (for simplicity henceforth habitats) were used, separated by 7 500 - 9 500 m.

Four transects were set up at each edge running perpendicular to the edge, reaching 100 m into the forest/corridor and 100 m into the pasture (Fig 2). The distances between transects at an edge were 200 - 400 m and the minimum distance from a transect to another edge was 400 - 600 m (Fig. 2). We used a thin, dark green nylon thread along transects in forested areas so they could be located without clearing conspicuous trails. The thread was placed through the dense canopy and was thus well hidden and not possible to follow for predators. It was high enough (approximately 140 - 160 cm) for most animals to pass under, rheas (Rhea americana) excluded, and low enough to be reached by a hand an followed. A nest-station was marked every 25 m, (9 nest-stations per transect, 36 per edge), with one station being placed exactly at the border between forest and pasture, using knots on the nylon thread in forested areas and flagging tape in pastures. The flagging tape was tied to shrubs at least 10 m from nest-stations, a distance suggested not to effect predation rates by predators using visual cues (see Major and Kendall 1996).

The experiment was run for four consecutive trials, each lasting four days. Four days was chosen since it mimics egg-laying patterns of some passerines in the area, and is thus a period where the nests are left unattended by the parent birds for longer periods of time. In each trial, nine ground nests and nine shrub nests were randomly placed among the 36 nest-stations at each edge, so that one ground and one shrub nest was placed at each distance from the edge. All nests were relocated to other nest-stations along the transects for every new trial. A design with varied distances between nests at each trial was used to lower the risk that predators would develop a search-pattern over the trials (Yahner and Mahan 1996). Areas approximately 400 m into the forests and 400 m into the pastures were used as controls. Three 100 m transects were set up in each area extending from a centre-point, with nest-stations every 25 m (Fig. 2). During each trial, one ground and one shrub nest were placed on each transect at one of the marked nest-stations. A ground and a shrub nest were never placed at the same nest-station at the same trial, and each nest-station only received one ground and one shrub nest during the experiment. No studies on natural nest densities have been made in the area but are in progress (Meritt, unpubl.). We used on average one nest/ha/trial during the experiment.

The artificial nests were open cup canary nests of rattan woven through with millet (Vo-Toys Inc., Harrison, NI 07029, USA). They measured 103 mm ((3 mm, 1 SD, N = 10) in outer diameter and 44 mm ((3 mm, N = 10)) in outer height. The same type of nest was used in all habitats and for both ground and shrub nests. Shrub nests were wired to forked branches, using a light gauge steel wire, at a mean height of 140 cm ((12 cm, 1 SD, N = 156) in forested areas and 71 cm ((23 cm, N = 132) in pastures, depending on available vegetation. Ground nests were wired to bases of canopy trees in forested areas and bases of shrubs in pastures. Dominating plant species used as substrates were *Ruprechtia triflora* and *Acacia spp*. We used three types of eggs in this study; Quail eggs (length 35 mm, (1 mm, 1 SD; width 27 mm, (0.8 mm; weight 11 g, (0.9 g, N = 30); Clay eggs, made of non-hardening and non-toxic light-grey modelling clay (length 22 mm, (0.6 mm; width 15 mm, (0.5 mm; weight 3 g, (0.1 g, N = 30; AMACO Inc.), that were secured in the nest by a thin gauge steel wire (Darice Inc.); Light-blue hard plastic eggs (length 19.5 mm; width 12.5 mm; weight 1,5 g, N = 30). One egg of each type was placed in each nest during the experiment. Depredated eggs and nests were collected for later identification of predators. No attempts were made to conceal nests or mimic nests and/or eggs of a specific bird species. Rubber gloves and rubber boots were used to reduce human scent.

We classified a nest as depredated when one or more eggs were removed, broken or when the clay or plastic egg had marks on them. Twenty-two shrub nests that were disturbed by wind in pastures (the quail and the plastic egg was found beneath the nest after several days of strong winds) were classified as not depredated for the following reasons: The nests were still baited with the egg that performed best during the study; There were no signs of predation and the quail egg and plastic egg were found below the nest; Including these nests as not depredated in analysis may have introduced a bias and underestimated the predation rate in pastures since the clay egg did not capture 100 % of the predation in the study. However, excluding these nests would have increased the calculated predation rate for pastures and therefore, in our opinion, introduced a larger bias than if these nests were included in analyses.

Data Analysis

Ground nests and shrub nests were analysed separately. Two-tailed probabilities and a p-value of 0.05 were used in all statistical tests. Bonferroni correction for multiple comparisons was used when appropriate. There were no significant differences in nest predation between the three replicates so data was pooled for analysis.

We used two methods to test if nest predation events were independent, that is not influenced by the fate of neighbouring nests. The first method (modified from Hannon and Cotterill 1998) treated ground nests and shrub nests separately and looked at neighbouring nests on each transect and recorded in how many instances they were a) both depredated, b) one depredated and one not depredated or c) both not depredated, to get observed values for each event. Expected frequencies were calculated from the observed overall probability of predation for shrub (0.42) and ground nests (0.44) using a binomial distribution ($p^2 + 2pq + q^2$). p is the probability of a nest being depredated and q the probability of the nest escaping predation. p^2 is thus the expected frequency of two neighbouring nests both being depredated, 2pq is the expected frequency of one nest being depredated, the other not, and q2 is the expected frequency of two neighbouring nests escaping predation. Expected frequencies were multiplied by the total number of depredated nests to give expected values for each event.

Secondly, if the fate of a nest is influenced by the fate of its neighbour, then the mean distance between nests experiencing the same fate should be shorter than between neighbouring nests experiencing different fates. We thus calculated and compared the mean distance between neighbouring nests that experienced the same fate (both depredated, or both not depredated) and between those that experienced different fates (only one nest being depredated).

We used logistic regression to detect whether the risk of an individual nest becoming depredated was influenced by the following parameters: Type of edge, i.e. edge between contiguous forest and pasture and edge between forested corridor and pasture; Habitat, i.e. forest and pasture; Distance, i.e. distance from edge; Trial, i.e. during which trial the nest was placed.

Predators were divided into the following categories: 1) Large-gaped birds - the clay egg showed marks of bird predation and the quail egg was depredated, e.g. *Cyanocorax chrysops* and *Cariama cristata*; 2) Other birds - the clay egg showed marks of bird predation but the quail egg was intact, e.g. *Taraba major* and *Mimus triurus*; 3) Large-gaped mammals - judged from marks on clay eggs, e.g. *Pseudalopex gymnocercus* and *Eira barbara*; 4) Small-gaped mammals - rodents and possibly opossums; 5) Large-gaped unidentified - the clay egg was removed, had unidentifiable marks or were not depredated, and the quail egg was depredated; 6) Small-gaped unidentified - the clay egg was removed, had unidentifiable marks or were not depredated, and the quail egg was not depredated. No predator could be identified as a reptile. One nest that was completely destroyed with the eggs showing no signs of predation and 4 nests showing signs of multiple predation were omitted from analysis. The categories of predators were pooled into birds (group 1 and 2), mammals (group 3 and 4), large-gaped predators (group 1, 3 and 5) and small-gaped predators (group 2, 4 and 6) for analysis.

SYSTAT 8.0 statistical software and JMP statistics and graphics guide from SAS Institute were used for statistical analysis.

Results

Nest-predation

The average risk of predation was similar for shrub nests (41.7 %) and ground nests (43.8 %), see Table 1. No significant difference was found on predation rates between ground nests and shrub nests in any of the different habitats (Table 2). We nevertheless chose to analyse these separately since they are likely to be vulnerable to different predators (Söderström 1998) and pooling them may obscure differences that exist for a certain nest type. Both tests of independence of nest fates showed that the risk for predation of a nest was independent of the fate of its neighbour (ground nests, n = 120: (2 = 0.86, df =2, p = 0.65; Z = 0.41, p = 0.68; shrub nests, n = 121: (2 = 2.09, df = 2, p = 0.35; Z = 1.49, p = 0.14). Each nest was thus treated as an independent sample.

Logistic regression showed that the risk of a nest becoming depredated was influenced by

Table 1. Number of nests used in each habitat for ground nests and shrub nests, together with number of nests depredated. Numbers in parenthesis are percentage of depredated nests. FE-F: Forest edge, forested part; FE-P: Forest edge, pasture part; CE-F: Corridor edge, forested part; CE-P: Corridor edge, pasture part; F: Interior forest; P: Interior pasture.

	Ground nests		Shrub nests	
Habitat	n	$n_{depredated}$	n	$n_{depredated}$
FE-F	60	25 (41.7)	60	29 (48.3)
FE-P	48	15 (31.2)	48	9 (18.8)
CE-F	60	36 (60.0)	60	45 (75.0)
CE-P	48	18 (37.8)	48	10 (20.8)
F	36	21 (58.3)	36	22 (61.1)
P	36	11 (30.6)	36	5 (13.9)
Total	**288**	**126 (43.8)**	**288**	**120 (41.7)**

Table 2. Comparisons of predation rates between artificial ground nests and shrub nests in the different habitats, using χ^2 for two-way contingency tables. FE-F: Forest edge, forested part; FE-P: Forest edge, pasture part; CE-F: Corridor edge, forested part; CE-P: Corridor edge, pasture part; F: Interior forest; P: Interior pasture.

Habitat	χ^2 (DF = 1)	p
CE-F	3.08	0.079
CE-P	3.23	0.072
FE-F	0.54	0.46
FE-P	2.00	0.16
F	0.058	0.81
P	2.89	0.089

Table 3. Results of logistic regression comparing risk of predation by type of edge, habitat, distance from and trial (time). The model was significant for both ground nests (log likelihood of constants only = 147.90 and fitted model = 140.91, p = 0.007) and shrub nests (log likelihood of constants only = 147.63 and fitted model = 124.25, p < 0.001).

Type of nest Parameter	Coefficient	S.E.	p
Ground nests:			
Constant	2.98	1.02	0.003
Type of edge	-0.56	0.28	0.050
Habitat	-1.32	0.58	0.022
Distance	0.01	0.00	0.212
Trial	-0.21	0.13	0.103
Shrub nests:			
Constant	3.43	1.09	0.002
Type of edge	-0.80	0.31	0.011
Habitat	-1.79	0.62	0.004
Distance	-0.00	0.01	0.770
Trial	-0.01	0.14	0.945

Table 4. Results of logistic regression comparing risk of predation by type of edge, habitat, distance from and trial (time), with the edge-habitat interaction included. The model was significant for both ground nests (log likelihood of constants only = 147.90 and fitted model = 140.57, p = 0.012) and shrub nests (log likelihood of constants only = 147.63 and fitted model = 122.98, p < 0.001).

Type of nest Parameter	Coefficient	S.E.	p
Ground nests:			
Constant	4.00	1.61	0.013
Type of edge	-1.24	0.87	0.155
Habitat	-2.03	1.04	0.051
Distance	0.01	0.00	0.210
Trial	-0.21	0.13	0.102
Type of edge x habitat	0.48	0.58	0.407
Shrub nests:			
Constant	5.53	1.74	0.001
Type of edge	-2.20	0.94	0.019
Habitat	-3.31	1.16	0.004
Distance	-0.00	0.00	0.768
Trial	-0.01	0.14	0.945
Type of edge x habitat	1.04	0.65	0.110

Table 5. Comparisons of predation rates between interior forests and forested parts of the edges and between interior pastures and pasture parts of the edges for artificial ground nests and shrub nests, using c^2 for two-way contingency tables. FE-F: Forest edge, forested part; FE-P: Forest edge, pasture part; CE-F: Corridor edge, forested part; CE-P: Corridor edge, pasture part; F: Interior forest; P: Interior pasture.

Comparison	χ^2 (DF = 1)	p
Ground nests:		
FE-F – F	2.50	0.11
FE-P – P	0.005	0.95
CE-F– F	0.026	0.87
CE-P– P	0.44	0.51
Shrub nests:		
FE-F– F	1.48	0.22
FE-P– P	0.35	0.55
CE-F– F	2.06	0.15
CE-P– P	0.68	0.41

type of edge and habitat for both ground and shrub nests (Table 3). Nest predation was higher for both ground and shrub nests in forests than in pastures. Predation rates were also higher for both ground and shrub nests at edges along forested corridors compared to edges neighbouring contiguous forests. Distance and trial did not influence the risk of predation. Following these results, we were it interested in seeing whether an interaction existed between type of edge and habitat. The interaction proved not significant for both ground nests and shrub nests (Table 4). The latter model did not improve the explanatory power of the model for either ground nests (difference in log likelihood (2 = 0.69, df = 1, p > 0.05) or shrub nests (difference in log likelihood (2 = 2.55, df = 1, p > 0.05). We therefore retain the first model (Table 3).

There were no significant differences between the risk of predation at the controls in the interior forests and interior pastures compared to the forested and pasture parts of the edges respectively (Table 5). No edge effect was thus detected for either ground nests or shrub nests neither within 100 m from the edges nor within 400 m from the edges.

Identification of Predator Categories

The clay egg captured on average 83.3 % of the total predation in this study, the plastic egg 75.2 % and the quail egg 62.6 %. The division of predators into categories means that category 2 and 6 (being distinguished from category 1 and 5 respectively by the fate of the quail egg) could have been exposed to some predation events by large-gaped predators that decided not to prey upon the quail egg. We believe this to be only a minor bias since the quail egg was the only egg that offered a reward for the predator, and would therefore rarely be left.

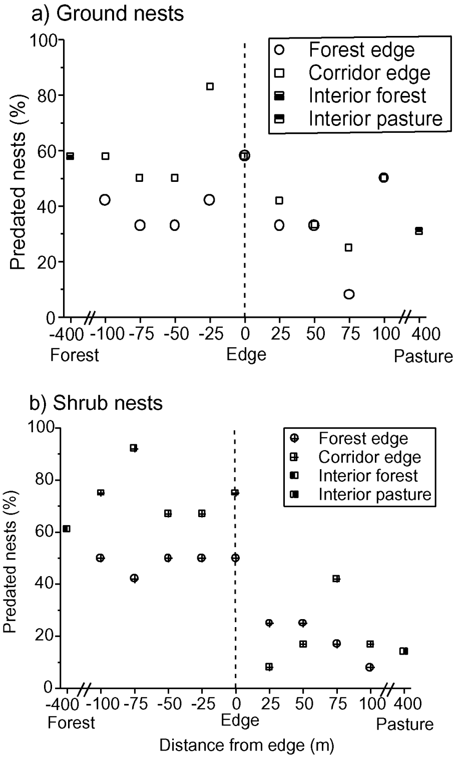

Fig. 3. Scatter-plots showing percentage depredated nests for a) ground nests and b) shrub nests at measured distances from the habitat edge.

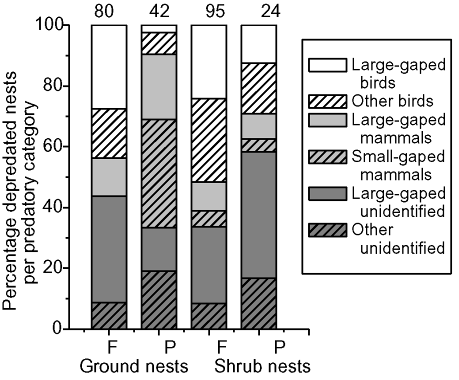

Fig. 4. Proportions of depredated nests per predator category for shrub and ground nests in pastures and forested areas and proportions of depredated nests per predator category for shrub nests in forested parts of forest edges and corridor edges. Numbers above bars denote number of depredated nests. F = Forests, P = Pastures, FE = Forest edge, CE = Corridor edge.

Table 6. Comparisons between predator categories on artificial ground nests and shrub nests in different habitats using Fisher's exact test. G-P: Ground nests in pastures; G-F: Ground nests in forested habitats; S-P: Shrub nests in pastures; S-F: Shrub nests in forested habitats.

	Mammals – Birds	Small-gaped – Large-gaped Predators
Habitats	p	p
G-P – G-F	< 0.0001[a]	0.0001[a]
G-P – S-P	0.0022[a]	0.074
S-P – S-F	0.69	0.82
S-F– G-F	1.00	0.036

[a] Significant after Bonferroni correction ($P_{\text{Bonferroni}}$ ^{3} 0.0062, n = 8).

Different habitats and nest-sites were vulnerable to different categories of predators (Fig. 4). Ground nests in pastures were more often depredated by mammals and less by birds than both shrub nests in pasture and ground nests in forested areas (Table 6). Ground nests in pastures were also relatively more depredated by small-gaped predators than ground nests in forested areas. Predators could unfortunately not be identified to species, and cameras would be needed to identify specific predators. No further analysis was made on the identity of predators due to small sample sizes.

Discussion

Edge and Habitat Effects

We found a difference in predation rates between habitats for both ground and shrub nests. Nests in forested parts of the edges ran a higher risk of being depredated than nests in pasture parts of the edges.

Although no difference in relative predator composition could be detected for shrub nests, there was a significant difference in number of nests depredated. We suggest two possible reasons for this difference. First, there was a higher number of birds in forested areas, where cover is abundant, than in pastures (Areskoug, unpubl.), and this seems to be the case also for potential avian nest predators (personal observation). Many bird species may avoid open areas with reduced cover in pastures, even when a food resource, such as an artificial nest, is available only a short distance from the forested areas. The cover and height of vegetation types in pastures did not influence the level of predation (Eriksson, unpubl.), even though large shrubs may provide good perching sites for avian predators. Second, some potential mammal predators may be excluded from predation on shrub nests in pastures, since branches may be too weak for larger predators to climb on. The shrubs in pastures are also more dense and spiny in their lower regions then the trees that were used as substrates in forested areas and thus make it more difficult for potential predators to reach the nests. This is supported by the relatively high frequency of mammal depredation on ground nests in pastures. This leads to a relatively low predation by both birds and mammals on shrub nests in pastures.

There was a difference in relative predator composition for ground nests in forests compared to pastures. Mammals were relatively more important as predators in pastures, whereas birds were major predators in forested areas. Mammals may be more prone to use pastures for travelling and foraging than birds. This is supported by Areskoug (unpubl.) who found significantly more bird species in forested areas than in pastures, with distinct bird communities in the two habitats, whereas most mammal species were at least occasionally found also in the pasture.

There were differences in predation rates on both ground and shrub nests between the two types of edges, as corridor edges demonstrated significantly higher predation. Both types of edges might act as pathways for predators, but the forested corridors may channel these in higher concentration compared to the forest edge. These corridors are narrow, possibly consisting only of edge-habitat for the species of concern. Even though no edge effect was detected, the exposure of double edges at the corridors, in addition to a possible congregation of moving predators, appear to render birds nesting in corridors more vulnerable to predation. Major et al. (1999) also concluded that linear strips of remnant woodland habitat (50 - 90 m wide) at a study-site dominated by agriculture in New South Wales, Australia, seemed disadvantageous as habitat for breeding birds due to increased risk of nest predation. We could not determine whether the higher risk of predation in forested corridors was due to higher concentrations of predators or due to more effective foraging patterns. There is a need for future studies to estimate predator compositions and concentrations and also to study movements and behaviour of predators in the different habitats and type of edges. Further studies are needed with a focus on predation risk on natural nests.

No increase in nest predation were found closer to edges between pastures and forested areas (Fig. 3a and 3b, Tab 3). Such edge effects have been documented (Gibbs 1991, Paton 1994, King et al. 1998), but so has the lack of such an effect (Nour et al. 1993, Marini et al. 1995, Bayne and Hobson 1997). Many studies have used quail or chicken eggs (See Paton 1994). There are recent studies suggesting that edge effects might disappear when small-gaped predators are important nest predators, since these may be more important in the interior of habitats (Haskell 1995, Nour et al. 1993). Small predators are often not able to depredate quail eggs and we suggest that small eggs should be included whenever the aim is to detect predation events by all predator categories. Our sample sizes did not allow for different predator categories to be analysed separately. We found six other studies that used eggs of modelling clay or plasticine and included distances from edges in their designs. Five of these (Nour et al. 1993, Bayne and Hobson 1997, Hannon and Cotterill 1998, Keyser et al. 1998, Matthews et al. 1999) failed to detect an edge effect, whereas Møller (1989) found that exposed ground nests in forests near forest-agricultural edges experienced higher predation rates.

The lack of an edge-effect in our study could also be an effect of the dry Chaco's short history of forest fragmentation. We performed this study in a forest-dominated landscape recently (1970s) exposed to forest clearings. It is thus possible that there has as yet been little adaptation of the predator fauna to an increased amount of open landscape. Andrén (1995) in a review found nine studies that suggested that increased predation close to forest-farmland edges was an effect of farmland predators (e.g. corvids) penetrating into the forest. These studies were performed in Scandinavia and North America, regions with a long history of human-induced fragmentation as compared to our study-site. Many areas that are valuable for conservation purposes today do however experience a similar situation as the dry Chaco, with a recent and very rapid rate of deforestation, where there will be little time for species to adapt to the altered environment.

Some predators may develop a search pattern during a nest predation experiment, which may lead to changed levels of predation at the latter stages of the experiment. We found no difference in nest predation as the experiment proceeded, i.e. number of trials. We therefore conclude that the development of a search pattern did not influence the results of this study.

Most research on corridors have focused on their function as movement channels between remnant habitat patches, and few have discussed the fate of species and/or individuals using these corridors. The result of this study is in support of Major et al. (1999) and Vander Haegen and DeGraaf (1996) who conclude that corridors (50 - 90 m) and narrow riparian buffer strips (< 150 m), respectively, should not automatically be seen as beneficial for wildlife. If nesting bird species become exposed to higher predation risks in forested corridors than in other forested areas, as suggested for shrub nesters in this study, the value of a corridor as movements channels must be balanced against such costs (Simberloff and Cox 1987).

Artificial nest predation studies tend to focus on forested habitats and have predominantly been performed in the Northern Hemisphere (see Paton 1994, Söderström 1999). Söderström (1999) suggested in his review that mammals may play a comparatively larger role in nest predation in tropical forests as compared to temperate zones. We found birds to be a major predator category in forested areas at our study site on both ground and shrub nests. Our study-site, with its comparatively simple vegetation structure, may be more justly compared to temperate conditions with a high proportion of predation events by visually searching predators.

The dry Chaco is listed as a global 200 ecoregion by the World Wildlife Fund. It is a unique and very diverse faunal landscape (Redford et al. 1990) and to a high extent very poorly studied. In Paraguay, there is fortunately still time to address the issues of fragmentation, edge effects and corridors, since much natural habitat is still intact. But the rate of fragmentation is high and occurs on a large scale. For the purpose of management advice regarding ecosystem connectivity and landscape planning, research should start today.

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Distribution and diversity of arbuscular mycorrhizal fungi in traditional agriculture on the Niger inland delta, Mali, West Africa.

Sara Friberg

Friberg, S. 2001. Distribution and diversity of arbuscular mycorrhizal fungi in traditional agriculture on the Niger inland delta, Mali, West Africa. – CBM:s Skriftserie 3: 53–80.

A diverse community of arbuscular mycorrhizal fungi (AMF) produces a beneficial and stable symbiosis with most plant communities. In this study, we determined diversity, richness and relative abundance of AMF species in the semi-arid Niger inland delta of Mali, West Africa.

The 10 sites ranged from annually inundated fields to arid fields of rice, sorghum, millet and natural vegetation, and were sampled using four transects per site. To determine possible correlations with soil characters we analysed pH, extractable phosphorus (P), total P, organic matter and particle fractions. The plant parameters assessed were density, species diversity and richness. A 4.5 months pot culture with *Sorghum bicolor* was used to enhance sporulation of indigenous AMF species. By comparing this with INVAM references (International Culture Collection of Arbuscular and Vesicular-Arbuscular Mycorrhizal Fungi), we could identify seven AMF species: *Glomus aggregatum, Glomus clarum, Glomus claroideum, Glomus occultum,* an undescribed *Glomus* species, *Acaulospora morrowiae* and an undescribed *Entrophospora* species.

The undescribed *Glomus* species had the greatest range for every measured parameter, was totally dominant in three samples and produced most spores in both the arid and inundated sites. AMF species richness ranged from 1 to 5 per 2500 m^2 site, showing no correlation to plant species richness. Intense AMF root colonisation and sporulation were found in the interval pH 5.6 to 7.1 and 0 to 13mg P kg^{-1} soil. To investigate the most important variables influencing AMF, we used a multivariate principal component analysis. The highest and most consistent AMF data was found in the annually inundated sites. The study showed that traditional, monospecific, low input, untilled agriculture of inundated rice, sorghum and millet is promoting an extremely high and relatively diverse inoculum potential of AM fungi.

Sara Friberg, Swedish Biodiversity Centre, Swedish University of Agricultural Sciences,
P. O. Box 7007, SE-750 07 SWEDEN. E-mail: axebo@hotmail.com

Introduction

Arbuscular mycorrhiza in general

Mycorrhiza (modern Latin of Greek words *mykes* = fungi, *rhiza* = root) were discovered 100 years ago, but were not seriously included in the multidisciplinary science of biology until the 1980's. The very special mycorrhizal group considered here, arbuscular mycorrhiza (AM) is often still neglected when issues of botany, soil biology or microbial ecology are discussed. One reason may be that the methods available today for studying AM are very specific and time consuming. From a conservation perspective, a reason for neglect may be the assumed global abundance of AM fungi (AMF), although the functional diversity and the effects of local species extinction of AMF have not been studied. Nevertheless, research and interest have expanded exponentially during the last two decades, especially in agricultural sciences.

There are seven groups of mycorrhizal fungi, all of which build a living bridge between plant roots and bulk soil in most ecosystems. In 1973, Rambelli suggested the term "mycorrhizosphere" to substitute "rhizosphere" because of the significant and dynamic microbial interactions found in the soil of mycorrhizal roots. The morphologically and functionally different groups of mycorrhizal fungi are distinguished by having the plant exchange compartment either outside (ectomycorrhiza) or inside (endomycorrhiza) the root epidermis cells (Smith and Read 1997). AM is an endomycorrhiza and has got its name from the distinct fungal tree-shaped, short-lived structure that develops in plant root cells (arbus = tree). Earlier, the name vesicular-arbuscular fungi (VAM) was used, but since not all fungi in the group produce vesicles, the term AMF is preferred. AM is the most widespread group, found from the Arctic's to the tropics, and is the dominating mycorrhiza in deserts, grasslands, agroecosystems and broad-leaved forests in temperate to tropical biomes (Smith and Read 1997). On the other hand, AMF is the least diverse group of mycorrhizal fungi on a species level, containing only 154 species in the order Glomales of the division Zygomycetes (Morton and Benny 1990). The species concept used is phylogenetic, based on the inherited morphology and biochemistry of AMF spores (Morton *et al.*1995). Distinct from the other groups of mycorrhizal fungi, AMF lack sexual reproduction. Furthermore, AMF lack plant host specificity and are obligate symbionts, germinating but not growing in the absence of responding plant roots (Smith and Read 1997). The wide range of hosts has only been marginally screened, but a compilation by Trappe (1987), based on 6500 plant species (e.g. 3% of the unknown but estimated number of angiosperms), suggested that the range covers 50% of the dicots and 50% of the monocots. Many bryophytes (Smith and Read 1997) and pteridophytes (Gemma *et al.* 1992) also develop AM symbiosis. There are reports of AM-plants with such different adaptations as being aquatic (Cooke and Lefor 1998), epiphytic (Gemma and Koske 1995), halophytic or desert cacti, rainforest trees (Smith and Read 1997), C_3 and C_4-grasses (Hetrick *et al.* 1991), and agricultural crops (Smith and Read 1997). One of the first terrestrial plants, *Aglaophyton,* in a 400 million year old fossil, shows arbuscules identical to the type found in roots today (Pirozynski and Dalpé 1989, Taylor *et al.* 1995). The long co-evolutionary history of plants and AMF, as proved by this finding, probably explains the lack of host specificity and the global distribution of AMF.

When it became known that AM-plants show increased fecundity compared to non-AM plants, the interest for AM symbiosis arose, especially in agricultural research. An AMF mycelium increases the absorptive root surface area of a plant 100-fold (Smith and Read 1997). AM-plants thus have increased macro- and micronutrient content (Clark and Zeto 1996, Solaiman and Hirata 1996). Due to unknown reasons, this is also seen at low soil phosphorus levels (Smith and Read 1997) or low to high pH-levels (Clark and Zeto 1996). In general, AMF-plants also exhibit an increased rate of photosynthesis (Dixon *et al.* 1994), and tolerance to drought (Osonubi *et al.* 1992) and salinity (Rosendahl and Rosendahl 1991). Resistance to root pathogens also increases (Smith and Read 1997), primarily due to AMF occupying the root niche and to increased plant vigor. Another feature important in the establishment of seedlings is the transport of photoderivatives from an unshaded to a shaded plant via the AMF mycelium (Eissenstat and Newman 1990).

As AM is a mutualistic symbiont, AM fungi drain up to 20% of photosynthetic carbon (Jakobsen and Rosendahl 1991) and in return, provide plants with large amounts of nutrients (P, N, K, Zn etc) and water from the soil. AMF also produce glycoprotein extracellularly on the mycelia in the bulk soil, which together with the physical network of hyphae, helps to aggregate soil (Wright and Upadhyaya 1998), thus improving aeration and water percolation. The carbon inflow to soil attracts soil microbes; altogether producing a functionally diverse and dynamic soil biota (Schreiner *et al.* 1997), which is fundamental for plant nutrition in natural systems and sustainable agriculture.

The benefit of an AM symbiosis depends on when in a plants life stage its roots are colonised by AM fungi (Solaiman and Hirata 1996). The outcome is also affected by the growth rate of both the fungi and plant. Moreover, the AM symbiosis is also influenced by the composition of plant and fungal species (Schreiner *et al.* 1997), by the hierarchical structure of AMF species in the root niche, and by their inherited genetic and functional diversity (Smith and Gianinazzi-Pearson 1988). Additionally, the outcome of an AM symbiosis is affected by soil properties, soil and plant treatments, and the presence, and amount, of soil microbes being mutualists, commensalists, inhibitors or parasites. The above ground macro- and microclimate are also factors influencing the symbiosis.

An AM fungus cannot be regarded as an individual. What we may call an intact AM fungus is in fact a community of thousands of individually distinct, motile DNA-nuclei, building and inhabiting a network of non-septate (non-cross walled) hyphae inside and between root epidermis cells. Intact hyphae have been proved to extend at least 12 cm from a colonised root (Jakobsen *et al.* 1992).

A new AMF infection of roots can start from anywhere, when all compartments are considered as independent propagules. But the life cycle of an AM fungus starts from an asexually produced, thick-walled spore, produced on a hyphal tip either inside the root or in the bulk soil, depending on the fungal species. When mature, the spore separates from the hypha and is totally dependent on passive dispersal. If the spore is produced in the soil surface layer, it may be spread by wind, water or by any soil digging animal such as humans, voles, earthworms and root collecting birds (Terwilliger and Pastor 1999; Koske and Gemma 1990). AM spores can be produced more than 1.20m down in the soil profile (Thompson 1991) and are then heavily dependent on the frequency of passing roots to grow. Without plants, AM fungi can survive for a few years in the form of spores if not heavily parasitized (Smith and Read 1997).

Depending on the AMF family, one to several germ tubes grow a few millimetres from the AM spore, carrying the stored lipid content and hundreds to thousands of nuclei. But an AMF spore is unable to metabolise its own reserves without the presence of a root (Bécard and Piché 1989). It is not known what type of signal system the AM symbionts are using, but McArthur and Knowles (1992) showed that ethylene production in potato roots, promoted by high levels of soil phosphorus, prevented AMF colonisation. If an AM responding plant root is present, germination and hyphal growth is promoted, directing the germ hyphae towards the fine root tips. An appressorium is developed, which is used as an attachment onto the root surface. From the appressorium, an intraradical mycelium develops between and inside the plant cells in the epidermal layer of the root. In the plant cells, the hyphae produce arbuscules by dichotomous branching and a simultaneous plant response invaginating the cell plasmalemma. The AM symbiosis is thus established. Via the vast absorptive surface area of the arbuscule/plasmalemma, carbon is delivered from the plant, promoting growth of the mycelial network in the bulk soil. Water and protein bound phosphorus is transported from the bulk soil back to the arbuscular compartment and delivered to the plant. The AMF stores some photosynthetic derivatives as lipids in elliptical vesicles produced by many fungi on both intraradical and extraradical hyphae. When a threshold level of colonisation is achieved (e.g. a certain amount of carbon is allocated), most AMF species start to sporulate (Gazey *et al.* 1992; Pearson and Schweiger 1993).

Arbuscular mycorrhiza, diversity and disturbance

To understand the contributions of AMF to ecosystems (including agriculture) and how to manage them, Abbott *et al.* (1995) stressed the importance of assessing its diversity, as it has been shown that the exchange activity and beneficial outcomes vary with fungal and plant species composition. Rarely one AM fungal species, but mostly three and occasionally nine species of different families and suborders, occupy the root system at the same time (Morton *et al.* 1995). The AMF diversity does not follow, but may regulate, patterns of plant diversity: if one AMF species or indigenous species becomes extinct in a habitat, there may be significant shifts in how plants acquire resources in that habitat (Allen *et al.* 1995). The interspecific genetic diversity of AMF probably overrides the intraspecific diversity, which is why conservation and research should also deal with the adaptations of isolated species. As the molecular methods to describe specific and interspecific diversity are so far only developed for a few AMF species, taxonomy still must rely on the time consuming methods of morphology and histochemistry.

High AMF diversity ranges from 10-18 species per 25g subsample in 1m^2 plots of dry tropical forest, forest edge and grassland in Costa Rica (Johnson and Wedin 1997), to 43 species found in apple rootstock plantings across 18 states of the US (Miller *et al.* 1985). Along a 355km latitudinal gradient along the eastern US, 4.6 species on average, and 23 species in total, were found associated with two plant species along 1km transects across Atlantic barrier dunes (Koske 1987). A relatively low species richness of AMF has been found in true semi-arid to arid areas. However, Stutz and Morton (1996) showed that AMF species richness in arid ecosystems could be comparable to the richness found in most other plant communities if an adequate root soil sampling technique and several successive trap cultures were used to propagate the slow-growing and/or non-sporulating fungi. AMF diversity has been reported to decrease with the moisture gradient of a tall grass prairie (Anderson *et al.* 1984) and with temperature gradients in coastal sand dunes (Koske 1987). Some species, like *Glomus intraradices*, are reported to have a vast soil parameter range, while others, like *Acaulospora* species, are restricted to acidic soils in the tropics. Wang *et al.* (1997) showed that spores of *Glomus* species have different temperature and pH preferences for germination.

As AMF are below ground organisms, they spread slowly over short distances, using plants as "stepping stones". The distribution that we see today therefore can be said to rely on historical processes (Ricklefs and Schuluter 1993; Morton *et al.* 1995). Plants have better means of dispersal in time and space than AMF, as seeds and pollen are produced above ground and have co-evolved with the behaviour of above ground animals. However, proof of AM symbiosis in more than 90% of the endemic flora of the isolated Hawaii islands (Koske and Gemma 1990), suggests a historical long-distance co-dispersal of plants and AM fungi by oceanic waters, winds and birds (Koske *et al.* 1992; Gemma and Koske 1995).

When a plant establishes itself, the plant and the soil dwelling AMF community must co-adapt to develop a symbiosis (Allen *et al.* 1995). Allen *et al.* (1995) state that plants of arid and semi-arid regions are facultatively mycorrhizal in comparison to most tropical trees that are believed to be obligatory AM, and thus it seems less likely that the fungi control the plant's distribution in such areas. This statement is a bit contradictory, as semi arid to arid environments have an extremely patchy distribution of vegetation, which may even differ from year to year, so the survival of AM fungi and the establishment of AM symbiosis may be locally obstructed. As vegetation in such areas is patchily distributed due to the spatial heterogeneity of nutrients being too easily volatilised, leached or too firmly bound, they theoretically would depend more on AMF for establishment than plants in rich or nutrient homogenous environments. Moreover, plants in disturbed areas of low fertility would benefit from a diverse AMF community, as there is then a larger chance of adaptation to environmental changes (Abbott and Gazey 1994). As an example, AMF that are scarce in undisturbed areas may increase after disturbance and mitigate disturbance effects (Jasper *et al.* 1989). In the subtropics, one such periodical disturbance is the shift from the rainy to dry season. Dodd *et al.* (1990) report that the number of AMF spores in tropical savannahs decreases during the dry season due to wilt of the vegetation, which prevents carbon allocation to AM fungi and hence hinders growth and sporulation. Additionally, soil surface temperatures above 60°C kill AMF spores (Thompson 1989) which decreases the infectivity potential in the surface layer.

Periodical inundation is another disturbance affecting the distribution of plant diversity. Until recently, inundation was thought to prevent AMF development, but Cooke and Lefor (1998) now report that young plants on developing shorelines were colonised by AM fungi, suggesting that this phenomenon is common in the development of vegetation associated with fluctuating water, nutrient and oxygen conditions.

Subtropical and tropical soils often have low amounts of available phosphorus, due to long-term exposure to optimal weathering conditions. The availability of phosphorus is also constrained by acidity (pH <6.5) and alkalinity (pH >7.5), which are both common features of tropical and subtropical soils. Less than 1% of the total soil phosphorus is available in the soil solution (Mullen 1998), serving as the central conversion point between the geochemical and biological pools in the overall phosphorus cycle. Phosphorus is an essential macronutrient to all living organisms, making up the backbone structure of DNA. Phosphorus assimilated by an organism will be recycled by other organisms during decomposition, either directly or indirectly. AM fungi are as effective in finding and delivering phosphorus from uniformly distributed fertilisers as from enriched patches in the soil (Cui and Caldwell 1996) if and when the AM symbiosis is established.

Agricultural management is another disturbance affecting the development and function of AM. Abiotically, tillage disrupts the hyphal network, which delays the AMF infectivity rate on plant roots in the coming season (Jasper *et al.* 1989). Biotically, inter-cropping of a legume with a cereal promotes AMF proliferation more than monocropping either of them (Harinikumar *et al.* 1990). The importance of soil parameters to AMF species diversity is not well known, but overall AMF production in the form of spore propagules may increase with soil pH, organic carbon (Johnson *et al.* 1991) and clay (Day 1987), and decrease with increasing amounts of soil phosphorus (Johnson *et al.* 1991). Superphosphate is reported to have a negative effect while rock phosphate enhances the AMF indigenous inoculum (Barea *et al.* 1980). Harinikumar and Bagyaraj (1989) showed that root colonisation and spore numbers increased during the season following treatment with farmyard manure and straw. Likewise, Douds *et al.* (1995) found a higher species richness in soils treated with farmyard manure compared to when inorganic fertilisers were used, but what process is causing the differences is not clear. Joner and Jakobsen (1995) report that the branching and growth of AMF hyphae was stimulated by the encounter of microsites rich in organic matter. An increased percentage of oxygen in the soil gas, due to aggregation stability and enhanced aeration, may be one factor (Smith and Read 1997). Alternatively, the transformation and decomposition rate of soil organic material, increasing the respiration of carbon dioxide, has been proven to stimulate AMF (Bécard and Piché 1989).

Objective of the study

The objective of this study was to assess the diversity and relative abundance of AMF in representative traditional agriculture sites on the Niger inland delta of Mali. We also wanted to investigate if the AMF species present, and their relative abundance, were correlated with the status of soil phosphorus, pH, organic matter, plant diversity, plant density and any agricultural treatments, such as fallow or water regime. Additionally, the aim of the study was to discuss possible agricultural benefits of the AMF inoculum found at the different sites, and cautionary aspects when converting traditional agriculture to modern methods.

Study area and methods

Study area

The study area was located in the Sahel belt of Mali in West Africa, where the Niger River forms an inland delta (Fig 1a, 1b). In total, 10 sites were sampled, all situated within a 25km radius from the village Niafunké (4 00’W, 15 59’N). The bushland of the Sahel, rich in woody herbs, grasses and scattered leguminous trees, is extensively used as grazing land for large herds of primarily cow. The annual inundation of the river creates temporary lakes and wetlands. African and asian rice (*Oryza glaberrima* Steud., *O. sativa* L.) are sown in depressions either before or after inundation. In the latter case, the rice nursery is established on the shore and rice is then transplanted up to three times, following the receding waterline. Close to the villages, millet (*Pennisetum glaucum* (L.) R.Br., syn. *P. typhoides*) and sorghum (*Sorghum bicolor* (L.) Moench.) are sown on the sand dunes after the heavy rains in July-August (200mm year^{-1} in the area of Niafunké). After harvest, all fields are freely grazed and additional manure is rarely added. Crops are not rotated in time nor space, but intercrops are cultivated when seeds are available on the market. On the dunes, the wild water-melon (*Citrullus lanatus* (Thunb.) Matsumara & Nakai) is sown as an intercrop. In the inundated depressions, Bambara groundnut (*Vigna subterranea* (L.) Verdc.), potatoes (*Solanum tuberosum* L.) and gombou (*Abelmoschus esculentus*

Table 1: Plant and management data (For site codes, see Fig.1). Total species richness includes crops and native plants. Total average distance is an estimate of plant density/plant cover, also given as an estimated number of individuals per site. The crop and water regimes in brackets indicate what treatment was used before the fallow started in 1973 for iLN and 1993 for iG1-3r

Site	Tot species richness Nov. -98	Tot average distance (m) Nov. -98	Total no. individuals (50x50m)	Major crop (per year)	Crop distance (m)	Water regime (per year)
*I*LR	1	0.2	62500	rice	0.2	inundation
*I*LS	4	0.9	3075	sorghum	1.0	inundation
*I*LM	8	0.7	5100	millet	1.0	inundation
*i*LN	13	0.5	10000	natural veg.	–	(inundation -73)
*i*G1r	5	5	100	fallow (rice)	(0.2)	(inundation - 93)
*i*G2r	0	50	1	fallow (rice)	(0.2)	(inundation - 93)
*i*G3r	9	10	25	fallow (rice)	(0.2)	(inundation - 93)
*A*MN	3	40	1.5	natural veg.	–	arid
*A*MM	22	0.7	5100	millet	1.0	arid
*A*NM	21	0.7	5125	millet	1.0	arid

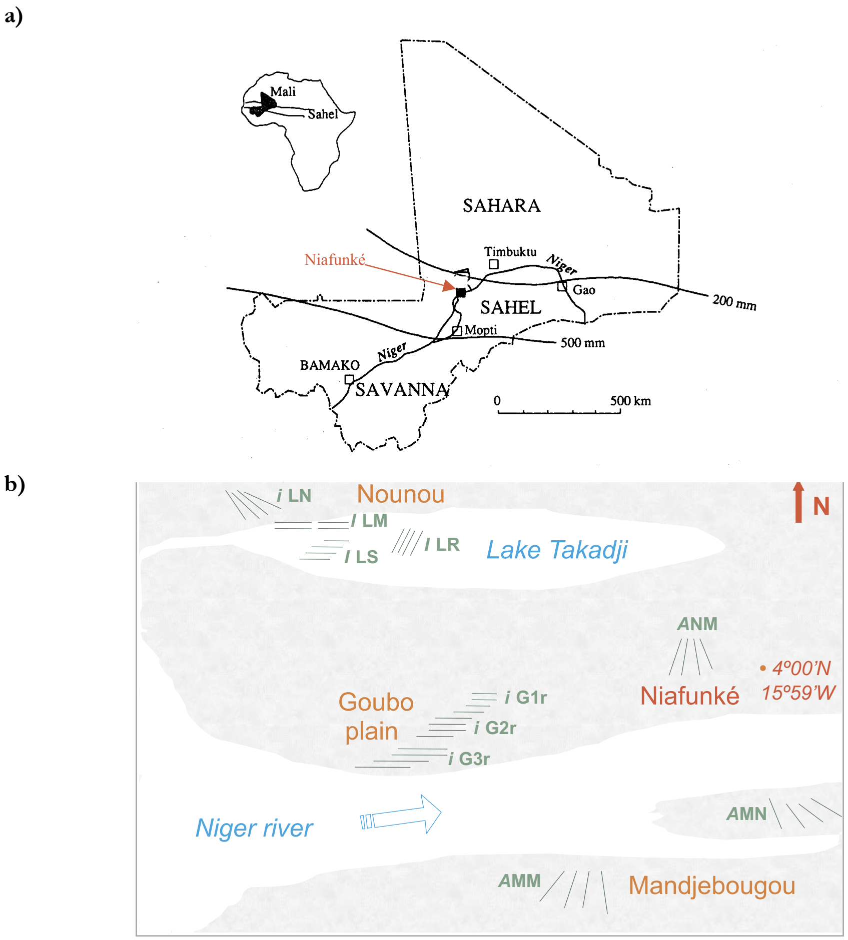

Figure 1: **a)** Mali in West Africa. **b)** Study area in the semi-arid Niger inland delta (4°00'W, 15°59'N). Bars represent transects (n = 4/site). Site codes: 1st letter signifies the water conditions being either I = inundated yearly since historical time, i= historically inundated but now arid (iLN since -73, iG1-3r since -93), and A = historically arid; 2nd letter signifies area or village being either L = Lake Takadji, G = Goubo (field no. 1, 2 and 3), N = Niafunké and M = Mandjebougou; and 3rd letter signifies the vegetation type being either R = rice, r = fallow from rice, S = sorghum, M = millet or N = natural vegetation.

(L.) Moench.) are often sown as intercrops. Perennial intercrops such as cassava (*Manihot esculenta* Crantz), laurel (*Laurus nobilis* L.), henne (*Indigofera tinctoria* L.) and mango (*Mangifera indica* L.) are sometimes planted along the upper rim of the inundated depressions. The native annuals and perennials on the dunes are cut back at time of crop establishent, but are never totally removed. Some are collected as fodder, medicine or wood for charcoal production, or left detached on the ground as wind erosion traps. Sometimes, especially on the dunes, pit traps for wind deposition are dug. So far, tillage has never been used in the traditionally cultivated study area. In one site, a fungicide (*Sijolan* in French) was mixed with millet seeds before sowing to prevent mildew and black soot.

In co-operation with the staff of the

Table 2. Soil properties at 10 traditional agricultural sites (n=4) in the semi arid Niger inland delta, Mali, West Africa. The value given is the average ± 1 standard deviation, counted on 2:1 top:subsoil. (For site codes, see Fig.1). Extractable P was assessed using NaCO3. * Preliminary assessment based on 1 transect sample/site.

Site	Depth (cm)	pH (2:1 aq.dest)	SOM (%)	Extract. P (mg/kg soil)	Total P* (mg/kg soil)	Ex. P: Tot. P (%)	Soil type* (% fraction)
*I*LR	0–40	5.8 ± 0.1	7.6 ± 1.2	6.0 ± 1.1	27.0	22.2	Sand
*I*LS	0–40	6.0 ± 0.3	10.6 ± 0.5	11.8 ± 2.7	27.7	42.7	Clay
*I*LM	0–45	7.0 ± 0.1	2.6 ± 0.3	3.4 ± 1.4	9.50	35.5	Sandy loam
*i*LN	0–45	6.2 ± 0.1	8.6 ± 0.5	6.4 ± 1.0	25.4	25.11	Clay
*i*G1r	0–25	5.4 ± 0.2	6.8 ± 0.4	5.4 ± 2.2	43.5	12.5	Clay
*i*G2r	0–25	5.9 ± 0.1	6.7 ± 0.3	1.4 ± 0.7	34.8	4.0	Clay
*i*G3r	0–25	5.8 ± 0.4	6.8 ± 0.2	3.3 ± 2.6	43.8	7.5	Clay
*A*MN	0–25	5.5 ± 0.4	7.3 ± 0.2	5.8 ± 3.8	23.8	24.3	Clay
*A*MM	0–30	8.0 ± 0.2	1.1 ± 0.3	28.7 ± 9.3	62.3	46.1	Sandy clay
*A*NM	0–45	7.0 ± 0.1	0.7 ± 0.1	2.5 ± 1.2	5.3	46.7	Sand

multidisciplinary development project of the lake district of Niafunké (PDZL-II) and a parallel swedish minor field study-project (MFS) of soil properties (Friberg *et al* 2000), four agriculturally representative villages were chosen (Fig. 1b). The field sampling was carried out in November and December 1998, in the dry season (18 to 30°C), just before the inundation of the Niger River. Site locations and site codes are given in Fig. 1b.

Site information on crop and management regimes is presented in Table 1. Soil properties assessed in the MFS-project, using the same sampling regime and time, as here, are presented in Table 2. For transect data see Appendix 1.

Soil sampling

To cover the spatial heterogeneity of each 2500 m^2 site, soil was sampled along four transects (a, b, c, d), each with a length of 40 meters and situated 10 meters apart (Fig. 1b), giving four pooled soil samples per site. Each pooled sample was produced by collecting soil with a traditional hoe from dug pits along a transect in one bucket, and then mixing the soil was cautiously before subsampling ca 200g of soil for physical and chemical analyses. This procedure was done twice per transect, giving one top soil sample collected from 20 dug pits and one sub soil sample collected from 10 deepened pits. The depth of pits at each site differed, due to variation in root depth between sites, and varied between 25 and 45cm. The soil content of the top soil and sub soil buckets were mixed after subsampling, giving a mixed AMF transect sample of 2:1 (top soil: sub soil) of 400g of soil to use as a pot culture inoculum. Additionally, roots (assumed to contain more AMF propagules than bulk soil) were gathered from each transect to counteract a possible low AMF inoculum potential when setting up the pot culture. All samples were air dried in the shade for one week before transport.

Soil analyses

The physical and chemical soil properties were assessed in a separate MFS project. For further details, see Friberg *et al* 2000. A brief description of the methods is given here: Soil pH was analysed in air dried, 2mm sieved soil after 24 hrs in 2:1 water and two repeated 30 minute shakes. The amount of extractable phosphorus (P) in the soil was measured using the P-Olsen Method (Olsen *et al.* 1954). Following Olsen and Sommers (1987), the total amount of soil P was assessed on one topsoil subsample and one subsoil subsample from each site, as a preliminary screening. The percentage of soil organic material (SOM) in the 2mm sieved soil was indirectly measured by comparing the dry weight after 6 hrs at 105°C with the dry weight after 4 hrs at 550°C (the standard Loss on Ignition Method). Some water adsorbed to clay may be included in the results for SOM. A rough estimate of the soil types was based on a top soil subsample from each site, where dispargation, sedimentation and hydrometry were used to achieve soil particle fractionating (Gee and Bauder 1986) and the international soil textural triangle.

Plant taxonomy and plant density

Data on vernacular names, crop history, agricultural treatments, vegetation periods, crop distances etc were collected during field walks and interviews with farmers. Voucher specimens of native plants occurring within the 2500m^2-site (50´50 m) were collected. After identification, the herbaria sheets were deposited at the Uppsala Herbaria (UPS) in Sweden for storage. The plant species diversity was investigated according to taxonomic literature of Western and Northern Africa (Maire 1957; Hutchinson 1958; Hubbar and Milne-Redhead 1959; Berhaut 1967; Bondet *et al.* 1986; El Amin 1990; Maydell 1992; Hedberg and Edwards 1995), as there is no flora of Mali at present. As the chosen time of sampling was in the dry season, after harvest and grazing, no specimens of cultivars could be collected at any of the sites. Despite the grazing, most native plants were still identifiable. Plant sampling was carried out two weeks after soil sampling, which is why no native specimens could be collected from the sites at Lake Takadji (*I*LR, *I*LS and *I*LM), as they had been competely inundated in the meantime.

Overall plant density per site was roughly estimated as the average distance (m) between plants, based on observations of the amount of native plants and the distance between crops made during fieldwork.

AMF pot culture

A pot culture, with each pot representing a single transect, was set up at the Swedish University of Agricultural Sciences (SLU), Department of Microbiology, Uppsala. There are several reasons for setting up a pot culture. Firstly, we wanted to dilute the parasitic pressure on the AMF propagules in the soil. Secondly, our aim was to induce AMF sporulation in all samples at the same time, in order to get spores of similar developmental stages. Thirdly, by maximizing the availability of roots for AMF colonization, and by optimizing the conditions for nutrient, water, light and temperature, we intended to promote AMF sporulation. The "trap culture" was set up according to the recommendations of Morton *et al.* (1993), based on the experiences at INVAM (International collection for Arbuscular and Vesicular-arbuscular Mycorrhizal fungi), West Virginia, USA. The recommended host genera is sorghum, due to the fact that 1000 AMF isolates, of 98 species in all six genera, have been able to grow and sporulate in pots with *Sorghum sudanense* (Piper) Stapf at INVAM (Morton 1993).

A subsample of 200g from each transect soil inoculum (see Soil sampling) was diluted with 800g autoclaved medium sized sand and mixed before being poured into a one liter pot. Sand was chosen as a diluting substrate, as it is inert and does not affect inoculum pH, which was confirmed by a trial. After 24 hrs of incubation with water, a local sorghum variety from Northern Mali (group durra membranaceum, CIRAD, Bamako, Mali) was sown as a host plant, at a density of 25 plants pot^{-1}. Each pot was then covered with coarse, autoclaved sand to prevent unintentional dispersal of AMF. The 10x4 pots were randomly placed in a climate chamber, where subtropical conditions were imitated as follows: 75% humidity, 12 hrs of 24°C and 480 mmol m^{-2}s^{-2} light intensity and 12 hrs of 18°C in darkness. After seedling emergence, the pots were watered daily with deionized water to keep 60% of the Water Holding Capacity (WHC). Every second week, the pots were given diluted UWA nutrient solution poor in phosphate according to Hill *et al.* (1979). The total amount of minerals given in successive doses were: 74.0 N, 58.5 K, 6.2 Ca, 4.8 Mg, 14.5 P, 32.9 S, 10.9 Cl, 3.7 Mn, 1.3 Zn, 0.53 Cu, 0.08 Mo, 0.13 Na (in kg ha^{-1}).

The pot culture was run for 4.5 months. During the last week, the moisture regime was successively lowered to 30% of WHC to stop the growth of plants and to enhance sporulation of the existing AMF species.

AMF root colonisation

To assess the success of the AMF inoculum in the pot cultures, we determined root colonisation one month after sowing. From each pot, three core borer samples (Æ1.5cm, 7cm deep) were collected. The roots were rinsed, cut, mixed, cleared and stained for fungal structure (Kormanik and McGraw 1982) and placed in a petri dish. The hairline intersect counting method (Newman 1966) was used on 15 random spots per petri dish, covering 0.15m of 1m roots per sample. As we considered that the root colonisation percentage was too low, we added a small amount (0.1g) of dried, cut root pieces from the vegetation of the associated transects in Mali. Suspended in water, the roots were added to each pot two months after sowing.

After harvest and taxonomic sampling, we determined the AMF root colonisation again in each pot by sampling a section on each side of where the AMF taxonomy section had been sampled 5.5 months from sowing. The WHC had been kept at 10% and the pots stored at room temperature over the month after harvest. We used the same clearing and staining method as above, but did the counting according to Giovanetti and Mosse (1980) and Kormanik and McGraw (1982), using a gridline intersect method where 0.85m of 1m root sample was covered.

AMF taxonomy

At 4.5 months from sowing, a section (1/4) of the trap culture was cut out, chopped and mixed. A subsample of 50ml was taken for AMF spore extraction by centrifugation in sucrose gradients (Daniels and Skipper 1982). Diluted with water, we counted intact spores on 30 random fields of view per petri dish by microscopy to obtain the relative abundance per species and the total spore numbers g^{-1} freshweight soil. The spore morphotypes were separated and transferred to object glasses and identified by investigating the range of, and mean, spore and saccule sizes, colours and distances between spore and saccule. To further examine the organisation and histochemistry of spore subcellular structure, we mounted slides with 2´30 spores to PVLG media and Melziers' reagent, according to Schenck and Pérez (1990). INVAM isolates and voucher specimens were used as taxonomic references.

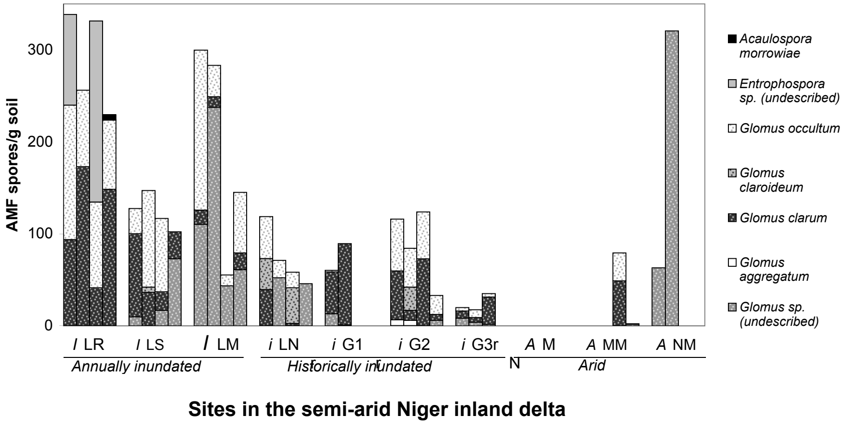

Figure 2. Species diversity and spore abundance of arbuscular mycorrhizal fungi after 4.5 months of trap culture. Each pot represents a transect. The sites are arranged according to water regime. (For site codes see Fig.1b)

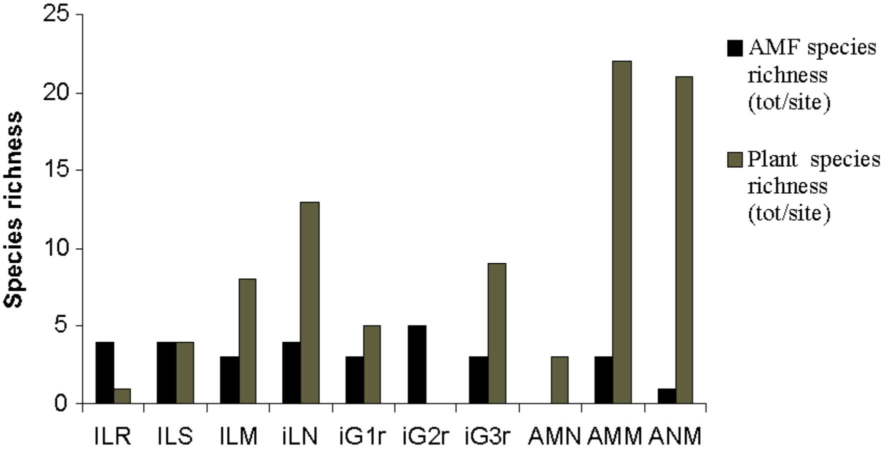

Figure 3. Species richness comparison. Site codes see Fig. 1b.

Statistical analyses

Means and standard deviations (StDev) were produced in Microsoft Excel (Windows 97). Correlation within and between the soil parameters and the AMF data were initially determined by performing linear regressions in Microsoft Excel (Windows 97). A single ANOVA analysis was simultaneously carried out to prove the validity of the regression.

A multivariate principal component analysis (PCA) was performed according to Wold *et al.* (1987) in the Unscrambler – program (Camo AS 1996) for all quantitative data (See Appendix 1). The first component, *X-axis,* explains the greatest part of the total variation in the data set and consequently directs the grouping of samples from left to right in the graph. The second component, *Y-axis,* explains the grouping of samples from bottom up in the graph. It is calculated differently from component one, using residual variation instead of the least square fit, to describe the second most influential direction of maximum variation in the data set. The variables furthest away from the origin are the most influential, meaning that they are either parallel (cos 0 = 1) or oppositely angled (cos

Table 4: Data on arbuscular mycorrhizal fungi (AMF) after 4.5 months of trap culture with Sorgum bicolordurra membranaceum in soil from the Niger inland delta in the Sahel belt of Mali, West Africa. (For site code, see Fig. 1).

Site	% Root colonisation (1 month)	% Root colonisation (4.5 months)	No. Spores per g fw soil (4.5 months)	Species richness (4.5 months)
*I*LR	5.9 ± 7.2	73.0 ± 4.4	169.9 ± 31.9	2.8 ± 0.5
*I*LS	5.3 ± 4.6	46.2 ± 11.1	72.4 ± 11.2	2.8 ± 0.5
*I*LM	3.8 ± 3.5	55.0 ± 5.9	115.0 ± 68.4	2.8 ± 0.5
*i*LN	7.4 ± 7.9	32.8 ± 12.1	43.1 ± 18.9	2.3 ± 1.0
*i*G1r	1.9 ± 1.0	1.1 ± 0.4	0	0
*i*G2r	1.2 ± 1.0	1.1 ± 1.9	12.0 ± 23.1	1.0 ± 1.2
*i*G3r	0.4 ± 0.6	3.2 ± 1.3	22.0 ± 26.4	1.3 ± 1.5
*A*MN	1.0 ± 0.7	24.7 ± 26.4	51.1 ± 22.8	3.0 ± 0.8
*A*MM	0.6 ± 0.8	11.4 ± 22.8	10.5 ± 8.4	2.3 ± 1.5
*A*NM	2.5 ± 1.4	14.0 ± 8.4	56.4 ± 89.8	0.5 ± 0.6

Table 3. Plant diversity. (For site codes, see Fig.1). Authors are given after family and species name. Abbreviations: * voucher specimens deposited at the Uppsala Herbaria (UPS) in Sweden; AM = reported in literature to develop arbuscular mycorrhiza; (F) vernacular name in French; (S) Souraï; MC = major crop; IC = inter crop; X = Native plant; F= >5 individuals/site; mc, ic, x, xf = as above, but not present in 1998, although frequent in the years before.

PLANT FAMILY	Plant species and authority	ILR	ILS	ILM	iLN	iG1r	iG2r	iG3r	AMN	AMM	ANM
AIZOACEAE	*Glinus lotoides* L. *		X		X			X			
	Zaleya pentandra (L.) Jeffrey *									X	
AMARANTACEAE	*Aerva Sp.* *										X
	A. javanica (Burm. f.) Juss ex Schultez *				X						
	Alternantera sessilis (L.) R. Br. ex Roth *				XF			X			
	Amaranthus graecizans L. *									X	
ANACARDIACEAE	*Mangifera indica* L.			IC							
ASCLEPIADACEAE	*Leptadenia hastata* (Pers.) Decne. *				X					X	X
	L. pyrotechnica (Forsk.) Decne. *				X					X	X
	Pergularia daemia (Forssk.) Chiov. *				X						
BALANITACEAE	*Balanites aegyptiaca* (L.) Del. *									X	X
BORAGINACEAE	*Heliotropium baclei* Johnston *		X							X	
	H. subulatum (Hochst. ex A. DC.) Vatke *										X
CAPPARIDACEAE	*Boscia angustifolia* A. Rich. *										X
	B. salicifolia Oliv. *										X
	Maerua crassifolia Forssk. *									X	X
CELASTERACEAE	*Maytenus senegalensis* (Lam.) Exell *									X	
COMPOSITAE	*Pulicaria undulata* L.*				X						
	*Sp.**										X
CONVOLVULACEAE	*Sp.**							X			
CUCURBIATACEAE	*Citrullus lanatus* (Thunb.) Matsumara & Nakai *										XF
	Cucumis Sp. L. * ^{AM}				XF						
	*Sp.**							X			
CYPERACEAE	*Cyperus rotundus* L. ("*eu-rotundus*" Maire & Weiller) * ^{AM}				X			XF			
	*Sp.**				X					X	X
ELATINACEAE	*Bergia suffruticosa* (Del.) Fenzl. *		X		XF			XF	X	XF	
EUPHORBIACEAE	*Euphorbia thymifolia* L. *									X	X
	Manihot esculenta Crantz ^{AM}			IC							

Table 3. continued

PLANT FAMILY	Plant species and authority	*I*LR	*I*LS	*I*LM	*i*LN	*i*G1r	*i*G2r	*i*G3r	*A*MN	*A*MM	*A*NM
GRAMINEAE	*Cenchrus biflorus* Roxb. * ^{AM}				X				X	XF	XF
	Chloris lampropriata Stapf *				X						
	Echinocloa stagnina ? "Le Bourgou" (F)					xf	xf	xf			
	Eragrostis tremula Hochst. ex Steud. *									X	X
	Hyparrhenia rufa (Nees) Stapf *										X
	Oryza glaberrima Steud. *	xf				xf	xf	xf	X	XF	
	O. sativa L. ^{AM} cult. Chinois, Maître D'Oro (F)	MC				mc	mc	mc			
	Pennisetum glaucum (L.) R.Br. ^{AM} cult. Haini (S)			MC						MC	MC
	Sorghum bicolor (L.) Moench. ^{AM} cult. Saba, Sotta, Hambo (S)		MC								
	Tragus berteronianus Schult. *									XF	
LEGUMINOSAE	*Acacia albida* Del. * ^{AM} (Syn. *Faidherbia albida*)									X	
	A. ehrenbergiana Hayne *										X
	A. raddiana Savi (syn. *A. tortilis* Hayne) *										X
	Aeschynomenae sp. *					XF					
	A. tambacoundensis Berh. *							XF			
	Alycicarpus zeyheri Harv. *									X	X
	Indigofera tinctoria L.			IC							
	I. senegalensis Lam. *					X					
	Prosopis juliflora (Sw.) DC. * ^{AM}										X
	Vigna subterranae (L.) Verdc.			IC							
LAURACEAE	*Laurus nobilis* L.			IC							
MALVACEAE	*Abutilon pannosum* (Forstf.) Schlechtend. *									X	
MALVACEAE ?	"L'Oseil rouge" (F)			IC							
PALMAE	*Hyphaene thebaica* Mart. *									X	
POLYGALACEAE	*Polygala crisptera* DC. *										X
SOLANACEAE	*Solanum tuberosum* L. * ^{AM}			IC							
RHAMNACEAE	*Zizyphus mauritiana* Lam. *									X	
TILIACEAE	*Corchorus fascicularis* Lam. *					XF					
ULMACEAE	*Celtis integrifolia* Lam. *									X	
?	"L'Aimé du lapin" (F)			X							
Total number of plant species per site:		2	4	8	13	6	2	10	3	22	21
Total number of plant families per site:		1	4	8	8	4	2	9	2	15	11

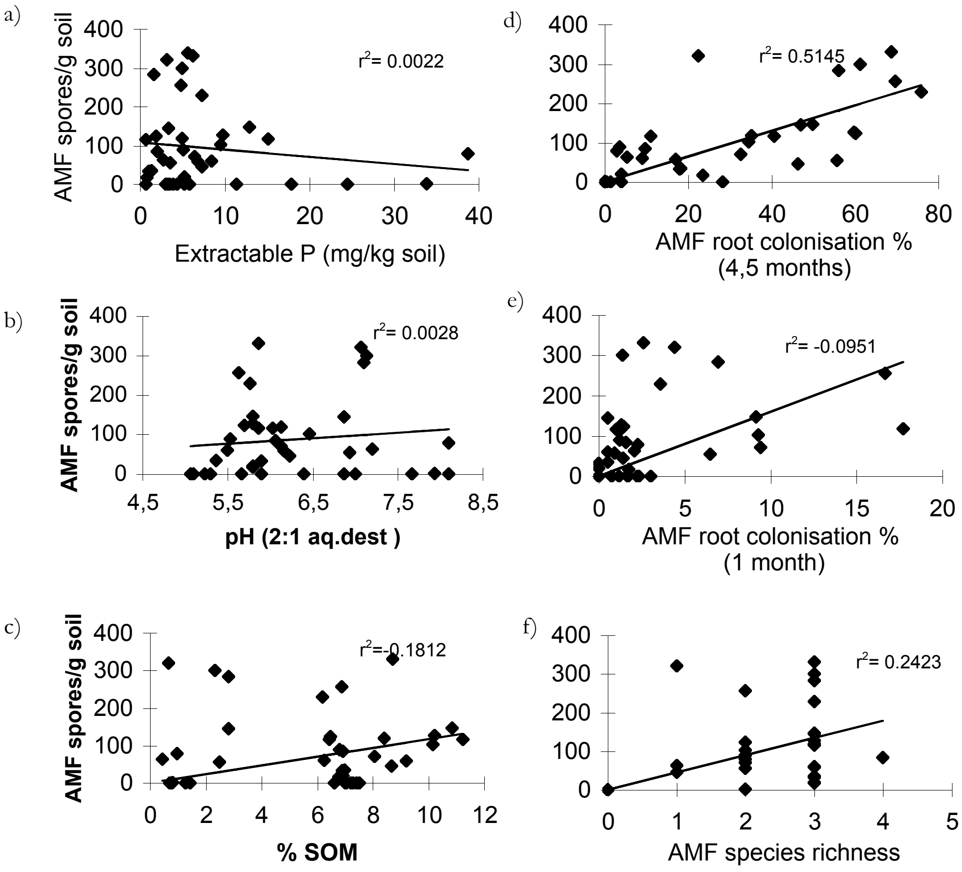

Figure4: Regression analyses: a, b, c) Correlations of AMF and soil parameters. The clustering of data may be more important than the correlation. d, e, f) Correlations of AMF parameters. The r-square value obtained is given in each figure

180 = -1) to the components. When site samples are grouped around a variable, it means they score high values of it.

A mathematical transformation of variables was performed when necessary to achieve a normal distribution as a base for linear statistics, in order to give them all the same possibility to influence the multivariate model (Ö(*AMF spore numbers g-1 soil*), Ö*(% AMF root colonisation 4.5 months*); $\log_{10}$ (*plant distance, m*)). We did not include the variables *Extractable P* and *% AMF root colonisation at 1 month* in the model, as they both had a very low influence (appearing close to the origin) and only disturbed the relationship between the other parameters. As the data used were of different units, types and ranges, a standardisation (each transect-data subtracted by the site mean and divided by the site standard deviation) was performed on transformed data to give all variables the same chance to influence the estimation of the components (Camo AS 1996).

Results

AMF data

After 4.5 months of trap culture, AMF root colonisation and sporulation was found in nine of 10 sites, with species richness ranging in total

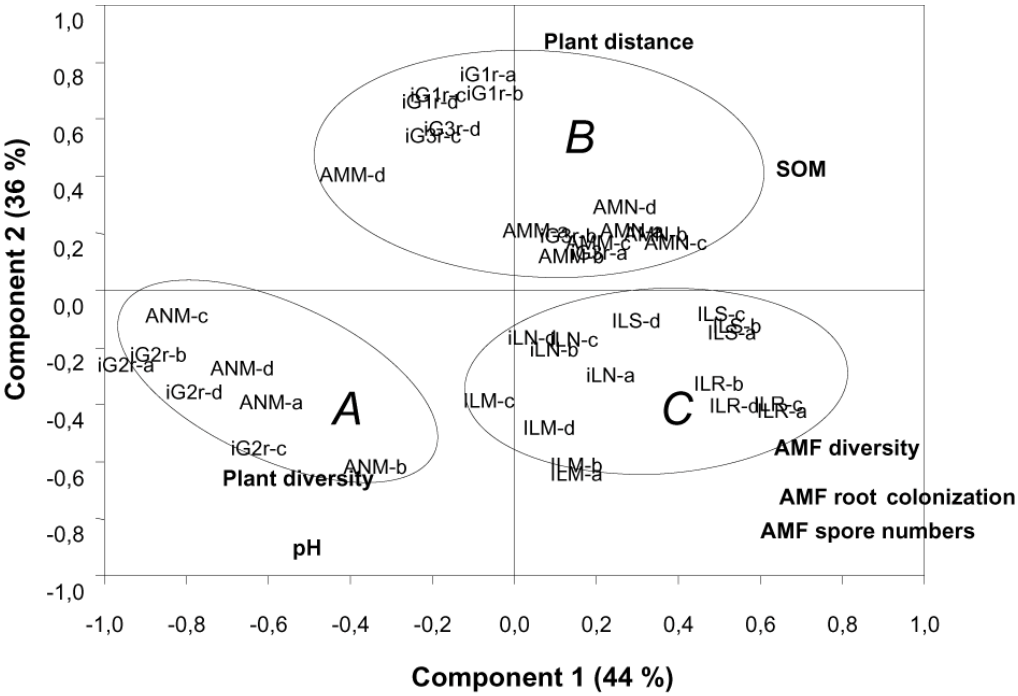

Figure 5. Principal component analysis(PCA) of AMF-, soil-, and plant-data from 10 (n=4) sites in traditional agriculture in the semi-arid Niger inland delta of Mali, West-Africa. (Site codes see Fig. 1; Raw data see Appendix 1). The grouping of data by PCA is interpreted by the authors in the following way with circles representing: A) historically arid sites; B) uncovered historically arid or flooded sites; and C) covered historically flooded sites now arid (iLN) or still yearly flooded.

from 1 to 5 in those sites. The species richness varied within the site. When comparing the transects, the site species richness ranged from 0.5±0.6 to 2.3±1.5 and 2.8±0.5. (Table 3). AMF root colonisation per site obtained after one month ranged from 0.4 to 7.4% whereas 1.1 to 73.0% of roots where colonised at the final harvest (4.5 months) (Table 3). The total numbers of AMF spores produced by the site inoculum varied between 17.9±14.3 and 288.9±54.4 g^{-1} soil (Table 3). For parameter results per transect, see Appendix 1.

In total, the trap culture revealed seven species of AM fungi (see Fig. 2). Five of them belonged to the Glomus genera in Glomaceae and the other two belonged to different genera in the Acaulosporaceae family. The species were *Glomus aggregatum* (Schenk and Smith), *Glomus claroideum* (Schenck and Smith), *Glomus clarum* (Nicolson and Schenck) (synonymous with *Glomus manihotis* according to Morton and Bentivenga, unpublished), *Glomus occultum* (Walker), an undescribed *Glomus* species, *Acaulospora morrowiae* (Spain and Schenck) and an undescribed *Entrophospora* species. The distribution of species communities within sites and the relative abundance of spore numbers are shown in Fig. 2. The most frequent species were *Glomus occultum*, *Glomus clarum* and the undescribed *Glomus* species, occurring in 80% of the sites. Less frequent were *Glomus claroideum* (30%), followed by *Glomus aggregatum*, *Acaulospora morrowiae* and the *Entrophospora* species, found in 10% of the sites. The glomacean family dominated, found in 90% of the assessed area.

At INVAM, monospecific cultures of the following species and sites were set up for live voucher collection and multiplication: *Glomus* *clarum* from site *I*LR and *A*MM; *Glomus occultum* from *I*LR; *Glomus claroideum* from *i*LN; the undescribed *Glomus* species from *A*MM and the undescribed *Entrophospora* species from *I*LR. A minimum of 125 spores is needed, so not all species could be accessed on this occasion.

AMF response to plant and soil parameters

The relationship between plant species richness (found in Nov-98) and AMF species richness is shown in Fig. 3 and shows no correlation. The scientific names of the plants found per site are presented in Table 4). Plant species richness was up to seven times higher in the arid sites compared to the inundated sites (Fig 3 and Table 4). One exception to this was the completely open *A*MN, situated in the middle of an island in the Niger river. This sampled site had only five plant individuals per 2500m^2 (Table 1). The site most diverse in terms of AMF species was one of the uncovered, formerly inundated sites in fallow after rice cultivation (iG2r), closely followed by annually inundated sites of low plant species richness (*I*LR, *I*LS, *I*LM), and the formerly inundated site now rich in natural vegetation species (*i*LN) as well as one of the arid sites of high plant species richness (*A*MM) (Fig 2 and 3). It should be remebered that plant species richness and plant density does not correlate (Table 1).

By using regression analysis, it was found that there was no correlation's between the investigated soil parameters and AMF (Fig. 4 a,b,c). The only linear correlation found was between AMF spore numbers and AMF root colonisation percentage after harvest ($r^2 = 0.6$) when comparing the whole data set (N=40) (Fig 4 d,e,f). But when considering the clustering of data, another picture appears: AMF spore numbers >100g^{-1} were only found at 1.4 to 7.3 mg P kg^{-1} soil (Fig 4 a), and at soil pH of 5.6 to 7.1 (Fig. 4 b), but within a wide range of SOM (0.6 to 8.7%) (Fig. 4 c). Final AMF root colonisation of >50% was only found at low to moderate P-levels (1.6 to 12.9 P mg kg^{-1}), at soil pH of 5.6 to 7.1, and at a wide range of SOM (2.5 to 10.2%) (See Appendix 1).

The multivariate analysis of soil, plant and AMF variables for the different sites is shown in Fig. 5 Together, the components explain 80% of the grouping of data. The principal component analysis enabled separation of inundated, arid and bare fallow sites. The variable "plant species richness", "pH", soil organic matter and all the AMF parameters all exerted a high influence on component one. "Plant distance", measured in meters (m) was the only variable with influence on component two. There were two outlier transects in the data set, meaning that they have a high influence. One was *A*NM-b, which was from an arid site, but had extreme sporulation numbers by one single, dominating species (the undescribed *Glomus* species). The other outlier transect, *i*G2r-b, was from a site with no plant cover, but delivered the highest AMF species richness found in any sample (four species).

Discussion

AMF response to sampling and trap culture

Data of soil biota often differ as much within a site as between sites (Stenberg 1999), which is why the aims of the study must direct the sampling procedures. If the aim is to assess the field level diversity, a transect-sampling technique, like the one used in this study, would be accurate, preferably complemented by a split of the pooled transect samples into sub replicates. All 10 sites were sampled metrically, despite differences in plant cover, which may have diluted the AMF inoculum in sparsely vegetated sites, but gives an estimate of the average field level diversity. The addition of roots after two months of culturing may have been an important counteraction to overcome the differences in inoculum propagule density. The aim of the trap culture was not to mimic the actual conditions of the sites, but to optimise the conditions for AMF propagules in general. The relatively high numbers of colonisation, sporulation and species richness, achieved after 4.5 months, proved that the pot culture method was successful in culturing many, if not all, dwelling AMF fungi. No control pots were used, but contamination seems to have been avoided, as there was no sporulation found in

11 of the randomly placed 40 pots. The variation and inconsistency in the arid to semi-arid sites confirms the need for successive pot culture cycles (e.g. several periods of water treatments to respond and channel the allocated carbon into hyphal growth, colonisation and sporulation) as suggested by Stutz and Morton (1996).

AMF response to inundation

The annually inundated sites on the Niger inland delta of Sahel (*I*LR, *I*LS, and *I*LM*)* had the highest and most consistent scores of AMF root colonisation, AMF spore numbers, and AMF species richness (Table 3, Fig. 2). Additionally, the number of spores produced per g soil in the study area were up to 10 times higher than in reports from semi-arid to arid areas (see Stutz and Morton 1996, Jakobsen 1997). However, in contradiction, Hayman (1982) reported that the infectivity of AMF propagules decreases in wet and anoxic soils. Another common feature of inundated soils is high organic material content, attracting a wide array of soil organisms and enhancing the parasitic pressure on AMF spores (Smith and Read 1997). The longer the soil is submerged under water, the more AMF viability is decreased (Ilag *et al.* 1987). Consequently, rice has been considered an unsuitable pre-crop when managing AMF in rotation systems (Brandon and Mikkelsen 1979, Thompson 1991). All these reports contradict our results.

Recently though, it has been confirmed that AMF are present, and even are beneficial to plants, in waterlogged ecosystems. For example, Solaiman and Hirata (1996) report that AMF innoculated paddy rice plants have higher grain yield, P level and micronutrient content (Zn, Cu, Fe, and Mn) than non-mycorrhizal plants throughout all growth stages. According to Solaiman and Hirata (1996), soil fertility dictates at which life stage AMF colonisation of rice roots is most successful. The less fertile the soil, the earlier a successful root colonisation was established by inoculated AM fungi in transplanted rice. In a more fertile soil, AMF root colonisation rate had an extended lag phase. The same authors reported in 1995 that to benefit most from an AM symbiosis, rice should be innoculated as early as possible in the nursery, because their observations were similar to those of Ilag *et al.* (1987), that AMF root colonisation rate decreases with increased time of paddy conditions. It is not clear though if a decrease in root colonisation rate is only due to rapid growth of plant roots, or if AM fungi simply stop growing at a certain point in paddy conditions and allocate carbon to sporulation? Rice has roots similar to several cyperaceae species, producing an air filled tube cover where AM fungi have been found to thrive. Such roots were dense in *I*LR, where the highest scores of all AMF parameters were obtained, despite the long inundation time (four months) compared to the other less inundated sites. What is important to consider is the cropping system used in Lake Takadji, called *riz de decrue*, meaning that rice plants are transplanted successionally (up to three times) before being established at the site after inundated water has receded (through infiltration and evaporation). Probably, each rice plant has been colonised both in the nursery site and in the transplanted site by AM fungi. That may be one reason why the soil of *I*LR had such a diverse and fast growing AMF population, responding very well to the trap culture technique used Why would periodic waterlogging increase the AMF diversity and inoculum potential? If deteriorated every season, the transplanting of rice, and possible dispersal by water and wind, may add a considerable amount of AMF propagules to the inundated soils from the surroundings. Water has been suggested as an important medium for the dispersal of AMF propagules (and other soil micro-organisms) to soils (Koske *et al.* 1992). Dispersal by water may cover distant areas, but is probably also important within and between sites. In Lake Takadji, the water rises from, and recedes back to, a Niger River inlet, crossing the bottom of a depression where rice is cultivated and where the highest consistent AMF data was obtained. Smaller and larger depressions, like the ones in Sahel, are filled with surface run-off during the rainy season. This surface run-off contains nutrients, clay and possibly AMF propagules from surrounding dunes. Likewise, suspended material eroded by wind may be deposited on the slopes of the depressions when dry, and on the water surface during inundation. Wind-eroded material may contain AMF propagules from the surrounding landscape. Efficient dispersal of AM fungi is also achieved by freely moving large herds of animals and by humans working on the fields. But why was the AMF inoculum from the inundated sites of our study higher in comparison to the inoculum from drained or arid sites in the area? Could there be unknown direct or indirect effects of waterlogging that are beneficial to the development of AM fungi? The water shelters the surface soils from high temperature fluctuations and slows down decomposition rates, allowing broader, more time consuming, successive resource scavenging by more functionally diverse microbial populations. Inundation can also be considered as a disturbance, inducing a temporary shift in the soil environment from aeroby to anaeroby, directing the soil biota to alternative, slower respiratory pathways or to dormancy or death. When the water recedes, a new disturbance regime takes place, allowing for niche and resource competition. Nutrients from the "bank" of organic material are quickly released through the fast aerobic respiration process, having a fertilising effect on the plants, and attracting more microbes and mesofauna. Additionally, the carbon dioxide respiration rate in the soil increases with a more numerous, diverse and active microbial community, which has been proven to have a stimulating effect on AMF hyphal growth (Bécard and Piche 1989), and indirectly promote the rate of root colonisation.

AMF response to aridity

In arid sites, the high surface soil temperature has an almost sterilising effect on the alluvial (A) horizon, only possibly sustaining crustaceans, some saprophytic or parasitic fungi and free-living diazotrophic bacteria. In contrast to wet soils, the decomposition rate of organic material in/on arid soils will be more similar to a burning process, where substances are quickly lost to the atmosphere. A study of the AMF communities in dunes in the Namib Desert revealed that moisture is important for opportunistic growth in arid sites as well, but on a microsite level (Jakobson 1997). Jacobson showed that more resilient spores were produced in the dunes when moisture was low, which assures AMF survival when plants are lost due to drought. In our study, we assessed three formerly inundated sites that had been arid for five years (*i*G1r, *i*G2r and *i*G3r) and three truly arid sites (*A*MN, *A*MM and *A*NM). All sites had a remarkably low amount of AMF root colonisation, AMF spore productivity and AMF diversity in comparison with the annually inundated sites, although individual transect inoculum samples varied from having zero to very high scores. The multivariate analysis separated the truly arid soils of Mandjebougou and Niafunké into unvegetated or plant diverse soils, while the now drained soils of Goubo were held intact, but grouped together with the unvegetated and organically rich *A*MN soils. The reasons are probably complex

AMF response to soil organic matter, pH and phosphorus

This study cannot show why there is a higher and more consistent AMF development and spore production in soils rich in organic matter. *A*MN, the only site where sporulation was not discovered, was rich in soil organic matter (7.8%), but was instead lacking plant cover for a very long time, which is why we conclude that next to inundation, plant cover is the second most important factor affecting the presence of AMF. Then thirdly comes the influence of soil organic matter.

Soil organic matter shelters the soil from insolation and binds water. Soil organic matter also has a buffering capacity, retaining and releasing nutrients as well as humic acids and carbon dioxide, which can act as solvents of inorganic nutrients bound to the clay. Soil organic matter contains organic forms of nitrogen. Ortas *et al* (1996) showed that the phosphorus uptake by AM colonised sorghum plants was enhanced by increased nitrogen availability. That would in turn increase the plant growth and likewise the allocation of carbon to the AMF, which may explain the more opportunistic growth of AMF fungi in soils rich in organic matter, in the presence of roots.

Soil pH and extractable phosphorus may be more influential than this study could reveal, and were difficult to compare due to their extreme differences in varying water regimes, soil types and plant cover. Apparently, soil pH and phosphorus do influence certain fungal species and their ability to colonise roots (Fig. 4). Sylvia *et al.* (1993) observed a decrease in all AMF parameters; by different AM fungi from a wide array of habitats, when extractable P exceeded 10-mg kg^{-1} soil. Only two sites in our study had P^{Olsen} >10 mg kg^{-1} soil (*I*LS 11.8±2.7 and *A*MM 28.7±9.3, see Table 2), which may explain why extractable P did not have much influence in our study. The rough estimates of total soil phosphorus in our study, ranging from 5 to 62 mg kg^{-1} (extractable P contributing with 4 to 47%, see Table 2), were extremely low compared to values from many other areas in the world, ranging from 350 to 4700 mg kg^{-1} (McCullum 1996). It is very important to investigate this further, to know if the plants, with the help of AMF, are actually mining the soil for its phosphorus content, as suggested by van der Pol and Traoré (1993). If so, rock phosphate must be added to the soils to maintain both plants and AMF in the area.

AMF response to plant density and plant species richness

To maintain productive AMF communities, plant cover seems to be more important than plant diversity or plant species richness, but less important than inundation and the presence of soil organic material. As AMF propagules cannot survive by themselves for more than one to a few years in the soil, revegetation is essential for AMF survival. Koske and Gemma (1997) found a total lack of AMF propagules in unvegetated sites, but after planting with inoculated grass species, an AMF population was established in less than a year. Al Agely and Reeves (1995) showed that the AMF root colonisation of *Oryzopsis hymenoides* (Gramineae), a common plant on inland dunes in the western US, was positively correlated to plant cover in comparison to diversity. In site *A*MN of this study, which was a dune isle naturally unvegetated since the sorghum fields were abandoned 100 years ago and probably only ever had very scattered annuals after the rains each year, showed a complete lack of AMF spores. A very low percentage of root colonisation indicated that AMF were still present, but unable to reproduce even when the soil was densely seeded with sorghum plants in the trap culture experiment. The reason for this is probably a combination of low AMF potential and that the AMF species present in the arid sites are (or have turned into) K-strategists

A denser plant community helps the colonising obligate AMF to spread extensively, with less propagule being lost to passive stochastic dispersal. A denser plant cover also produces a higher litterfall and greater amount of root biomass to the soil organisms, hence directly increasing the percentage of organic material in the soil and indirectly assuring soil system sustainability. However, plant diversity may be important in maintaining a diverse AMF community - and vice versa. Van der Heijden *et al.* (1998) showed that AMF diversity determined plant diversity, ecosystem variability and productivity in European calcareous grassland and in some North-American old-fields. In European calcareous grassland, eight of 11 plant species were dependent on certain AMF taxa to produce enough biomass to stay competitive in the plant community. This result was roughly equal in microcosms with the most effective single combinations of plant-AMF species as when mixing all the actual plant and AMF taxa. Although AMF diversity has been proven to dictate plant diversity, as discussed above, plants ultimately regulate AMF communities. To study how individual plant species influence the community structures of AMF, a sampling technique comparing mycorrhizosphere soils of several plant species in different sites would be needed. In our study, we were not studying specific diversity relationships, but were looking for congruent patterns of plant and AMF species richness, but, as mentioned, no such correlation's were detected.

In the Niger inland delta in the Sahel belt of Mali, overall plant species richness and plant cover increases after rainfall or inundation, which is why the results obtained in the dry season before inundation may be underestimations of these parameters, but are still comparable as site differences probably remain proportionally the same throughout the year.

AMF communities

AMF species richness was as high in one of the arid sites (*A*MM) as in any of the inundated sites, indicating that AMF diversity may be as high, but less evenly distributed, in arid sites (Stutz and Morton 1996). When present in an arid site, AMF can also produce spore numbers as high as in inundated sites (>300 g^{-1} soil). If correctly assessed (see paragraph 4.8), the actual *Glomus* species in *A*NM produced those spore numbers despite a rather low root colonisation (<25%).

Rice roots were dense in all transects of the rice field (*I*LR), which was the only site where *Entrophopora* species and *Acaulopora morrowiae* were detected, the latter genera frequently found in acid soils (Allen *et al.* 1995). *Acaulospora* species have been reported from upland rice (Ammani and Rao 1996). *Glomus clarum* is reported to have increased the plant biomass of *Acacia albida* (syn. *Faidherbia albida*) and *A. nilotica* during drought stress in sterile soil (Osonubi *et al.* 1992), both tree species being very important to the Sahel ecosystem. *Glomus aggregatum*, and *Glomus clarum* have been found in irrigated and dryland rice in Brazil (Pozzebon, *et al.* 1992).

Two undescribed species of AMF

The undescribed *Glomus* species (Glomaceae) were present in 80% of the sites. Mostly, it shared a niche with *Glomus clarum* and/or *Glomus occultum*, but in three cases it dominated completely, ability not found in other AM fungi in the study. The spores of the undescribed *Glomus* species are externally very similar to *Glomus intraradices*, but have one extra cell wall layer when studied subcellularly. The environmental range where this species was found on the Niger inland delta of Mali, was very broad. It occurred in inundated, drained and arid clays, loams and sands of 0.5 to 11% SOM, 5.4 to 7.9 soil pH and 0.8 to 33.8 mg P kg^{-1}soil. It was also found in uncovered sites as well as in sites with the highest plant species richness. It was not found in the rice field, but in the five years of fallow after rice. Earlier, these undescribed *Glomus* species had only been found in arid sites; once in the Namib desert in Africa; twice in the semi arid region of the western U.S.; and once in the dunes of the Assategue island outside Virginia, eastern U.S. (INVAM database). In this study, the undescribed *Glomus* species was the most productive sporulater in both arid and inundated sites (*A*NM-b: 320.5 g^{-1}, *I*LM-b: 237.5 g^{-1}). What is not known is to what extent it is beneficial to the plants.

Another undescribed species, *Entrophospora* species (Acaulosporaceae) only occurred in two replicates in the inundated rice field (*I*LR), the only site where the undescribed *Glomus* species could not be detected. This *Entrophosphora* species was the second best sporulater in the study (197.2 g^{-1}), and shared a root niche with *Glomus clarum* and *Glomus occultum*.

Agricultural and conservation importance of the AMF found

In human society, the combination of natural conditions and soil degradation, together with the colonially created fatalism and poverty, have led to an agricultural situation where nutritional losses are greater than the inputs. Crop yields are reported to mine the soil, even when fertilised (Van der Pol and Traoré 1993). Phosphorus deficiency in soils in tropical areas is one of the limiting factors in the establishment of tree plantations and agricultural crops (Sanchez 1995). In such systems where nutrients are low, AM fungi are a resource to rely on and should be cautiously maintained. Locally adapted species should not be suppressed or allowed to become extinct by unconsciously introducing new crops, AMF inoculum from elsewhere or new agricultural methods and treatments. In restoration of grasslands, AMF are important (Miller and Jastrow 1992). Likewise, in restoration of watersheds AM fungi should not be underestimated (Cooke and Lefor 1998). The unknown status of soil phosphorus on the Niger inland delta in Mali, led us to assess not only the soil phosphorus but the species richness and abundance of the indigenous arbuscular mycorrhizal fungi. These data need to be complemented by local studies of growth yield responses to AMF in different fertiliser regimes and intercropping systems, but can still serve as a practical indication for agriculture. To maintain and increase the local diversity and inoculum potential, phosphorus levels should be kept low (<20 mg/kg soil), land kept vegetated (not less than one plant m^{-2} if annuals) or periodically inundated. The pH range of 5.6 to 7.1 where AMF respond the most, is not easy to regulate in naturally acidic or alkaline soils. But, denser vegetation on the dunes, where pH is often high, would decrease the pH locally by root exudes. Additionally, increased plant cover would add organic material to the soil, which facilitates aggregation and infiltration. The AMF species found might have adaptations that are suggested for further study. For instance, the co-evolution of AM fungi and African rice, *Oryza glaberrima*, originating from the area, and the functional diversity of the two undescribed species, especially the undescribed *Glomus* species abundant in arid and inundated sites, are suggested. Additionally, the intercropping of AM trees and annual or perennial rhizobium-symbiosed legumes, all preferably native species from Northern or Western Africa, would together maintain and stimulate the AM fungi and, indirectly, the agricultural crops and the ecosystem as such.

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Appendix 1. Raw soil, plant and AMF data from 10 sites in the semi-arid Niger inland delta, Mali, West Africa. (Site codes see Fig.1b).

Site	Depth	Pot	% Root col.		Spores	Extr P		Tot P	SOM	pH	Soil	Main	Water
transect	cm	No.	1m	4.5m	/g soil	mg/kg	%	mg/kg	%	aq 2:1	type	Crop 98	regime
*I*LR-a	0-40	1	0.91	77.55	338.5	5.64	20.89	27.00	8.48	5.87	Sand	rice	flood
*I*LR-b	0-40	2	16.67	69.66	256	4.79			6.87	5.63		rice	flood
*I*LR-c	0-40	3	2.60	68.73	331.3	6.24			8.70	5.87		rice	flood
*I*LR-d	0-40	4	3.59	75.89	229.3	7.32			6.18	5.77		rice	flood
*I*LS-a	0-40	5	1.30	59.82	127.3	9.77	35.27	27.71	10.21	5.80	Clay	sorghum	flood
*I*LS-b	0-40	6	9.15	49.91	146.8	12.91			10.85	5.80		sorghum	flood
*I*LS-c	0-40	7	1.30	40.55	116.6	15.11			11.22	5.87		sorghum	flood
*I*LS-d	0-40	8	9.28	34.55	101.9	9.52			10.14	6.47		sorghum	flood
*I*LM-a	0-45	9	1.38	61.21	299.8	4.95	52.07	9.50	2.34	7.13	Sandy loam	millet	flood
*I*LM-b	0-45	10	6.97	56.10	283.1	1.62			2.83	7.10		millet	flood
*I*LM-c	0-45	11	6.49	55.68	55.1	3.57			2.50	6.93		millet	flood
*I*LM-d	0-45	12	0.51	47.03	145.1	3.33			2.83	6.87		millet	flood
*i*LN-a	0-45	13	17.73	35.24	118.5	4.95	19.46	25.42	8.40	6.13	Clay	nat.veg.	(flood -73)
*i*LN-b	0-45	14	9.41	32.57	70.9	6.44			8.05	6.13		nat.veg.	(flood -73)
*i*LN-c	0-45	15	0.92	16.95	58.2	6.85			9.20	6.17		nat.veg.	(flood -73)
*i*LN-d	0-45	16	1.42	46.38	45.6	7.29			8.67	6.23		nat.veg.	(flood -73)
*i*G1r-a	0-25	25	0.53	8.99	60.2	8.44	19.42	43.46	6.25	5.50	Clay	fallow (rice)	(flood -93)
*i*G1r-b	0-25	26	1.23	3.49	89.3	5.11			6.81	5.53		fallow (rice)	(flood -93)
*i*G1r-c	0-25	27	0	0.00	0	5.20			7.01	5.30		fallow (rice)	(flood -93)
*i*G1r-d	0-25	28	0	0.14	0	3.03			7.29	5.07		fallow (rice)	(flood -93)
*i*G2r-a	0-25	29	1.02	10.95	115.9	0.68	1.95	34.83	6.43	6.03	Clay	fallow (rice)	(flood -93)
*i*G2r-b	0-25	30	1.58	9.63	84.2	2.01			6.93	6.07		fallow (rice)	(flood -93)
*i*G2r-c	0-25	31	1.44	60.19	123.5	1.88			6.49	5.70		fallow (rice)	(flood -93)
*i*G2r-d	0-25	32	0	17.98	32.9	1.01			6.90	5.90		fallow (rice)	(flood -93)
*i*G3r-a	0-25	33	0	3.90	19.6	5.23	11.93	43.79	6.93	5.80	Clay	fallow (rice)	(flood -93)
*i*G3r-b	0-25	34	1.76	23.49	17.1	0.83			6.78	5.80		fallow (rice)	(flood -93)
*i*G3r-c	0-25	35	0.54	18.22	34.9	1.31			6.98	5.37		fallow (rice)	(flood -93)
*i*G3r-d	0-25	36	0	0.00	0	5.83			6.62	6.40		fallow (rice)	(flood -93)
*A*MN-a	0-25	17	0.76	0.44	0	3.89	16.33	23.84	7.40	5.10	Clay	nat.veg.	arid
*A*MN-b	0-25	18	1.72	3.95	0	3.45			7.51	5.23		nat.veg.	arid
*A*MN-c	0-25	19	3.03	0.00	0	4.36			7.21	5.67		nat.veg.	arid
*A*MN-d	0-25	20	2.24	0.00	0	11.40			7.04	5.90		nat.veg.	arid
*A*MM-a	0-30	21	0	0.13	0	24.51	39.34	62.29	1.29	8.10	Sandy clay	millet	arid
*A*MM-b	0-30	22	0.75	1.34	0	17.84			1.45	7.67		millet	arid
*A*MM-c	0-30	23	2.26	2.81	79.2	38.71			0.97	8.10		millet	arid
*A*MM-d	0-30	24	1.66	0.00	1.9	33.81			0.80	7.93		millet	arid
*A*NM-a	0-45	37	2.06	5.26	62.7	2.76	52.57	5.25	0.46	7.20	Sand	millet	arid
*A*NM-b	0-45	38	4.41	22.35	320.5	3.17			0.66	7.07		millet	arid
*A*NM-c	0-45	39	2.33	0.00	0	3.24			0.78	6.87		millet	arid
*A*NM-d	0-45	40	1.18	28.27	0	0.64			0.71	7.00		millet	arid

Appendix 1. Continued

Site transect	Plant ssp	AMF ssp	AMF species diversity GLOMACEAE					ACAULOSPORACEAE
*I*LR-a	1	3		*G. clarum*		*G. occultum*		*Entrophospora sp.*
*I*LR-b		2		*G. clarum*		*G. occultum*		
*I*LR-c		3		*G. clarum*		*G. occultum*		*Entrophospora sp.*
*I*LR-d		3		*G. clarum*		*G. occultum*		*Acaulospora morrowiae*
*I*LS-a	4	3		*G. clarum*		*G. occultum*	*G. sp.*	
*I*LS-b		3		*G. clarum*	*G. claroideum*	*G. occultum*		
*I*LS-c		3		*G. clarum*		*G. occultum*	*G. sp.*	
*I*LS-d		2		*G. clarum*			*G. sp.*	
*I*LM-a	8	3		*G. clarum*		*G. occultum*	*G. sp.*	
*I*LM-b		3		*G. clarum*		*G. occultum*	*G. sp.*	
*I*LM-c		2				*G. occultum*	*G. sp.*	
*I*LM-d		3		*G. clarum*		*G. occultum*	*G. sp.*	
*i*LN-a	13	3		*G. clarum*	*G. claroideum*	*G. occultum*		
*i*LN-b		2				*G. occultum*	*G. sp.*	
*i*LN-c		3		*G. clarum*	*G. claroideum*	*G. occultum*		
*i*LN-d		1					*G. sp.*	
*i*G1r-a	5	3		*G. clarum*		*G. occultum*	*G. sp.*	
*i*G1r-b		2		*G. clarum*			*G. sp.*	
*i*G1r-c		0						
*i*G1r-d		0						
*i*G2r-a	0	3	*G. aggregatum*	*G. clarum*		*G. occultum*		
*i*G2r-b		4	*G. aggregatum*	*G. clarum*	*G. claroideum*	*G. occultum*		
*i*G2r-c		2		*G. clarum*		*G. occultum*		
*i*G2r-d		3		*G. clarum*		*G. occultum*	*G. sp.*	
*i*G3r-a	9	3		*G. clarum*		*G. occultum*	*G. sp.*	
*i*G3r-b		3		*G. clarum*		*G. occultum*	*G. sp.*	
*i*G3r-c		3		*G. clarum*		*G. occultum*	*G. sp.*	
*i*G3r-d		0						
*A*MN-a	3	0						
*A*MN-b		0						
*A*MN-c		0						
*A*MN-d		0						
*A*MM-a	22	0						
*A*MM-b		0						
*A*MM-c		2		*G. clarum*		*G. occultum*		
*A*MM-d		2				*G. occultum*	*G. sp.*	
*A*NM-a	21	1					*G. sp.*	
*A*NM-b		1					*G. sp.*	
*A*NM-c		0						
*A*NM-d		0						

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An ethnobotanical study of medicinal plants used by the Zay people in Ethiopia

Mirutse Giday

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An ethnobotanical survey was carried out to collect information on the use of medicinal plants by the Zay people of Ethiopia, who live on islands and along the shore of Lake Ziway in the Ethiopian Rift Valley. Vegetation surveys were also conducted to investigate the habitat and status of the reported medicinal plants in the area. A total of 33 species of medicinal plants were reported in the area. Leaf material forms the major component of plant parts collected. The majority of remedies are prepared in the form of a juice from freshly collected plant parts. Most of the remedies are prepared from a single species and are mainly taken orally. Most of the medicinal plants are harvested from the wild. Of the 33 medicinal plants, 10 were reportedly scarce locally. Environmental degradation and intense deforestation have been reported as the main causes for the depletion of medicinal plants in the area. As the Zay people are still partly dependent on medicinal plants, the loss of these medicinal plants and the associated knowledge will, to a certain extent, hamper the existing health care system in the area.

Mirutse Giday, National Herbarium, Addis Ababa University, P.O. Box 3434, ETHIOPIA

Introduction

The Ethiopian flora is estimated to contain between 6500 and 7000 species of higher plants, of which about 12% are endemic (Tewolde B.G. Egziabher, 1991). The country is well known for its significant geographical diversity which has favoured the formation of different habitat and vegetation zones. Ethiopia is also a home to many languages, cultures and beliefs which have in turn contributed to the high diversity of traditional knowledge and practices of the people which, among others, includes the use of medicinal plants.

Plants have been used as a source of medicine in Ethiopia from time immemorial to treat different ailments. Due to its long history, traditional medicine has in fact become an integral part of the culture (Pankhurst, 1965). It is not unusual for people living in the countryside to treat some common ailments using plants available around them (e.g. *Hagenia abyssinica* (Bruce) J.F. Gmel. to expel tapeworm). Dawit Abebe and Ahadu Ayehu (1993) reported that 80% of the Ethiopian population depends on traditional medicine for their health care. More than 95% of traditional medical preparations are of plant origin (Dawit Abebe, 1986).

Despite its significant contribution to society, traditional medicine has experienced very little attention in modern research and development, and less effort has been made to upgrade the practice. It is only recently (Worku Abebe, 1984) that the Ethiopian health authorities have shown an interest in promoting and developing it. In 1979, a Co-ordinating Office for Traditional Medicine (recently promoted to the Drug Research Department) was established under the Ministry of Health (Dawit Abebe, 1996). The aims of the Office, among others, were to conduct chemical screening of medicinal plants, co-ordinate activities regarding traditional medicine and carry out a census of traditional medical practices, as well as to evaluate traditional medicine (Vecchiato, 1993; Meseret Shiferaw, 1996). Up until 1996, the Drug Research Department had collected and documented over 600 medicinal plants (Dawit Abebe, 1996).

Today, continued deforestation and environmental degradation of habitats in many parts of the country has brought about the depletion of medicinal plants and associated knowledge. Medicinal plants such as *Hagenia abyssinica* (Bruce) J.F. Gmel., *Securidaca longepedunculata* Freser., *Clerodendrum myricoides* (Hochst.) R.B. Br. ex Vatke, *Cucumis aculeatus* A. Rich. and *Warburgia ugandensis* Sprague, are among the threatened species in Ethiopia due to environmental degradation and overexploitation (Costentinos Berhe Tesfu et al., 1995; Fassil Kebebew and Getachew Addis, 1996). According to an FAO report (IUCN, 1996), the present rate of deforestation in Ethiopia is estimated at 2000 km^2/year. If the current trend is allowed to continue, the country will lose all its existing natural forests (which is now less than 2.7% of the total land area) within the coming 15 to 20 years (Kidane Mengistu, 1998). The actual part of the medicinal plants that is collected also poses a serious threat to the survival of the species. The species *Dracaena steudneri* Engler, *Hagenia abyssinica* and *Securidaca longepedunculata* are becoming scarce in the wild as a result of excessive harvesting of their roots, bark or whole parts (Costentinos Berhe Tesfu et al., 1995). Loss of the associated knowledge has been aggravated by the expansion of modern education, which has made the younger generation underestimate its traditional values. Migration from rural areas to towns and resettlement of people from drought-stricken regions to fertile areas have also resulted in the deterioration of traditional practices (Dawit Abebe, 1986). In countries like Ethiopia, where there are no adequate hospitals and formally trained doctors, a weakening of traditional medical practices will greatly affect the national primary health care system.

Recent works in the country have recorded medicinally important plants (e.g. Jansen, 1981; Mesfin Tadesse, 1986; Gelahun Abate, 1989; Dawit Abebe and Estifanos Hagos, 1991; Mesfin Tadesse and Sebsebe Demissew, 1992; Dawit Abebe and Ahadu Ayehu, 1993; Abbink, 1995; Tesfaye Awas and Zemede Asfaw, 1999). The Zay people are one of the minority nationalities

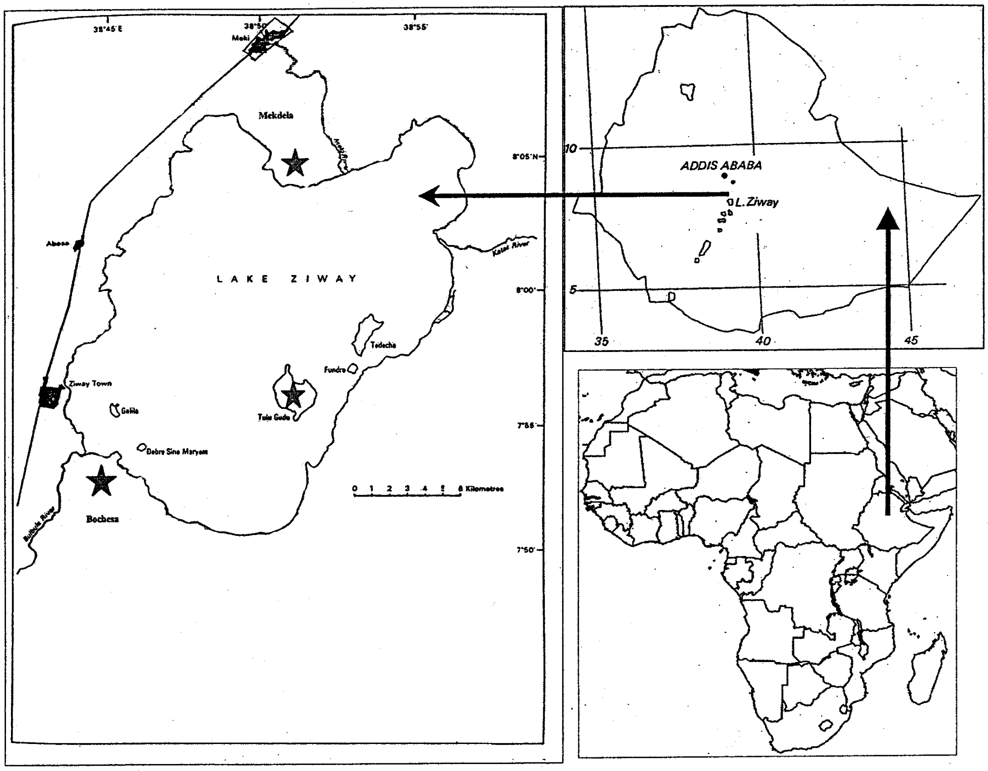

Figure 1. Map of the study area (modified from Makin et al., 1976).

in Ethiopia, with a population estimated to be around 5000 (Grimes, 1996). Zay, one of the Semitic languages which are mainly spoken in the north and partly in the central and eastern parts of the country, is the language of the Zay people.

According to local traditions, as compiled by Tuma Nadamo (1982), the Zay people are a result of a joining of three streams of people that crossed the water to the islands of Lake Ziway sometime between the early 14th and the middle of the 17th century for different reasons.

The economy of the Zay people is mainly based on subsistence agriculture and traditional fishing. Frequently cultivated crops in the area are maize, sorghum, finger millet, tef, pepper and barley. The Zay people also keep cattle, goats, sheep, donkeys and chicken, and use animal dung as their main source of fertilizer. Papyrus-made local boats are used as the main means of transport for the Zay people living on the islands, as donkeys and horses are for those residing on the shore. Fishing is widely practised in the area both for domestic use and trade.

According to informants and personal observations, the main health problems of the Zay people are malaria, schistosomiasis, diarrhoea and respiratory diseases. Black leg, anthrax, pasteurolosis and intestinal parasitic infections are some of the common livestock diseases in the area. Access to modern health services is very limited.

Like many other Ethiopians, the Zay people use medicinal plants for their primary health care. Ethnobotanically, these people have remained unexplored and no comprehensive account of their traditional practices (including ethnomedicine) is available. As is happening elsewhere in the country, both the traditional knowledge and the plants utilised by these people are under threat due to reasons mainly attributed to degradation, deforestation and cultural shifts.

In this study, we compiled the traditional knowledge of the Zay people on medicinal plants, looked into factors affecting the practice of traditional medicine and assessed the current status/abundance of medicinal plants and their possible threats in the area.

Description of the study area

The Zay people live on two relatively large islands and two shore areas of Lake Ziway (7° 52' N, 38° 47' E), located about 160 km south of the Ethiopian capital, Addis Ababa, at an altitude of 1630 m a.s.l. With an area of 434 km^2, Lake Ziway is one of seven lakes situated along the Ethiopian Rift Valley. (Tesfaye Edetto, 1988).

There are five islands on Lake Ziway, namely Galila, Debre Sina, Tullu Guddo, Taddacha and Funduro. Galila and Debre Sina are found on the western side of the lake, whereas Tullu Guddo, Taddacha and Funduro are found on the eastern side (Tesfaye Edetto, 1988). Currently, the two larger islands, Tullu Guddo and Taddacha, are occupied by the Zay people, whereas the other three islands have been abandoned because of over-population and a shortage of agricultural land. The Zay people who moved out from these islands have mainly settled on two shore areas, locally known as Bochesa and Mekdela, found along the southeastern and northeastern sides of the lake respectively. Currently, about 2000 Zay people reside in Taddacha, 1500 in Tullu Guddo, 1000 in Bochesa and 500 in Mekdela. There is still a continuous influx of people from the occupied islands to the mainland in search of arable land.

The study area covered one island (Tullu Guddo) and two mainland villages (Bochesa and Mekdela), found at altitudes between 1700 and 1830 m a.s.l. (see Figure 1).

Climate

The area surrounding Lake Ziway, like other Rift Valley areas, has a wet season from July to September, the main rainy season, and a dry and windy season from October to January. There is also irregular, highly variable rainfall from February to June. Generally, the Lake Ziway basin is characterized by an arid climate, with a mean annual rainfall of around 600mm. The mean annual temperature is 19.3°C (Makin et al., 1976; EWNHS, 1996).

Flora and fauna

The Rift Valley is well known for its rich flora and fauna. The country's national parks, game reserves and sanctuaries are mainly concentrated in this area. Open *Acacia* woodland is characteristic of the Rift Valley area. Because of the increased need for farmland and cutting of trees for different purposes (e.g. charcoal making and construction of houses), the area around Lake Ziway, which used to be covered by a variety of woody plants (personal communication with local elders), has now been left with only remnant woodland and bushland patches dominated by *Acacia tortilis* (Forssk.) Hayne, *A. seyal* Del., *A. albida* Del. and *Balanites aegyptiaca* (L.) Del. (Makin et al., 1976).

Lake Ziway is also a refuge for many species of bird. Great white pelican, Marabou stork and Fulvous whistling duck are some of the most common species (EWNHS, 1996). Lake Ziway is also home for hippopotamus and some fish species such as *Tilapia nilotica* and several *Barbus* spp., of which *Barbus zwaicus* is probably endemic (Sayer et al., 1992). The shore areas are rich in *Paspalidium geminatum*, *Typha domingensis* Pers. (bulrush), *Cyperus papyrus* L. (papyrus), *Nymphaea nouchali* Burm. f. (blue water lily) and *Aeschynomene elaphroxylon* (Guill. & Perr.) Taub (ambatch). Bulrush is used for thatching houses, whereas ambatch and papyrus are used for construction of boats. The underground part of *Nymphaea nouchali* is edible, but is only eaten when there is a severe shortage of food.

Materials and Methods

Ethnobotanical information

Ethnobotanical data were collected between January and August 1999, based mainly on semi-structured interviews with selected knowledgeable elders (Martin, 1995; Cotton, 1996).

Most of the interviews and discussions were conducted in Amharic, the official language of the country, and a few in the Oromo language with the help of a translator. On each day, the time allotted for interview with one informant was about three hours. Interviews were conducted in a place where the informants were most comfortable. Information regarding the gathering, preparation, use, status/abundance, trends and cultivation practices of medicinal plants and their marketability was also collected. Additional discussions were conducted with the informants in order to understand the traditional health system of the people and its organization. At the end of each interview, specimens of plants mentioned for their medicinal uses were collected and identified. Voucher specimens for most of these medicinal plants are stored at the National Herbarium, Addis Ababa University.

In this ethnobotanical study, 17 knowledgeable elders (16 men and one woman), between the ages of 41 and 77, were involved from the three study areas (three from Tullu Guddo, four from Mekdela and the remaining 10 from Bochesa) and served as key informants. These elders knowledgeable on medicinal plants were chosen from the different sites with the assistance of local administrators and community elders. During the course of the study, each informant was visited three times in order to verify the reliability of data obtained. If what was said during the first visit concerning the use of a particular medicinal plant by an informant did not agree with what was said during the second or third visit, the information was considered unreliable and was rejected. Repeated visits also helped to gather additional information that was not mentioned during earlier interviews.

The relative popularity of each medicinal plant species was evaluated based on the proportion of informants who independently reported its medicinal use (informant consensus) in the area. For each species, the proportion of informants who independently reported its use against a particular disease/disease category was also assessed following approaches used by Adu-Tulu et al. (1979) and Trotter and Logan (1986).

Additional interviews were also conducted with two groups of different age classes. The first group comprised 20 people aged between 18 and 40, and the second group of 20 people above the age of 40. All the participants in these interviews were randomly picked from the residents of Bochesa village. The aim of the interviews was to compare knowledge of medicinal plants (its depth and breadth) between the two age groups. Every member of the two groups was interviewed separately for about 20 minutes. According to the local elders, parents start passing on their knowledge about medicinal plants to their children at the age of 10, and this continues up to the age of 18. Commencing at the age of 18, children are expected to know what their fathers or mothers know, unless they are not willing to learn or are denied the chance (privilege) by their parents.

A preference ranking technique was employed to rank some selected medicinal plants according to their degree of scarcity. Preference ranking, according to Martin (1995), is one of the simplest analytical tools, which involves asking people to think of five to seven items and then arrange those items according to a given criterion (in this case, medicinal plants were ranked according to their degree of scarcity). Each rank is given an integer value (1, 2, 3 and so on) with the most important item (the most scarce medicinal plant in this case) given the highest value, while the least important is assigned a value of 1. These numbers are summed for all respondents, giving an overall ranking for the objects by the selected group of respondents. For this purpose, 10 individuals were randomly selected from the people that had already served as key informants. Each one of the informants was provided with fresh specimens of six scarce medicinal plants and asked to rank them according to their degree of scarcity. The six plants were selected from a list of medicinal plants that were already reported as scarce by most of the key informants, based on information obtained from key informants, vegetation studies and observation.

Interview responses were recorded in a notebook and sometimes a tape recorder was used.

Some photos were also taken when considered necessary.

Vegetation sampling

In order to classify and describe the existing plant communities and assess the abundance and distribution of the reported medicinal plants in the area, a vegetation survey was carried out between 21st and 27th of March 1999. A total of 30, 20x20 m sample plots were established in all three study sites (11 in Mekdela, nine in Tullu Guddo and 10 in Bochesa), at altitudes between 1700 and 1830 m, following a sampling approach as described by Muller-Dombois and Ellenberg (1974). The sample plots were established systematically in order to cover all habitat types and plant communities occurring in the area (agrib cultural plots, hilltops, grazing areas, wet and dry areas etc.). The homogeneity of each tree stand was checked through observation before laying down a sample plot. For each tree species, individuals encountered within each relevé were counted and percentage cover estimated. For those plants which were not trees (shrubs, herbs, vines, trailing species etc.), only percentage cover was estimated. Herbarium specimens were collected for those plants that were not identified to species level at the time, for later determination at the National Herbarium, Addis Ababa University.

Data analysis

A descriptive statistical method was employed to analyse and summarise the ethnobotanical data on the reported medicinal plants. The programme SYN-TAX, ver. 5 (Podani, 1994), was used to analyse and classify the vegetation data obtained from the relevés. Using classification, similar individual sample stands are grouped into categories which are as homogenous as possible (Greig-Smith, 1980). The percentage cover values, estimated while recording the species in the field, were converted into cover-abundance values according to a 1-9 modified Braun-Blanquet scale (van der Maarel, 1979) (see Table 1).

Table 1. Modified Braun-Blanquet scale for cover-abundance values (van der Maarel 1979).

Scale	Cover/abundance
1	rare
2	occasional
3	abundant
4	very abundant
5	cover 5–12.5%
6	cover 12.5–25%
7	cover 25–50%
8	cover 50–75%
9	cover > 75%

Results

The plants and their application

During the present ethnobotanical survey, 33 plant species were reported by the informants for their medicinal uses (see Tables 2 and 3), representing 32 genera and 23 families. Four species belonged to the family *Boraginaceae* and three to the family *Fabaceae*. The families *Apocynaceae*, *Cucurbitaceae*, *Euphorbiaceae*, *Solanaceae* and *Poaceae* were represented by two species each, whereas the other 16 families were represented by a single species each. Eighty-eight percent of the medicinal plants were reported with their local names and most of them were known only by their Oromo or Amharic names. Four of the plants (12%) have names in the Zay language. Analysis of the data based on their habits shows that 18 species (55%) are herbs, 11 species (33%) are trees and shrubs and four species (12%) are climbers.

Of the 33 reported medicinal plants, 28 species were used against human ailments and 11 species were used against cattle and equine diseases. Some of the medicinal plants were used for both human and veterinary purposes (see Tables 2 and 3). Efforts have been made to find equivalent medical terms in English for each of the local disease names. For such purposes, some medical and veterinary doctors were consulted, although for some local terms, corresponding English names could not be found. Local diseases names are given in small caps.

For human use – Eight species are used as remedies against gastrointestinal problems, seven species against MICH (febrile illness), four species against skin diseases and three species each against chest pain and snakebites. One to two species each were reported as being used for a number of different ailments such as tonsillitis, toothache and haemorrhoids (see Table 2).

For veterinary use – Ten species are used as remedies against four kinds of cattle diseases, of which four species are used to treat skin problems and three species against anthrax (ABA SENGA). One species is used as a treatment against the only reported equine (donkeys and horses) disease, locally called GEREGELCHA (see Table 3).

Analysis of the data revealed that *Solanum incanum* and *Withania somnifera* are applied to a wide range of ailments. *Solanum incanum* is used against six different ailments (stomach problems, snakebites, chest pain, tonsillitis, MICH and skin wounds of cattle) and *Withania somnifera* is a used for five types of diseases (chest pain, MICH, anthrax, typhoid and evil eye). The other reported medicinal plants (31 species) have one or two uses each.

Plant parts used and method of preparation

Leaves are the most widely used plant parts, accounting for 48% of the reported medicinal plants uses, followed by roots (33%), flowers (9%), fruits and seeds (9%), above ground parts (9%) and the whole plant (9%).

A majority of remedies are prepared in the form of a juice from freshly collected plant parts. The juice is usually prepared by pounding or crushing the plant parts in a wooden or stone mortar and pestle. Water is mostly used to dilute the juice. Few remedies are prepared from dried, and subsequently ground plant parts. Usually, the Zay people do not store remedies for a prolonged period of time. When the need comes, they go out and collect the plant, prepare the remedy and apply it to the animal or person who needs the treatment. Most of the remedies were reportedly prepared from a single species. Detail information on how to prepare each remedy is available from the first author.

Route of administartion and dosage

Most remedies are taken orally, accounting for 79% of medicinal plant use, followed by external application (applied topically on skin) (36%) and nasal application (9%). One species (*Calotropis procera*) is given anally to treat haemorrhoids. The mode of applications of two remedies, *Senna occidentalis* and *Withania somnifera* (used for repelling snakes and in preventing the spread of typhoid respectively), do not fit into either of the above categories since they are meant for prevention rather than treatment. Dried leaves of *Withania somnifera*, for example, are fumigated in the house of the sick person in order to minimize the transmission of the disease to others, while fresh or dried *Senna occidentalis* leaves are kept in a pocket to prevent snakes.

To improve the acceptability of certain oral remedies, additives are frequently used. The juice prepared from the crushed leaves of *Cynoglossum lanceolatum*, for instance, is usually taken with coffee to reduce its bitterness. The remedy prepared with female *Hagenia abyssinica* flowers is mixed with a jelly scraped from a freshly debarked stem of a plant locally called 'deqono', so that the preparation can be swallowed without much difficulty.

Some of the informants reported that restrictions are imposed when certain types of remedies are taken by patients. For example, a patient who takes a remedy against snakebites prepared from the root of *Solanum incanum*, should not sleep the first night after treatment. It is believed that sleeping reduces the efficacy of the remedy. Food is not given to a patient who takes a remedy against tapeworm (prepared from *Hagenia abyssinica*) until the proglottids are expelled from the intestine. The drug is thought to be more effective when the proglottids are made to starve.

For most of the remedies, a full dose is taken at once. The dose given to the patient depends on age, physical and health conditions. Lack of agreement among the informants on doses of certain remedies prescribed was sometimes noted. For example, three crushed leaves of *Cordia monoica* mixed in a cup of water was

Table 2. List of medicinal plants used against human ailments, alphabetically arranged by scientific names (please note that Amh. stands for Amharic and Or. for Oromo).

Scientific name	Family	Zay name	Amharic or Oromo name used by Zay people	Habit	Application	Plant part used	Route of administration
Achyranthes aspera L.	Amaranthaceae	ambulale	dergu arba (Or.)	climber	skin wounds	leaves	skin
Acokanthera schimperi (A. DC.) Schweinf.	Apocynaceae		qereru (Or.)	tree	tonsillitis	leaves	oral
Allium sativum L.	Alliaceae		nech shinkurt (Amh.)	herb	influenza	bulb	oral
					headache	bulb	oral
					chest pain	bulb	oral
Asparagus africanus Lam.	Asparagaceae		seriti (Or.)	climber	skin lesions	cladodes	skin
Calotropis procera (Ait.) Ait. f.	Asclepiadaceae		tobiaw (Amh.)	shrub	haemorrhoids	stem (latex)	anal
Carissa edulis (Forssk.) Vahl	Apocynaceae		agamsa (Or.)	shrub	rheumatism	root	oral
Cordia monoica Roxb.	Boraginaceae	ira	menchera (Or.)	tree	MICH*	leaves	oral and nasaloral
					eye diseases	leaves	
Croton macrostachyus Del.	Euphorbiaceae		bekanisa (Or.)	tree	retained placenta	leaves	oral
					MICH*	root	oral
Cucumis ficifolius A. Rich.	Cucurbitaaceae		holoto (Or.)	trailer	chest pain	root	oral
Cynoglossum lanceolatum Forssk.	Boraginaceae		yemich kitel (Amh.)	herb	MICH *	leaves	oral and nasal
Dyschoriste radicans Nees	Acanthaceae	–	–	trailer	toothache	whole plant	oral
Eleusine coracana (L.) Gaertn.	Poaceae		dagusa (Amh.)	herb	diarrhoea	seeds	oral
Euclea schimperi (DC.) Dandy	Ebenaceae		miessa (Or.)	shrub	MICH*	root	oral
Euphorbia crotonoides Boiss.	Euphorbiaceae		guri (Or.)	herb	stomach problems	root	oral
Hagenia abyssinica (Bruce) J.F. Gmel.	Rosaceae		kosso (Amh.)	tree	tapeworm	flowers (female)	oral
Heliotropium aegyptiacum Lehm.	Boraginaceae	ambachirara		herb	dandruff	leaves	skin
Heliotropium pterocarpum DC.	Boraginaceae		yeamara yemich kitel (Amh.)	herb	MICH*	leaves	oral
Indigofera spicata Forssk.	Fabaceae	–	–	trailer	stomach problems	root	oral
Kedrostis foetidissima (Jacq.) Cogn.	Cucurbitaceae		holobido (Or.) yetirign kitel (Amh.)	climber	chest pain	whole plant	oral
Linum usitatissimum L.	Linaceae		telba (Amh.)	herb	retained placenta	seeds	oral
Ocimum urticifolium Roth.	Lamiaceae		chebicha, wehale (Or.)	herb	MICH*	leaves and skin	oral
Pavetta gardeniifolia (Hiern) Verdc.	Rubiaceae		galo ajeftu (Or.)	shrub	snakebites	leaves	oral
Ruta chalepensis L.	Rutaceae		tena adam (Amh.)	herb	stomach problems	leaves	oral
Senna occidentalis (L.) Link	Fabaceae	–	–	herb	to repel snakes	leaves	–

*MICH – It is a febrile disease. The main symptoms, according to the local elders, are fever, headache and sweating.

Table 2. Continued...

Scientific name	Family	Zay name	Amharic or Oromo name used by Zay people	Habit	Application	Plant part used	Route of administration
HelSolanum incanum L.	Solanaceae		hidi (Or.)	herb	stomach problems	root	
					snakebites	root	oral
					chest pain	root, root bark	oral and skin
					tonsillitis	flowers, fruits	oral
					MICH*	leaves	oral
Sorghum bicolor (L.) Moench	Poaceae		zengada (Amh.)	herb	diarrhoea	seeds	oral
Vernonia amygdalina Del.	Asteraceae	iIbicha		tree	skin wounds	leaves	oral
Withania somnifera L.	Solanaceae		kumo (Or)	herb	chest pain	root	oral
					MICH*	leaves	oral and skin
					typhoid	root	–
					evil eye	root	nasal

*MICH – It is a febrile disease. The main symptoms, according to the local elders, are fever, headache and sweating.

Table 3. List of medicinal plants used in traditional veterinary medicine, alphabetically arranged by scientific names.

Scientific name	Family	Zay name	Amharic or Oromo name used by Zay people	Habit	Application	Plant part used	Route of administration
Acacia sieberiana DC.	Fabaceae		lafto (Or.)	tree	skin diseases	flowers	skin
Agave sisalana Perrine ex Engel.	Agavaceae		alge (Or.)qacha (Amh.)	herb	blackleg	root	oral
Aloe trichosantha Berger	Aloaceae		hargisu (Or.)	herb	anthrax		
Asparagus africanus Lam.	Asparagaceae	seriti (Or.)		climber	GEREGELCHA[1]	root and cladodes	oral
Calotropis procera (Ait.) Ait. f.	Asclepiadaceae		tobiaw (Amh.)	shrub	blackleg	stem (latex)	skin
Capparis tomentosa Lam.	Capparidaceae		gora (Or.)	shrub	skin diseases	leaves	skin
Commicarpus plumbagineus (Cav.) Standley	Nyctaginaceae		gale, qoricha simbira (Or.)	climber	skin diseases	above ground	skin
Kedrostis foetidissima (Jacq.) Cogn.	Cucurbitaceae		holobido (Or.) yetirign kitel (Amh.)	climber	ALOYE[2]	leaves	oral
Senna occidentalis (L.) Link	Fabaceae		-	herb	anthrax	leaves	oral
Solanum incanum L.	Solanaceae		hidi (Or.)	herb	skin wounds	leaves	skin
Withania somnifera L.	Solanacaeae		kumo (Or.)	herb	anthrax	root	oral

[1] GEREGELCHA - an equine disease where mucous continuously comes out of the nose of the sick animal.

[2] ALOYE - a cattle disease. The main symptoms are loss of hair, skin lesions, constipation, failure to urinate and swelling of the body.

cited as a full dose against a disease called MICH by one informant, whereas another informant reported that a handful of leaves of the species should be taken as a full dose to treat the same ailment. Besides, the units (e.g. handful of leaves, some leaves) employed to measure the amount of the plant or plant parts used in the preparation of most of the remedies are rough and therefore lack precision.

No side effects were reported by the informants as a result of the use of the different remedies, except for three species (*Hagenia abyssinica*, *Kedrostis foetidissima* and *Vernonia amygdalina*) that cause vomiting and diarrhoea. Two species (*Solanum incanum* for its fruit used in treating tonsillitis and *Calotropis procera* for its white latex used in treating haemorrhoids) were reported as poisonous to humans if not handled with proper care.

Informants consensus

The results of the study show that some medicinal plants are more popular than others. Accordingly, *Solanum incanum* is the most popular, cited by 10 informants (59%) for its medicinal value, followed by *Withania somnifera* and *Cordia monoica* mentioned by nine (53%) and eight (47%) informants respectively. Each one of the other reported medicinal plants was mentioned by one or two informants.

Similarly, some remedies are more familiar to the informants than others for use against a particular ailment or health problem. Informant consensus for those remedies that were mentioned by two or more informants as being used for the same purpose is given in Table 4. *Cordia monoica* was the most frequently cited remedy, where eight out of the 17 key informants (47%) independently reported its use against MICH, whereas each one of the other reported remedies was only cited by three or less informants.

Comparison of knowledge of medicinal plants between age groups

Knowledge of medicinal plants between two age groups (18 to 40 years and above 40 years) was compared. The sample size for each age group was 20 people. The results revealed that members of the age group above 40 mentioned more medicinal plants than the other group. Eighteen of the interviewees (90%) from this age group cited at least one medicinal plant each (two on average). A total of 10 medicinal plant species were mentioned by this group. Every member of this group who reported to have knowledge of medicinal plants knew the identity of each plant species that they cited, the location where it is collected, its preparation and route of administration.

Nine of the interviewees (45%) from the other group, between the ages of 18 and 40, cited at least one medicinal plant each (one on av-

Table 4. List of medicinal plants confirmed by two or more informants as being used for a particular ailment

Scientific name	Ailment	No. of informants
Cordia monoica	MICH	8 (47%)
Solanum incanum	chest pain	3 (18%)
	tonsillitis	2 (12%)
	stomach problems	2 (20%)
Withania somnifera	evil eye	3 (18%)
	chest pain	2 (12%)
	MICH	2 (12%)
	anthrax*	2 (12%)
Capparis tomentosa	skin disease*	2 (12%)
Commicarpus plumbagineus	skin disease*	2 (12%)
Ocimum urticifolium	MICH	2 (12%)
Hagenia abyssinica	tapeworm infection	2 (12%)
Cynoglossum lanceolatum	MICH	2 (12%)

*cattle diseases

Table 5. Three categories of medicinal plants based on their degree of abundance, as reported by informants.

Rarely encountered (30% of the total)	Occasionally encountered (27% of the total)	Commonly encountered (39% of the total)
Acacia sieberiana	*Achyranthes aspera*	*Agave sisalana*
Acokanthera schimperi	*Aloe trichosantha*	*Allium sativum*
Asparagus africanus	*Calotropis procera*	*Cucumis ficifolius*
Carissa edulis	*Capparis tomentosa*	*Cynoglossum lanceolatum*
Cordia monoica	*Commicarpus plumbagineus*	*Eleusine coracana*
Croton macrostachyus	*Dyschoriste radicans*	*Heliotropium aegyptiacum*
Euclea schimperi	*Euphorbia crotonoides*	*Heliotropium pterocarpum*
Kedrostis foetidissima	*Indigofera spicata*	*Linum usitatissimum*
Pavetta gardeniifolia	*Ruta chalepensis*	*Ocimum urticifolium*
Vernonia amygdalina		*Senna occidentalis*
		Solanum incanum
		Sorghum bicolor
		Withania somnifera

erage), although some were not sure about the plant part used or modes of preparation and application. A total of six medicinal plants were reported by the group. The rest of the interviewees from this group (55%) responded that they did not have any knowledge of medicinal plants and hence could not mention any species.

Habitat, current status and trend of the medicinal plants

Results of this study show that there is little practice of cultivating medicinal plants in the area. Most of the medicinal plants (82%) are, therefore, harvested from the wild. It was noted that only six medicinal plants (*Agave sisalana*, *Allium sativum*, *Linum usitatissimum*, *Ocimum urticifolium*, *Ruta chalepensis* and *Sorghum bicolor*) are under cultivation in the area, either in home gardens or farming plots, of which only one species (*Ocimum urticifolium*) is cultivated primarily for its medicinal use. The medicinal plants *Cordia monoica* and *Acokanthera schimperi* were seen in one or two home gardens, grown from seedlings brought from the wild, mainly for other purposes.

Most of the medicinal plants collected from the wild are available in areas not very far from the Zay villages. There is one highland species (*Hagenia abyssinica*) that is not naturally occurring in the area, but utilized by the people as a vermifuge against tapeworm. When the need arises, the remedy is purchased from the nearby towns.

Thirty percent of Zay medicinal plants which formerly were forest-inhabiting species are now only rarely encountered in the area as remnants on farm plots, edges of farm plots and other disturbed areas (see Table 5). Their quantity was reported to have been decreasing from time to time. Sixty-six percent of the noted medicinal plants are commonly or occasionally found in the area. Most of them are wild herbs that grow in disturbed areas such as fallow lands, roadsides and around home gardens. Favoured by the ever-increasing habitat disturbance, the abundance of these plants in the area was reported to have been increasing during the past years.

Preference ranking values, obtained from the overall ranking for the six medicinal plants (*Acacia sieberiana*, *Acokanthera schimperi*, *Asparagus africanus*, *Carissa edulis*, *Cordia monoica* and *Euclea schimperi*) by the selected respondents (10 informants), showed that *Acokanthera schimperi*, *Cordia monoica* and *Carissa edulis* are the most scarce species in the area (see Table 6). The six plants were selected from a list of medicinal plants that were already reported as scarce by the key informants.

Marketability of the Zay medicinal plants

Ninety seven percent of the Zay medicinal plants are used locally within the community. They were

Table 6. Preference ranking values (based on their degree of scarcity) of the six selected medicinal plants in the study area.

	Key informants (coded A to J)										Total score	Ranking
List of medicinal plants	A	B	C	D	E	F	G	H	I	J		
Acacia sieberiana	3	3	2	2	2	2	1	2	2	4	23	5th
Acokanthera schimperi	5	4	6	6	5	5	6	6	5	5	53	1st
Asparagus africanus	1	1	3	3	1	6	2	5	3	2	27	4th
Carissa edulis	4	6	4	5	4	3	3	3	4	1	37	3rd
Cordia monoica	6	5	5	4	6	4	5	4	6	6	51	2nd
Euclea schimperi	2	2	1	1	3	1	4	1	1	3	19	6th

reported as not being sold in markets, close or distant, by the Zay people, and it is only one species (*Hagenia abyssinica*) that is purchased from markets, since it is does not grow in the area.

Vegetation classification and distribution of medicinal plants

A total of 96 plant species were recorded from the 30 sample plots. Based on the composition and cover-abundance data of the species, the sample plots were classified into five recognized vegetation or community types, 1–5.

1. *Aeschynomene–Typha–Agrostis* community: *Aeschynomene elaphroxylon*, *Typha domingensis* and *Agrostis lachnanta* Nees are the characteristic species of this community. This type of community was found in two of the three study sites; a mainland shore area at Mekdela and a shore area of Tullu Guddo. These are very marshy areas, to the extent that plants growing in these areas are partly covered by water. This plant community is found at an altitude of 1700 m. There were no medicinal plants recorded from this community.
2. *Cynodon–Nymphaea* community: *Cynodon dactylon* (L.) Pers. and *Nymphaea nauchali* are the characteristic species of this community. This type of community occurred in all the three study sites (Tullu Guddo, Bochesa and Mekdela). These are mainly wet grazing areas, bordered by shores of the lake and farming lands. This community occurs at an altitude of 1700 m. Two medicinal plants, *Withania somnifera* and *Heliotropium aegyptiacum*, were recorded from this community. The species are considered rare because of their low mean cover-abundance values.
3. *Cynodon–Cyperus* community: *Cynodon dactylon* and *Cyperus rigidifolius* Steud. are the characteristic species of this community. *Acacia albida* is also abundant. This type of community occurs in the two Zay villages (Bochesa and Mekdela) found on the mainland shore areas of Lake Ziway. It is a community utilised as both grazing areas and farming plots. This community occurs at altitudes between 1700 and 1730m. The medicinal plants *Solanum incanum*, *Senna occidentalis*, *Achyranthes aspera* and *Ocimum urticifolium* were recorded from this community. *Solanum incanum* was found in abundance.
4. *Acacia–Hypoestes* community: *Acacia tortilis* and *Hypoestes forsskoli* are the characteristic species of this community. This type of community occurred in two of the three study sites (Tullu Guddo and Bochesa). It covers hilly areas with estimated slopes between 30° and 40°, though the stony slopes are still being used as farming plots due to the critical shortage of farming land in the area. This community occurs at altitudes between 1700 and 1830m. The medicinal plants *Heliotropium aegyptiacum* and *Solanum incanum* are rarely encountered in this type of community.
5. *Heliotropium* community: This is a farming plot found in Tullu Guddo where the medicinal plant *Heliotropium aegyptiacum* is

the characteristic species, with a very high mean cover-abundance value (7.000). This community occurs at an altitude of 1700 m.

Only nine (all herbs except one) out of the 33 reported medicinal plants were encountered in the 30 sample plots. Their mean cover-abundance values (also indicative of their frequency) were very low, except for *Heliotropium aegyptiacum* and *Solanum incanum* (see Table 7). Out of the nine medicinal plants, eight were recorded from three communities (community number 3, 4 and 5) that were predominantly agricultural areas. There was no medicinal plant recorded from community 1. As a result of their rare occurrence during the time when the vegetation survey was carried out, the rest of the cited medicinal plants were not encountered in the sample plots.

Discussion

Medicinal plants and associated knowledge

The reported number of medicinal plants (33 species) being used by the Zay people is not small, taking into account the small population size and the extent of deforestation and degradation, and acculturization that has occurred in the area through the years. In a similar study (Abbink, 1993) that was carried out on people called Me'en, whose population size was estimated to be 51,000 and inhabited an area with relatively better vegetation cover in the southwestern part of the country, 52 species of medicinal plants were reported. Tesfaye Awas and Zemede Asfaw (1999) also conducted a similar study on the Berta people of the Benishangul Gumuz Region in Western Ethiopia and their preliminary results showed 24 medicinal plants.

All the informants agreed that more medicinal plants were in use in the past than those reported now. This has happened as a result of continued deforestation, degradation and acculturization that has taken place in the area over several years. This situation gave way to the local loss of some medicinal plants and the associated knowledge. The shore areas of Lake Ziway that are currently inhabited by the Zay people were reported to have been covered by many tree species such as *Acacia tortilis*, *Acacia albida*, *Acacia tebaica*, *Balanites aegyptiaca*, *Ficus* spp., *Rhus glutinosa* and *Maytenus senegalensis*. Most of these trees have been destroyed, mainly due to the expansion of agriculture and widely practised charcoal making. Few of them are now found scattered on farmlands as remnants. One informant reported that a medicinal plant (local name not given), which was used as remedy against rabies, was lost as a result of the continued deforestation in the area. The informant was not sure whether the plant could be found in some other places in the country or not.

A rich knowledge of medicinal plants has also disappeared, because this knowledge was not properly passed down to the next generation by specialized healers of that time. These healers had a strong tendency of keeping their knowledge secret. Five informants, for instance, reported that the identity of one medicinal plant, which was used as a remedy against snakebites, was lost because holders of the knowledge kept it secret and died without releasing the information to anybody.

Today, there are no professional Zay healers in the area that regularly serve the community. Most of the knowledge is held by elders (picked up from their fathers and grandfathers), who mainly use it to keep the well being of their respective families. Occasionally, they offer help to other people within the community when a request comes. Most of these knowledgeable elders are men. Costentinos Berhe Tesfu et al. (1995) reported that the practice of traditional medicine in Ethiopia is dominated by men. According to Zemede Asfaw (personal communication), however, there are many female healers taking care of family level treatments even though the high level professional healing is mainly practised by men.

Result of interviews conducted on two groups of different age classes showed that older people are more knowledgeable on medicinal plants than the younger ones. The younger generation is more exposed to modernisation

Table 7. Mean cover-abundance values of recorded medicinal plants in the five clusters (community types).

Species name	Mean cover-abundance value in each of the five communities 1	2	3	4	5
Withania somnifera	0	0.28571	0	0	0
Heliotropium aegyptiacum	0	0.28571	0	0.18182	7
Solanum incanum	0	0	2.5556	0.90909	0
Senna occidentalis	0	0	0.66667	0	0
Achyranthes aspera	0	0	0.22222	0	0
Ocimum urticifolium	0	0	0.22222	0	0
Pavetta gardeniifolia	0	0	0	0.63636	0
Agave sisalana	0	0	0	0.36364	0
Indigofera spicata	0	0	0	0.18182	0

(e.g. modern education) and is therefore not interested in learning and practicing traditional medicine. Similar situations have been observed elsewhere. In Nepal, for example, the impact of modernization has been so widespread that only older people have a knowledge of traditional medicine (Manandhar, 1995).

The fact that most of the medicinal plants are known by either their Amharic or Oromo names gives us room to suspect that the major source of knowledge of the medicinal plants of the Zay people are both the peoples of Amhara (northern part of the country) and the Oromo (central part of the country). This might have occurred as a result of their long-standing historical relationship with the Amharic speaking people in the earlier times (Tuma Nadamo, 1982), and later on the close interaction they had with the neighbouring Oromo people. The younger generation of Zay community inhabiting the shore areas of Lake Ziway use Oromo language more frequently than their own (Zay language) in their day-to-day communication. This shows the strong relationship they have established with the Oromo people. This does not mean that the Zay people are using these medicinal plants exactly the same way they have been used by the peoples of Amhara and Oromo. Some modifications are expected to have happened in the process as traditional knowledge itself is dynamic and, in fact, we observed some changes in the way some medicinal plants are used in the area. In the treatment of haemorrhoids, for instance, the Zay people use the white latex of *Calotropis procera* (a recently introduced weed to the area), whereas the Amhara people use powdered seeds of *Calotropis procera* as a remedy against the same ailment.

Thirty-nine percent of the reported medicinal plants are used for the treatment of gastrointestinal problems and MICH. Gastrointestinal disorders and MICH are among the most highly prevalent diseases in the study area. According to Dawit Abebe and Ahadu Ayehu (1993), a certain complaint with several alternative drugs might indicate a preponderance of that particular health problem.

Solanum incanum and *Withania somnifera* are the two most frequently used species as remedies against a variety of complaints in the area. The high diversity of use of these two species could be attributed to their relative abundance in the area. The high consensus of the key informants on the medicinal use of the species *Solanum incanum*, *Withania somnifera* and *Cordia monoica* shows the importance of these plants to the Zay people. The high salience or familiarity of *Cordia monoica* (cited by 47% of the key informants) for use as a remedy against a particular ailment, MICH, might indicate its efficacy. According to Trotter and Logan (1986), pharmacologically effective remedies are expected to have greater informant consensus. According to Johns et al. (1990), however, confirmation is not a single true measure of the potential efficacy of any remedy. There is a great probability of a common plant, reported to treat a common disease, to be cited more frequently than a rare plant that is used to treat a disease of limited occurrence.

Most of the reported Zay medicinal plants (70%) are also used elsewhere in Ethiopia for their medicinal value, of which six species (*Allium sativum*, *Calotropis procera*, *Eleusine coracana*, *Hagenia abyssinica*, *Solanum incanum* and *Withania somnifera*) are in many instances used in the same way as they are used by the Zay people. The fact that some medicinal plants are used for the same purpose by more than one community (we may call it 'community consensus') might indicate the pharmacological effectiveness of these remedies. Thirty-seven percent of the plant remedies that were cited during the course of this study were also reported to have been used medicinally by authors in other parts of the world (Lal and Yadav, 1983; Johns et al., 1990; Ghazanfar and Al-Sabahi, 1993; Sequeira, 1994; Barrett and Kiefer, 1996; Karehed and Odhult, 1997; Weimann and Heinrich, 1997; Ballero and Pole, 1998). The active substances of some of the Zay medicinal plants are already known from other studies carried out elsewhere (Dawit Abebe and Estifanos Hagos, 1991).

Preparation, dosage and route of administration

Most of the reported preparations in the area are drawn from a single plant; mixtures are used rarely. In other parts of the country, the use of mixtures of plant species in treating a particular ailment is fairly common (Dawit Abebe, 1986). Synergic interaction or potentiating effect of one plant on the other, when in prescription of multiple sources, is well-recognized in Ethiopian traditional medical practice (Dawit Abebe and Ahadu Ayehu, 1993).

Lack of precision in the determination of doses has been noted in the area. According to Dawit Abebe and Ahadu Ayehu (1993), the major drawbacks in traditional medicine stem mostly from a lack of precision in dosage.

The majority of the remedies are taken orally. This agrees with the results of a study carried out by Dawit Abebe and Ahadu Ayehu (1993). They found that the main administration route of all the reported remedies used in Northern Ethiopia is an oral route, accounting for 42%.

Habit of the medicinal plants used

More than half of the Zay plant remedies were reported to have been obtained from herbs. This might indicate that the people have come to rely on herbs because they are relatively common in the area as compared to tree species. It takes much more time and effort to harvest medicinal trees. Dawit Abebe and Estifanos Hagos (1991) compiled a list of 51 medicinal plants used in the traditional health practices of Ethiopia, of which 30 species (56%) were herbs.

The most widely sought after plant part in the preparation of remedies in the area is the leaf. Collecting leaves does not pose a great danger to the existence of an individual plant when compared with the collection of an underground part, stem or whole plant. Studies have shown that removal of up to 50% of tree leaves does not significantly affect the growth of the species studied (Poffenberger et al., 1992). However, the popularity of roots including bulbs and rhizomes, barks and stems has grave consequences from both an ecological point of view and for the survival of the species (Dawit Abebe and Ahadu Ayehu, 1993). Costontinos Berhe Tesfu et al. (1995) reported that some plant species, such as *Dracaena steudneri*, *Hagenia abyssinica* and *Securidaca longepedunculata*, that are harvested for their roots, bark or whole part in many parts of the country have become scarce and thus difficult to find.

Habitat and status of the medicinal plants

Most of the medicinal plants utilized by the Zay people are harvested from the wild. This is also true in many other parts of the country. Tesfaye Awas and Zemede Asfaw (1999) reported that 71% of the medicinal plants of the Berta people in western Ethiopia were obtained from the wild. Zemede Asfaw (1998) reported that only six percent of plants maintained in home gardens in Ethiopia are primarily cultivated for their medicinal value, even though many other plants grown mainly for non-medicinal uses turn out to be important medicines when health problems are encountered. The fact that most of the remedies are only found in the wild poses a significant threat to their existence if the mass destruction of their habitats continues. The continued cutting of plants for different reasons has resulted in a scarcity of some medicinal plants in the study area (e.g. *Acokanthera schimperi* and *Cordia monoica*). Even those species that seem relatively common (those that favour disturbed areas) may soon be endangered. An increasing need to use more herbicides (especially on the mainland shore areas) and the continued use of farming plots for cultivation without leaving land fallow (as there is a shortage of farming plots in the area as a result of over-population) could also be potential threats to the existence of the Zay medicinal plants normally growing in agricultural fields in the area.

Analysis of the vegetation data collected from the relevés showed that almost all of the medicinal plants reported from the study area are rarely encountered. As most of the medicinal plants reported from the area are seasonal herbs, with the timing of the data collection being in the dry season, many of the were dry and, therefore, had low a probability of being encountered in the relevés. They are abundant towards the end of the long rainy season (August and September). Much time and effort is needed to harvest medicinal plants during the dry season. We were told that some medicinal plants only grow immediately after the rainy season, but these were not included in our survey because their identity was not known.

Medicinal plants and trade

There is no threat to Zay medicinal plants arising from trade, as they are only harvested for local use. But, the same medicinal plants could be available in markets elsewhere in the country. There are a number of Ethiopian medicinal plants (e.g. *Hagenia abyssinica*, *Embelia schimperi* and *Glinus lotoides*) that are widely traded for their domestic use (Kloos, 1976; Kloos et al., 1978). The only significant recorded medicinal plant export from Ethiopia is khat (*Catha edulis*), but it is traded primarily for its properties as a stimulant (TRAFFIC International, 1998).

Conclusion

The Zay people are partly dependent on medicinal plants to fulfil their day-to-day health care needs. A loss of medicinal plants and associated knowledge will, to a certain extent, hamper the existing health care system in the area, as there is no adequate modern health care programme that can fully shoulder this responsibility.

However, the knowledge of medicinal plants is declining in its depth and breadth and less and less medicinal plants are being utilized as generation goes by. The introduction of modern education to the area has partially contributed in making the younger generation undermine traditional medicinal knowledge and practices because such practices have been considered backward.

The environmental degradation and intense deforestation that have continued for a century, as a result of increased needs for farming lands, fuel wood and construction materials in the area, have been the main causes for the reduction in quantity (depletion) of medicinal plants. As a result, there has been a major shift in the type of medicinal plants used in the area, from forest-derived species to those growing in disturbed habitats (mostly herbs), such as roadsides and fallow land.

As environmental degradation and deforestation continue, there is a high probability of losing some of the rarely encountered medicinal plants from the area (e.g. *Acokanthera schimperi* and *Cordia monoica*). In the area, there is little practice of bringing medicinal plants under cultivation.

There is no real threat to the medicinal plants in the area as a result of over-harvesting for their medical purposes. They are only used locally and therefore harvested in small quantities. Furthermore, since most of the Zay remedies are obtained from leaves, the probability of survival of individual plants after harvest is expected to be high.

Most of the Zay medicinal plants are also widely used elsewhere in the country for their medicinal value (some of them even for the same medicinal use). The wide use of these medicinal plants could be attributed to their effective medicinal properties.

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Bee diversity along a gradient of disturbance in tropical lowland forests of Southeast Asia

Lee Hsiang Liow

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Bees are believed to be dominant pollen vectors in tropical forests, yet studies specific to bees in Southeast Asia are rare. Regeneration and restoration of the rapidly disappearing lowland forests of this region are reliant on bees thus there is an urgent need for forest bee community-level data.

I surveyed bee communities of eight forested sites in Johor (Malaysia) and Singapore three times each from Feb–Aug 1999 at the below-canopy level. These sites ranged from relatively undisturbed primary lowland dipterocarp forests to late secondary forests and exotic forests, including an oil palm plantation.

I attempted to elucidate the environmental factors that determined the distribution of bees in these forests. I also attempted to determine if there was a correlation between bee and bird diversity.

Bee abundance, in particular that of Apidae, was significantly higher in larger primary forests than other types of forests. However, bee species richness was higher in disturbed forests. The distribution of bees in surveyed forests was influenced by variables closely related to forest disturbance and resource abundance such as the density of big trees (dbh 30–40 cm), temperature, and flowering intensity of trees and shrubs. Large trees and more constant ambient conditions are more conducive to many trigonid bees which may have the ability to survive inter-mass flowering conditions (tolerant of lower flowering intensities) and utilize abundant resources during mass flowering, which in turn allows cross-fertilization among con-specific trees. No significant correlations between bird and bee species richness and abundance were found, probably due to a small sample size.

The differences between the bee communities in forests of urban Singapore and primary forests in Johor may indicate that ecological processes, in particular pollination, in Singapore may be declining. However pollination may not be totally intact in the primary forests surveyed, as their bee communities seem to be depauperate.

Lee Hsiang Liow, The Swedish Biodiversity Centre, CBM, Box 7007, SE-750 07 Uppsala, SWEDEN and the Dept. of Biological Sciences, National University of Singapore, Kent Ridge 119260, REPUBLIC OF SINGAPORE

Introduction

Threats to tropical lowland forests of Peninsula Malaysia and Singapore

Deforestation in tropical Southeast Asia is rapid and the rate was 1.6% between 1981-1990 compared with 0.9% in the rest of the tropics (Groombridge 1992). In particular, the island state of Singapore has largely been urbanized except for small forested areas, totaling to about 20 km^2 or 3% of Singapore's total land area (Lum 1999). There are also intensive land-use changes in Peninsular Malaysia since the 1970s and now the total lowland evergreen broadleaf forest (including disturbed natural forests) stands at 31.7% of which only 9.0% (2.9% of the total land area of Peninsular Malaysia) is protected (Anon.1999). In Johor, Malaysia, most of the original dipterocarp forests have been logged for timber or cleared for plantations. Oil palm plantations alone accounted for 525 360 ha (26.3%) of land in Johor in 1990 (Sukaimi et al. 1993). Little is known how this extensive habitat loss will affect species diversity and ecological processes. Floral and faunal inventories have not been comprehensive even in Peninsular Malaysia and Singapore where biological research had a fairly long history.

Why insects?

Invertebrates, the bulk of which are insects, may be much more important than vertebrates for the maintenance of vital ecosystem processes (Wilson 1987). However, few intensive surveys of tropical insect diversity have been made (Holloway et al. 1992, Kremen et al. 1993). The direct conservation of tropical insect fauna is also rare (Janzen 1987) although there are recent efforts to generate interest in insect conservation (Collins & Thomas 1991, Samways 1994). It is also a recent trend to use insect taxa (including butterflies, tiger beetles and termites) as habitat or environmental quality indicators (e.g. Holloway & Barlow 1992, Pearson & Cassola 1992, Eggleton et al. 1996).

Why bees and pollination?

Anthropogenic changes such as the conversion of native habitats and the introduction of exotic species will have more apparent effects through the loss of original vegetation architecture and native species than the loss of ecological processes (Kearns & Inouye 1997). However, the loss of ecological processes, e.g. pollination, is equally, if not more destructive than physical changes, to a natural ecosystem. Detrimental effects of pollinator declines (genetic erosion, decreases in species richness and ecological diversity) were discussed by Buchmann & Nabhan (1996) and Allen-Wardell et al. (1998). Threats of habitat alteration, agriculture, grazing, habitat fragmentation and alien introductions to native bees have also been recently reviewed (Kevan 1993, Verma 1993, Kearns & Inouye 1997). This study deals with bees also because they are believed to be the most dominant pollen vectors in tropical forests (Bawa 1990, Renner & Feil 1993, Roubik 1993a). For instance, 74% of the insects visiting flowers in Sumatra are apid bees (Inoue et al. 1990).

The bee fauna of the oriental region is the poorest (89 genera) in the world (Michener 1979) and accordingly, the bee fauna in tropical Southeast Asia is also species poor, despite an extremely high plant species richness (Whitmore 1984). However, tropical bee communities are more ecologically diverse (Roubik 1989, 1992). This means that each bee species in the tropics plays more roles in their ecosystem and may have a greater part in maintaining the angiosperms than bees in other regions (Michener 1979).

Despite their purported roles as dominant pollen vector, studies specific to bees in tropical Southeast Asia are rare, in contrast to the neotropics (e.g. Bawa et al. 1985, Roubik 1993b, Frankie et al. 1997 and references therein). There are many botanical and anecdotal accounts of bee-pollinated plants in Southeast Asia (e.g. Jackson 1981, Appanah 1987, Momose et al. 1997) but few studies specifically deal with the pollinators themselves. Exceptions include studies done in Sarawak (Kato 1996, Inoue & Hamid 1997, Nagamitsu & Inoue 1997), Peninsular Malaysia (Appanah 1981), Brunei (Roubik 1996) and Sumatra (Sakagami et al. 1990, Salmah et al. 1990), but these are concerned mainly with the family Apidae.

Objectives of this study

There is no comprehensive inventory, systematic comparison between sites or study on the habitat requirements of bees in Malaysian and Singaporean forests. We attempt to partly fill these gaps.

First, I ask if there are differences in the assemblage of bee species found at the different sites, in particular between undisturbed and disturbed sites. I test the hypothesis that primary forests are richer than disturbed forests in species richness and abundance of bees. Second, I ask whether there are habitat preferences for bees. I test whether vegetation structure and/or microclimate variables affected the distribution of the bee species. Third, I ask whether both total bird species richness and richness in different feeding guilds correlated with bee species richness and abundances to determine if both these taxa show similar distribution patterns. Finally, I attempt to make generalizations on the bees found at the below-canopy level in forests of varying disturbances in the southern Malay Peninsula and discuss what the results of this study spell for the conservation of this region.

Materials and methods

Study sites

Eight sites were surveyed, five in Singapore and three in Johor, Malaysia (Fig. 1), to represent a range of tropical lowland forests of varying degrees of anthropogenic disturbances. A summary of the forest types (definitions based on Whitmore 1984) and background information of the eight sites are given in Table 1.

Bee surveys

Preliminary studies were conducted between December 1998 and January 1999 to optimize sampling methods. Three yellow funnel traps and three yellow floating platforms on petri dishes were set up at MacRitchie, Singapore with baits (honey solutions, sugar solutions and banana pulp) in December (1998) to test the feasibility of trapping and/or attracting bee individuals. The traps were set 50 m apart with funnels alternating with the petri dishes. Some bees were trapped after entering the funnel or by the surface tension of the liquid. Both methods rendered the bees wet, making taxonomic identification difficult. The average trap rate (± S.E.) were 9.0 ± 2.4 and 8.3 ± 4.3 for individuals/trap/day for funnel traps and perti dishes respectively. Bees were not attracted to banana pulp.

Honey baiting on vegetation was also tested. Honey-salt-water and sugar-salt-water solutions of varying concentrations were made and sprayed on vegetation 1–2 m from the ground at both sites. At MacRitchie there were three baiting spots of about 1 m in diameter for different concentrations of honey or sugar solutions while at Bekok there was one of each. The baiting spots were about 10 m apart at each site.

It was found that a solution of honey diluted in the ratio of 1:2 (honey:water, V:V) and solutions diluted in the ratio of 1:4 (honey:water and sugar:water), with salt concentration constant at 2 cm^3 in 500 ml of solution sprayed on vegetation, did not have significantly different recruitment rates for different morphospecies of bees. It was also found that the method of baiting on vegetation was more efficient at attracting bees than that of baited funnels type traps and petri dishes. During each check, approximately 20.0 ± 2.8 trigonid bees were counted at individual vegetation baiting spots.

For the actual bee surveys, one to three transects of 0.5–1 km were set-up at each site (see Table 1 for transect lengths). Honey solution (1:4, honey:water) with 2 cm3 salt/500 ml of solution, standardized with a hand refractometer was used to attract bees. Thirty jets (20 ml) of this solution were sprayed on the vegetation marked with colored flagging tape every 100 m along the transacts. The baited spots were about 1 m in diameter and between 1–2 m above the ground. The baits were replenished every other time the transects were checked by spraying 15 jets of the solution on the same previously sprayed spots. If the solution was washed away

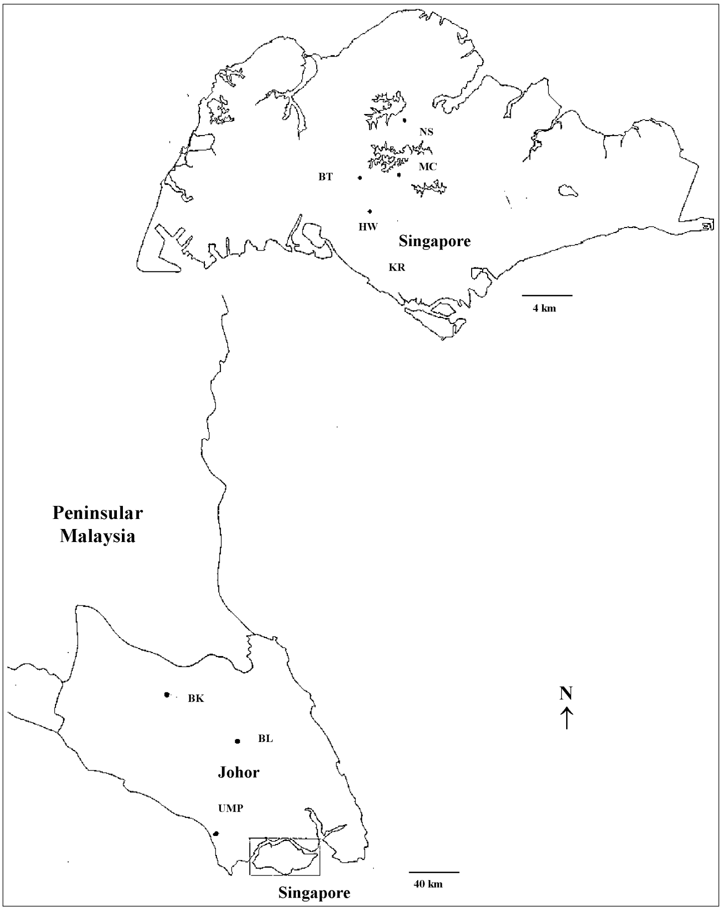


Fig. 1. The eight study sites where BK = Bekok, BL = Belumut, BT = Bukit Timah Nature Reserve, HW = Holland Woods, KR = Kent Ridge, MC = MacRitchie, NS = Nee Soon, and UMP = UMP oil palm plantation.

by rain, the baiting spots were sprayed at least half an hour before the transects were surveyed again. Bees attracted to each of these baited spots were caught with a standard insect net four times a day (between 0730 and 1700h), during a maximum of three minutes. The time lapse between bait application and collection ranged from 30 minutes to 16 h (e.g. when the bait was left over-night). I waited at each baited spot for 20 seconds to scan the area for bees and moved on if there were none. Bees spotted when I was walking along the transects were also collected and the substrates on which they were caught were recorded. Each collection cycle at a particular site ran for three consecutive days. I visited each study site three times between February and August 1999 (Table 1). Temperature, humidity and light intensity were measured every 200 m of a transect during the first and the third check of the transect during the day using a thermo-hygrometer and an illumination meter.

The collected bees were identified with the help of R. W. Brooks (Snow Entomological Museum at the Kansas State University) and are now deposited at the Raffles Museum of Biodiversity Research (RMBR) of the National University of Singapore and the Snow Entomological Museum of the Kansas State University.

Floral resource availability

To determine if floral resource availability affected the numbers of bees caught, the flowering intensity every 200 m along the transacts were recorded on the second day of each bee collecting cycle. Binoculars were used to scan a circular area (8 m radius = approx. 200 m^2 ground area) and trees (more than 2 m in height) with open flowers were counted. A 50 m^2 area was divided into ten sectors and the number of sectors with flowering shrubs recorded. In both cases, open flowers are defined as single flowers or parts of inflorescence with anthers and/or stigmas no longer being concealed by the corolla and/or calyx but before the corolla and/or calyx falls off. When the perianth was not obvious, open flowers were taken to be single flowers or parts of the inflorescence with mature anthers or stigmas.

Vegetation sampling

To determine if vegetation structure is a factor in determining bee species distribution, the following variables were measured and recorded along transacts at 150 m intervals.

1) The canopy cover of the forest, using a spherical densiometer, according to Lemmon (1957)
2) The dbh (density at breast height) of trees having more than 2 cm. I also visually estimated if these trees are more or less than 10 m in height.
3) The number of trees having less than 2 cm dbh.
4) The number of dead trees.
5) The number of palms.
6) The percentage ground cover.
7) The leaf litter depth that was obtained by gently inserting a ruler vertically into the leaf litter at twelve random points in each plot.

Bird surveys

To determine if bee species diversity correlated with resident bird species diversity, bird surveys were carried out on four days (between about 0730-1100 h) at each site. The bird species recorded during these surveys were used to generate a species list (Appendix 1) for each of the eight study sites. Only resident birds (including introduced bird species that are known to have established breeding populations in the study sites) were used for analyses.

Data analyses

The Kruskal-Wallis test was used to determine if the catch-rate of bee species and number of bee individuals at the eight study sites were significantly different. On finding that there were significant differences, the catch-rates were manually ranked and Duncan's multiple range test was used to determine which sites were different from the others. The two catching methods (netting at baits and netting along transects) were compared using the Mann-Whitney U test. All these tests were performed using SAS version 6.12. Bee diversity indices (Margalef's, Menhinick's, Simpson's, Berger-Parker, McIntosh's, Brioullin's and Shannon's indices) were hand calculated according to Magurran (1988). Each set of indices was ranked and Kendall's coefficient of concordence, W, calculated according to Siegel & Castellan (1988).

The bee species presence-absence data from 21 transects in the eight study sites were subjected to a Cluster Analysis using PC-ORD version 2.0. This analysis used Euclidean distance and Ward's method. Similarly, the presence-absence data of the Apidae species from my eight study sites and those from Brunei (Roubik 1996) and Sumatra (Salmah et al. 1990) were also subjected to a Cluster Analysis. Twenty-four environmental variables (the mean dbh and density of trees < 10 m height/plot, the mean density of palms < and > 10 m height/plot, the mean dbh and density of trees > 10 m height/plot, the mean number of tress < 2 cm dbh/plot, the mean number of dead trees/plot, shrub and canopy cover, leaf litter depth, the density of trees with dbh < 10 cm, between 10-20 cm, 20-30 cm, 30-40 cm and > 40 cm, the number of flowering trees/m2, the flowering density index of shrubs, mean and standard deviation of temperature, humidity, and light intensity) were correlated using SAS. From all groups of variables with a Pearson correlation coefficient > 0.50, only one variable was retained for ordination analysis. The retained variables were the ones that were most biologically relevant: the mean density of trees < 10m height per plot, leaf litter depth, the mean density of trees with dbh between 30-40 cm, the number of flowering trees/m^2, flowering density index of shrubs and the mean temperature.

To determine the factors affecting the distribution of bee species, Canonical Correspondence Analysis (CCA) (ter Braak 1986) in PC-ORD 2.0 was performed using data matrices of log-transformed bee species abundance data and the six environmental variables retained. Axis scores were standardized using Hill's (1979) method and scaled to optimize the representation of species.

The number of bird and bee species recorded, the absolute number and rate of collection of bees were correlated using Spearman correlation coefficients (SAS). Similarly, the number of bee species recorded and the rate of collection of bees were correlated with the number of insectivorous, necterivorous and frugivorous birds (data from del Hoyo et al. 1992, Jeyarajasengam & Pearson 1998) recorded during this study.

Results

Overall species diversity

Forty-five morphospecies and 1613 individuals from five bee families (Anthophoridae, Apidae, Colletidae, Halictidae and Megachilidae) were collected during 71 days (279 h). The three most abundant species in the eight sites combined were *Trigona (Tetragonula) geissleri* Friese 1918, *T. (T.) melina* Gribodo 1918 and T. (T.) laeviceps Smith 1857 with 412, 202 and 546 individuals collected, respectively, while seven species, *T. (Lepidotrigona) ventralis* Smith 1857, *T. (Geniotriogona) thoracica* Smith 1857, two species of *Nomia (Maculonomia)*, two species of Lipotriches and one species of Halictidae were collected only once each during the collection period (Appendix 2). The total number of species collected at each site ranged from four at Nee Soon to 22 at MacRitchie. The total number of individuals collected ranged from 63 individuals at Kent Ridge Park to 444 individuals at Belumut (Appendix 2).

One nest each of five species was encountered at three sites. The nests of *Trigona (Heterotrigona) itama*, *T. (Tetrigona) apicalis*, *T. (Tet3ragonula) meilna* and *T. (Lepidotrigona) terminata* were found in trees with dbh from 50 cm while that of *T. (Tetragonula) laeviceps* was found in the ground (Appendix 3).

The cumulative collection curves (Fig. 2) at Bekok, Belumut, Bukit Timah, Holland Woods, Kent Ridge appear to have reached their asymptotes during this study. However, those at MacRitchie, Nee Soon and the UMP oil palm plantation are still rising. Only bees of the honeybee family, Apidae, were encountered at the two large primary forest tracts in Johor while the family Halictidae dominated in the oil palm plantation, an exotic forest (Figs. 3a and 3b). *Apis mellifera* Linn. 1758, the globally widespread exotic honeybee, was not found.

Comparisons between bee capturing methods

The mean numbers (± SE) of bees caught at baits and along transects were 5.62 ± 2.65 and 1.08 ± 0.39 inds. h-1, respectively. The baiting method was significantly more efficient at catching bees than just netting bees sighted along transects (Mann Whitney's U = 10.426, df = 7, $P < 0.0012$). The mean number of Apidae caught at baits (3.83 ± 4.63 individuals per hour) was significantly higher than the mean number of non-Apidae bees caught at baits (0.09 ± 0.07) (U = 29.011, df = 7, $P < 0.0001$). Of the all bees caught while they were approaching or foraging on flowers, 80.2% were caught on only four species of continuously flowering plants. These were *Dillenia suffructicosa* (Griff.) Martelli, *Melastoma malabatricum* Linn., *Asystasia instrusa* Blume and *Stacytarpheta indica* Vahl., of which the first two are plants of early secondary forests and the last two are weeds found in open areas. All are native plants except S. indica that originated from South America.

Bee diversity

The number of individuals and species collected per hour varied from 1.63 ± 0.22 and 0.38 ± 0.11

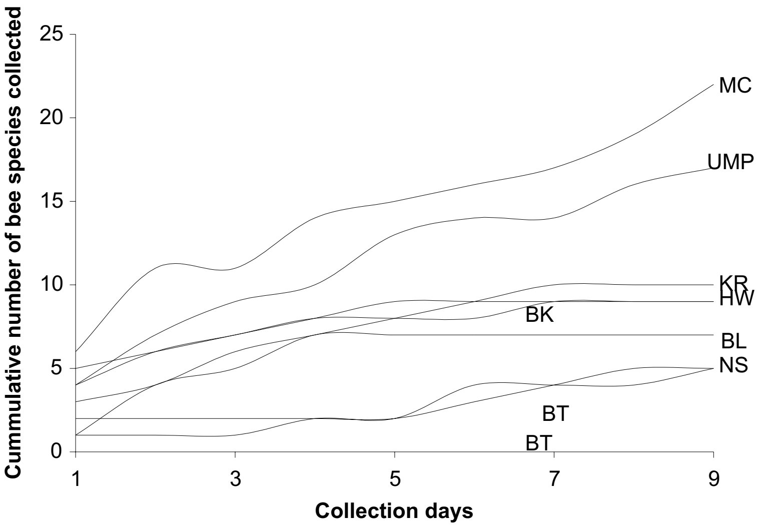


Fig. 2. The cumulative number of bee species collected at the eight study sites. For site abbreviations see Table 1.

(Holland Woods and Bukit Timah) and that of individuals varied from 12.15 ± 1.48 to 0.95 ± 0.26 (Bekok and Bukit Timah), respectively (Figs. 4a and 4b). The mean numbers of bee species caught per hour differed significantly among sites (KW = 44.763, df = 7, $P < 0.0001$). Duncan's multiple range test showed that the ranked mean number of bee species caught per hour at Belumut, NeeSoon and Bukit Timah were significantly lower than that at Holland Woods, MacRitchie, Bekok and Kent Ridge ($P < 0.05$). The mean numbers of bee individuals caught per hour differed significantly among sites (KW = 40.673, df = 7, $P < 0.0001$). Duncan's multiple range test showed that the ranked mean number of bee individuals caught per hour at Bekok and Belumut were not significantly different from each other but were significantly higher than that at the remaining sites ($P < 0.05$), with the exception of Nee Soon.

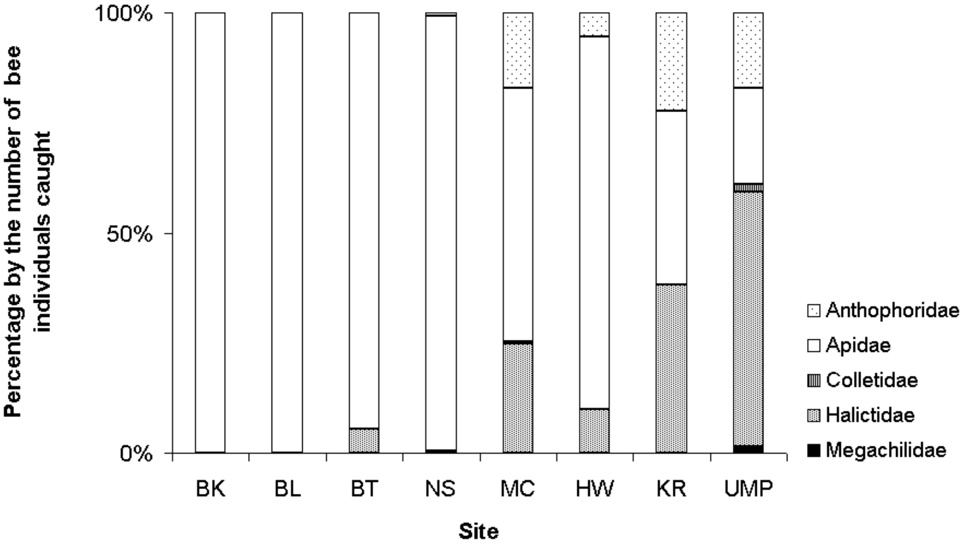
Bee diversity indices for sites

Of the eleven diversity indices calculated, six gave the most disturbed forest, the oil palm plantation the highest diversity value and Nee Soon, a late secondary forest the lowest diversity value (Table 2). The Kendall coefficient of concordence, W was significant ($W = 0.453$, $P < 0.0001$), indicating reasonably good consensus among indices. Averaging the ranks of the sites (using the 11 indices and the total number and species of bees collected at each site), the most diverse site was MacRitchie, a secondary forest while the least diverse site was Bukit Timah Nature Reserve, a small primary forest (Table 2).

Bee community similarity among sites

Three of the more disturbed forests (Kent Ridge, Holland Woods and the UMP Oil Palm Plantation) and transects A and B from MacRitchie (a secondary forest) formed the first main cluster in the dendrogram drawn using presence-absence data of all bee species found. The remaining sites consisting of the three primary forest sites (Bekok, Belumut and Bukit Timah), one secondary forest site (Nee Soon) and transect C from MacRitchie formed another main cluster. Five out of six transects from the two large tracts of primary forests (Bekok and Belumut) were very similar while many transects from the closed forests in Singapore grouped together (Fig 5).

A dendrogram of bees of the family Apidae (including *Trigona* and *Apis*) was drawn using presence-absence data separated the sites from this study (Singapore and Johor) from the a)



b)

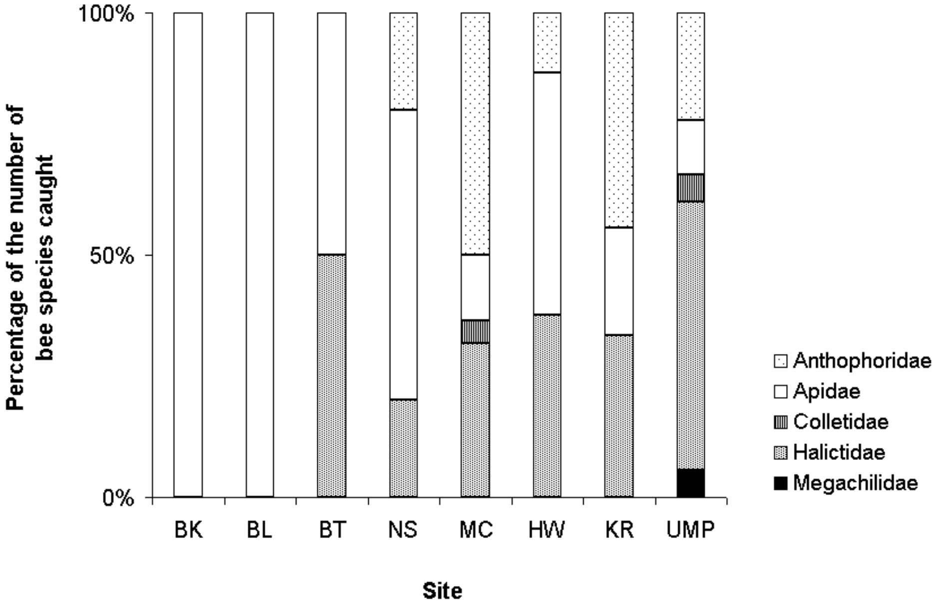


Fig. 3. a) Proportion of bee families collected at each site (based on number of individuals collected) and b) Proportion of bee families collected at each site (based on number of species collected). For site abbreviations see Table 1.

Table 1. Summary of information on study sites surveyed for bees from February to August 1999 including: 1) The names, state and countries of the study sites and abbreviations used in the text; 2) the description of the forest type (based on Whitmore 1984); 3) the landscape of the matrix surrounding the surveyed forest; 4) the geographical co-ordinates of the sites; 5) the size of the sites; 6) the dates of the bee surveys; transact lengths at each site and 7) approximate age of the forests.

Name and location of site and abbreviation used in text	Description	Surrounding matrix	Coordinates	Size (ha)	Dates of bee surveys (1999)	Transact Length, km (hrs surveyed)	Approx. age
Belumut, Johor Malaysia (BL)	primary hill Dipterocarp forest	Oil palm and rubber plantations and logged forests	2°03.90N 103°31.57E	>2000	9-11 Feb; 25-27 May; 3-5. Aug	1.2 (16.04) 1.1 (4.63) 0.5 (13.99)	Never logged
Bekok, Johor Malaysia(BK)	primary lowland /hill Dipterocarp forest	Oil palm and rubber plantations and logged forests	02°20.84N 103°09.41E	>2000	17-19 Jun; 13-15 Jul; 11-13 Aug	1 (13.80) 1 (16.59) 1 (13.26)	Never logged
Bukit Timah Nature Reserve, Singapore (BT)	Primary hill Dipterocarp forest	Urban areas 103°50'E	1°20'N	87 20-22 Apr; 28-30 Jun	3-5 Mar; 1 (12.80) 1 (11.39)	1 (12.24)	Never logged
MacRitchie, Singapore (MC)	Secondary forest with primary patches	Urban areas and secondary forest		521	24-26 Feb; 12-14 Apr; 22-24 Jun.	1 (12.04) 1 (10.32) 1 (12.41)	60-80 yrs
Nee Soon, Singapore (NS)	Secondary forest with primary patches	Urban areas and secondary forest		794.6	16-18 Mar; 26-28 Apr; 6-8 Jul	1 (16.16) 1 (14.34) 1 (14.64)	60-80 yrs
Holland Woods, Singapore (HW)	Secondary forest mixed with (*Albizia* spp.) exotic forest	Urban areas		41.5	5-7 May; 8-10 Jun; 26-28. Jul	1.8 (24.42)	20-40 yrs
Kent Ridge Park, Singapore (KR)	Secondary forest and open parkland	Urban areas		27.2	30 Mar-1 Apr; 18-20 May; 1-3 Jul	1 (10.96) 1 (11.88)	20-40 yrs
UMP , Oil Palm Plantation Johor (UMP)	Uniform oil palm) stand(*Elaeis guineensis*	Pineapple,rubber and fruit trees plantations	1°35.81N 103°27.57E	2105.6	12-14 Mar; 12-14 May; 20-22 Jul	1 (11.75) 1 (12.45) 1 (13.13)	Cleared: 1946/7

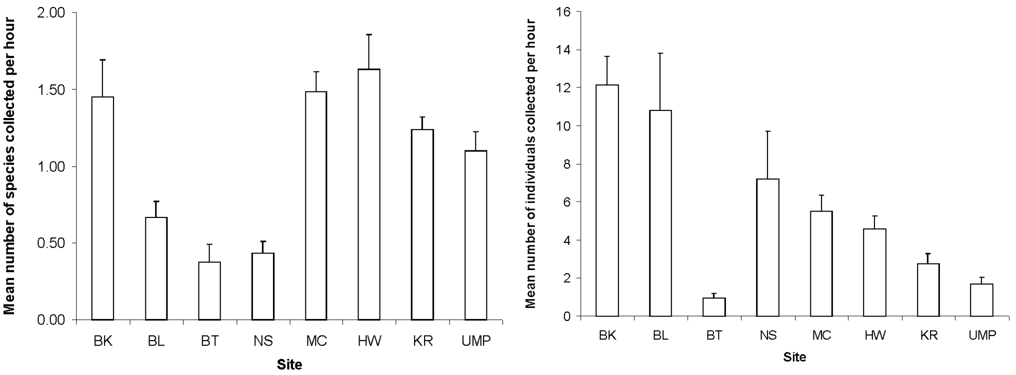


Fig. 4. a) Mean number of species collected per hour at each site and b) Mean of number of individuals collected per hour at each site. For site abbreviations see Table 1.

Sumatran sites (data from Salmah et al. 1990) and those in Brunei (data from Roubik 1996) (Fig. 6). Within the sites from the present study, the primary forests in Johor were clearly distinguished from the rest of the sites in Singapore and the oil palm plantation in Johor. Within the Sumatran and Bornean sites, the pristine primary forests formed a separate cluster (Fig 6).

Environmental factors affecting bee distribution

A Canonical Correspondence Analysis (CCA) was performed on a primary data matrix consisting of log transformed numbers of bee individuals collected per hour for 45 bee species and a secondary matrix with six environmental variables. The first two CCA axes explained 28.2% and 22.4% of the variation in the data sets, respectively (Table 3). Both the first and second axes had high loadings of the mean temperature of the sites and the flowering density index of shrubs (Table 3). Five groups of bees can be distinguished, namely the honey bees (group 1), the 1st group of stingless bees (group 2, including *melina*, *itama*, *reepeni*, *ventra* and *terminata*), the 2nd group of stingless bees (group 3, including geisslerei and laeviceps), the 1st group of Megachilids and Anthophorids (group 4, including *Nomia*, *Cerat-*

Table 2. Bee species richness (S), absolute numbers of bees (N) collected at each site (see Table 1 for abbreviations) and diversity indices calculated according to Magurran (1988). D (Mg) = Margalef's index, S (Mn) = Menhinick;s index, 1/D(S) = inverse of Simpson's index, N/Nmax = inverse of Berger-Parker's index, U (McIn) = McIntosh's index in general form, D (McIn) = McIntosh's dominance measure, E (McIn) = McIntosh's evenness, HB = Brillouin index, E of HB = Brillouin's evenness index, H? = Shannon's index and E of H? = Shannon's evenness index.

Sites	S	N	D (Mg)	D (Mn)	1/D (S)	N/ Nmax	U	D (McIn)	E (McIn)	HB (McIn)	E of HB	H'	E of H'
BK	9	419	1.32	0.44	3.39	2.07	228.07	0.48	0.68	0.373	0.71	1.543	0.256
BL	7	444	0.98	0.33	2.12	1.77	305.59	0.33	0.5	0.66	0.27	0.881	0.145
BT	5	42	1.07	0.77	1.6	1.27	33.44	0.24	0.36	0.282	0.2	0.765	0.205
NS	5	232	0.73	0.33	1.1	1.05	221.09	0.92	1.55	0.098	0.14	0.249	0.046
MC	22	242	3.83	1.41	4.96	2.95	109.48	0.59	0.7	0.819	0.65	2.018	0.368
HW	9	111	1.7	0.85	3.85	2.41	57.3	0.53	0.73	0.643	0.76	1.598	0.339
KR	10	63	2.17	1.26	4.12	3	31.73	0.57	0.73	0.622	0.74	1.608	0.388
UMP	17	64	3.86	2.13	8.88	4.92	22.58	0.74	0.85	0.881	0.82	2.259	0.543

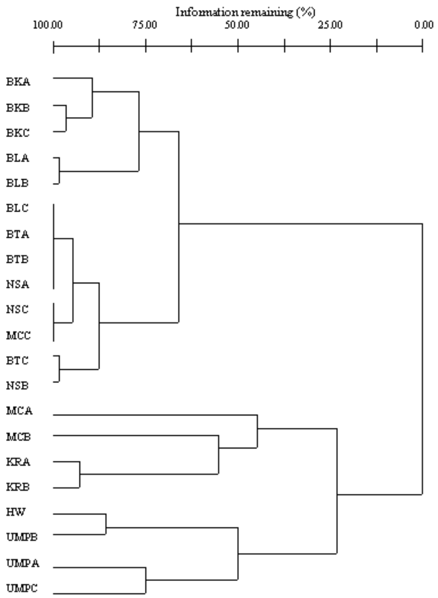


Fig 5. A dendrogram of bee species recorded along the transects of the eight study sites (See Table 1 for abbreviations).

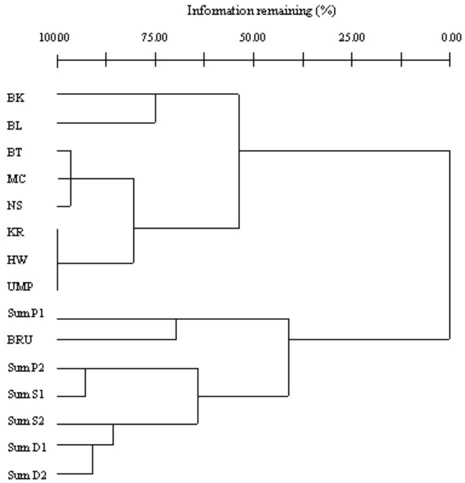


Fig. 6. A dendrogram of the distribution of Apidae in 14 sites, where BK, BL, BT, MC, NS, HW, KR, UMP are from this study, (see Table 1 for abbreviations), Sum P1= Primary forest, Sum P2 = Primary forest mixed with secondary forest, Sum S1 = Secondary forest, Sum S2 = Secondary forest mixed with other disturbed habitats, Sum D1 = coconut plantations and orchards, Sum D2 = villages (Sumatran sites from Salmah *et al.* 1990) and Bru = Brunei primary forest (Roubik 1996).

ina, *Amegilla*, *Xylocopa*) and the 2nd group of Megachilids and Anthophorids (group 5, including *Lipotriches* and *Lassioglossum*) (Fig. 7). Both the groups of stingless bees increased in abundance with the increase in the number of big trees (the density of trees with dbh between 30-40 cm), and decreased with increasing temperature and flowering intensity of both trees and shrubs. The honey bees appear to prefer average conditions or may not be strongly affected by the measured variables. Group 5 increases in abundance with increasing flowering intensity and temperature and tolerates the low density of larger trees (Fig 7).

Correlation of birds and bees

The species richness of birds and bees, and the absolute abundance and catch rate of bees were not correlated. However, bird species richness increases with bee abundance. There are also no significant correlations between the number of insectivorous, nectarivorous, frugivorous birds and the bee species richness or catch rates of bees. Although, again, the number of insectivorous bird species increases with the abundance of bees. This may be due to the limitation of a small sample size (N = 8). Plotting bird richness and bee abundance along a disturbance gradient shows that both values decrease with disturbance (Fig. 8), especially when the outlier, BT (Bukit Timah) is removed.

Discussion

Bee community characteristics at the eight sites

Within the limitations of the collecting methods used, it can be seen that disturbed forests tend to have greater absolute bee species richness. These disturbed habitats may also attract more ”tourists”, i.e. bees that do not reside within the habitat under investigation and those with potentially greater foraging ranges (e.g. the trap-lining *Amegilla* and *Xylocopa* spp.). However, the relatively undisturbed lowland Dipterocarp primary and secondary forests have greater absolute abundance of bees.

The Apidae, especially the genus Trigona, is

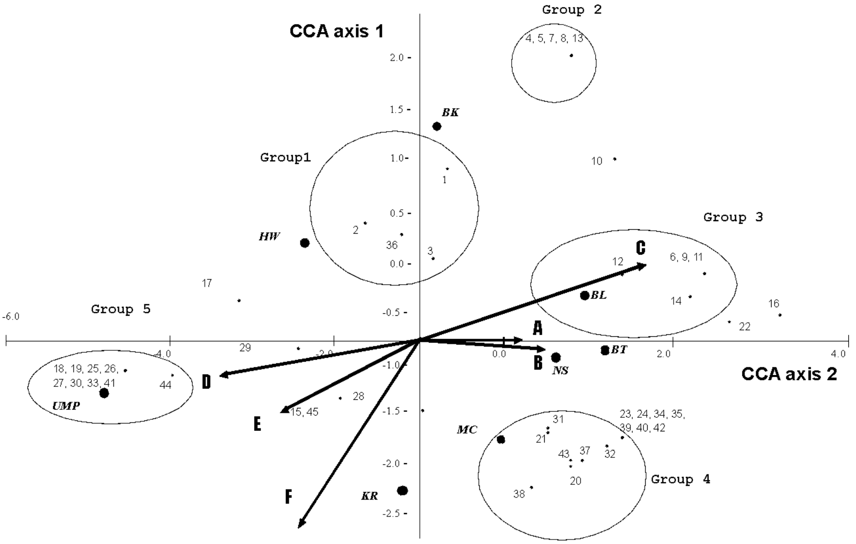


Fig 7. The ordination diagram from the CCA of a primary matrix of the log transformed numbers of bees collected per hour and a secondary matrix of six environmental variables and their canonical coefficients. Solid circles refer to sites (for abbreviations, refer to Table 1), small diamonds refer to bee species (refer to Appendix 2), the arrows A-F refer to environmental variables where A = Density of trees < 10 m in height, B = leaf litter depth, C = density of trees with dbh between 30-40 cm, D = flowering tree/m^2, E = flowering density index of shrubs and F= temperature.

ubiquitous in the rain forest (Appanah et al. 1986) and are important pollinators, especially in the under-story (Bawa & Opler 1975, Appanah 1981). Both the primary and secondary forests habour a much greater proportion of Apidae: the more undisturbed by human activity the forests, the fewer non-Apidae bees can be found in the under-story. In fact, only *Apis* and *Trigona* of the family Apidae were recorded in Bekok and Belumut. In similar but smaller forests in Singapore, the Apidae were also relatively dominant (99.1% of all bees caught in Nee Soon and 95.2% in Bukit Timah Nature Reserve). MacRitchie, another late secondary forest in

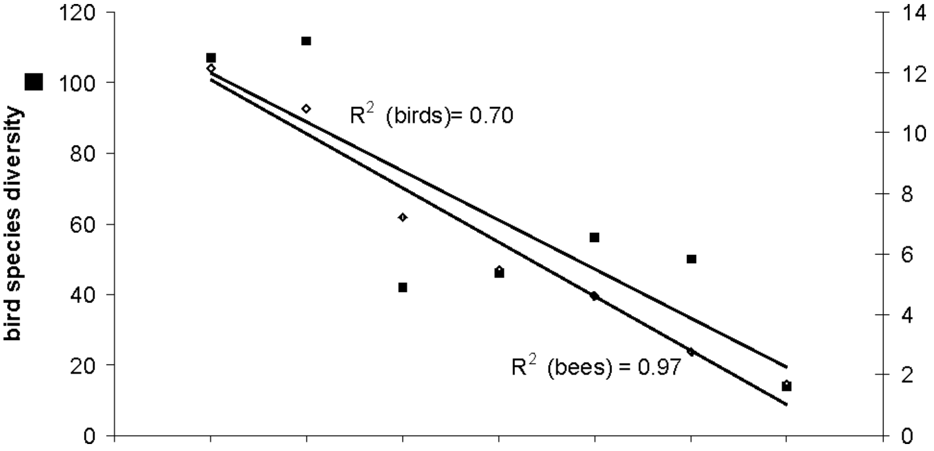


Fig. 8. Birds and bees along a disturbance gradient (minus outlier BT)

Table 3. Summary statistics of the 1st two CCA axes of the CCA performed with a primary matrix of the log transformed numbers of bees collected per hour and a secondary matrix of six environmental variables and their canonical coefficients.

Canonical Axis	1	2
Eigenvalue	0.668	0.529
% of variance in species data explained	28.2	22.4
Cummulative % of variance in species data explained	28.2	50.6
Pearson Correlation (Spp- Env)	0.995	0.999
Environmental variables (Abbreviation)	Canonical	coefficients
Density of trees <10m height (A)	-0.121	0.6
Leaf litter depth (B)	0.499	-0.326
Flowering trees/m2 (D)	2.08	-1.896
Flowering density index of shrubs (E)	-2.013	1.67
Temperature (F)	2.935	-4.204

Singapore has a somewhat mixed habitat. Two of its transects (A and B) were more open and haboured more weedy, constantly flowering shrubs and early pioneer species (pers. obs.). This observation is supported by the analysis which clustered these two transects with those from Kent Ridge Park a relatively young, open forest (Fig. 5). The two more abundant families of non-Apidae bees were the Anthophoridae and the Halictidae. The remaining two families (Colletidae and Megachilidae) were rarely collected or observed during this study. The Anthophoridae and Halictidae favoured the more open and disturbed forests. They are frequently caught on flowers of common early secondary plants and widespread weeds in open habitats. This is in contrast to Kato's (1996) observation in Sarawak where *Amegilla* of the Anthophoridae was noted as shade-loving. This may indicate that these bees are more adaptable than previously reported.

There is no reason to believe that Sumatra and Brunei have a different bee composition from Peninsular Malaysia with the exception of a few endemic species. But 13 out of 27 species of *Trigona* and *Apis* found in Sumatra and Brunei, and thus expected during this study, were never encountered. It is not known why this was so, despite a comparatively lengthy collection period that included months with a higher flowering intensity in the lowland forests (March to July, Medway 1972) and similar collection methods. Perhaps some species are becoming so rare, even in the primary forests of Johor, that chance encounters are very low. It must be born in mind that these primary forests of Johor are also forest fragments, albeit large ones, and they are surrounded by plantation forests. The alternative explanation is that population numbers of certain species may be low during inter-mass flowering periods, hence decreasing the number of chance encounters. On a positive note however, the feral *Apis mellifera* was never encountered during this study even in the most disturbed forest habitats.

The inadequacy of classical diversity indices

Diversity indices such as the ones calculated in this study are not adequate in reflecting the biological status of the habitat in consideration. The primary forest sites are ranked less diverse by these indices when the absolute abundance of bees may be more important in maintaining the ecosystem than the absolute number of species. The ecological roles of the species involved must be considered when deciding how undisturbed a habitat is.

Resources for foraging bees

Mass flowering in the lowland Dipterocarp forests of West Malesia is a well-known phenomenon (Appanah 1985), although it is little understood (Corlett 1990). During the inter mass flowering years, however, the level of flowering is kept more or less constant by a changing assortment of species and the peak flowering period during any year appears to be between March to July (Medway 1972). This study spans this period of high flowering intensity although it did not coincide with a mass flowering period, hence it sheds light on the bee community structure during 'normal' periods of flowering intensity in Bekok, Belumut, Bukit Timah, Nee Soon and MacRitchie, all of which have at least some resemblance to the forests described by Medway (1972). The Apidae must have some mechanisms for tiding over periods of low flowering and these may include storage of resources and/or the use of resources other than nectar and pollen (e.g. extra-floral nectaries) to maintain densities large enough to utilize efficiently the mass flowering phenomenon when it occurs.

In the three remaining sites, where plant species composition is different and species diversity lower, flowering of both trees and shrubs is quite constant. We may speculate that many solitary bee species from the Anthophoridae and Halicatidae found in these forests need not be adapted to store food because of a constant supply of open flowers.

Different species or even genera and families of bees are sometimes not very specific in their choice of resource. One of us (Liow) has seen bees from all the four major families (Apidae, Halictidae, Megachilidae and Anthophoridae) foraging on *D. suffructocisa*, *M. malabatrhicum*, *A. instrusa* and *S. indica* flowers despite differences in the architecture of the flowers. *Trigona* have been reported to be polylectic, visiting flowers of many different plant species (e.g. Kato 1996). This may be due to the unpredictability of flowering in the West Malesian tropics (Roubik 1992), requiring bees to be flexible in their resource use and thus to be primarily generalists instead of specialists (Waser et al. 1996).

However, the honey baits tended to attract mainly the honey bees (*Apis*) and stingless bees (*Trigona*). This could be indicative that the concentration and method of presentation of the sugars was attractive only to the Apidae.

Environmental parameters, forest disturbance and the distribution of bees

Many of the environmental variables, thought to be important in defining the habitat for bees, are related to the level of disturbance in the forest. In the relatively undisturbed forests, temperature and light intensity were lower, humidity higher, and all the three variables more constant than in the rest of the sites. This is due to a closed canopy that results from the higher density of sub-canopy and canopy trees. Hardly any understory plants or trees were observed flowering during this study. Under these conditions, only bees of the Apidae were collected in the understory. The species richness within Apidae in Bekok and Belumut were higher (nine and seven respectively) than that in the other sites. Out of the total of 14 species of Apidae collected at these two sites, eight were not collected elsewhere. In particular, *T. melina*, an abundant species collected at Bekok appears to be a species restricted to primary forests, as also indicated by the Sumatran study (Salmah et al.1990). This species may be restricted by its small foraging range, (common to most if not all trigonids e.g. Roubik & Aluja 1983, van Nieuwstadt & Iraheta 1996) and fragile nest structure (Appendix 3).

The CCA indicates that many of the stingless bees favour forests with larger trees and lower temperatures. In the case of some Trigona it has been shown that nest sites are limiting factors for their density (Inoue et al. 1990). In other words, these stingless bees characterize the bee community in closed native forests. They seem to be tolerant of the apparent lack of flowering resources. This may be due to their ability to store food in their nests to tide over times of meagre resources during inter-mass flowering episodes.

Many of the trigonid nests observed during this study had nest entrances made of resinous material and trigonids have been observed to collect resins from trees. There appears to be much more available resin on trees in the primary forests of Johor. This may be because the trees are older, larger and more frequently utilized by beetles, woodpeckers and fungi, causing the resins to be exposed and available for bees to collect. It is not known if bees are specific in the choice of resins for nest building.

In the intermediately disturbed forests of Singapore, the physical parameters were more variable as there were more gaps in the canopy. Growth of open area species such as *Dicranopteris linearis*, a fern and *Clidemia hirta*, an exotic shrub, were also apparent. MacRitchie in particular was abundant in shrubs and treelets constantly flowering. Both Nee Soon and Bukit Timah are in a physiognomic and a bee compositional sense (mainly Apidae) similar to the primary forests in Johor although species richness is lower. MacRtichie, consisting of a mix of open and closed habitats, is much more bee species rich, as can be expected of a mixed habitat. It has also a more even distribution of bee families. Bukit Timah Nature Reserve deserves a separate mention because despite its primary forest status, it is very small (87 ha with a lot of edge habitats) and apparently very poor in both species richness and abundance. *Trigona laeviceps*, which has been described to the most commonly found trigonid species (Inoue et al. 1984) especially in disturbed areas, dominated both Bukit Timah and Nee Soon.

At the other end of the spectrum, Kent Ridge, Holland Woods and the UMP oil palm plantation are more or less dominated by exotic plants (by ornamental plants in Kent Ridge, *Albizia* sp. in Holland Woods and *Elaeis guineensis* in the oil palm plantation). Under these conditions, the family Halictidae and Anthophoridae were more commonly caught. They seem to require higher temperatures and light intensity, and lower humidity levels. They also increase in abundance with greater flowering intensities both in the low-lying vegetation and in trees. They apparently do not require larger trees.

The relationship between bird diversity, forest condition and the bee community

Correlations between species richness in different taxa have been found to be significant (e.g. Pearson & Cassola 1992) or absent (Lawton et al. 1998). In this study no correlation was found between birds and bees although one might speculate that the number of insectivorous birds should be positively correlated with bee abundance, if bees can act as an indicator of insect diversity in general. One might also speculate that the number of nectarivorous birds should reflect positively the number of nectar collecting bees since they are using the same resource. There is a trend that bird diversity and bee abundance decrease with disturbance.

Conservation implications

It has been reiterated that baiting methods are biased (Southwood 1978). In particular, this study could not investigate the bee community in the canopy of trees, especially in the less disturbed forests where trees were commonly more than 20 m in height. It was also biased by the non-randomness of the transects chosen. However, the collection methods were standardized throughout the eight sites and it is possible to compare the bees collected from the sites of varying disturbances. The physical architecture of forests is determined mainly by plants but the underlying perpetuation of plants is dependent on pollinators especially in the tropics where many plants are dioecious (Renner & Feil 1993) and where wind-pollination is very rare (Whitmore 1984). Animal pollination is an important ecological process dominated by bees. It is still not known how bees are affected by habitat change though inferences can be made from this study and some other previous studies. In particular, larger trees and more constant ambient conditions are more conducive to many trigonid bees that may have the ability to survive inter-mass flowering conditions and utilize abundant resources during mass flowering. This in turn allows cross-fertilization among con-specific trees. Nest sites/materials (e.g. resins) and foraging sites may be limited when forest conversions occur.

Are there enough pollinators surviving for the process of pollination to continue in regenerating forest fragments or logged forests? If, as this study show, the bee community composition is largely different in disturbed and undisturbed forests, are disturbed forests such as secondary forests adequate to meet the pollination requirements of regenerating forests? During the period of study, it has been observed that there are many more T. laeviceps individuals immediately outside the forest of Bukit Timah foraging on exotic, ornamental flowering plants along the road than in the interior of the Nature Reserve. This may indicate that T. laeviceps is favouring a richer and more constant food source in the matrix of the small forest fragment and may hence neglect to visit forest plants that flower much less frequently. The five Singaporean forest sites studied are quite different in bee community structure as compared with the primary forests in Johor. This is probably an indication that ecological processes in forests of Singapore are changing. Trigonids, dominant in closed forests, were absent from the oil palm plantation, a habitat that is rapidly becoming all pervading in Peninsular Malaysia. However, even in the primary forest sites in Johor, the bee community is not as complete as it should be. There is a need to study the bee community in relation to the matrix surrounding these undisturbed forests. We can only speculate at this moment that the matrix (i.e. plantations) surrounding these forests, may not provide adequate nest sites for many forest bee species. These negative trends, which can also be seen in the South American tropics (Frankie et al. 1997), should be rectified before the process of pollination grinds to a dangerous low. The only way of rectification that can be suggested based on our present knowledge of tropical ecology is to preserve larger tracts of undisturbed tropical lowland forests.

Research directions

We need to study the mechanisms of resource storage by social bees, especially during the mass flowering periods which may allow them to maintain a steady population throughout the long inter mass flowering period. Do these bees forage more intensively during mass flowering periods and are there mechanisms through which they increase their worker populations to tap nectar and pollen resources? We also need to study the effects of forest fragmentation on bees and their pollination functions. Exactly how selective are bees for nest sites and are they limiting for bees? Is it true that the bees found in disturbed habitats cannot respond to mass flowering in native forests? What are the consequences of small forests with differing matrices for bees with various foraging ranges? How important is the recruiting behaviour in social bees like trigonids for utilizing fluctuating resources in the mass flowering tropics?

All these questions should be answered to help us manage the remaining bee populations and understand the role of pollination in regeneration and restoration of mass-flowering lowland tropical Southeast Asian forests.

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Appendix 1 . Table of the bird species recorded at the eight study sites (see Table 1 for abbreviations), their dates of survey and the habitat preference of the bird species where FW = fresh water habitat, P = Primary forest, S = Secondary forest and forest edge, GR =grassland and open areas.

	Common Name	Scientific Name	Site								Habitat			
	Resident Species		NS	MC	BT	HW	KR	UMP	BL	BK	FW	P	S	GR
1	Purple Heron	*Ardea purpurea*					1				1			
2	Striated Heron	*Butorides striatus*					1				1			
3	Brahminy Kite	*Haliastur indus*				1	1				1		1	
4	White-bellied Sea-Eagle	*Haliaeetus leucogaster*	1	1	1		1	1			1			
5	Grey-headed Fish-Eagle	*Ichthyophaga ichthyaetus*	1								1	1		
6	Crested Serpent-Eagle	*Spilornis cheela*		1					1	1	1	1	1	1
7	Changeable Hawk-Eagle	*Spizaeetus cirrhatus*	1	1	1				1			1	1	1
8	Black-thighed Falconet	*Microhierax fringillarius*							1			1	1	1
9	Red Junglefowl	*Gallus gallus*							1	1		1	1	
10	Great Argus	*Argusianus argus*							1	1		1	1	1
11	Red-legged Crake	*Rallina fasciata*				1					1	1	1	
12	White-breasted Waterhen	*Amaurornis phoenicurus*				1	1	1			1			1
13	Thick-billed Pigeon	*Treron curvirostra*							1	1		1		
14	Little Green Pigeon	*Treron olax*							1			1		
15	Pink-necked Green-Pigeon	*Treron vernans*	1	1	1	1	1				1		1	1
16	Green Imperial Pigeon	*Ducula aenea*							1			1	1	
17	Spotted Dove	*Streptopelia chinensis*			1	1	1	1	1				1	1
18	Peaceful Dove	*Geopelia striata*						1					1	1
19	Green-winged Pigeon	*Chalcophaps indica*							1	1		1	1	
20	Long-tailed Parakeet	*Psittacula longicauda*	1	1	1	1			1		1	1	1	1
21	Blue-rumped Parrot	*Psittinus cyanurus*	1		1				1	1	1	1		
22	Blue-crowned Hanging-Parrot	*Loriculus galgulus*			1	1				1	1			1
23	Indian Cuckoo	*Cuculus micropterus*					1		1			1	1	
24	Banded Bay Cuckoo	*Cacomantis sonneratii*			1	1						1	1	1
25	Rusty-breasted Cuckoo	*Cacomantis sepulcralis*				1						1	1	
26	Violet Cuckoo	*Chrysococcyx xanthorhynchus*	1	1	1					1		1	1	
27	Drongo Cuckoo	*Surniculus lugubris*	1		1							1	1	
28	Common Koel	*Eudynamys scolopacea*			1		1						1	1
29	Black-bellied Malkoha	*Phaenicophaeus diardii*								1		1	1	
30	Chestnut-bellied Malkoha	*Phaenicophaeus sumatranus*		1	1							1	1	

Appendix 1. Continued.

	Common Name	Scientific Name	Site								Habitat			
	Resident Species		NS	MC	BT	HW	KR	UMP	BL	BK	FW	P	S	GR
31	Raffles's Malkoha	*Phaenicophaeus chlorophaeus*							1	1		1	1	
32	Chestnut-breasted Malkoha	*Phaenicophaeus curvirostris*								1		1	1	
33	Short-toed Coucal	*Centropus rectunguis*								1		1	1	1
34	Greater Coucal	*Centropus sinensis*	1			1		1		1			1	1
35	Lesser Coucal	*Centropus bengalensis*		1		1							1	1
36	Reddish Scops-Owl	*Otus rufescens*							1	1		1		
37	Collared Scops-Owl	*Otus lempiji*			1				1	1		1	1	
38	Barred Eagle-Owl	*Bubo sumatranus*								1		1	1	
39	Brown Hawk-Owl	*Ninox scutulata*			1							1	1	
40	Spotted Wood-Owl	*Strix seloputo*							1			1	1	1
41	Gould's Frogmouth	*Batrachostomus stellatus*								1		1		
42	Javan Frogmouth	*Batrachostomus javensis*								1		1		
43	Malaysian-Eared Nightjar	*Eurostopodus temminckii*							1			1		
44	White-bellied Swiftlet	*Collocalia esculenta*							1			1	1	1
45	Brown Needletail	*Hirundapus giganteus*							1		1	1	1	1
46	Silver-rumped Swift	*Rhaphidura leucopygialis*							1	1	1	1		
47	House Swift	*Apus affinis*			1	1	1							1
48	Asian Palm-Swift	*Cypsiurus balasiensis*				1	1					1	1	1
49	Grey-rumped Treeswift	*Hemiprocne longipennis*				1	1		1	1		1	1	
50	Whiskered Treeswift	*Hemiprocne comata*								1		1	1	1
51	Red-naped Trogon	*Harpactes kasumba*							1			1	1	
52	Diard's Trogon	*Harpactes diardii*							1	1		1	1	
53	Scarlet-rumped Trogon	*Harpactes duvaucelii*							1	1		1	1	
54	Blue-eared Kingfisher	*Alcedo meninting*							1		1	1		
55	Blue-banded Kingfisher	*Alcedo euryzona*								1		1		
56	Oriental Dwarf Kingfisher	*Ceyx erithacus*			1					1	1	1		
57	Banded Kingfisher	*Lacedo pulchella*							1	1		1		
58	Stork-billed Kingfisher	*Halcyon carpensis*		1							1			
59	White-throated Kingfisher	*Halcyon smyrnensis*	1	1	1	1	1	1			1		1	1
60	Collared Kingfisher	*Halycon chloris*				1	1				1		1	1
61	Rufous-collared Kingfisher	*Actenoides concretus*							1	1		1		
62	Blue-tailed Bee-eater	*Merops philippinus*	1		1	1	1				1			1

Appendix 1. Continued.

	Common Name	Scientific Name	Site								Habitat			
	Resident Species		NS	MC	BT	HW	KR	UMP	BL	BK	FW	P	S	GR
63	Blue-throated Bee-eater	*Merops viridis*	1	1	1	1	1		1	1	1	1		1
64	Red-bearded Bee-eater	*Nyctyornis amictus*							1			1	1	
65	Dollarbird	*Eurystomus orientalis*	1	1	1	1	1					1	1	
66	White-crowned Hornbill	*Berenicornis comatus*								1		1		
67	Bushy-crested Hornbill	*Anorrhinus galeritus*								1		1		
68	Wreathed Hornbill	*Rhyticeros undulatus*							1	1		1		
69	Rhinoceros Hornbill	*Buceros rhinoceros*							1	1		1		
70	Helmeted Hornbill	*Rhinoplax vigil*							1	1		1		
71	Gold-whiskered Barbet	*Magalaima chrysopogon*							1	1		1		
72	Red-crowned Barbet	*Megalaima rafflesii*	1	1	1					1		1	1	
73	Red-throated Barbet	*Megalaima mystacophanos*								1	1	1	1	
74	Blue-eared Barbet	*Megalaima australis*							1	1		1	1	
75	Coppersmith Barbet	*Megalaima haemacephala*				1	1					1		1
76	Brown Barbet	*Calorhamphus fuliginosus*							1		1	1	1	
77	Rufous Woodpecker	*Celeus brachyurus*	1	1		1	1		1	1		1	1	1
78	Laced Woodpecker	*Picus vittatus*				1						1	1	
79	Crimson-winged Woodpecker	*Picus puniceus*							1	1		1	1	
80	Chequer-throated Woodpecker	*Picus mentalis*							1	1		1		
81	Banded Woodpecker	*Picus miniaceus*	1	1	1	1	1		1	1		1	1	
82	Common Goldenback	*Dinopium javanense*	1			1	1					1	1	
83	Buff-rumped Woodpecker	*Meiglyptes tristis*							1			1	1	
84	Buff-necked Woodpecker	*Meiglyptes tukki*								1		1	1	
85	Great Slaty Woodpecker	*Mulleripicus pulverulentus*							1			1	1	
86	White-bellied Woodpecker	*Dryocopus javensis*		1								1	1	
87	Maroon Woodpecker	*Blythipicus rubiginosus*								1		1	1	
88	Dusky Broadbill	*Corydon sumatranus*								1		1		
89	Black-and-red Broadbill	*Cymbirhynchus macrorhynchus*								1	1	1	1	
90	Banded Broadbill	*Eurylaimus javanicus*							1	1		1	1	
91	Black-and-yellow Broadbill	*Eurylaimus ochromalus*							1	1		1	1	
92	Green Broadbill	*Calyptomena viridis*							1	1		1	1	
93	Pacific Swallow	*Hirundo tahitica*	1	1	1	1	1				1			1
94	Red-rumped Swallow	*Hirundo daurica*		1	1						1			1

Appendix 1. Continued.

	Common Name	Scientific Name	Site								Habitat			
	Resident Species		NS	MC	BT	HW	KR	UMP	BL	BK	FW	P	S	GR
95	Bar-winged Flycatcher-Shrike	*Hemipus picatus*							1			1	1	
96	Black-winged Flycatcher-Shrike	*Hemipus hirundinaceus*							1	1		1	1	
97	Large Wood-Shrike	*Tephrodornis virgatus*							1	1		1	1	
98	Bar-bellied Cuckoo-Shrike	*Coracina striata*							1			1	1	
99	Lesser Cuckoo-Shrike	*Coracina fimbriata*							1	1		1	1	
100	Pied Triller	*Lalage nigra*			1		1						1	1
101	Fiery Minivet	*Pericrocotus igneus*							1	1		1		
102	Scarlet Minivet	*Pericrocotus flammeus*			1				1	1		1		
103	Green Iora	*Aegithina viridissima*							1	1		1	1	
104	Common Iora	*Aegithina tiphia*	1	1		1	1						1	1
105	Great Iora	*Aegithina lafresnayei*								1		1	1	
106	Lesser Green Leafbird	*Chloropsis cyanopogon*			1				1	1		1	1	
107	Greater Green Leafbird	*Chloropsis sonnerati*			1				1			1	1	
108	Blue-winged Leafbird	*Chloropsis cichinchinensis*	1	1	1				1	1		1	1	
109	Straw-headed Bulbul	*Pycnonotus zeylanicus*			1						1	1	1	
110	Black-headed Bulbul	*Pycnonotus atriceps*							1			1	1	
111	Black-crested Bulbul	*Pycnonotus melanicterus*			1							1	1	
112	Grey-bellied Bulbul	*Pycnonotus cyaniventris*							1	1		1	1	
113	Red-whiskered Bulbul	*Pycnonotus jocosus*					1						1	1
114	Yellow-vented Bulbul	*Pycnonotus goaivier*	1	1	1	1	1	1	1				1	1
115	Olive-winged Bulbul	*Pynonotus plumosus*	1	1	1	1	1			1		1	1	1
116	Cream-vented Bulbul	*Pycnonotus simplex*	1	1	1				1	1		1	1	
117	Red-eyed Bulbul	*Pycnonotus brunneus*		1	1				1	1		1	1	
118	Spectacled Bulbul	*Pycnonotus erythropthalmos*							1	1	1	1	1	
119	Finsch's Bulbul	*Criniger finschii*								1		1		
120	Grey-cheeked Bulbul	*Criniger bres*							1	1		1	1	
121	Yellow-bellied Bulbul	*Criniger phaecocephalus*							1	1		1	1	
122	Hairy-backed Bulbul	*Hypsipetes criniger*							1	1		1	1	
123	Buff-vented Bulbul	*Hypsipetes charlottae*							1	1		1	1	
124	Streaked Bulbul	*Hypsipetes malaccensis*							1	1		1		
125	Ashy Bulbul	*Hypsipetes flavala*	1		1		1		1			1	1	
126	Bronzed Drongo	*Dicrurus aeneus*								1		1	1	

Appendix 1. Continued.

	Common Name	Scientific Name	Site								Habitat			
	Resident Species		NS	MC	BT	HW	KR	UMP	BL	BK	FW	P	S	GR
127	Greater Racquet-tailed Drongo	*Dicrurus paradiseus*	1	1	1	1			1	1	1	1	1	
128	Dark-throated Oriole	*Oriolus xanthonotus*							1	1		1	1	
129	Black-naped Oriole	*Oriolus chinensis*	1	1	1	1	1	1					1	1
130	Asian Fairy-Bluebird	*Irena puella*	1	1	1				1	1	1	1	1	
131	Crested Jay	*Platylophus galericulatus*								1		1		
132	Large-billed Crow	*Corvus macrorhynchos*	1	1	1	1	1	1	1		1			1
133	Sultan Tit	*Melanochlora sultanea*							1	1		1	1	
134	Velvet-fronted Nuthatch	*Sitta frontalis*			1				1		1	1		
135	Black-capped Babbler	*Pellorneum capistratum*							1	1		1	1	
136	Short-tailed Babbler	*Trichastoma malaccense*	1	1					1		1	1	1	
137	Horsfield's Babbler	*Trichastoma sepiarium*							1			1		
138	Abbott's Babbler	*Trichastoma abbotti*		1		1						1	1	
139	White-chested Babbler	*Trichastoma rostratum*	1						1		1	1	1	
140	Moustached Babbler	*Malacopteron magnirostre*							1	1	1	1	1	
141	Sooty-capped Babbler	*Malacopteron affine*								1		1	1	
142	Rufous-crowned Babbler	*Malacopteron magnum*							1	1		1		
143	Grey-breasted Babbler	*Malacopteron albogulare*								1	1			
144	Chestnut-backed Scimitar-Babbler	*Pomatorhinus montanus*							1			1		
145	Striped Wren-Babbler	*Kenopia striata*							1		1	1		
146	Large Wren-Babbler	*Napothera macrodactyla*							1			1		
147	Eyebrowed Wren-Babbler	*Napothera epilepidota*							1			1		
148	Rufous-fronted Babbler	*Stachyris rufifrons*							1			1	1	
149	Grey-headed Babbler	*Stachyris poliocephala*								1		1	1	
150	Chestnut-rumped Babbler	*Stachyris maculata*							1	1		1		
151	White-necked Babbler	*Stachyris leucotis*							1			1		
152	Black-throated Babbler	*Stachyris nigricollis*								1		1		
153	Chestnut-winged Babbler	*Stachyris erythroptera*	1	1					1	1		1	1	
154	Striped Tit-Babbler	*Macronus gularis*	1	1	1	1	1		1	1		1	1	
155	White-bellied Yuhina	*Yuhina zantholeuca*							1	1		1	1	
156	Malaysian Rail-Babbler	*Eupetes macrocerus*							1	1		1	1	
157	Oriental Magpie Robin	*Copsychus saularis*					1	1	1	1			1	1

Appendix 1. Continued.

	Common Name	Scientific Name	Site								Habitat			
	Resident Species		NS	MC	BT	HW	KR	UMP	BL	BK	FW	P	S	GR
158	White-rumped Shama	*Copsychus malabaricus*	1						1	1		1	1	
159	Chestnut-naped Forktail	*Enicurus ruficapillus*								1	1			
160	Flyeater	*Gerygone sulphurea*					1		1	1		1	1	
161	Common Tailorbird	*Orthotomus sutorius*				1	1	1					1	1
162	Dark-necked Tailorbird	*Orthotomus atrogularis*	1	1	1	1	1		1	1	1	1	1	
163	Ashy Tailorbird	*Orthotomus sepium*			1			1			1		1	1
164	Rufous-tailed Tailorbird	*Orthotomus sericeus*				1			1	1		1	1	
165	Yellow-bellied Prinia	*Prinia flaviventris*				1					1		1	1
166	Grey-chested Flycatcher	*Rhinomyias umbratilis*							1		1	1	1	
167	Grey-headed Flycatcher	*Culicicapa ceylonensis*							1	1		1		
168	Spotted Fantail	*Rhipidura perlata*							1			1	1	
169	Pied Fantail	*Rhipidura javanica*				1							1	1
170	Blacked-naped Monarch	*Hypothymis azurea*							1	1		1	1	
171	Rufous-winged Monarch	*Philentoma pyrhopterum*							1	1	1	1		
172	Asian Paradise-Flycatcher	*Terpsiphone paradisi*		1	1							1	1	
173	Philippine Glossy Starling	*Aplonis panayensis*	1	1	1	1	1						1	1
174	Common Myna	*Acridotheres tristis*					1						1	1
175	Hill Myna	*Gracula religiosa*	1	1		1	1		1	1		1	1	
176	Brown-throated Sunbird	*Anthreptes malaccensis*	1	1		1	1			1	1		1	1
177	Red-throated Sunbird	*Anthreptes rhodolaema*								1		1	1	
178	Ruby-cheeked Sunbird	*Anthreptes singalensis*								1		1	1	
179	Purple-naped Sunbird	*Hypogramma hypogrammicum*							1	1		1	1	
180	Purple-throated Sunbird	*Nectarinia sperata*	1	1		1						1	1	1
181	Olive-backed Sunbird	*Nectarinia jugularis*				1	1				1		1	1
182	Crimson Sunbird	*Aethopyga siparaja*	1	1	1	1	1					1	1	
183	Little Spiderhunter	*Arachnothera longirostra*	1	1	1				1	1		1	1	
184	Long-billed Spiderhunter	*Arachnothera robusta*							1			1	1	
185	Spectacled Spiderhunter	*Arachnothera flavigaster*								1		1	1	
186	Grey-breasted Spiderhunter	*Arachnothera affinis*							1	1		1	1	
187	Yellow-breasted Flowerpecker	*Prionochilus maculatus*							1	1		1	1	
188	Crimson-breasted Flowerpecker	*Prionochilus percussus*							1	1	1	1	1	
189	Orange-bellied Flowerpecker	*Dicaeum trigonostigma*	1	1	1				1	1		1	1	1

Appendix 1. Continued.

	Common Name	Scientific Name	Site								Habitat			
	Resident Species		NS	MC	BT	HW	KR	UMP	BL	BK	FW	P	S	GR
190	Scarlet-backed Flowerpecker	*Dicaeum cruentatum*		1	1	1	1					1	1	
191	Everett's White-eye	*Zosterops everetti*							1	1		1	1	
192	White-rumped Munia	*Lonchura striata*							1		1		1	1
193	Scaly-breasted Munia	*Lonchura punctulata*		1			1	1			1		1	1
	Introduced species (naturalized)													
194	Red Lory	*Eos bornea*					1						1	
195	Rainbow Lorikeet	*Trichoglossus haematodus*				1							1	
196	Blossom-headed Parakeet	*Pstittacula roseata*				1							1	
197	Rose-ringed Parakeet	*Psittacula krameri*		1		1	1						1	1
198	Red-breasted Parakeet	*Psittacula alexandrii*				1							1	
199	Tanimbar Corella	*Cacatua goffini*				1							1	
200	White Cockatoo	*Cacatua alba*				1							1	
201	House Crow	*Corvus splendens*		1		1	1							1
202	Greater Necklaced Laughingthrush	*Garrulax pectoralis*					1						1	
203	White-crested Laughingthrush	*Garrulax leucolophus*			1	1	1					1	1	
204	Hwamei	*Garrulax canorus*				1							1	
205	White-vented Myna	*Acridotheres javanicus*	1	1	1	1	1	1	1				1	1
206	Oriental White-eye	*Zosterops palpebrosa*				1	1					1	1	
		Total	42	46	52	56	50	14	112	107				
		Transect length (km)	4.5	5.5	1.9	1.7	2.6	3.0	3.0	2.5				
		Dates of surveys (d-m-y)	9.2.98 10.2.98 7.7.98 7.8.98	14.7.97 16.8.97 7.1.98 27.11.98	22.10.97 30.12.97 17.4.98 3.7.98	1.6.99 29.9.98 30.11.98 25.3.99	17.7.97 2.11.97 15.1.98 5.8.98	12.5.99 13.5.99 21.7.99 22.7.99	27.7.99 28.7.99 15.8.99 16.8.99	29.7.99 30.7.99 5.8.99 6.8.99				

Appendix 2. Absolute abundance of 45 bee morphospecies collected at each transect in the eight study sites. (See Table 1 for site abbreviations).

	Family	Species	BK			BL			BT			NS			MC			HWKR			UMP		
		Transects	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	A	B	A	B	C
1	Apidae	*Apis cerana* Fabricius 1793	40	0	19	0	3	3	0	0	0	0	0	0	0	0	0	29	0	0	4	3	6
2		*A. dorsata* Fabricius 1793	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	15	0	0	1	0	0
3		*A. adreniformis* Smith 1858	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	44	1	3	0	0	0
4		*Trigona (Leipdotrigona) terminata* Smith 1878	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5		*T. (L.) ventralis* Smith 1857	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
6		*T. (Homotrigona) fimbriata* Smith 1857	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
7		*T. (Tetragonula) reepeni* Friese 1918	0	0	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8		*T. (Heterotrigona) itama* Cockerell 1918	0	0	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9		*T. (Genotrigona) thoracica* Smith 1857	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10		*T. (Tetrigona) apicalis* Smith 1857	0	10	5	2	6	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0
11		*T. (Tetragonula) atripes* Smith 1857	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12		*T. (T.) geisslerei* Friese 1918	37	7	33	95	118	38	1	1	0	1	0	2	18	8	26	6	10	11	0	0	0
13		*T. (T.) melina* Gribodo 1893	39	41	122	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
14		*T. (T.) laeviceps* Smith 1857	25	1	9	42	88	44	12	14	7	72	36	113	20	15	47	0	0	0	0	0	0
15	Halictidae	*Halictus*	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
16		Halictidae?	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
17		*Lassioglossum (Ctenonomis)* sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	4	5
18		*Lassioglossum (Evylaeus)* sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	8	3
19		*Lassioglossum* sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0
20		*Pachyhalictus* sp.	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	2	0	0	0
21		*Nomia (Curvinomia)* sp.	0	0	0	0	0	0	0	0	1	0	0	0	27	14	6	4	7	14	0	2	0
22		*Nomia (Maculonomia)* sp. 1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
23		*Nomia (Maculonomia)* sp. 2	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
24		*Nomia (Maculonomia)* sp. 3	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
25		*Lipotriches* sp.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
26		*Lipotriches* sp. 2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0
27		*Lipotriches* sp. 3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
28		*Lipotriches (Lipotriches)* sp.	0	0	0	0	0	0	0	0	0	0	0	0	1	3	0	0	0	0	1	0	1
29		*Pseudapis*	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	2	0	1	1	1	3

Appendix 2. Continued.

Family	Species	BK			BL			BT			NS			MC			HWKR			UMP		
	Transects	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	A	B	A	B	C
30 Megachilidae	*Chalicodoma* sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
31 Anthophoridae	*Amegilla (Zonamegilla) korotonensis* (Cockerell)	0	0	0	0	0	0	0	0	0	0	0	0	8	0	0	0	0	0	1	0	0
32	*A. (Z.) andrewsi* (Cockerell)	0	0	0	0	0	0	0	0	0	0	0	0	10	1	0	0	0	1	0	0	0
33	*A. (Z.) flammeozonata* (Dours)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
34	*A. (Glossamegilla) insularis* (Smith)	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0
35	*A. (G.) fulvohirta* (Meade-Walde)	0	0	0	0	0	0	0	0	0	0	0	0	4	1	0	0	0	0	0	0	0
36	*Thyreus himalayus* Radcloz.	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	6	0	0	0	0	0
37	*Ceratina (Ceratinidia) nigrolateralis* Cockerell	0	0	0	0	0	0	0	0	0	0	0	0	2	3	0	0	1	1	0	0	0
38	*Ceratina* sp.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
39	*Ceratina* sp.2	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
40	*Ceratina* sp. 3	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
41	*Ceratina (Pithitis)* sp.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
42	*Ceratina (Pithitis)* sp.2	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
43	*Xylocopa (Platynopoda) latipes* (Drury)	0	0	0	0	0	0	0	0	0	0	0	2	2	2	1	0	3	7	0	0	0
44	*Xylocopa (Kortortosoma)* sp.	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	6	0	2
45 Colletidae	*Hylaeus* sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0

Appendix 3: Descriptions of trigonid nests encountered during this study. See Table 1 for site abbreviations .

Species	Site	Description of nest entrance	Description of nest location
Trigona (Teragonula) melina	BK	Delicate, extensive, resinous tube with a total length of 33.8 cm. Mouth of entrance 1.8 by 3.3 cm.	In trunk of tree (dbh 180 cm, ht. >20 m), entrance 81 cm above ground.
T. (Lepidotrigona) terminata	BK	Solid tubular structure 5 cm in length opening out into a delicate, resinous trumpet like exit 4.2 cm in length. Mouth of entrance 1.9 by 2.0 cm.	In trunk of tree (dbh = 222 cm, ht. > 20m), entrance 60 cm above ground
T. (Heterotrigona) itama	BK	Solid tubular structure 7 cm in length. Mouth of entrance 1.2 by 1.2 cm.	In trunk of tree (dbh = 100 cm, ht. > 20 m), entrance 103 cm above ground.
T. (Tetrigona) apicalis	BTNR	Vertically flattened trumpet like opening without a tube, 18.0 by 2.5cm.	In trunk of tree (dbh = 50 cm, ht. ca. 20 m) entrance 47 m above ground.
T. (Tetragonula) laeviceps	NS	Solid short tube inserting into loose soil. Mouth of entrance 1.0 by 1.0 cm.	In loose soil camouflaged by leaf litter.

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Choice of methodology for marine pollution monitoring in intertidal soft-sediment communities

Nelly Krassulya

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The changes in macrobenthic communities due to organic pollution stress were studied in Proper Bay, South Australia. I tested several choices of biological variables and associated statistical methods with the aim of identifying the most sensitive and cost-effective approach to designing marine pollution assessment and monitoring programs. Data for the study was collected at Proper and Boston Bays, South Australia, in summer 1998 and autumn 1999. Changes in soft-sediment intertidal macrobenthic communities from three impacted sites were analysed in comparison to six control sites. Results of both one-way and two-way Analysis of Variance (ANOVA) for univariate measures (number of individuals, number of species and species diversity) were inconsistent. Rank-abundance methods (log-normal distribution and k-dominance curves) applied to the summer data confirmed typical patterns of distribution of individuals of species in stressed communities, but the results for the autumn data were inconsistent. All three multivariate methods tested (Hierarchical Agglomerative Clustering, Multi-Dimensional Scaling (MDS) and Analysis of Similarities (ANOSIM)) were successful in discriminating between impacted and control sites. Analysis of variability among replicates, by examination of MDS plots and Index of Multivariate Dispersion, revealed an increased variability only for autumn data. Different taxonomic resolutions (species level, class level and species from selected taxa) were tested as possible methods of cost reduction. Results of all three multivariate methods, when applied to data using different taxonomic resolutions, were consistent and no significant information was lost in comparison with traditional species level identification. In conclusion, I recommend that analysis of community structure using multivariate methods on class level (or a selected group such as Polychaeta) is the most effective and inexpensive methodological choice.

Nelly Krassulya, Swedish Biodiversity Centre, P. O. Box 7007, SE-750 07 Uppsala, SWEDEN

Introduction

Macrobenthic communities inhabiting intertidal flats are attractive for the detection and monitoring of organic pollution as they are known to be responsive to organic enrichment and are relatively easy to sample. Properly designed methods, based on an understanding of processes occuring in communities affected by organic pollution, could give us a cheap and reliable approach for environmental impact monitoring. As different characteristics of a community behave in different ways in response to different types of disturbance, the choice of biological variables to be measured and particular methods associated with them is a crucial component in any monitoring process and is presently heavily debated (Keough and Quinn 1991, Warwic 1993).

Diversity

One of the most commonly used methods for assessing changes in communities is estimation of species diversity. This is based on the relationship between the diversity of a community and it's stability - the more diverse and complex the community, the more stable it is (though this theory is not always supported by data (ie May 1975)). Pollution, or other types of human disturbance, affect the stability of a community and this may be detected by a change in diversity. Overviews of diversity measurements are given in Magurran (1988) and Washington (1984). The most widely used parameters, species richness (S), species diversity (Shannon's Diversity Index, H') and evenness, show a clear correlation with increasing or decreasing pollution levels in many cases (Rygg 1985, Gray et al 1990). However, these parameters may respond differently to changing replication and may have different power characteristics (Bernstein and Zalinsky, 1986). In some cases, such as an impact study of mining on coral reef fish communities in the Maldives (Dawson-Shepherd et al. 1992), the mean Shannon's Index did not differ between mined and control sites where multivariate analysis showed a clear-cut difference. Additionally, it may be extremely difficult, especially in Australia (see above), to identify all species in samples. Thus, it was tested whether this method could be applied on levels higher than species, or only for selected taxa (Polychaeta for example, which are usually well represented in samples and have a high abundance).

Rank abundance methods

There are two commonly used methods for graphically presenting distribution of individuals among species: log-normal distribution and k-dominance curves (Nelson 1987, Gray 1981, Clarke 1990). Both of these methods give promising results for the detection of pollution-induced changes in communities. A good log-normal fit of distribution represents ecological equilibrium of an undisturbed community where most species rarely respond to the stochastisity of environmental and biological interactions. Disturbance in the form of pollution produces a skewed distribution, where the commoner species become more abundant and the rarer species more scarce.

Multivariate approach

Hierarchical agglomerative clustering and multi-dimensional scaling (MDS) are two of the most frequently used multivariate methods. Both of these are based on similarity coefficients calculated between every pair of samples. The first method facilitates a classification or clustering of samples into groups which are mutually similar, while the second method maps the samples (in two or three dimensions) in such a way that the distances between pairs of samples reflects their relative dissimilarity in species composition (Clarke & Warwick 1994). The less frequently used ANOSIM (analysis of similarities) is built on a simple non-parametric permutation procedure, which is applied to the similarity matrix underlying the ordination or classification of samples (Clarke, 1993). Using numerous examples, Clarke and Warwick (1994) showed that multivariate methods of data analysis were more sensitive in detecting differences in community structure between samples in space, or changes over time, in comparison to univariate techniques. The major drawback of the multivariate approach is the necessity to identify all species in samples. However, this can be overcome if lower taxonomic resolution proves to be applicable and sensitive enough to detect changes in macrobenthic communities.

Variability

It has been shown in a variety of environmental impact studies that variability among samples collected from impacted sites is much greater than that from controls. Warwick and Clarke (1993) described an increase in variability of four different types of marine communities (meobenthos, macrobenthos, corals, reef-fish). They compared variance/mean or standard devation/ mean ratio of the number of individuals of all species and diversity indices (H'). The most marked results were obtained for meobenthos and macrobenthos communities. In all cases, a pronounced increase in variability between replicate samples was revealed by analysis of MDS plots and suggested Index of Multivariate Dispertion (IMD).

One of the major difficulties researchers and environmental managers face when considering macrobenthic communities is the costly and time consuming sampling process, especially species identification. This task becomes even more complicated in areas such as Australia, where an extremely high diversity of macrobenthic fauna is insufficiently taxonomically described. Due to a lack of up-to-date taxonomic keys, identification to species level is also becoming extremely difficult and expensive. One of the approaches presently being discussed widely in the scientific press (James et al 1995, Somerfield & Clarke 1995, Ferraro&Cole 1990, Chapman 1998, Olsgard et al 1997, Vanderklift 1996) is the reduction of the level of taxonomical resolution. In other words, the identification of macrofauna to levels higher than species, family, order, class or even groups with relatively similar roles in the ecosystem. Another approach, which would allow significant savings in time and effort, is the identification and analysis of species only from selected groups or taxa, instead of a whole community. Polychaeta would be a useful group, as they are ubiquitous in virtually all marine sediments, are typically present in high numbers and are represented by many species.

The main purpose of this study was to 1) estimate the changes in macrobenthic communities under organic pollution stress in Proper Bay, Port Lincoln and 2) identify the most cost-effective and sensitive choice of biological variables and associated methods.

The following biological variables and associated methods were considered with respect to their sensitivity and applicability to routine environmental monitoring.

Study area and methods

Study area

Samples were collected from nine stations, three impacted and six controls (Figure 1), at the end of December 1998. Three stations (impacted site P3, controls C1 and C2) were sampled again in April 1999. A description of the sites, with sources of contaminants, is given in Table 1. The first impacted site was located at an outlet from an area of the intertidal flat that has been separated from the sea by a railway embankment for several decades. This area, called "the wetland", has accumulated run-off from an emu farm and a dirt road for many years. A limited exchange of water between the wetland and the sea has resulted in an accumulation of black, sulfur-enriched sediments covered with a shallow layer of extremely saline water (65-70 %). The second and third impacted sites were near outfall pipes from a fish-processing factory. The sediment structure (dead shells, sand, gravel and mud) was similar at all three impacted locations. At all impacted sites, algae cover indicative of organic pollution was observed. Control sites in Proper Bay were chosen at a distance from impacted sites (the closest site, C1, was approximately 10 km away from site P3) and were chosen regardless of gradient and without visible signs of contamination (ie algae growth).

We also decided to use two control sites outside of Proper Bay to avoid possible confusion, but it was impossible to find physically similar sites. Thus, control sites 5 and 6 have a quite different sediment structure in comparison with the other locations.

Sampling methods

At each site, a total of eight cores in the summer and six cores in the autumn were taken, giving a total of 72 samples for December and 18 for April. Replicates at each site were collected randomly along a 50m transect parallel to the shore (50m from the highest tide mark). For impacted sites, transects were centered on the outfall and extended 25m in either direction. This sampling design was chosen to avoid any confusing zonation effect on the distribution of the intertidal macrofauna. Samples were taken at low tide using a 10cm diameter hand core. All samples were then sieved on a 500(mesh screen and fixed in 5% formalin.

Individuals were identified to the lowest possible level (species or morphospecies) except for Anthozoans, Nemerteans, Sipuncules and Oligochaetes. With the exception of Oligochaetes, all these taxa were comparatively rare.

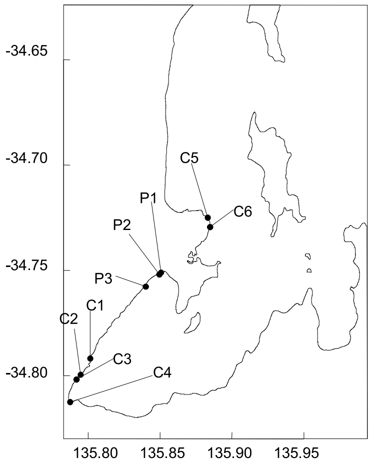

Figure 1. Sampling site locations

Statistical analysis

Univariate approaches

In addition to total number of individuals and total number of species, two further diversity indices were also calculated: Hill's N1 (the exponential of the Shannon-Wiener function H') and Hill's N2 (Simpson's reciprocal D). Hill's N1 was chosen as an index most sensitive to changes

Table 1. Description of sampling sites

Site	Location	Sediment structure*)	Sample date (No. of replicates)	Source of impact
Impacted 1 (P1)	Proper Bay	Medium sand, silt	December 1998 (8)	"Wetland" outfall (see text)
Impacted 2 (P2)	Proper Bay	Medium sand, silt	December 1998 (8)	Fish-processor outfall
Impacted 3 (P3)	Proper Bay	Medium sand, silt	December 1998 (8)	
April 1999 (6)	Fish-processor outfall			
Control 1 (C1)	Proper Bay	Medium sand, silt	December 1998 (8) April 1999 (6)	
Control 2 (C2)	Proper Bay	Medium sand, silt	December 1998 (8)	
Control 3 (C3)	Proper Bay	Medium sand, silt	December 1998 (8)	
Control 4 (C4)	Proper Bay	Medium sand, silt	December 1998 (8) April 1999 (6)	
Control 5 (C5)	Boston Bay	Fine sand	December 1998 (8)	
Control 6 (C6)	Boston Bay	Fine sand	December 1998 (8)	

*)by Holme&McIntre, 1971

in rarer species, while Hill's N2 was used as most sensitive to changes in dominant species (Peet 1974). With these univariate measures as response variables, a simple one-way ANOVA model was used to test for differences between impacted and control sites for the December samples. For the April samples, and a matched subset of the December samples, a two-way ANOVA to test was also used for time effects and any site-time interactions. If significant effects were detected, a Post Hoc Test (Student-Newman-Keuls) was applied to all variances used.

Homogeneity of variance was tested for using Leven's Test of Equality of Error Variance. The data was not homogeneous both before and after transformations (log (x+1), fourth root). Furthermore, mostly untransformed data were used (fourth root transformation was used in some cases for multivariate analysis).

Rank Abundance methods

Two commonly used methods for graphical presentation of distribution of individuals among species were applied:

1. Plots of x 2 geometric species abundance classes against number of species,
2. K-dominance curves (x-logged, y-cumulative % dominance).

Graphs were produced for each site for both summer and autumn data. To show general trends, all control sites were pooled into one group and impacted sites into another and the two curves compared for the summer data.

Multivariate approaches

Hierarchical agglomerative clustering, multidimensional scaling (MDS) and ANOSIM (Analysis of Similarities) were used in separate analyses for the summer and autumn data. Variability among samples was analysed using Multi-Dimensional Scaling ordination of replicates and calculation of Index of Multivariate Dispersion (IMD) (as described in Warwick & Clarke 1993). PRIMER (Plymouth Marine Laboratory, 1996) software was used to test for statistically significant differences between sites.

Taxonomic resolution

To test how taxonomic resolution affects the sensitivity of multivariate methods for detecting changes in benthic communities, multivariate statistical analyses (Hierarhical clustering, MDS and ANOSIM) were applied to three sets of data:

1) All individuals identified to species/morphospecies level,

2) Individuals only classified to class level,

3) Only species/morphospecies of Polychaeta.

Results

Number of individuals, number of species and species diversity

A total of 12675 individuals were collected from all sites, comprising 99 species / morphospecies. In December, the highest abundance of benthic macrofauna was found at impacted site P1, with a slightly lower abundance at impacted sites P2 and P3 and at approximately the same level at the controls C1 and C4 (Table 2). The remaining controls were characterized by uniformly low abundance.

ANOVA performed on the number of individuals revealed a significant difference between sites (Table 3). A Post Hoc Test (Table 4) identified two distinct groups of stations: C2, C3, C5, C6 (low abundance) and P1, P2, P3, C1, C4 (high abundance).

The highest species richness during the summer was found at the control sites C2 and C3. The number of species was also comparatively high at the impacted sites P1 and P3, whereas impacted site P2 and controls C4 and C6 were characterised by comparatively low abundances (Table 2). One-way ANOVA recognized significant difference between sites (Table 3), but the grouping of stations by a Post Hoc Test was confusing (Table 4), whilst impacted and control sites were mixed without any visible pattern.

Generally, both diversity indices were lower at impacted sites in comparison with controls in both seasons (Table 2, Figure 2), with the exception of control C4 in the summer, where diversity was the lowest because of the highly dominant gastropod S. solidus. One-way ANOVA performed on summer data revealed a statistically significant difference between sites for both indices N1 and N2 (Table 2) and Post Hoc Tests recognised four significantly different groups of stations for N1 and five groups for N2 (Table 3). With the exception of the first group, where impacted site P2 was merged with controls, for both indices three (shaded) different impacted sites were in the same groups. A Post Hoc Test failed to clearly separate them from controls.

Generally, results of one-way ANOVA tests performed on different variables (number of individuals, species richness and species diversity indices Hill's N1 and N2) were inconsistent. Though in most cases a significant difference was revealed between sites, Post Hoc Tests failed to clearly separate impacted and control sites.

A lower abundance of benthic macrofauna was found in autumn at all three sampled stations compared to in summer, with the lowest abundance at impacted site P3. Two-way ANOVA performed on the number of individuals at sites P3, C1 and C4, and between the two seasons, revealed a significant (p<0.05) difference between seasons but not between sites (Table 4).

Species richness was also lower in the autumn, with the lowest number of species at control C4. Two-way Analysis of Variance for the number of species distinguished (p<0.05) between sites and seasons (Table 4), but a Post Hoc Test failed to separate impacted sites and controls.

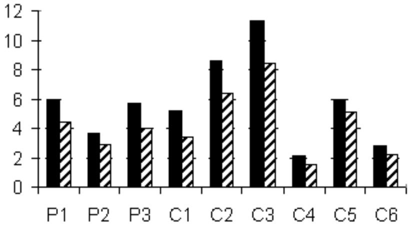

Figure 2. Values of Hill's N1(solid) and N2

Values of both diversity indices were low in the autumn at all sites and slightly higher at the controls in comparison with impacted sites. Two-way ANOVA and a Post Hoc Test performed on diversity indices for autumn data revealed significant differences between sites and seasons for Hill's N1, but failed to distinguish between seasons in the case of Hill's N2. Student-Newman-Keuls Test failed to separate the impacted sites from the controls (Table 4).

Generally, results of two-way ANOVA for different univariate measures (number of individuals, species richness, two diversity indices) were confusing and inconsistent. Even though

Table 2. Univariate Indices Values of the stations in summer and autumn.

Site	Summer								Autumn							
	No. of individuals		No. of species		Hill's N1		Hill's N2		No. of individuals		No. of species		Hill's N1		Hill's N2	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
P1	351.5	112.2	13.7	0.7	6.0	0.7	4.4	0.5								
P2	226.8	42.2	8.1	0.7	3.7	0.3	2.9	0.3								
P3	280.8	39.7	14.6	1.1	5.7	0.3	4.0	0.4	94.6	52.2	7.1	1.5	3.1	0.3	2.3	0.3
C1	267.0	24.1	15.2	0.7	5.2	0.4	3.4	0.3	234.0	11.3	9.1	0.4	3.4	0.2	2.5	0.2
C2	47.5	19.7	12.8	2.1	11.3	0.9	8.4	0.9								
C3	53.5	7.0	16.6	1.2	8.6	0.8	6.4	0.6								
C4	285.6	54.6	10.0	1.1	2.1	0.2	1.5	0.1	211.6	13.5	8.1	0.4	3.2	0.3	2.5	0.2
C5	16.5	5.1	7.3	1.5	5.9	1.1	5.1	0.9								
C6	15.0	8.3	4.0	1.0	2.8	0.4	2.2	0.3								

Table 3. One-way ANOVA for summer data

	Number of individuals					Number of species				
Source	Type III SS	df	Mean Square	F	Sig.	Type III SS	df	Mean Square	F	Sig.
SITE	1179129.694	8	147391.212	8.424	.000	1150.944	8	143.868	11.920	.000
Error	1102281.625	63	17496.534			760.375	63	12.069		

Subsets grouped by S-N-K test

P1	P2	P3	C1	C4	C2	C3	C5	C6
—	—	—	—	—				
					—	—	—	—

P3	C3	C1	C2	P1	C4	P2	C5	C6
—	—	—	—	—				
					—	—		
			—	—	—			
						—	—	—

	Hill's N1					Hill's N2				
Source	Type III SS	df	Mean Square	F	Sig.	Type III SS	df	Mean Square	F	Sig.
SITE	525.331	8	65.666	17.397	.000	299.811	8	37.476	13.855	.000
Error	237.794	63	3.775			170.412	63	2.705		

Subsets grouped by S-N-K test

P1	P3	C1	C5	P2	C4	C6	C2	C3
				—	—	—		
—	—	—	—	—				
							—	
								—

P1	P3	P2	C1	C6	C4	C2	C5	C3
		—	—	—	—			
—	—	—	—	—				
—	—	—	—			—	—	
						—	—	
								—

*In all cases significance of S-N-K test <0.05

in most cases seasonal changes were revealed, the test failed to clearly differentiate impacted and control sites.

Rank abundance

Plots of geometric abundance classes for all sites are given in Figure 3. Curves are steep at all control sites, indicating that many species are only represented by single individuals and very few abundance classes are represented. Curves for impacted sites have a completely different shape due to a low abundance of rare species and being extended over more abundance classes. Figure 4 shows k-dominance curves for the same data. Curves plotted separately for each site look confusing, particularly for controls C1 and C4, but the graph for pooled data reveals a clear pattern, with the curve for impacted sites elevated, indicating lower diversity in comparison to controls.

The pattern of distribution of individuals among species in the autumn is similar for sites P3 and C1, but less obvious in the case of control C4 (Figure 3 (c)). K-dominance curves for autumn data look even more confusing, with curves for control sites slightly above those for polluted sites (Figure 4(c)).

Generally, results of rank abundance methods applied to the data confirmed typical patterns of distribution of individuals among species in disturbed macrobenthic communities. All three impacted sites sampled in the summer were characterized by a lower number of rare species and more abundant common species in

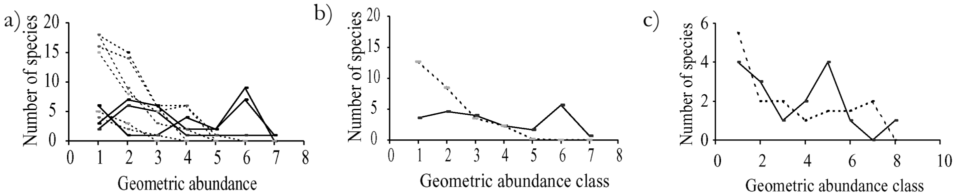

Figure 3. Plots of x2 geometric species abundance classes (solid lines – impacted sites, broken lines – controls): (a) all sites in summer; (b) all sites pooled into two groups: impacted and controls in summer; (c) sites pooled into two groups: impacted and controls in autumn.

comparison to control sites. However, results for the autumn data were confusing, which could be explained by an insufficient number of samples containing low numbers of individuals and species.

Community structure

With respect to broad taxonomic groups, gastropods were most abundant (35.9% of total abundance), while malacostracans, polychaetes and bivalves represented 19.8%, 14.6% and 10.5% of the sampled individuals respectively. Figure 5 shows the relative abundance of the major taxa at three impacted sites and six controls. Other taxa were comparatively rare.

In the summer, the impacted sites were

Table 4. Two-way ANOVA results for univariate values, autumn

	Number of individuals					Number of species				
Source	Type III SS	df	Mean Square	F	Sig.	Type III SS	df	Mean Square	F	Sig.
SITE	37523.762	2	18761.881	1.931	.163	63.389	2	31.694	4.542	.019
TIME	57192.722	1	57192.722	5.887	.021	186.778	1	186.778	26.768	.000
SITE * TIME	31467.995	2	15733.998	1.620	.215	47.389	2	23.694	3.396	.047
Error	291429.208	30	9714.307			209.333	30	6.978		
Subsets grouped by S-N-K			P3 C1 C4 ————————			P3 C1 C4 ————— —————				

	Hill's N1					Hill's N2				
Source	Type III SS	df	Mean Square	F	Sig.	Type III SS	df	Mean Square	F	Sig.
SITE	17.880	2	8.940	8.969	.001	6.916	2	3.458	4.880	.015
TIME	6.545	1	6.545	6.566	.016	.980	1	.980	1.383	.249
SITE * TIME	17.371	2	8.685	8.714	.001	8.996	2	4.498	6.348	.005
Error	29.902	30	.997			21.258	30	.709		
Subsets grouped by S-N-K			P3 C1 C4 ————— ——			P3 C1 C4 ————— ——				

*Statistical significance of S-N-K test in all cases <0.05

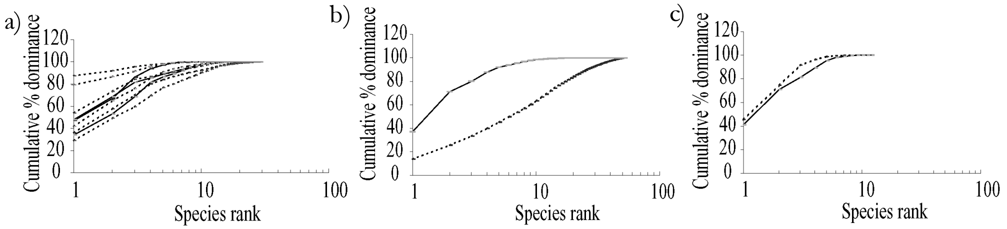

Figure 4. K-dominance curves (x-logged), (solid line-impacted sites, broken line-controls): (a) all sites in summer; b) all sites pooled into two groups: impacted and controls in summer; (c) sites pooled into two groups: impacted and controls in autumn.

characterised by the dominance of so-called opportunistic species, such as the polychaete Capitella capitata, Polydora sp., unidentified Oligochaetes and amphipods Corophium sp. The gastropods Solinator soludus, Zeocumanthus sp. and several species of bivalves, which were comparatively rare at the impacted stations, were dominant at control sites C1 and C4. Other control sites were characterised by a comparatively balanced community structure without expressed dominants.

In the autumn, species composition changed at site P3: the gastropod S. solidus became dominant, whilst the formerly abundant polychaete opportunistic species (Capitella capitata, Polydora sp.) were replaced by species of Lumbrinereidae and Orbinidae (Figure 5). The formerly dominant Amphipode Corophium sp. was also replaced by another species. In contrast, at controls C1 and C4 the community structure remained the same in comparison with the summer situation.

Multivariate approach

Figure 7(a) shows the results of a hierarchical clustering of summer data (no transformation). The three impacted sites form a distinctly separate group. Sites C1 and C4 form a second group, while the controls C2, C3 and C5, C6, despite their distant location and different sediment structure, remain more similar to each other than to the impacted sites.

The pattern for MDS ordination is less clear, with controls C1 and C4 located close to impacted sites (Figure 8(a)). The group of impacted sites became much more distinct from the controls after the data were transformed (fourth root) (Figure 8(b)). ANOSIM test performed on two groups of replicates from impacted and controls sites resulted in global R=0.276 with a significance level of 0.001%. Results of a pairwise test (Appendix 1) suggest that impacted sites are more similar to each other than to controls (sign level <0.001%), with the exception of the pair of sites P3 and C6.

When data collected in April from stations P3, C1 and C4 were added to the initial summer matrix, site P3 formed a group with samples from C4-summer. Samples from C1 in both seasons formed a separate group, closely attached to C4-autumn (Figure 7(b)).

MDS ordination of the 36 replicates from the three sites sampled in the summer and the autumn (Figure 9(b)), shows a clear separation of site P3-summer and half of the replicates from P3- autumn, whilst replicates from both controls in both seasons occupy positions close to each other. MDS plot for fourth root transformed data revealed a more distinctive pattern. Replicates from site P3 in both seasons formed a separate group with the exception of two autumn replicates positioned far from all the others. Samples from controls formed three distinctive groups: C1-summer, C4-summer and both sites in the autumn largely in one group.

Analysis of similarities performed on two groups of samples, impacted site P3 in both seasons and controls C1 and C4 in both seasons, resulted in global R=0,671 and a significance level of 0.0%. Results of a pairwise test for three sites

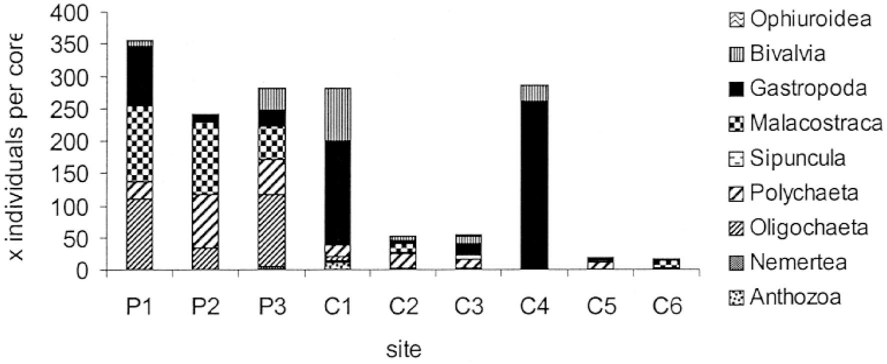

Figure 5. Abundance of macrofauna at impacted and control sites in December 1998

(P3, C1, C4) in both seasons were not significant. Once again, as was shown by the rank-abundance method, the difference between impacted and control sites in the autumn was less obvious in comparison to the summer situation.

Variability

Figure 9(a) presents results of MDS ordination of replicates for all sites in the summer. The replicates from impacted sites were not more scattered than those from the controls. Results of calculations of Index of Multivariate Dispersion are presented in Tables 5 and 6. Index of Multivariate Dispersion has a maximum value of +1 when all similarities between impacted samples are lower than any similarities between controls. The converse case gives a minimum IMD of -1 and values near zero imply no difference between treatment groups (Warwick & Clarke 1993). In this study, the average IMD values between impacted and control sites and between controls were both negative (-0.2 and -0.47 respectively). The only more or less high positive value among pairwise comparisons was between P3 and C4 (0.65) (Table 6). Average values of Relative Dispersion for impacted and control sites were 0.86 and 0.81 respectively - ie no difference was found.

Opposite to the case of the summer data, replicates from impacted site P3-autumn were much more scattered in comparison with replicates from C1-autumn and C4-autumn, which formed a very tight group. Index of Multivariate Dispersion for pairwise comparison was as follows: between P1 and C1 = 0.636, between P1 and C4 = 0.662, and between two controls = -0.076. Both comparisons between impacted and control sites gave high positive

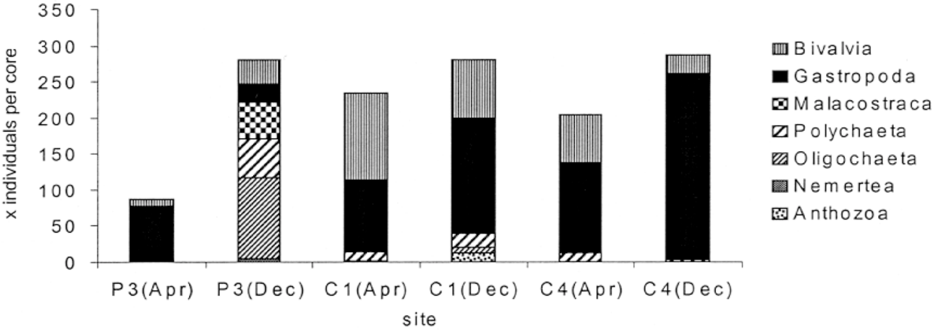

Figure 6. Abundance of macrofauna at impacted site P3 and controls C1 and C2 in April 1999

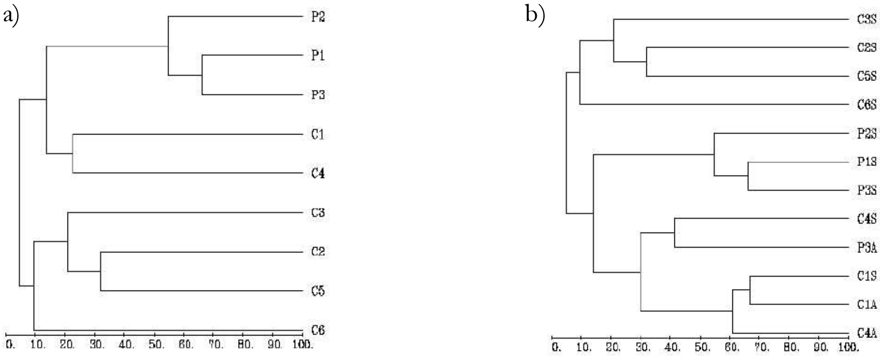

Figure 7. Dendrogram of: (a) nine stations in the summer; (b) nine stations in the summer plus three stations resampled in the autumn; both using group average clustering from Bray-Curtis similarities on untransformed abundances.

values, whereas comparisons between control sites themselves did not reveal much difference. The same pattern was confirmed by Relative Dispersion values, where dispersion for impacted sites was much higher (Table 5).

Generally, all three multivariate methods tested were much more successful in discriminating between impacted and control sites then univariate methods. An increased variability among replicate samples was only revealed for autumn data. Fourth root transformation was found helpful in clearly discriminating patterns in some cases.

Taxonomic resolution

Figure 10 shows the results of a hierarchical clustering of summer data classified to (a) class level and (b) separately for Polychaeta species (no transformation used). In both cases, the impacted sites P1, P2 and P3 are clearly separated from all controls. However, the arrangement of controls into groups differs from the case at species level (Figure 7(a)), especially for Polychaetes. The group of impacted sites remains clearly separated from the controls on both plots of MDS ordination of summer data at class level (Figure 11(a)) and for Polychaetes (Figure 12 (a)). Fourth root transformation of data for class level had little effect in revealing a more obvious pattern (Figure 11(b)). ANOSIM test applied to two groups of impacted and control sites on class level and Polychaetes resulted in global R=0.279 and 0.358 respectively with a significance level of 0.0% (which is similar to global R=0.276 in the case of species level). In both cases, a pairwise comparison revealed an insignificant difference

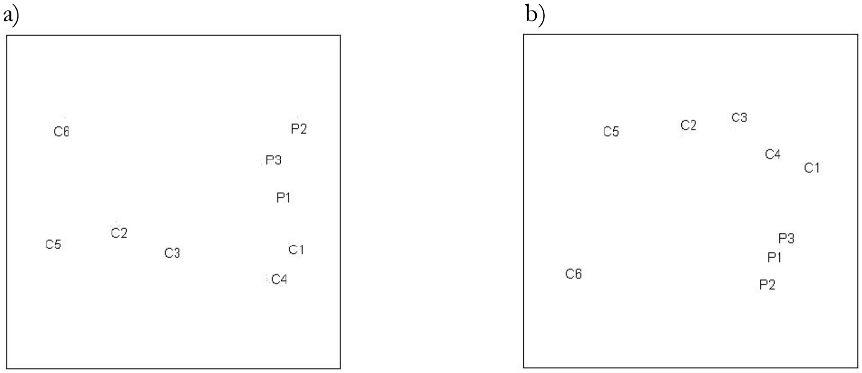

Figure 8. MDS ordination of the nine sites based on: (a) untransformed; (b) fourth root transformed abundances and Bray-Curtis similarities (stress 0.06).

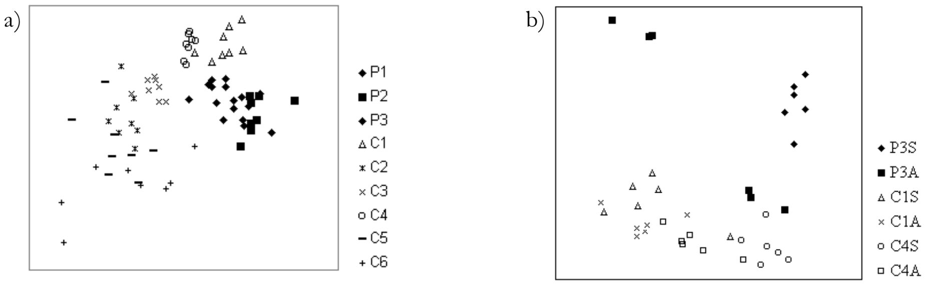

Figure 9. MDS ordination of replicates from all sites: (a) summer; (b) summer and autumn; no transformation.

between impacted sites and a significant difference between almost every pairing of impacted and control sites (Appendix 1).

MDS ordination of autumn and summer data for sites P3, C1 and C4 on class level (Figure 12(b)) revealed a pattern highly similar to that of species level. In both cases, all replicates from P3-summer and three replicates from P3-autumn were clearly separated from both controls in both seasons. ANOSIM results for a pairwise comparison were insignificant, the global R between impacted and control sites in the autumn being 0.448.

Generally, all three multivariate methods applied to data on class level and Polychaeta only succeeded in distinguishing between impacted and control sites in all cases. In this respect, no significant information was lost in comparison with an analysis at species level.

Discussion

The principle aims of this study were 1) to estimate the changes in macrobenthic communities under organic pollution stress, in Proper Bay, Port Lincoln and 2) to identify the most cost-effective and sensitive choice of biological variables and associated methods.

The study succeeded in distinguishing between impacted and control sites with a high degree of significance and compared different methods with respect to their sensitivity. Even though a decrease in species richness and an increase in the number of individuals are widely acknowledged characteristics of stressed communities, this was not observed in the present study. The main cause of this inconsistency was the great variability between control sites themselves. This supports the idea of so-called MBACI sampling design (Underwood 1994, Keough &

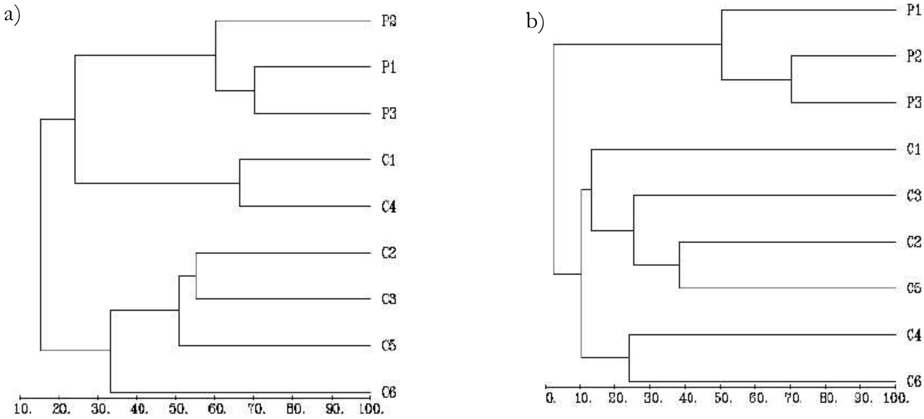

Figure 10. Hierarhical clustering of summer data classified to: (a) class level; (b) only Polychaeta species.

Table 5. Relative Dispersion of impacted and control sites in summer

Order of group	Relative Dispersion (summer)	Relative Dispersion (autumn)
C4	0.50	0.81
P3	0.68	
C1	0.71	0.77
P2	0.73	
C3	0.86	
P1	1.18	1.42
C2	1.25	
C6	1.54	
C5	1.55	

Table 6. Pairwise comparison of IMD values for impacted and control sites in summer

P1									
P2	0.47								
P3	0.51	0.06							
C1	0.46	0.03	0.00						
C2	-0.05	-0.59	-0.62	-0.54					
C3	0.36	-0.19	-0.29	-0.23	0.51				
C4	0.65	0.31	0.26	0.26	-0.75	-0.50			
C5	-0.38	-0.84	-0.87	-0.81	-0.40	-0.87	-0.91		
C6	-0.43	-0.76	-0.79	-0.76	-0.42	-0.84	-0.85	-0.13	
	P1	P2	P3	C1	C2	C3	C4	C5	C6

Quinn 1995), which suggests the use of more than one (the more the better) control site. This point was additionally illustrated by comparison of the results of diversity indices. At three control sites, diversity indices were higher than at any impacted site, whilst at two controls they were approximately on the same level, slightly lower at one. Any evidence of impact would not have been detected if sites with low diversity were used as controls and our assumptions were based only on diversity indices. Analysis of community structure revealed a well-known pattern of increased abundance of opportunistic species (*Corophium sp.*, *Capitella capitata*, *Polydora sp*, Oligochaeta) at impacted sites, but univariate methods associated with the first three variables tested did not succeed in recognising these changes.

Both rank abundance methods tested were more successful, and confirmed results from other studies showing trends in distribution of individuals among species in stressed communities (ie Gray 1981, Clarke 1990). However, patterns among control sites themselves were again highly variable and in the case of the three sites sampled in the autumn, k-dominance curves for control sites behaved in a way opposite to expected. In this respect, caution should be taken when dealing with data containing a low number of individuals and species, and a sufficient number of control sites should be used. Also, another drawback of rank abundance methods is the difficulty of expressing results in understandable and convincing values or indices.

All multivariate methods that were tested succeeded in distinguishing between impacted and control sites with a high level of confidence both in graphical and numerical representations. Analysis of variability was also found to be useful. Visual examination of MDS plots of replicates did not confirm the pattern of greater variability in stressed communities for the

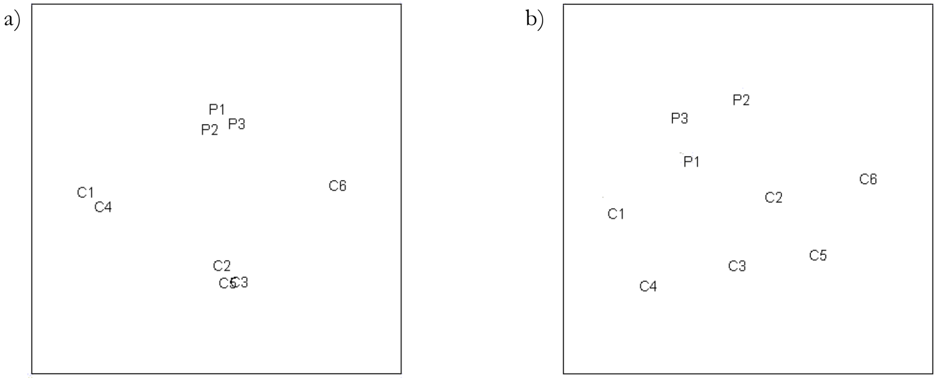

Figure 11. MDS ordination of summer data classified to class level: (a) no transformation, stress 0.01; (b) fourth root transformation, stress 0.08.

summer data, although in the autumn, replicates from impacted sites were more scattered than those from controls. Results of calculations of Index of Multivariate Dispersion were also different for summer and autumn data. In the autumn, a higher Relative Dispersion was revealed for impacted sites in comparison with controls, whilst in the summer, average Relative Dispersion was almost identical for impacted and control sites. The IMD values for comparisons between impacted and control sites in the autumn were strongly positive but negative in the summer. In other words, increased variability among replicates from impacted sites in comparison with controls was revealed for the autumn situation, but not for the summer.

Even though both rank abundance and multivariate methods proved to be sensitive to changes in communities, the major difficulty connected with them is the tedious and costly process of species identification. The two possible methods of cost reduction tested in this study (identification of all individuals to class level and use of species only from a selected group, eg. Polychaeta) both resulted in patterns highly similar to those for traditional species level and no significant information was lost.

According to the results of this study, the most cost-effective and sensitive methodological choice is an analysis of community structure using multivariate methods either at the class level or using only the Polychaete assemblage (Table 7).

Our results are consistent with the conclusions of other researchers in this area. A majority of authors (Somerfield & Clarke 1995, Vanderkliff et al. 1996) agree that identification

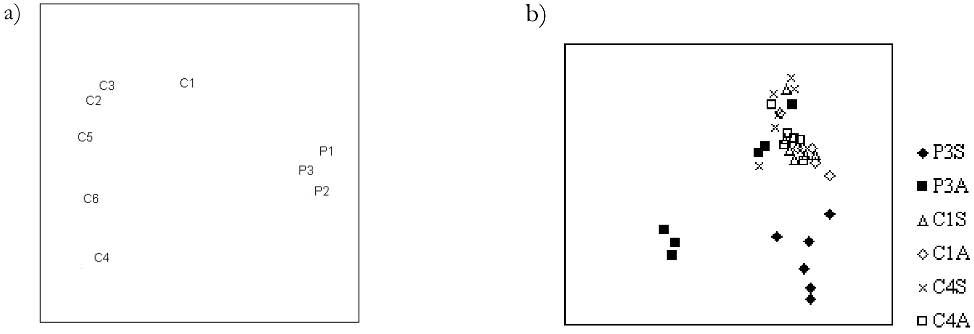

Figure 12. (a) MDS ordination for Polychaeta sampled in summer, stress 0.04, no transformation; (b) MDS ordination of replicates from three sites (P3, C1 and C4) sampled in the summer and autumn, no transformation, stress 0.09, class level.

Table 7. Advantages/disadvantages of choice of particular biological variables and sensitivity of associated methods as shown by this study

Variable	Methods associated with variable	Advantages/Disadvantages	Sensitivity to changes from the results of this study
Number of individuals	ANOVA	No species identification required	Not sensitive
Number of species	ANOVA	Species identification required	Not sensitive
Species diversity	Diversity Indices, ANOVA	Species identification required	Not sensitive
Distribution of individuals among species	Rank abundance methods	Species identification required, no simple understandable values	Sensitive, caution should be taken
Community structure (species level)	Multivariate methods	Species identification required	Sensitive
Variability in community structure among replicates (species level)	Analysis of MDS plots, Index of Multivariate Dispersion	Species identification required	Results are inconclusive
Community structure (class level)	Multivariate methods	Identification is fast and simple	Sensitive
Polychaeta assemblages	Multivariate methods	Identification takes less time than identification of all species	Sensitive

of macrofauna to family level has little or no effect, but further aggregation produces differing results in different studies, although interpretable results are possible even on the phylum level. Ferraro & Cole (1990) compared univariate measures from areas with different degrees of impact. They suggested that different taxonomic levels could be used for different situations, using a coarse resolution for harsher impacts and a finer resolution for moderate impacts and so on. They believed that biological response to stress has a hierarchically structured nature. As stress increases, the adaptability of first the individual, then the species, genus, family, etc. is exceeded. Consequently, increasing stress is manifested at higher and higher levels of biological organisation. Warwick (1988) considered that analysis of pollution effects on higher taxa minimises the confounding effects of natural variables (water depth, sediment structure and so on). This relies on the assumption that such variables usually influence the fauna more by species replacement than by changes in the proportion of major taxa present. Chapman (1998) produced positive results when studying the relationship between spatial patterns of benthic assemblages at traditional species level resolution and when all taxa were divided into nine groups according to their phylogeny and ecology.

Identification to a level higher than species drastically reduces the cost of impact assessment or monitoring. Ferraro & Cole (1995) found that the cost of genus, family, order and phylum level identification were respectively 23%, 55%, 80% and 95% less than for species level identification. According to our estimation, identification to class level is about 80-85% less costly that to species level and does not require special training. It is agreed that identification to family level could reveal a more detailed picture, but for the purpose of rapid impact identification, class level is probably sufficient. Besides, coarser taxonomic resolution releases time and money which can be used for sampling more control sites, which, according to our results, is extremely important.

Identification of species from a selected group has not been widely discussed in the literature, and it has been suggested that such an approach could be misleading (Warwick 1993). However, our results were highly consistent and more research is now needed to ensure that changes detected in selected groups are indicative of changes in the community as a whole.

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Appendix 1

One-way ANOSIM results for different levels of taxonomic resolution (no transformation, number of permutations = 5000)

Groups	Species R=0.770	Class R=0.753	Polychaeta R=0.551
(P1, P2)	0.505*	0.456	0.431
(P1, P3)	0.441	0.383	0.244
(P1, C1)	0.667*	0.411*	0.364
(P1, C4)	0.554*	0.403*	0.518*
(P1, C2)	0.921*	0.732*	0.729*
(P1, C3)	0.779*	0.711*	0.780
(P1, C5)	0.867*	0.888*	0.754*
(P1, C6)	0.690	0.838*	0.460*
(P2, P3)	0.318	0.323	0.142
(P2, C1)	0.997*	0.993*	0.888*
(P2, C4)	1.000*	1.000*	0.648*
(P2, C2)	0.992*	0.723	0.859*
(P2, C3)	1.000*	0.983*	0.981*
(P2, C5)	0.893*	0.902*	0.893*
(P2, C6)	0.755*	0.897*	0.585*
(P3, C1)	0.992*	0.931*	0.723
(P3, C4)	0.995*	0.979*	0.649*
(P3, C2)	0.952*	0.728	0.827*
(P3, C3)	1.000*	0.940*	0.949*
(P3, C5)	0.877*	0.877*	0.866*
(P3, C6)	0.752*	0.944*	0.593*
(C1, C4)	0.800*	0.286	0.565*
(C1, C2)	0.984*	0.927*	0.649
(C1, C3)	0.976	0.997*	0.629*
(C1, C5)	0.894*	0.969	0.744
(C1, C6)	0.762*	0.992	0.488*
(C4, C2)	0.974*	0.969*	0.400
(C4, C3)	1.000*	0.967*	0.573*
(C4, C5)	0.901*	0.991	0.408*
(C4, C6)	0.755	0.992*	0.184
(C2, C3)	0.800	0.509*	0.586*
(C2, C5)	0.200	0.110	0.139
(C2, C6)	0.632*	0.627*	0.233
(C3, C5)	0.775*	0.669*	0.583
(C3, C6)	0.744*	0.874*	0.383*
(C5, C6)	0.371	0.337	0.098

* significant (< 0.0%)

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Soyoung Park

Park, S. 2001. Habitat-based population viability analysis for the Asiatic black bear in Mt. Chiri National Park, Korea. – CBM:s Skriftserie 3: 149–165.

The Asiatic black bear population in Korea has been reported to be close to extinction and is in urgent need of effective management. Suitable bear habitat in Mt. Chiri National Park and adjacent areas was assessed based on data from field surveys. When incorporated with demographic data, this data was fed into a habitat-based, stage-structured, stochastic model in Ramas/GIS. A population viability analysis was performed in this model to investigate the effects of poaching on the viability of the population and the potential of a restoration programme of the bear population by supplementation. Generally, the simulation results show that the risk of extinction is small when the carrying capacity and the population growth rate are large and the environmental stochasticity is small within the parameter ranges used in this model.

In conclusion, population viability analysis of a hypothetical Asiatic black bear population in the Mt. Chiri National Park area raises two points. Firstly, Mt. Chiri National Park can support a viable bear population in a demographic sense, though is probably inadequate for long-term survival in a genetic sense. Secondly, a viable bear population, in a demographic sense, may be restored through supplementation. Simulation results confirm that there can be a significant difference between a no supplementation policy and one of supplementing only a few individuals.

Soyoung Park, Swedish Biodiversity Centre, Box 7007, SE-750 07 Uppsala, SWEDEN.
E-mail: p_soyoung@hotmail.com

Introduction

Seven subspecies of Asiatic black bear are distributed over much of southern Asia including Pakistan, Afghanistan, northern India, China and Southeast Asia (Ellerman and Morrison-Scott 1968). Separate populations are also known to be present in eastern Russia, Korea, Taiwan and Japan (Servheen 1989). Throughout most of its range, conservation efforts aimed at the Asiatic black bear are almost nonexistent and legal protection is seldom enforced.

At present, there is no exact estimate of the wild Asiatic black bear population. Servheen (1989) considered that data on the Asiatic black bear was minimal and the validity of distribution information was questionable. Bunnell and Tait (1981) also commented on the lack of data on this species. Some studies have focused on foraging habits and consequent forest damage (Watanabe and Komiyama 1976, Watanabe 1980, Torii et al. 1989, Reid et al. 1991, Mizoguchi et al. 1996, Hashimoto and Takatsuki 1997). Other researchers have reported on the distribution, demographics and home range of the Asiatic black bear (Mizuno et al. 1972, Torii 1975, Nozaki et al. 1979, Hazumi et al. 1981, Nozaki and Mizuno 1983, Ma 1986, Liu and Xiano 1986, Ishida 1995).

The status of the Asiatic black bear population in Korea (*Selenarctos thibetanus ussuricus* Heude) is similar to that in other Asian countries. Servheen (1989) concluded that 'the Asiatic black bear is very close to extinction with a population estimate of 57 individuals in 1982 separated into five separate populations'. This species is listed as 'Natural Monument No. 329' by the Korean government and has been under legal protection since 1982 (Lee et al. 1994). Despite these efforts, the bear population decreased dramatically and it was considered to be extinct in the wild. However, traces of bears, such as footprints on the snow, scats and scratches on trees, were then found at Mt. Chiri and Mt. Odae where bears were once found. The exact number of remaining bears is unknown, but some experts estimate the number to be between 5 and 20 individuals. There has been almost no research on bears and bear populations in Korea.

The Korean government has attempted to control poaching by abandoning all unused or informal mounting trails, strictly controlling the use of firearms and the construction of ecological infrastructure, such as underpasses and eco-bridges. Some experts have insisted that all the wild Asiatic black bears in Korea should be caught and kept in captivity for protection and breeding, being reintroduced later, since the number of individuals is too small to sustain a viable population. Others have recommended the supplementation of individuals from China or Southeast Asia to avoid inbreeding depression.

These suggested management options can be summarised as:

1) anti-poaching;
2) establishing ecological infrastructure between fragmented habitat areas;
3) supplementation.

In addition to these actions, public education about the bear and the focusing of the efforts of a diverse group who have different interests, towards a management objective that will be beneficial to the bear, are also important. However, since the resources for conservation efforts are limited, the effect of diverse management options should be evaluated. Population viability analysis (PVA) is a quantitative method that makes it possible to evaluate the effects of management options through simulation (Shaffer 1990, Norton 1995, Possingham and Davies 1995). Effective management of a population largely depends on an understanding of habitat requirements as well as population dynamics. There are an increasing number of studies on these subjects, but few have tried to connect these two fields.

The objectives of thisstudy were to 1) compile all currently available knowledge, including habitat requirements and demographic data, on the black bear, 2) assess the suitable bear habitat in Mt. Chiri National Park and adjacent areas, 3) incorporate the habitat data and demographic data into a metapopulation model and perform a population viability analysis, and 4) evaluate the effects of poaching on population viability

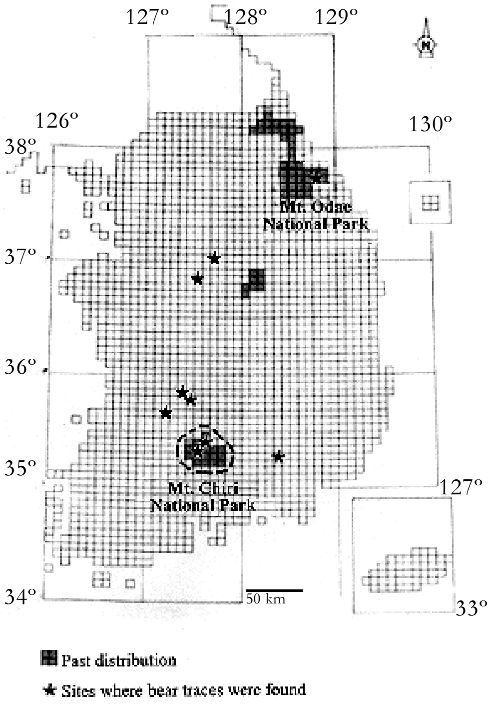

Figure 1. Distribution of *Selenarctos thibetanus ussuricus* Heude in South Korea.

and investigate the possibilities of restoration of the bear population, by supplementation, in Mt. Chiri National Park.

Methods

Study area

Mt. Chiri was designated as National Park No. 1 in 1967, and is located in the southern part of the Sobaek mountain range. It includes the second highest peak in S. Korea (1 915 m) and is the largest of the country's National Parks (about 440 km^2).

The past distribution of the Asiatic black bear and sites where traces have been found recently are shown in Figure 1. Mt. Chiri National Park and Mt. Odae National Park are both located within the former range of the bears, and some of the recent observations of bear signs were found within these areas. This study focused on Mt. Chiri National Park and the adjacent area, since it is the largest National Park in Korea and the main vegetation comunity of Mt. Chiri is dominated by *Quercus* that is known to be more suitable for the bear, whereas the main vegetation community at Mt. Odae National Park is dominated by *Abies* species. It was thought that some areas outside of the National Park might be suitable habitat for the bear, though these are not protected at present. Thus the areas adjacent to the Mt. Chiri National Park were also included in this study.

GIS database

The GIS Database consists of topographical and vegetation data. I used the digitised topographic maps (1:25000 or 1:5000) prepared by the Korean National Geographic Institute (NGI). These maps were integrated and converted into a raster (grid) format with a resolution of 50m, based on the home range size of bears and landscape heterogeneity (Layman and Barrett 1986). I analysed elevation (m), slope (°), aspect (°, 0 for north, 90 for east, 180 for south, and 270 for west) and distance from roads (m) and water (m) from this raster map.

A Digitised Actual Vegetation map (i.e., *Quercus mongolica* community, *Pinus densiflora* community), which was produced by the Ministry of Environment, and a Forest Type map (including age of forest, average diameter of trees and the density of trees), produced by the Forestry Service, were also converted to raster format with a resolution of 50m in Arcview (version 2.0).

These raster maps were converted into an ASCII format in Arcview and then converted into TXT format for use in the Ramas/GIS program.

Habitat requirements and habitat suitability index map

I chose environmental factors for analysing habitat suitability by reviewing literature on the Asiatic black bear and the American black bear (Torii et al. 1989, Reid et al. 1991, Clark et al. 1993, Rudis et al. 1995, Mizoguchi et al. 1996, Hashimoto and Takatsuki 1997). The factors chosen for use in the analysis were elevation, slope, aspect, distance from road and water, actual vegetation, forest type, age of forest, average diameter of trees and density of trees.

I collected absence and presence data for traces of the Asiatic black in the Mt Chiri National Park. In total, I found 12 traces of bears (i.e. denning site, bark scratches, broken branches) with the help of local people who have been moni toring the traces of bears since 1995. I recorded the geographical position of these traces using a portable GPS receiver (Model: Trimble Ensign GPS) and subsequently used as locations for presence data. During the field survey, vegetation type was recorded at each trace for comparison with a published map, which was converted. into a raster format. After locating each position on the raster map, environmental factors were then recorded for each point.

The National Park Authority (Anon. 1998) has identified and delineated 14 separate areas within Mt. Chiri National Park where bear traces have been found. Additional data was then gathered based on this literature. I digitised the boundary lines for these areas and set a 1 km buffer area around these boundaries to prevent collection of absence data within 1 km of these areas. Next, a point was located in the center of each trace area and these points (14 in total) were added to the presence data set. For absence data, 21 points were evenly placed outside the trace and buffer areas. No points were located far from the National Park, since most of those areas are developed or used for agriculture.

Next, I analysed correlations between existence data (absence and presence data) and environmental factors. A Mann-Whitney U test was used for elevation, slope, aspect, distance from road and water and existence data, and a Chi square test for other factors. Then, a multiple logistic regression analysis was used to calculate a habitat suitability function. A significance level of $p=0.05$ was used in both cases (correlation and logistic regression). SPSS (version 8.0) was used for statistical analysis. This habitat suitability function was used in Ramas/GIS (version 3.0) to predict the distribution of suitable habitat.

Population Viability Analysis (PVA) Simulation

Ramas/GIS

Ramas/GIS consists of 5 subprograms (Landscape data, Habitat dynamics, Metapopulation model, Sensitivity analysis, and Comparison of result) and combines spatial landscape data with demographic data of a population into a metapopulation model (Akçakaya 1998).

The landscape data program imports spatial data on the landscape (i.e. elevation, slope, aspect, vegetation etc.) and converts it into a habitat suitability map using the habitat suitability function. The landscape data program then identifies habitat patches in the habitat suitability map, within a given threshold habitat suitability (HS) and a neighbourhood distance that may relate to the foraging distance of the species.

The metapopulation model program then combines the habitat patch map with the demographic data (i.e. survival rates, fecundity, density dependence etc.). Simulations of management alternatives then estimate the risk of extinction within a projected time (e.g. 100, 500 or 1000 years) or time to extinction etc. Simulation scenarios can include several levels of poaching, population supplementation and natural catastrophes. Available literature on the black bear was reviewed and parameters, which were used in the simulation, were estimated. Each parameter had medium, lower and upper estimates (medium ±1/2SD). The medium estimate, in this case, refers to the average value from those that have been reported in different studies and the SD (standard deviation) refers to the variation among different studies.

Identifying habitat patches

After estimating a habitat suitability (HS) function, a threshold HS and a neighbourhood distance were used for identifying habitat patches. I used a threshold HS of 0.5 (0.45 for lower and 0.55 for upper estimates) and a neighbourhood distance of 1697m (SD=1544), based on the available literature (Young and Ruff 1982, Nozaki and Mizuno 1983, Ishida 1995). This means that bears can survive in areas where the habitat suitability value is 0.5 or above and individuals move up to 1697m when foraging.

Carrying capacity and initial abundance

I estimated the carrying capacity of the study area based on the average bear density (0.664/km^2, SD=0.838) that was reported in studies of the Asiatic and American black bear (Lecount 1982, Reid et al. 1991, Wang et al. 1994, Uh pers. comm. 1999). I assumed that these estimated densities reflected 80% of the carrying capacities. I used values of 100, 500 and 1000 for the carrying capacity in different simulations, as well as estimated values (78, 216 and 355 for lower, medium and upper estimates). I interviewed local people to estimate initial abundances. Values between 3 and 13 were obtained, with 3, 5 and 13 being chosen for lower, medium and upper estimates.

Stage structure

I modelled the dynamics using a stage-structured (juvenile and adult), stochastic matrix model. The parameter values (Table 1) in this model were based on the literature (Watanabe et al. 1976, Lecount 1982, Hellgren and Vaughan 1989, Wang et al. 1994, Powell et al. 1996). The standard deviation (variation among different studies) for each parameter was between 20 and 25 percentage of the average value. This standard deviation was used for simulating environmental stochasticity. I assumed that one third of juveniles would become breeding adults and that adult bears would breed every other year. Thus, the period between litters would be two years, which is shorter than the 2.4 years that was chosen for a PVA of the Asiatic black bear in Taiwan (Wang et al. 1994).

Environmental stochasticity

Environmental stochasticity can affect the vital rates, carrying capacity and dispersal among populations in the Ramas/GIS. I introduced environmental stochasticity by using the standard deviation of estimates in the stage matrix, so environmental stochasticity will affect only the vital rates such as survival rates and fecundity.. The three levels of environmental stochasticity were modelled by manipulating the standard deviation matrix (abbreviated to S, 1/2S, and 1/3S). At each time step during the simulation, the Ramas/GIS program chose a value for vital rates randomly from a distribution, which was limited only by the average value and its standard deviation (S).

Density dependence and Allee effect

I assumed a ceiling-allee model for all simulation scenarios. This means that each population will grow exponentially in a stochastic way until it reaches the ceiling or carrying capacity. If the population increases above the carrying capacity, it will be decreased back to, or below, the carrying capacity. But, if the population is much below the carrying capacity, it will then be affected by an allee effect and drawn towards extinction. The allee effect was incorporated by setting a local extinction threshold of 10% of the carrying capacity. A subpopulation in the metapopulation that has fewer individuals than this threshold will be considered extinct, but these individuals will be included in the total and will participate in breeding.

Poaching

I assumed that poaching would take place throughout the simulation period, of a constant

Table 1. Parameter value estimation for the stage matrix.

Parameters		Lower estimate		Medium estimate	
Juvenile fecundity	Adult fecundity	0.096	0.405	0.119	0.503
Juvenile survival	Adult survival	0.590	0.830	0.665	0.935
Population growth rate		1.026		1.074	

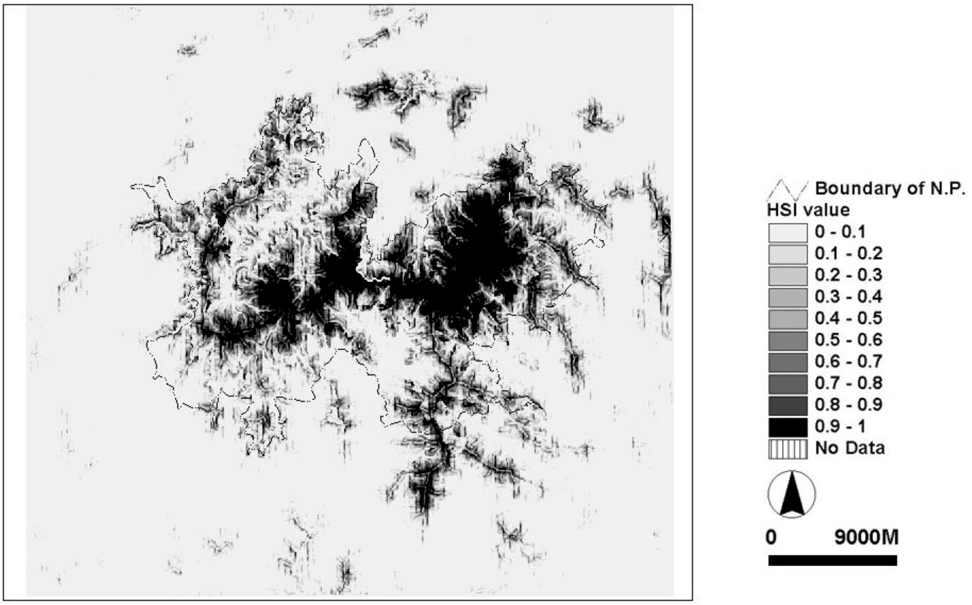

Figure 2. Habitat suitability index map for the Asiatic black bear in Mt. Chiri National Park.

proportion of the population, rather than a fixed number of individuals. I examined the effects of poaching levels of 1% and 2% of the population when the population growth rate was 1.026, and 1%, 5% and 7% when the population growth rate was 1.074. Poaching was modelled as a harvest in the Ramas/GIS program.

Supplementation

The objective of supplementation is to achieve a population with the same viability as a population at its carrying capacity, even though the initial population size is small. Three scenarios of supplementation were considered, with releases of 1/2K, 1/4K and 1/10K bears respectively. Supplementation was simulated every year during the first ten years. Thus, the actual numbers of supplemented individuals were 11 (1/2K), 5 (1/4K) and 2 (1/10K) per year when the carrying capacity was 216, and 25 (1/2K), 12 (1/4K) and 5 (1/10K) per year when the carrying capacity was 500. Both juvenile and adult bears were supplemented, corresponding to a stable demographic distribution.

Estimates of all parameters are shown in Table 2. Every simulation for each scenario (scenario and results are shown in Appendix 1, Appendix 2 and Appendix 3) was replicated 500 times and each replication projected the abundance of each population over 100 years. The upper estimate of population growth rate (λ) was not employed in simulations, as in these cases, populations could grow more than 23% per year. These populations would seldom go to extinction without severe poaching or catastrophes, which seems unrealistic.

Results

Habitat suitability index map

Among the habitat variables, only elevation (ELV), slope (SLP), distance from road (DRD) and actual vegetation (VEG) were significantly correlated with the absence and presence data of bear traces. A logistic regression function with four variables (ELV, SLP, DRD and VEG) was highly significant (p=0.0001) and the predictability was also very high. However, two of the regression coefficients (SLP and DRD) were not

Table 2. Estimates of parameters used in the model (For the choice of parameters, shaded areas were taken together as one estimate and un-shaded cells was taken separately for each parameter. Supplementation was simulated during the first ten years).

Parameter	Estimates Lower	 Medium	 Upper
Threshold HS	0.45	0.50	0.55
Neighborhood distance (m)	925.32	1696.89	2468.46
Dispersal distance (km)	9.253	16.969	24.684
Density (individuals/km^2)	0.245	0.664	1.083
Carrying capacity	78	216	355
Initial abundance	3	5	13
Population growth rate	1.026	1.074	1.234
Environmental stochasticity (Standard deviation matrix)	1/3S	1/2S	1S
Poaching level	0.01	0.02/0.05	0.07
Supplementation level (No. of individuals/year) (K=216/355/500)	2/3/5	5/9/12	11/18/25

statistically significant, so the DRD variable was excluded. The results of this logistic regression analysis with three variables are summarised in Table 3.

The logistic regression function is highly significant (p=0.0001). The predictability is also very high (91.49%, cut value for presence is 0.5) and all regression coefficients are statistically significant.

The probability for the presence of bear traces (habitat suitability) was calculated as:

$$P = 1-[1/\{\exp(ELV*0.0129+SLP*0.1919-VEG*3.6730-14.3114)+1\}] = HS$$

A habitat suitability index (HSI) map based on the HS is shown in Figure 2 and the HS histogram is shown in Figure 3. Only 13.58% of the total number of cells have a value greater than 0.50 and the average HS for the whole area is 0.15. Most of the suitable areas are concentrated inside the National Park but some areas with high HS values are situated outside the National Park boundary. Some of these areas are

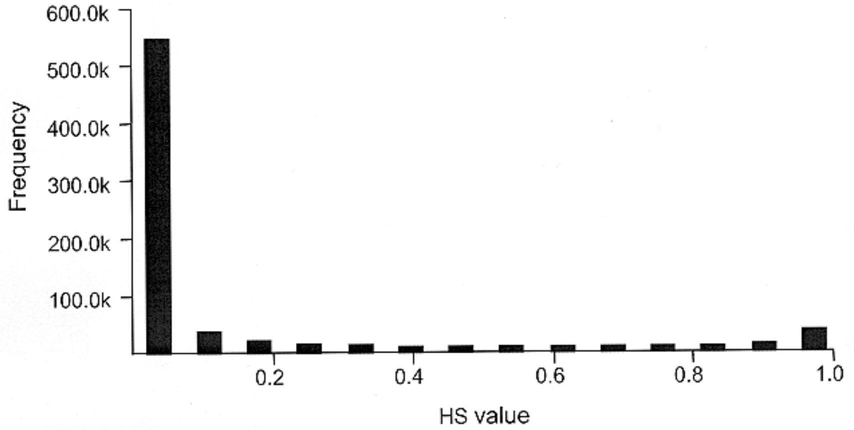

Figure 3. Frequency distribution of habitat suitability for the Asiatic black bear in the Mt. Chiri National Park area.

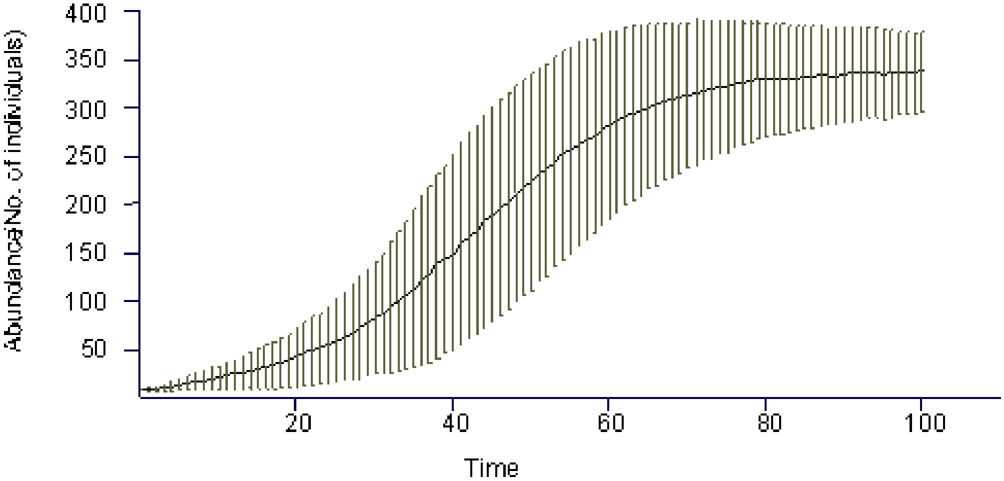

Figure 4. Trajectory summary for a hypothetical Asiatic black bear population (K=355, Init. abundance=13, population growth rate=1.0741, environmental stochasticity=1/3S; Appendix 1).

connected to the National Park, while others are isolated.

Using 0.5 as a threshold HS, three distinct habitat patches were found. Total HS, carrying capacity (K) and area (km^2) are shown in Table 4. Patch 2 covers the National Park and occupies 95.46% of the total suitable area. Some areas, which are not part of the National Park but connected to it, are included in this patch.

Population Viability Analysis

In general, the model predicted that the risk of extinction for a hypothetical Asiatic black bear population would be small when the carrying capacity (K) and the population growth rate (λ) are large and the environmental stochasticity is small, within the range between the lower and upper estimates used in this model (Figures 4 and 5).

Table 3. Results of logistic regression for a habitat suitability function with three variables.

Variables	Reg. coefficient	S.E.	Wald	p
ELV	0.0129	0.0050	6.6817	0.0097
SLP	0.1919	0.0947	4.1074	0.0427
VEG	-3.6730	1.3822	7.0617	0.0079
Constant	-14.3114	6.0016	5.6863	0.0171

Without poaching and natural catastrophes (such as fire, flood or typhoon), the model predicted that a hypothetical Asian black bear population, initially at its carrying capacity, would have a low risk of extinction ($p<0.05$), except if the carrying capacity and the population growth rate (λ) are both very low and the environmental stochasticity is high (K=78 and 100, population growth rate=1.0261, environmental stochasticity=S). Other hypothetical populations with a low initial abundance have a high risk of extinction, except if the carrying capacity and the population growth rate are very high and the environmental stochasticity is very low (K≥216, population growth rate=1.0741, environmental stochasticity=1/3S; Figure 6 and Appendix 1).

The effect of poaching was severe when the poaching level approached the value of the population growth rate. When population growth was assumed to be 7.41% per year, poaching of 5% of the population caused a large effect on population viability. Even in a hypothetical population initially at its carrying capacity, the model predicted that this population would have a high risk of extinction when the poaching level was 7% (Figure 7). Even with a lower poaching level, the risk of extinction can be high for a population with a small carrying capacity and a low population growth rate (Appendix 2).

Table 4. Summary of habitat patches (0.5 was used for threshold HS).

Patch	Total HS	Average HS value	K	Area (km^2)	Percentage of the total suitable area	Percentage of the landscape
1	3104	0.75	9	10.3	3.98	0.54
2	82324	0.83	206	247.9	95.46	12.96
3	393	0.68	1	1.5	0.56	0.08
Sum	85821		216	259.7	100	13.58

The model also predicted that the risk of extinction for a hypothetical population with a low initial abundance could be decreased by supplementation (Figure 8 and Appendix 3). It is possible to decrease the risk of extinction from 0.46 to 0.001 by supplementing the population with a number of individuals equivalent to a quarter of the total carrying capacity (initial abundance=5, K=216, population growth rate=1.0741, poaching=0.01, environmental stochasticity=S; Appendix 3).

Discussion and management implications

In this model, habitat suitability was a function of elevation, actual vegetation and slope. Distance from the road was correlated with the existence of bear traces but it was excluded, since the habitat suitability function was not significant statistically. As a result, habitat suitability does not reflect anthropogenic impacts on habitat. Forest type, such as old growth forest, and water resources that usually seem to be critical for the survival of wildlife, were not included in this model. Only 12 of the 47 presence and absence data points are based on personal observation, with others taken from the literature. But, I still obtained a statistically significant and highly predictable (91.49 %) habitat suitability function. However, it would be useful to have more data, especially from field surveys, to develop a habitat function that incorporates natural environmental factors and anthropogenic factors.

All the data used in the population viability analysis originated from literature on the American black bear and the Asiatic black bear in Japan, China and Taiwan. Thus, the data included

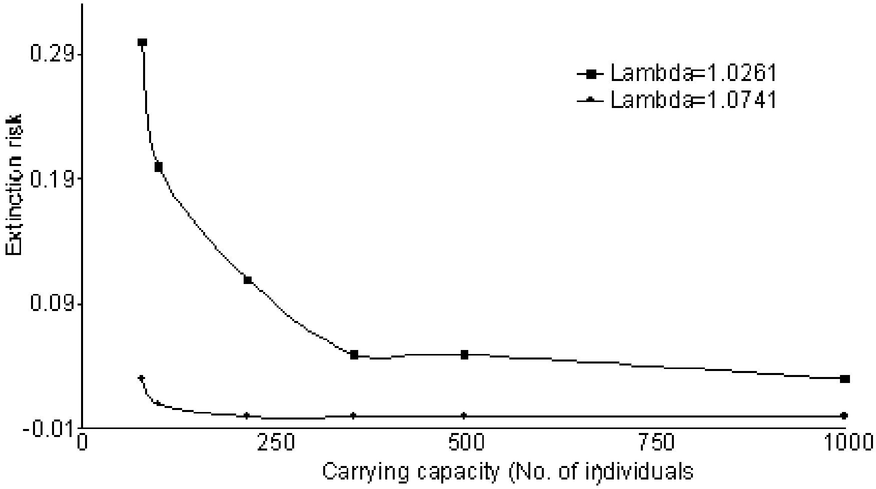

Figure 5. Comparison of extinction risks for a hypothetical Asiatic black bear population (init. abundance=K, population growth rate=1.0261 and 1.0741, environmental stochasticity = S; Appendix 1).

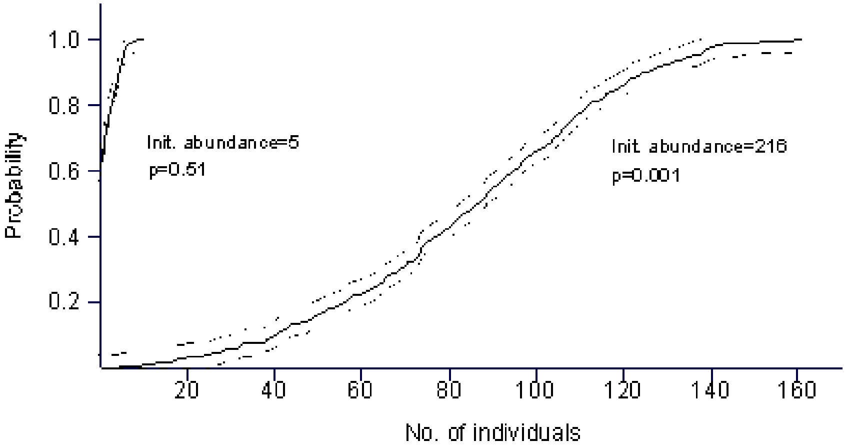

Figure 6. Comparison of interval extinction risk between two hypothetical populations (K=216, init. abundance=5 and 216, population growth rate=1.0261, environmental stochasticity = 1/3S; Appendix 1).

a wide range of different habitats, subspecies and even species. Future field surveys on this specific bear population would be helpful in improving this model.

The carrying capacity of the Mt. Chiri area can be calculated directly as a function of habitat suitability, or from the density of bears per unit area. I used the latter method, but limited the area to the suitable habitat as predicted by the habitat suitability function. But the density, which was used for calculating the carrying capacity, pertained to total area rather than just suitable area. Thus, actual carrying capacity may be underestimated.

Shaffer (1981) suggested that systematic pressures and stochastic perturbations, such as demographic stochasticity, genetic stochasticity, environmental stochasticity and natural catastrophes, contribute to the extinction process of a species.

In this population viability analysis, I only considered demographic stochasticity, environmental stochasticity and poaching as a systematic pressure. So, the risk of extinction as shown in this analysis, might be an underestimate. In spite of these limitations, it was

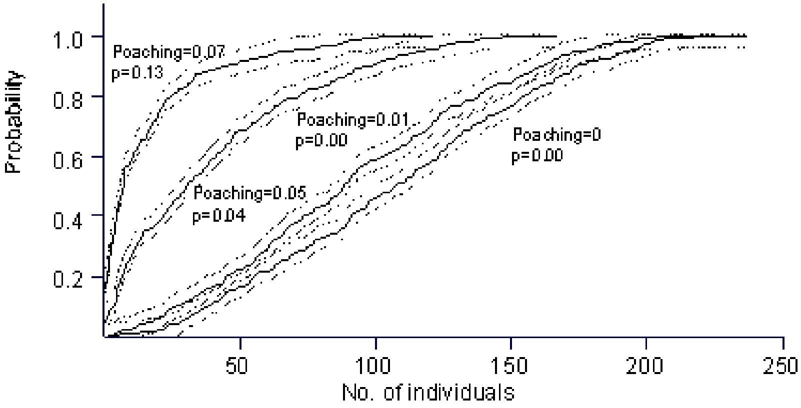

Figure 7. Comparison of interval extinction risk between four hypothetical populations with different poaching levels (K=355, init. abundance=355, population growth rate=1.0741, environmental stochasticity = S; Appendix 2).

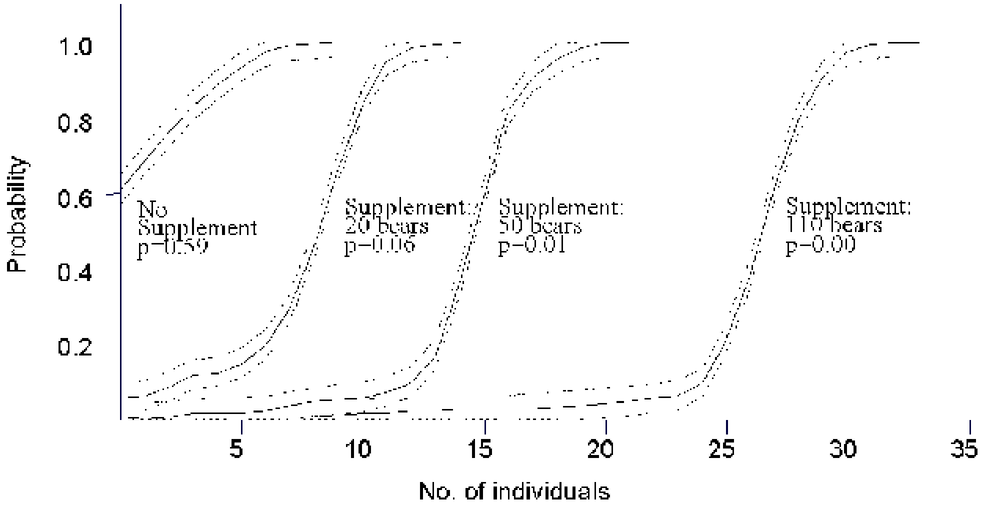

Figure 8. Comparison of interval extinction risk of supplemented hypothetical populations (K=216, init. abundance=5, population growth rate=1.0261, poaching=0.01, environmental stochasticity=1/2S; Appendix 3).

generally predicted, within a range of parameters values, that the risk of extinction for a hypothetical Asiatic black bear population would decrease with a relatively high population growth rate (λ), low environmental stochasticity and a large carrying capacity and initial abundance.

Franklin (1980) proposed that a genetically effective population size of 500 could be enough to maintain sufficient genetic variability to adapt to changing environmental conditions, and a genetically effective population size of 50 could be enough to maintain short-term fitness. This means that population size should be more than 150-500 individuals to sustain short-term fitness. But results from the present study show that a population size of 500 or 1000 is not enough if this is combined with high environmental stochasticity, low population growth rate and a high level of poaching. This theoretical population would then go extinct. This indicates that to attain sufficiency and long-term survival, population size should be larger and there may be a need to connect isolated populations to other areas with suitable bear habitat to promote geneflow. These genetic aspects are very important for small populations, but other factors, such as systematic pressures, demographic stochasticity and environmental stochasticity, should also be highlighted for species conservation.

Akçakaya and Atwood (1997) suggest two practical uses of this model. One is that sensitivity analysis can give information about which parameters need to be more carefully estimated, and through this careful estimation the model can be continuously improved by incorporating new data. Shaffer (1981) also suggested that if the information for the simulation is gathered over a long period time, it is possible to ensure that it is representative of the full range of conditions that the population is subject to and the simulation will provide a more realistic alternative to population viability analysis. Other studies suggest, based on a sensitivity analysis, that adult survival, especially female, is critical and insist that increased adult survival should be a principal management objective (Powell et al. 1996, Wiegand et al. 1998). The other use of the model is to rank management options in terms of the predicted effect on the viability of the target species. Since it is not always possible to experiment with a species, especially when considering large or rare animals, a population viability model can be an effective alternative for predicting the effect of management options and aid decision making.

In conclusion, the population viability analysis of a hypothetical Asiatic black bear population in the Mt. Chiri National Park area raises two points. Firstly, Mt. Chiri National Park can support a viable bear population in a demographic sense, though it is probably insufficient for long-term survival in a genetic sense. This condition might be improved by enlarging the National Park to support more individuals, or connecting it with other populations to promote gene flow. Secondly, a viable bear population, in a demographic sense, may be restored through supplementation. Results from a population viability analysis show that a few supplemented individuals can possibly make a significant difference.

According to this model, the management of a bear population should be aimed at maintaining a high population growth rate and controlling poaching to a level much less than the population growth rate. Other studies suggest that female adult survival is critical to maintain a high population growth rate and insist it should be a primary management objective (Powell et al. 1996, Wiegand et al. 1998).

I suggest that the poaching of adult bears should be strictly prohibited. A public awareness or environmental education program could be an effective way of preventing poaching. The enhancement of suitable habitat within the National Park may be another option, primarily by decreasing human access to suitable bear habitat and eliminating roads. Some areas of high suitability are found outside the National Park, but still connected to it, and I suggest that these areas should be included in the National Park.

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Appendix 1. Probability of extinction of a hypothetical Asiatic black bear population without poaching and supplementation.

K	Population growth rate	Initial abundance	Environmental stochasticity		
			1/3S	1/2S	S
78	1.0261	3	0.69	0.74	0.85
78	1.0741	3	0.51	0.51	0.63
78	1.0261	78	**0.01**	**0.03**	0.30
78	1.0741	78	**0.00**	**0.00**	**0.03**
100	1.0261	3	0.69	0.74	0.81
100	1.0741	3	0.50	0.33	0.47
100	1.0261	100	**0.01**	**0.01**	0.20
100	1.0741	100	**0.00**	**0.00**	**0.01**
216	1.0261	5	0.51	0.61	0.74
216	1.0741	5	**0.05**	0.15	0.29
216	1.0261	216	**0.00**	**0.00**	**0.11**
216	1.0741	216	**0.00**	**0.00**	**0.00**
355	1.0261	13	0.25	0.32	0.59
355	1.0741	13	**0.01**	0.07	0.17
355	1.0261	355	**0.00**	**0.00**	**0.05**
355	1.0741	355	**0.00**	**0.00**	**0.00**
500	1.0261	13	0.25	0.32	0.57
500	1.0741	13	**0.01**	0.07	0.16
500	1.0261	500	**0.00**	**0.00**	**0.05**
500	1.0741	500	**0.00**	**0.00**	**0.00**
1000	1.0261	13	0.32	0.40	0.59
1000	1.0741	13	**0.00**	0.09	0.18
1000	1.0261	1000	**0.00**	**0.00**	**0.03**
1000	1.0741	1000	**0.00**	**0.00**	**0.00**

Appendix 2. Probability of extinction of a hypothetical Asiatic black bear population an initial abundance of K and poaching levels of 0.01 and 0.02 (when population growth rate = 1.026) and 0.01, 0.05 and 0.07 (when population growth rate = 1.074)

K	Population growth rate	Poaching	Environmental stochasticity		
			1/3S	1/2S	S
78	1.0261	0.01	**0.00**	**0.02**	0.32
78	1.0261	0.02	**0.03**	0.07	0.33
78	1.0741	0.01	**0.00**	**0.00**	**0.03**
78	1.0741	0.05	**0.01**	**0.01**	0.13
78	1.0741	0.07	**0.02**	0.07	0.24
100	1.0261	0.01	**0.00**	**0.01**	0.23
100	1.0261	0.02	**0.02**	**0.04**	0.27
100	1.0741	0.01	**0.00**	**0.00**	**0.02**
100	1.0741	0.05	**0.00**	**0.00**	0.10
100	1.0741	0.07	**0.01**	**0.02**	0.23
216	1.0261	0.01	**0.00**	**0.00**	0.14
216	1.0261	0.02	**0.00**	**0.00**	0.19
216	1.0741	0.01	**0.00**	**0.00**	**0.00**
216	1.0741	0.05	**0.00**	**0.00**	**0.03**
216	1.0741	0.07	**0.00**	**0.01**	0.07
355	1.0261	0.01	**0.00**	**0.00**	0.09
355	1.0261	0.02	**0.00**	**0.00**	0.17
355	1.0741	0.01	**0.00**	**0.00**	**0.00**
355	1.0741	0.05	**0.00**	**0.00**	**0.04**
355	1.0741	0.07	**0.00**	**0.00**	0.13
500	1.0261	0.01	**0.00**	**0.00**	0.07
500	1.0261	0.02	**0.00**	**0.00**	0.11
500	1.0741	0.01	**0.00**	**0.00**	**0.00**
500	1.0741	0.05	**0.00**	**0.00**	**0.02**
500	1.0741	0.07	**0.00**	**0.00**	0.09

Appendix 3. Probability of extinction of a hypothetical Asiatic black bear population with different levels of poaching, environmental stochasticity, and supplementation.

Carrying capacity	Initial abundance	Population growth rate	Poaching	Supplementation											
				1/2K			1/4K			1/10K			No		
				Environmental stochasticity											
				1/3S	1/2S	S	1/3S	1/2S	S	1/3S	1/2S	S	1/3S	1/2S	S
216	5	1.0261	0.01	**0.00**	**0.00**	0.09	**0.00**	**0.01**	0.16	**0.02**	0.06	0.23	0.51	0.60	0.73
216	5	1.0261	0.02	**0.00**	**0.00**	0.16	**0.01**	**0.02**	0.20	**0.04**	0.08	0.32	0.57	0.60	0.78
216	5	1.0741	0.01	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.01**	0.11	0.27	0.46
216	5	1.0741	0.05	**0.00**	**0.00**	**0.03**	**0.00**	**0.00**	0.05	**0.00**	**0.00**	0.09	0.17	0.30	0.49
216	5	1.0741	0.07	**0.00**	**0.00**	0.07	**0.01**	**0.01**	0.10	**0.01**	**0.02**	0.15	0.19	0.35	0.61
355	13	1.0261	0.01	**0.00**	**0.00**	0.09	**0.00**	**0.01**	0.10	**0.00**	**0.01**	0.17	0.27	0.35	0.59
355	13	1.0261	0.02	**0.00**	**0.00**	0.10	**0.00**	**0.00**	0.18	**0.01**	**0.02**	0.24	0.30	0.39	0.59
355	13	1.0741	0.01	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.02**	0.05	0.19
355	13	1.0741	0.05	**0.00**	**0.00**	**0.03**	**0.00**	**0.00**	**0.03**	**0.00**	**0.01**	0.08	0.07	0.14	0.34
355	13	1.0741	0.07	**0.00**	**0.00**	0.09	**0.00**	**0.00**	0.13	**0.01**	0.05	0.20	0.17	0.26	0.47
500	13	1.0261	0.01	**0.00**	**0.00**	0.06	**0.00**	**0.00**	0.08	**0.00**	**0.00**	0.14	0.24	0.31	0.54
500	13	1.0261	0.02	**0.00**	**0.00**	0.08	**0.00**	**0.00**	0.11	**0.01**	**0.02**	0.21	0.27	0.33	0.55
500	13	1.0741	0.01	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.01**	0.06	0.21
500	13	1.0741	0.05	**0.00**	**0.00**	**0.01**	**0.00**	**0.00**	**0.03**	**0.00**	**0.00**	0.06	0.07	0.11	0.34
500	13	1.0741	0.07	**0.00**	**0.00**	0.05	**0.00**	**0.00**	0.08	**0.01**	**0.02**	0.15	0.15	0.20	0.46