



PROCEEDINGS
OF THE
CENTER FOR TROPICAL FOREST SCIENCE – ARNOLD ARBORETUM
INTERNATIONAL FIELD BIOLOGY COURSE 2006



Sinharaja World Heritage Site, Sri Lanka
30 July – 28 August 2006

Edited by Min Sheng Khoo, Cynthia Hong-Wa, and Rhett D. Harrison

Cover photo: Organizers, resource staff and participants of the sixth CTFS-AA International Field Biology Course 2006 (IFBC-2006) at Sinharaja Forest Bungalow, after the opening ceremony on 31 July 2006. See more photos on page 9.

Preface

The CTFS-AA International Field Biology Course is an annual, graduate-level field course in tropical forest biology run by the Center for Tropical Forest Science – Arnold Arboretum Asia Program in collaboration with institutional partners in South and Southeast Asia. The CTFS-AA International Field Biology Course 2006 was held at Sinharaja World Heritage Area, Sri Lanka, from 30 July to 29 August and was hosted by the Forest Department, Sri Lanka, and the University of Peradeniya, Sri Lanka.

It was the sixth such course organized by CTFS-AA. Last year's the course was held at Khao Chong, Thailand, and previous courses have been held in Malaysia. Next year's course will be held at Xishuangbanna, Yunnan, China. The aim of these courses is to provide high-level training in the biology of forests in South and Southeast Asia. The courses are aimed at upper-level undergraduate and graduate students from the region, who are at the start of their thesis research or professional careers in forest biology. During the course, topics in forest biology are taught by a wide range of experts in tropical forest science. There is a strong emphasis on the development of independent research projects during the course.

Students are also exposed to different ecosystem types, as well as forest related industries, through course excursions. The CTFS-AA International Field Biology Course 2006 was attended by 21 students from nine countries (Malaysia, Thailand, Philippines, UK, Taiwan, China, India, Madagascar, and Sri Lanka) and a total of 27 resource staff from a variety of national and international institutions gave lectures and practical instruction. The course in 2006 was implemented by Dr. Rhett Harrison (CTFS-AA), Drs. Savitri and Nimal Gunatilleke (University of Peradeniya, Sri Lanka), Mr. Anura Sathurusinghe (Forest Department, Sri Lanka), and Ms Luan Keng Wang (Raffles Museum, Singapore). Due to their considerable efforts the course proved to be an enormous success.

The following report illustrates the hard work of the organizers and the enthusiasm and commitment of the students. We look forward to another successful course in 2007.

Stuart J. Davies

Director, Center for Tropical Forest Science

Acknowledgements

First, the organizers of the CTFS-AA International Field Biology Course 2006 wish to thank all the resource staff who gave their time to teach on the course. Without the commitment of these researchers, many of whom have now taught on the course each year for the past several years, to the success of the field course at Sinharaja, nothing could have been achieved. In particular we would like to thank Ms. Luan Keng Wang (Raffles Museum, Singapore), who as always assisted greatly in the smooth running of the course. We would also like to acknowledge the considerable help of the University of Peradeniya staff and field assistants, especially the following: Drs. Nirmal Weerasekera and Hashendra Kathriarachchi, Mr. Suranjan Fernando and Mr. Tiran Abewardena, who made the computer facility at Sinharaja possible; the field assistants Mr. T. M. N. Jayatissa, Mr. Anura Tennakoon, Mr. T. M. Ratnayaka, and Mr. R. Sirimanna; the drivers Mr. M. A. Gunadasa and Mr. T. Wickramasinghe; the field station caretaker Mr. Wimal Shantha Kumara; and the kitchen staff Mr. M. G. Jayaratna, Mr. K. G. Piyasena and his assistants in the Kudawa forest camp; Mr. Martin Wijesinghe and his family for their unreserved support before and throughout the workshop. A list of all the resource staff who contributed to the course appears at the end of these proceedings.

We would like to thank the Forest Department, Sri Lanka for the enormous support they gave to the course. Especially, The Conservator General of Forests, Mr. M. P. A. U. S. Fernando for whole heartedly supporting this field course at Sinharaja from its inception to the end; Mr. E. J. M. J. K. Ekanayake (Additional District Forest Officer), Mr. D. P. Prasad (Forester) and other staff at the Sinharaja (Kudawa) Forest Department Facility for acceding to every request we made and giving their very best to make the course a success.

For the course excursions, we received a great deal of support from various people. The staff at Minneriya Wildlife Sanctuary, especially Mr. P. M. Dharmatilleke (Assistant Director) and his staff at the Giritale Wildlife Training Centre, and Mr. M. H. Chirasena (Park Warden), who addressed the students, and his staff at the Minneriya National Park, who kindly hosted us at their respective facilities. Dr. Wolfgang Dittus and his staff at Polonnaruwa worked extremely hard to give the students both an excellent introduction to primate social ecology and a wonderfully enjoyable visit to the ancient capital (the cricket was a great hit!). As a result of our last minute change of schedule, Dr. S. Wijesundara (Director) was not available to host us at the Royal Botanic Gardens, Peradeniya and we are very grateful for the excellent tour given instead by Mr. D. M. U. B. Dhanasekara (Deputy Director) to these beautiful gardens. Dr. Hashendra Kathriarachchi excelled herself giving the course participants both an enormously enjoyable and informative hike around Horton Plains, rain and all. An idea of how much the excursions were appreciated can be gauged from the enthusiastic reports the students wrote about them. The organizers would like to thank all the above for hosting the course.

Financial support for the field course came from the Center for Tropical Forest Science – Arnold Arboretum Asia Program of the Smithsonian Tropical Research Institute and the Arnold Arboretum of Harvard University. Tunghai University very generously provided additional funds through a grant to Dr. I Fang Sun, and funded the flights of the Taiwanese participants. The Eco-lodge project through a USAID grant provided additional funding to cover the costs of the participants from their project. In addition to hosting the course the Forest Department, Sri Lanka and the University of Peradeniya covered the costs of their employees and facilitated the course in various other ways for which we are very grateful.

Thanks to all.
The organizers,

Rhett Harrison (Center for Tropical Forest Science –Arnold Arboretum)
Savi Gunatilleke (University of Peradeniya)
Nimal Gunatilleke (University of Peradeniya)
Anura Sathurusinghe (Forest Department, Sri Lanka)

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Field Course Program

Overview

Date	Program
30 July	<ul style="list-style-type: none"> • Arrival at Colombo Airport • Registration at Goodwood Plaza Hotel • Noon travel to Sinharaja
31 July	<ul style="list-style-type: none"> • Opening ceremony
31 July – 6 Aug	<ul style="list-style-type: none"> • Lectures & practicals • Group projects
7 Aug	<ul style="list-style-type: none"> • Travel to Peradeniya • Kandy Perahera procession (night)
8 Aug	<ul style="list-style-type: none"> • Travel to Minneriya National Park • Evening travel to Giritale
9 Aug	<ul style="list-style-type: none"> • Birding at Giritale Wildlife Training Centre • Visit the Polonnaruwa ruins
10 Aug	<ul style="list-style-type: none"> • Primates of Polonnaruwa
11 Aug	<ul style="list-style-type: none"> • Travel to Peradeniya • Visit Peradeniya Botanical Gardens • Travel to Horton Plains
12 Aug	<ul style="list-style-type: none"> • Visit Horton Plains • Travel to Sinharaja
13 – 20 Aug	<ul style="list-style-type: none"> • Lectures and practicals
21 – 24 Aug	<ul style="list-style-type: none"> • Independent student projects
25 – 26 Aug	<ul style="list-style-type: none"> • Data analyses and write-up
27 Aug	<ul style="list-style-type: none"> • Travel to Colombo • Presentations of course projects, at Hector Kobbekaduwa Agrarian Research & Training Institute, Colombo
28 Aug	<ul style="list-style-type: none"> • Visit to Ranweli Ecotourist Resort • Mangroves & bird-watching tour • Farewell party
29 Aug	<ul style="list-style-type: none"> • Depart Colombo Airport

Lecture & Practical Course**31 July – 6 Aug: Introduction to Tropical Forest Flora and Fauna**

31 July	09:00			Opening ceremony
	10:30	Dr. J. V. LaFrankie	Field practical	Plant identification
	14:00	Dr. N. Gunatilleke	Field practical	Introduction to Sinharaja
	19:30	Dr. S. Davies	Lecture	Introduction to CTFS
1 Aug	08:00	Dr. J. V. LaFrankie	Field practical	Plant identification
	19:30	Dr. J. V. LaFrankie	Lecture	Trees of tropical Asia database
	20:00	Dr. S. Gunatilleke	Lecture	Forests of Sri Lanka
2 Aug	08:00	Dr. J. V. LaFrankie	Field practical	Plant identification
	14:00	Drs. Gunatilleke	Field practical	Plant diversity across a habitat gradient
	19:30	Dr. D. Lohman	Lecture	Insects & insect sampling
3 Aug	08:00	Dr. D. Lohman <i>et al.</i>	Field practical	Insect sampling
	19:30	Dr. D. Lohman	Lecture	Lepidoptera and herbivory
	20:00	Ms. N. Gunawardene	Lecture	Ants
	20:30	Dr. S. I. Vitharana	Lecture	Termites
	21:00	Dr. R. D. Harrison	Lecture	Bees
4 Aug	06:00	Dr. S. Kotagama, <i>et al.</i>	Field practical	Bird identification
	09:00	Dr. S. Kotagama	Lecture	Birds
	10:00	Dr. S. Kotagama	Field practical	Bird ecology
	14:00	Dr. K. Manamendra-Arachchi	Lecture	Amphibians and reptiles
	15:00	Dr. K. Manamendra-Arachchi	Field practical	Amphibian ecology
	19:30	Students	Talks	Research topics (10 mins)
5 Aug	08:00	Mr. C. P. Ratnayke	Lecture	Vertebrate sampling
	09:00	Mr. C. P. Ratnayke	Field practical	DISTANCE sampling
	14:00	Dr. R. D. Harrison		Twenty questions
	17:00	Dr. R. D. Harrison		Proposals for group projects
	19:30	Students	Talks	Research topics (10 mins)
6 Aug	08:00	Dr. R. D. Harrison		Group projects

7 – 12 Aug: Excursion to Kandy, Giritale, Polonnaruwa and Horton Plains

7 Aug	06:00			Travel to Kandy
	17:00			Check in to Casamara Hotel, Kandy
	18:00		Excursion	Kanda Perahera Procession
8 Aug	08:00		Excursion	Visit Temple of the Tooth, Kandy
	11:00			Travel to Minneriya Wildlife Park
	15:00	Dr. R. Sukumar	Excursion	Visit Minneriya Wildlife Park
	18:00			Travel to Giritale
	20:00			Check in to Giritale Wildlife Training Centre
9 Aug	07:00			Birding around Giritale
	10:00	Dr. R. Sukumar	Lecture	Elephant ecology
	12:00			Travel to Polonnaruwa
	15:00			Check in to Gajaba Rest House, Polonnaruwa
	16:00	Dr. W. Dittus	Field practical	Fruits and flowers identification
	20:00	Dr. W. Dittus	Lecture	Primate behavioural ecology (video)
10 Aug	05:30	Dr. W. Dittus	Field practical	Primate behaviour
	11:00	Dr. W. Dittus	Lecture	Primate behaviour – data analyses and interpretation
	15:30		Excursion	Visit Polonnaruwa ruins
	17:30			Cricket at Dr. Dittus'
	20:00			Travel to Dambulla
	23:00			Check in to Gimanhala
11 Aug	06:00			Travel to Kandy
	10:00	Mr. D. Danasekara	Excursion	Visit Royal Botanical Gardens, Peradeniya
	14:00			Travel to Ohiya
	19:00			Check in to Anderson Bungalow (Ginihiriya), Ohiya Circuit Bungalow, & Swarnalily
12 Aug	06:00	Dr. H. Kathriarachchi	Excursion	Horton Plains
	14:00			Travel to Sinharaja
	22:00			Arrive Sinharaja

13 Aug – 20 Aug: Forest Ecology

13 Aug	09:00	Dr. C. Webb	Lecture	Introduction to R
	10:00	Dr. R. Corlett	Lecture	Basic statistics
	11:00	Drs. R. Corlett & C. Webb	Practical exercise	Basic statistics
	19:30	Dr. R. Corlett	Lecture	Tropical forests compared
14 Aug	08:00	Dr. R. Corlett	Lecture	Frugivory & seed dispersal
	10:00	Dr. R. Corlett	Practical exercise	Frugivory & seed dispersal
	19:30	Dr. P. Davidar	Lecture	Conservation biology
	20:30	Dr. C. Bambaradeniya	Lecture	Invasive species
15 Aug	08:00	Dr. D. Burslem	Lecture	Plant diversity in forests
	10:00	Dr. D. Burslem	Practical exercise	Seedling ecology
	19:30	Dr. D. Burslem	Lecture	Review of seedling ecology
16 Aug	08:00	Dr. C. Webb	Lecture	Phylogenetic methods
	10:00	Dr. C. Webb	Field practical	Community phylogeny
	19:30	Dr. S. Lum	Lecture	Evolutionary philosophy
17 Aug	08:00	Dr. S. Lum	Lecture	Molecular ecology
	09:00	Dr. S. Lum	Practical exercise	Population genetics
	19:30	Students		Proposals for student projects I
18 Aug	08:00	Dr. R. D. Harrison	Lecture	Fig biology
	10:00	Dr. R. D. Harrison	Practical exercise	Fig biology
	19:30	Dr. R. D. Harrison	Lecture	Pollination ecology
19 Aug	08:00	Dr. M. Ashton	Lecture	Forest regeneration
	10:00	Dr. M. Ashton	Practical exercise	Forest regeneration
	19:30	Dr. M. Ashton		Tropical forest silviculture
20 Aug	08:00	Dr. M. Ashton	Lecture	Tropical forest rehabilitation
	10:00	Dr. M. Ashton	Practical exercise	Tropical forest rehabilitation and sustainable management
	19:30	Students		Proposals for student projects II

ABSTRACTS

Sinharaja World Heritage Site

I. A. U. N. Gunatilleke
University of Peradeniya, Sri Lanka

Sinharaja, the 'Forest of the Lion King', recognized as one of the precious jewels in Sri Lanka's biodiversity crown, is the largest relatively undisturbed, primeval, lowland and lower montane rain forest left in the country. Today it is a mere 11,000 ha. Sinharaja was declared an International Man and Biosphere Reserve by UNESCO in 1978, a National Wilderness Area in 1988 and a World Heritage Site in 1989. The wet zone forests of Sri Lanka as a whole with the Western Ghats of Peninsular India, is identified as one of the 25 Biodiversity Hotspots in the world.

Among others, there are three reasons why the rain forests in Sri Lanka are biologically interesting.

The ancestry of the Sinharaja biota, including that in the southwestern lowlands, dates back to millions of years and to the Deccan Plate.

Today, in the whole of South Asia, southwest Sri Lanka alone has an ever-wet climate, essential to support the maintenance of rain forests.

The wet lowlands of Sri Lanka receive an average of over 100 mm rain per month. Notice the black areas above 100 mm (its annual rainfall varies between 4000 – 6000 mm rain). It has a minimum temperature that does not go below 18 degrees celsius. The only lowland forests in South Asia that meet these criteria are those in southwest Sri Lanka, and best represented by Sinharaja.

Sinharaja has a very high proportion of endemic (confined to Sri Lanka and found nowhere else in the world) plant and animal species. Among the woody plant species, in Sinharaja over 60 percent are endemic to the island. Among the animal species endemic to Sri Lanka, 50 percent of the butterflies, 40 percent of the fishes, 36 percent of the snakes, 95 percent of the birds and 58 percent of the mammals are recorded at Sinharaja.

Your visit to Sinharaja takes you through the Kudawa village, with **traditional home gardens, smallholder tea gardens**, a few **Cinnamon** plots and exotic *Pinus caribaea* plantations in the reserve's perimeter. In part of the Pine stand, a **restoration trial** was initiated in 1991, using selected rain forest canopy species and non-timber species (**Rattan**, a medicinal vine *Coscinium*, **Cardamom** and the **Fish Tail palm**, which provides **treacle and jaggery** (a sugar candy), flour and also ornamental **foliage relished by elephants**).

Along the access road to the reserve and within its north-western quarter constructed for selective logging between 1970 and 1977, the **forest fringe vegetation** is dense, almost impenetrable, harbouring species sought after by villagers. Climbing **carnivorous pitcher plants, rattans with thorny whips** that overtop tree crowns, **medicinal vines**, fast growing **pioneer shrub and tree species**, all scrambling for light, and herbaceous **ginger** species and a purple flowered ground orchid *Arundina*. At dawn and dusk this road provides vantage points to observe and/or hear the incessant chatter of **bird flocks**, comprising many different species, **feeding together**, moving elusively in different strata and some times crossing the road. Many beautiful species, like the **Blue Magpie** endemic to Sri Lanka, the **Trogon**, the **Crested Drongo** and the **Rufous Babbler** are regular species in these flocks.

Further Reading

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An Introduction to CTFS-AA

Stuart Davies
CTFS-AA, Arnold Arboretum

The Center for Tropical Forest Science of the Smithsonian Tropical Research Institute is a global initiative in long-term tropical forest research. The broad objectives of this research program are: (1) to develop a general theory of tropical forest diversity and dynamics, providing explanations of the relative importance of biotic and abiotic factors in controlling species distributions and the regulation of population and community dynamics; and (2) to develop models incorporating ecological and economic analyses for predicting human impacts on and optimizing sustainable utilization of tropical forests. These and many other fundamental ecological questions concerning tropical forests are best addressed by a comparative approach involving long-term, individual-based, mapped, permanent forest plots. The consortium of researchers and institutions collaborating within CTFS has established a pan-tropical network of 17 large-scale (50 ha) permanent plots in 14 countries representing the diversity of tropical forests.

The CTFS-Arnold Arboretum Asia Program includes eight core sites, each with a large-scale research plot. The sites were chosen to represent the major biogeographical areas of South and Southeast Asia. The plots are found across a gradient of climates, soil types, and natural disturbance regimes. Current CTFS-AA core sites are in Malaysia, Thailand, India, Sri Lanka, Philippines and Singapore. CTFS-AA also collaborates with associated sites in Taiwan and Thailand. In this talk, I discuss the comparative ecology of the forests in which the eight plots have been established. A wide range of research is now being conducted within the CTFS plots. An overview of these studies is provided in this talk.

Further Reading

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Field Practical on Tree Identification

Jim LaFrankie
CTFS-AA, Philippines

The subject will be covered in three sessions each of one-half day.

The diversity of plant life is introduced. The individual tree and the breeding population are the manifest reality. Populations can be aggregated and named at increasingly higher hierarchical levels in arrangement that mimics fractal geometric patterns if self-similarity. Higher levels of species, genera, families and orders can be meaningful or not. The principle clades of angiosperms are noted.

Within the outline of plant diversity we examine the diversity and abundance of trees in general and trees of tropical Asia.

We will then examine representatives of 20 families and 25 genera of tropical trees. Dipterocarps form the physical framework of the forest and they will be examined in detail. Other main families include the major representatives of the Sri Lankan forest. For each family we will note the level of diversity and abundance, globally, for Asian tropical forests and for the Sri Lankan forest. To this we will add the vegetative and floral features that characterize the family.

In the course of that survey we will enumerate the main vegetative features by which tree families and genera can be distinguished. Simultaneously, we will make a survey of tree morphology regarding the features of bark, wood, twig and leaf.

Finally, we will discuss the resources and tools available to make further progress in the study of tropical tree diversity.

Further Reading

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The CTFS-AA Trees of Tropical Asia Database

Jim LaFrankie
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The lecture presents a brief introduction to the database compiled through the CTFS-AA network of long-term ecological research plots. The database includes taxonomic and ecological information on thousands of species of trees. It also includes photographs and meta-data from the permanent plots such as tables and distribution maps. The database is organized in FileMaker Pro software which will be explained and demonstrated. This software is well-suited for individual record keeping as well as institutional projects. While the CTFS-AA database is still in its infancy, it is now growing rapidly and should within a year be a useful on-line tool for ecological research and reference.

Forests of Sri Lanka

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Situated between 6° – 10° N and 80° – 82° E, Sri Lanka for its small size (65,525 km²) and location harbours an exceptionally rich tropical flora and diverse forest types. This diversity results from its historical biogeography, varied topography, rising up to 2524 m on the peak of Pidurutalagala, and its contrasting climate types ranging from perhumid to seasonally dry.

The **mangroves** of the island, covering 12,189 ha, are dominated by species of *Rhizophora*, *Ceriops*, *Bruguiera*, *Acanthus*, *Lumnitzera* and *Avicennia*.

Tropical lowland **wet evergreen forests** or lowland rain forests, restricted to the southwest of the island are at present highly fragmented and reduced to 141,549 ha. Reaching 30 m – 45 m height, they are dominated at the lower elevations by two spp. of *Dipterocarpus* and at higher elevations by *Mesua* and *Shorea* spp. The common subcanopy species are *Cullenia* and *Myristica* and in the understorey tree layer *Xylopia* and *Garcinia*. In these forests 60 percent – 75 percent of the tree species are endemic to the island.

The **submontane forests** confined to middle elevations of the hill ranges are now reduced to about 69,616 ha. They are about 20 m - 30 m tall. Species of *Shorea*, *Calophyllum*, *Cryptocarya*, *Myristica* and *Syzygium* dominate these forests. Most of the species of the endemic genus *Stemonoporus* show a very localized distribution in these forests. The proportion of endemic tree species here is about 50 percent.

The **montane forests**, restricted to the uppermost elevations are limited to 3,108 ha. They are 10 m or less in height and their tree species are dominated by *Calophyllum*, *Syzygium*, *Symplocos*, *Neolitsea*, *Cinnamomum*, *Litsea* and *Actinodaphne*. In most areas, *Strobilanthes* and *Coleus* dominate the understorey. About 50 percent of the tree species here are endemic.

Tropical **moist evergreen forests**, about 20 m – 25 m tall, represent an ecotone between the aseasonal and seasonal forests. Only very small patches of this forest type now remain in the island. Their tree species are dominated by *Mangifera*, *Canarium*, *Filicium*, *Euphoria*, *Nothopegia* and *Girardinia*. Only about 17 percent of the tree species in these forests are endemic. Frequent anthropogenic fires in these areas have given way to parkland-like savannas with fire-tolerant medicinal tree species dominated by *Careya*, *Phyllanthus* and *Terminalia*.

Tropical **dry mixed evergreen forests** covering 1,090,981 ha of the country's dry zone in the North, Eastern, North Central and Southern Provinces are the most widespread of all the forest types in the island. Reaching to about 25 m height in the best stands, these forests become shorter towards the arid zone in the northwest and southeast of the country. Dominant canopy species here are *Manilkara*, *Chloroxylon*, *Schleichera*, and *Pleurostyliia* and in the understorey tree layer they are *Pterospermum*, *Drypetes* and *Dimorphocalyx*. A significant proportion of this flora is similar to that of India. Only about 13 percent of the tree species in these forests are endemic.

Thorn scrub forests in the arid zone in the southeast and northwest of the island up to about 5 m tall are dominated by *Salvadora*, *Acacia*, *Dichrostachys*, *Bauhinia*, *Eugenia*, *Phyllanthus* and *Ziziphus*. Endemic plant species are absent in these forests.

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Plant Diversity across a Habitat Gradient

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Introduction to the Forest Dynamics Plot: Spanning an elevational range of 151 m, the Sinharaja Forest Dynamics Plot (FDP) rises from 424 m to 575 m above sea level. It includes a valley lying between two slopes, a steeper higher slope facing the southwest and a less steep slope facing the northeast (Fig. 1). In this plot seepage ways, spurs, small hillocks, at least two perennial streams and several seasonal streamlets cut across these slopes.

The 25-ha FDP was established in 1993. It was demarcated on the horizontal plane into 625 quadrats of 20 x 20 m (400 m²) each. The trees in the plot were censused over the period 1994 - 1996, when the diameter of all free-standing stems > 1 cm diameter at breast height (DBH) was measured. Each stem was mapped and identified to species, using the National Herbarium of Sri Lanka, and Dassanayake and Fosberg (1980-2000).

Topographic Parameters and Habitat Categorization: Different habitats in the FDP were identified taking into consideration three physical parameters, viz., elevation (which ranged from 424 m to 575 m), slope (which ranged from 0° to 40.9°) and convexity (which ranged from -9.3 to 7.9) in each of the 20 x 20 m quadrats.

Each 20 x 20 m quadrat of the FDP was assigned to one of two categories each of elevation, slope, and convexity (Table 1, Fig. 1). The two elevation categories were high elevation (> the median elevation, 460 m) and low elevation (< 460 m). The two slope categories were steep (> 25°) and less steep (< 25°). The two convexity categories were spurs (convexity > 0) and gullies (convexity < 0). Using these variables, the plot was divided into eight habitats (Fig 1). They are: (i) high steep spurs; (ii) high less-steep spurs; (iii) high steep gullies; (iv) high less- steep gullies; (v) low steep spurs; (vi) low less-steep spurs; (vii) low steep gullies; and (viii) low less- steep gullies.

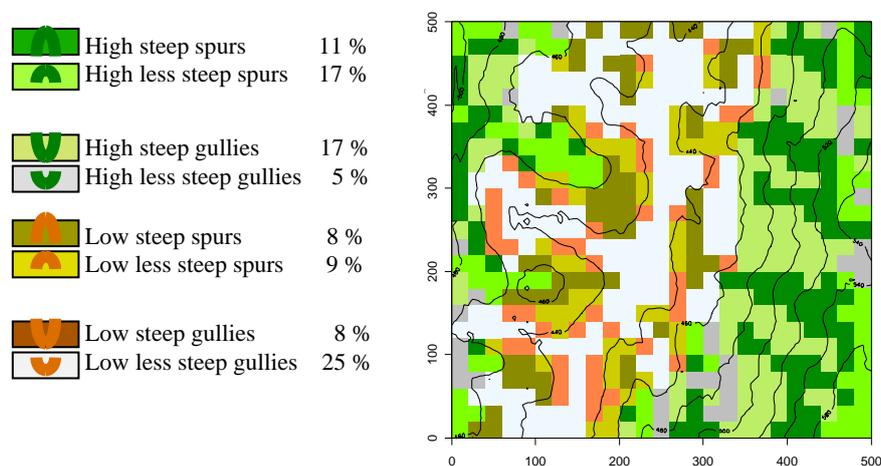


FIGURE 1: Distribution of habitat types in the Sinharaja Forest Dynamics Plot

Objectives of the Practical

In this practical, the students will examine whether two of the habitats, high steep spurs and high steep (or less steep) gullies identified on topographic variations also reflect vegetation differences. More specifically, the students will address the following hypotheses.

- i) The density of trees > 1 cm DBH in the two habitat types are different.
- ii) The diameter size of trees > 1 cm DBH in the two habitats are different.
- iii) The density of the dominant species varies in the two habitats.

Methodology

To test these hypotheses, trees > 1 cm DBH in one plot (5 m x 5 m in size) in each of the two habitats will be sampled by each group of students. Information collected by the different groups will be shared by the class.

In the information sheet students will record the following:

General physical features of the plot (rockiness, soil texture, slope and steepness)

Tree tag number

Tree DBH

Tree height

Identity of the tree (is the tree one of the dominant species (*Mesua nagassarium* (MESUNA), *Mesua ferrea* (MESUFE), *Humboldtia laurifolia* (HUMBLA), *Agrostistachys intramarginalis* (AGROIN) or not one of the dominant species (other).

Field data collected will be explored and analysed. The results will be summarized and possible explanations for results obtained will be discussed.



The Opening Ceremony of IFBC-2006.



Introduction to the Sinharaja World Heritage Site by Nimal Gunatilleke.



A



B



C



D



E

Botany lessons in the field. (A, B) The botany guru, Jim LaFrankie, imparting his skills; (C, E) Students getting hands-on plant identification experience and valuable tips from Stuart Davies and Nimal Gunatilleke; (D) Demonstration of specimen-processing by students with prior background and experience in botany.

Insects and Insect Sampling

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Insects are the most abundant and diverse macroscopic, terrestrial animals on the planet, and their species richness and high rate of reproduction make them ideal subjects for investigations in ecology, evolution, and behavior. We will discuss the traits that characterize insects and learn to identify several of the most important orders and families. Insects play a variety of key roles in every terrestrial and freshwater ecosystem, and we will investigate some of the ways in which their interactions with other organisms influence ecosystem functioning. Because of their varied life histories, there is no single best insect trapping method. We will review the various trapping methods and their relative merits before considering other logistical aspects of studying insects.

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Herbivory

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Insects are the most important herbivores in tropical forests, and methods for studying them have shifted in the past decade from sampling of adults to experimentally verified feeding records amassed on a large scale. Although the majority of research on insect-plant interactions has taken place in temperate areas, many of the lessons learned about plant defense, insect behavior, and coevolutionary dynamics also apply to tropical herbivores and their associated host plants and parasitoids. Systematic studies are few, but patterns of herbivory appear to differ between tropical and temperate ecosystems. We will discuss some of these latitudinal patterns as well as some of the recent advances in molecular aspects of plant-insect interactions.

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Ants

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Ants are social insects that form colonies in almost all bioregions of the world. Most species have a single queen who will produce all the sterile workers and reproductives of the colony. The workers are organized into castes which are responsible for the maintenance and feeding of the colony. This division of labour and complex communication abilities have allowed ants to dominate most ecosystems and play essential roles in the turnover of material. The species diversity of ants also demonstrates the numerous interactions they have with their environment and other organisms. Ants have become an accepted part of biodiversity assessments, are widely studied as indicators of ecosystem change and are closely linked with plant ecology.

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Termites (Order Isoptera)

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Termites (Order: Isoptera) are small to medium-sized, very soft-bodied insects. They are usually light in colour and live in social groups, or colonies which have highly developed caste system. Although they are referred to popularly as **white ants**, they are not closely related to true ants (Family: Formicidae) which are grouped with bees and wasps in a higher order of insects, the Hymenoptera. The social system of termites shows remarkable parallels with those of the Hymenoptera, but it has evolved independently.

1.0 Importance of termites: Termites are important in two ways:

1. They are destructive when they feed upon, and often destroy wooden structures or crops cultivated by man. When their original environment has been changed, like in the case of introduced species or those that have lost their original habitat due to deforestation, because they cannot adapt to the new environment easily, termites tend to seek shelter in protected, man-made environments such as cultivated crops or buildings and thus are likely to become the most serious pests in the new environment.
2. Termites are beneficial, in that they help to convert plant cellulose into substances that can be recycled into the ecosystem to support new growth.

Although of the nearly 2,000 known termite species only about 10 percent have been reported as pests, many of that group cause severe and extremely costly damage. For effective control, it is essential to determine whether the pest is a subterranean or wood-dwelling species or a plant infesting species, because treatment methods differ.

Pest Termites: Subterranean termites, dependent on contact with soil moisture, normally reach the wood in man-made structures through their foundations. The most common control used around a structure is a trench containing insecticide and covered by soil. Insecticides are useful around cracks and crevices in foundations and infested wood. Construction and design practices that can prevent the initial entry of subterranean termites into a structure include the use of pressure-treated wood, insecticide-treated concrete foundation blocks, and reinforced concrete foundations that extend at least six inches (15.2 cm) above the ground and have no cracks or contact with any outside wood.

Dry-wood termites, which nest in the wood on which they feed and do not invade a structure from the soil, are difficult to control. Preventive measures include the use of chemically treated wood in building construction and the use of paint or other durable finish to seal cracks in wood surfaces. Fumigation is the most effective method for exterminating dry-wood termites. Another method is to pour insecticides into small holes drilled into galleries of infested wood.

Some subterranean species attack live plants, eating the bark for their water needs mostly. An extreme situation is found in the case of and a few totally plant inhabiting species, also, referred to as live wood termites, particularly of the family Kalotermitidae, which termites do not have any contact with the soil, and transfer themselves from plant to plant either through root contact or by alates flying from plant to plant. The best examples are the live-wood tea termites of Sri Lanka.

No completely satisfactory method of termite control has been devised. In the past, most methods have depended heavily on chlorinated hydrocarbons. Bifenthrin, though not as long lasting as chlorinated hydrocarbons, has taken their place now. It is necessary that alternate, ecologically safer and effective methods of control are developed for all termite pests. Plant resistance has been exploited to the growers benefit in the case of tea termites.

2.0 World distribution of termites: Termites are distributed widely around the world, reaching their greatest abundance in numbers and species in tropical rain forests. About 1,900 living and 60 fossil species may inhabit moist subterranean or hot, dry locations. In North America termites are found as far north as Vancouver, British Columbia (*Zootermopsis*), on the Pacific coast, and Maine and eastern Canada (*Reticulitermes*) on the Atlantic coast. In Europe the northern limit of natural distribution is reached by *Reticulitermes lucifugus* on the Atlantic coast of France, although an introduced species, *Reticulitermes flavipes*, occurs as far north as Hamburg, Germany. The known European species of termites have a predominantly Mediterranean distribution and do not occur naturally in Great

Britain, Scandinavia, Switzerland, Germany, or northern Russia. In the Far East *Reticulitermes seperatus* ranges as far north as South Korea, Peking, and northern Japan.

Termites occur as far south as the Cape region of South Africa, Australia, Tasmania, and New Zealand.

Dispersal by human intervention: In addition to naturally occurring termites, many species have been transported inadvertently by man from their native habitats to new parts of the world. Termites, particularly *Cryptotermes* and *Coptotermes*, are transported in wooden articles such as shipping crates, boat timbers, lumber, and furniture. Because dry-wood termites (*e.g.*, *Cryptotermes* species) live in small colonies in wood and tolerate long periods of dryness, they can survive in seasoned wood and furniture and can easily be transported over long distances. Members of the family Rhinotermitidae (*e.g.*, *Coptotermes*) have been transported in shipping crates that have contact with moisture.

Coptotermes formosanus, widely distributed in Japan, Taiwan, and South China, has been introduced into **Sri Lanka**, the Pacific islands, South Africa, East Africa, Hawaii, and southern United States.

A termite native to the U.S., *Reticulitermes flavipes*, was found in the hothouses of the Royal Palace in Vienna, and the species was reported and described before it was discovered in the U.S. The termites presumably had been shipped from North America in wooden containers of decorative potted plants.

3.0 Termite Biology

Termites have a hemimetabolous metamorphosis and pass through a series of nymphal stages which are feeding and active throughout. Head structures like the dentition of the mandibles, and the presence or absence of individual caste members are used to distinguish termite families. Termite social castes (reproductives, sterile workers, and sterile soldiers) usually contain members of both sexes in equal numbers, and both males and females develop from fertilized eggs. The thorax in termites is joined broadly to the abdomen, without the “waist” characteristic of bees, ants, and wasps. Termites have two pairs of membranous wings, nearly equal in size, that break along a suture when shed, leaving only the wing base, or “scale,” attached to the thorax—probably the most distinguishing characteristic of isopterans.

3.1 Termite Nutrition: Cellulose

Termite mouthparts are modified for chewing. The food of termites is mainly cellulose, obtained from wood, grass, leaves, humus, manure of herbivorous animals, living plants and materials of plant origin (*e.g.*, paper, cardboard, cotton). Most lower termites and many higher ones feed on wood, either sound or partly decayed. A few termites (known as foragers or harvesters) collect and eat grass, leaves, and straw. Many higher termites (family Termitidae) are humivores, or exclusively humus feeders. Termites of all families (except Termitidae) known collectively as “lower termites”, harbour symbiotic flagellate protozoa in hindgut to digest cellulose. The protozoans secrete enzymes (cellulase and cellobiase) that break down cellulose into a simple sugar (glucose) and acetic acid. The species of the protozoa are characteristic of the termite species.

As with other social insects, not all members of a termite colony feed directly. Because, reproductives, soldiers, and the young nymphs in lower families (and all nymphs in Termitidae) cannot feed themselves directly, they must be fed by workers. Workers and the older nymphs or pseudergates in families without them (*e.g.*, Kalotermitidae) forage for the entire colony and transfer food to dependent castes either by mouth feeding or by anal feeding. Food transferred by mouth may consist of either paste like regurgitated chewed wood and saliva or a clear liquid. This method is used in all termite families. During anal feeding, present only among lower termites, a paste like liquid or droplet is discharged from the anus of the worker and licked away by the dependent castes. This liquid food, distinct from feces, consists of hindgut fluid containing protozoans, products of digestion, and wood fragments. Since the protozoans lost at the time of each molt are reacquired only through anal feeding, termites live in groups that allow contact of molting nymphs with infected, non-molting individuals. It is possible that the necessity for transfer of protozoans was responsible for the evolution of the termite society.

Higher termites lack symbiotic protozoans; only bacteria are present in the gut. Digestion may occur with the aid of bacterial cellulase and cellobiase enzymes, but the termites themselves may secrete the enzymes.

In addition to cellulose, termites require vitamins and nitrogenous foods (*e.g.*, proteins), which probably are supplied by fungi normally present in the decayed wood diet common to most termites. The fungi also may break down wood into components that are digested easily by termites, like in the case of live-wood termites of tea. Some others grow fungus gardens.

Fungus gardens: The Macrotermitinae (family Termitidae) cultivate symbiotic fungi (Termitomyces). The termites construct sponge-like “fungus gardens,” or combs, possibly of fecal matter rich in the carbohydrate lignin. The fungi grow on the combs, and the termites consume both fungi and combs. The fungi break down the fecal matter used to construct the combs into substances that can be reutilized by the termites. Nitrogen other than that from fungi is supplied by controlled cannibalism. The termites consume cast-off skins and dead, injured, and excess members of the colony.

3.2. Termite Form and function: Termites have a highly developed caste system which may contain reproductives, soldiers, and workers (or pseudergates). Reproductives shed wings after mating.

Castes and their roles The termite society, or colony, is a highly organized and integrated unit, with division of labour among its members differentiated by structure, function, and behaviour into castes. Of the major castes in the colony (reproductive, soldier, and worker castes) the soldiers and workers are sterile. The functional reproductives are of two types, primary and secondary (or supplementary).

a. Reproductives: The *primary reproductives* in a termite colony are usually one royal pair, a king and queen. They have developed from winged forms (alates) with hardened, pigmented bodies and large compound eyes. A pair of alates fly away from a

parent colony and shed their wings prior to founding a new colony. The primary reproductives have several important functions: reproduction, dispersal, and colony formation; in addition, during initial stages of colony formation, the primary reproductives perform tasks that are later taken over by the worker caste, such as construction, housekeeping, care of young.

If the king and queen die, they are replaced by several *supplementary reproductives* that are slightly pigmented, have either short wing pads (brachypterous) or none (apterous) and reduced compound eyes. These secondary reproductives, which develop from nymphs and may be called *neotenic*s, normally are not present in a colony as long as the primary reproductives function. If a primary reproductive is lost, a neotenic achieves sexual maturity without, however, attaining a fully winged adult stage or leaving the nest.

b. Workers: The sterile castes are the workers and soldiers. Both are wingless, usually lack eyes and, though of both sexes, usually lack fully developed reproductive organs. In some species the workers and soldiers are dimorphic (of two sizes); the larger is termed a major soldier or worker, the smaller a minor soldier or worker. A few species contain trimorphic soldiers. Most termite species have both soldier and worker castes.

The worker caste usually is the most numerous in a colony. Workers are pale in colour, soft-bodied, and with mandibles and mouthparts adapted for chewing. They feed all the other members of the colony, collect food, groom other colony members, and construct and repair the nest. The worker caste is responsible for the widespread destruction the termites can cause. In some primitive termite families (*e.g.*, Kalotermitidae) a true worker caste is absent, and its functions are carried out by immature individuals called pseudo-workers or *pseudergates*, which may moult without much change in size.

c. Soldiers: The primary function of the soldier caste is defense. Since most termite soldiers are blind, they probably locate enemies through tactile and chemical means. The termite soldier has a large, dark, hard-covered head; its long powerful jaws (mandibles) may be hooked and contain teeth. The head, the mandibles and their dentition, are used to defend the colony against predators, usually ants. The attacking mandibulate soldier makes rapid lunging movements, opening and closing its mandibles in a scissor-like action that can behead, dismember, lacerate, or grip a foe. In some mandibulate soldiers (*e.g.*, *Capritermes*) the mandibles are an asymmetrical, snapping type with the left mandible twisted and arched and the right blade-like. In defense, the mandibles lock together and release with a loud click, like the snapping of fingers. Some soldiers (*e.g.*, *Cryptotermes*) use their heads which are short and truncated in front (phragmotic), to plug the entrance holes of nests.

The higher termites (Termitidae) may supplement or replace mandibular defenses with chemical mechanisms that utilize sticky, possibly toxic, liquids secreted by either the salivary or the frontal glands. The whitish or brownish liquid becomes rubberlike after exposure to air and entangles enemies. The frontal gland of some termites (*e.g.*, *Coptotermes* and *Rhinotermes*) occupies a large portion of the abdominal cavity and opens by means of a frontal pore (fontanelle), through which the liquid is ejected. The liquid from the frontal pore of the minor soldier of *Rhinotermes* flows down a groove in the elongated labrum, rests at its hairy tip, and volatilizes as a repellent gas.

The mandibles of soldiers with exclusively chemical defense (*Nasutitermitinae*) have become reduced in size and nonfunctional; the head has become elongated into a long snout (nasus), and the frontal gland which occupies a major portion of the head, opens at the end of the snout. These nasute soldiers can fire a clear, sticky, resinous liquid accurately for many centimeters. A few genera lack a soldier caste; the mechanisms for defense in these groups are not known.

3.3. Colony organization: Mechanisms controlling differentiation of termites into castes are not understood fully. It is known that all young nymphs are genetically identical at hatching and that all could develop into any caste (reproductive, soldier, or worker). The castes in a colony are balanced and regulated closely; normally there are one pair of reproductives and a set ratio of soldiers to workers and nymphs. If members of any caste are lost, additional members of that caste develop from nymphs to restore the balance. Conversely, if overproduction of one caste occurs, selective cannibalism restores the balance.

Chemical substances such as pheromones and hormones play a role in differentiation, production, and regulation of castes. Both reproductive and soldier castes secrete a pheromone, a chemical substance that is transmitted through mutual licking (trophallaxis) to other members of the colony and inhibits development of reproductives or soldiers. If the caste balance of the colony is upset, some undifferentiated nymphs, which do not receive the "pheromone message" develop into reproductives or soldiers, thereby, restoring the balance. This **inhibition theory** has been confirmed by experiments with supplementary reproductive development in *Kalotermes* and *Zootermopsis*.

Activation of the corpora allata near the brain and the molt gland may be responsible for differentiation of a nymph into a soldier. In termites, therefore, hormones not only control molting and metamorphosis, as in other insects, but also play a role in caste-differentiation.

3.4. Termite Nests:

a. Internal features: Since termites have a soft cuticle and are desiccated easily, they live in nests that are warm, damp, dark, and sealed from the outside environment; their nests are constructed by workers or old nymphs. In addition to providing an optimum microclimate, the nest provides shelter and protection against predators. The high relative humidity in the interior of the nest (90 to 99 percent) probably is maintained in part by water production resulting from metabolic processes of individual termites. The temperature inside the nest generally is higher than that of the outside environment.

Since the anaerobic protozoans in the hindguts of primitive termites cannot tolerate high concentrations of oxygen, such termites have developed toleration for high concentrations of carbon dioxide, as high as 3 percent in some nests. Ventilation must occur in the nest, however, and may be facilitated by its architecture. For example, the subterranean nests of *Apicotermes* have an elaborate system of ventilation pores. Convection currents and diffusion through the nest wall also provide ventilation in large mounds.

b. Nest types: Although true wood dwellers never invade soil, and their nests have no soil connections, all other termites basically are subterranean; *i.e.*, they build their nests either in soil or with soil connections and exploit food sources away from the nest.

The family Kalotermitidae and the subfamily Termopsinae (family Hodotermitidae) make their nests in the wood on which they feed. These termites excavate irregular networks of galleries in the wood with no external openings (except for temporary ones through which they escape during swarming) many galleries have partitions made of faecal matter and are lined or coated with plaster made of faecal matter. Members of Kalotermitidae live in sound wood of stumps and branches of trees. Examples are *Neotermes tectonae* which attacks teak trees in Java, and *Cryptotermes* which bores into trees as well as furniture in various parts of the world and, *Postelectrotermes militaris*, *Glyptotermes dilatatus*, and *Neotermes greeni* all of which are endemic to Sri Lanka and attack live tea plants and other several trees species.

A few species of Termopsinae live in damp rotten logs. Many species of Rhinotermitidae build nests in wood that is buried in damp soil and from which a diffused network of tunnels to food sources may radiate into the soil or above the ground in the form of covered runways.

Arboreal nests are ovoid structures built of "carton" (a mixture of fecal matter and wood fragments). Carton may be papery and fragile, or woody and very hard. The inside of an arboreal nest consists of horizontal layers of cells, the queen occupying a special compartment near the centre. The nests always maintain connections with the ground through covered runways.

Many termites build diffused subterranean tunnels making up discrete and concentrated nests. Some nests rise partly above the ground as mounds or hills; others are totally underground or arboreal. Dirt, particles of fine clay, or chewed wood glued together with saliva or excreta are used to build nests. During nest construction a termite deposits fecal matter to cement particles in place. The large mounds or hills, a prominent landscape feature in the tropics, may be domelike or conical; some have chimneys and pinnacles. Longitudinal and horizontal chambers and galleries comprise the interior. Generally the outer wall is constructed of hard soil material, distinct from the internal central portion (or nursery), which is composed of softer carton material.

c. Symbionts and Commonsals: Many termite nests harbour various other invertebrates as guests (*e.g.*, beetles, flies, bugs, caterpillars, millipedes); some termed termitophiles, in fact, are unable to survive independent of their termite hosts. True termitophiles actually have evolved with their hosts and are species specific. Some beetles and flies have developed glands that secrete substances sought and licked by the termites. The termite nest, because it provides shelter and warmth, may be occupied also by lizards, snakes, scorpions, and some birds.

A few termites, known as inquiline species, live only in obligatory association with other termite species. Examples of such obligate relationships are *Ahamitermes* and *Incolitermes* species, which live only in the mound nests of certain *Coptotermes* species; the galleries of guests and hosts are completely separate. Inquiline species feed on the inner carton material of the host nests. *Incolitermes*, however, depend on the host species not only for food but also for exit holes from the nest during swarming. Such species' tolerance is highly unusual; normally, different species of termites are hostile to one another, and host termites may attack inquiline guests if partitions between galleries are broken.

3.4. Colony formation and development

a. Swarming: A new termite colony normally is founded by dispersion of winged adults (alates), which usually develop in a mature colony during certain seasons of the year. After molting into winged adults, alates group themselves in special chambers near the periphery of the nest for several days or weeks. Emergence and flight of alates usually is associated with high atmospheric humidity in combination with temperature, climatic, and seasonal factors that vary with the species. In some species one emergence a year may occur; in others there may be many successive flights.

Workers prepare tunnels to the surface and exit holes prior to emergence of the alates and sometimes construct launching platforms. During emergence the soldiers guard the exit holes, not only to prevent entry of enemies but also to prevent alates from re-entering the nest. At the time of emergence the alates, which normally avoid light, become attracted to it and fly out of the nest. They are weak fliers and, unless carried by the wind, descend within several hundred yards of the original colony. The flight, commonly called a nuptial or mating flight, is simply dispersal; mating occurs after the flight. Swarming from many colonies occurs simultaneously in a given area and may be synchronized closely in areas separated by hundreds of miles. An advantage of synchronization might be inter-colony mating.

Shortly after the alates alight, they shed their wings, leaving only the base of the wing scale attached to the thorax. During a short courtship, in which the female raises her abdomen and emits a sex-pheromone, the pair moves off in tandem (pairing), with the male following closely behind the female. The couple then seek a nesting site; together they find a crevice or dig a hole in wood or soil that has been softened by rain and seal the hole with fecal matter. Copulation takes place only after the establishment of this nuptial chamber. During copulation, which occurs intermittently throughout the lives of the king and queen, sperm are transferred and stored in the spermatheca of the female. Since the male has no external copulatory organ, sperm are released through a median pore on the ninth sternite, or abdominal plate.

After copulation the first batch of eggs, usually few in number, is laid. Those individuals that hatch out of the first batch eggs take over the functions of gallery making and other work of the nest. In some species the egg-laying capacity of the queen increases with time and her ovaries and fat bodies develop, and her abdomen enlarges (the process is called physogastry). Physogastric queens in more advanced families (*e.g.*, family Termitidae, especially *Macrotermes* and *Odontotermes*) may become 11 centimetres long. The queen may lay as many as 36,000 eggs a day for many years. Nowan "egg-laying machine," may produce The first young nymphs develop into workers or pseudergates and soldiers. Only after the colonies are mature do winged adults develop. During the initial stages of colony formation, the reproductives feed the young and tend the nest; but, as the colony becomes established, the young nymphs perform these duties.

Primitive termite families (e.g., Kalotermitidae) have small colonies—from hundreds to thousands of individuals. More advanced families (e.g., Rhinotermitidae, Termitidae) have colonies that may number thousands to millions of individuals; all members are produced by the single reproductive pair. Workers and soldiers may live two to five years. The primary king and queen in higher termite families may live 60 to 70 years. The entire colony may exist for many years in species that replace the primary king and queen with secondary reproductives.

b. Other colonizing methods: Sometimes new colonies are formed by budding, the division or accidental separation of part of a colony from an original nest; supplementary reproductives then take over as the reproductive pair. Another method of colony formation is sociotomy, or social fragmentation; workers, soldiers, and nymphs migrate or march to a new nesting site, and the fragment develops supplementary reproductives. Sometimes an original reproductive pair joins a migrating group.

4.0 Termite Communication: Among the members of a termite colony there is continuous exchange of information, such as alarm, indication of direction and presence of a food source, and, among reproductives, calling and pairing behaviour. Information is communicated by visual cues, vibrations, physical contact, and chemical signals (e.g., odour).

Many termite species leave their nests to forage for food. Workers (or older nymphs) and soldiers march in columns along the ground and carry grass, pine needles, and seeds for storage in the nest. The foraging trail between the nest and the food source may be indicated by deposits of fecal matter, covered runways over the trail, or pheromones secreted by a sternal gland.

5.0 Termite Evolution, paleontology, and classification: Termites are related to the roaches and probably have evolved from a primitive roach-like ancestor. The most primitive living roach, *Cryptocercus punctulatus*, has affinities with the primitive termites. *C. punctulatus* has the symbiotic, cellulose-digesting protozoans of the same genera as those found in the hindgut of primitive termites. The genitalia and certain internal structures of *Cryptocercus* have basic anatomic resemblances to those of the most primitive living termite, *Mastotermes darwiniensis*, from Australia. *Mastotermes* has further affinities with other roaches: its hind wing has a folded anal lobe, and its eggs are not laid singly as those of other termites but in clusters held together by a gelatinous material resembling the egg case of roaches.

Classification: The taxonomy and phylogeny of the Isoptera has been studied by several taxonomists. Kumar Krishna comprehensively reviewed the taxonomy of termites in 1970. A substantially modified taxonomy along with newly identified synapomorphies, has been presented by T.G. Mylesin 1998. Given below is a simplified classification of the nearly 2000 species of the termites in the world, as classified by Krishna.

1. Family Mastotermitidae (Primitive family)
 - 1 living species (*Mastotermes darwiniensis*) in Australia;
 - 13 Tertiary fossil species worldwide.
2. Family Kalotermitidae (dry-wood termites)
 - Wood-dwelling, wood-eating; survive dry conditions;
 - 292 living, 11 fossil species (some from Baltic amber).
3. Family Hodotermitidae
 - 30 living, 13 fossil species (1, the earliest known termite fossil, from Lower Cretaceous, Labrador); includes rotten-wood termites and harvester termites that forage and store food in nests; *Zootermopsis*, largest termite in North America, found in Rocky Mountains at altitudes of 2,000 to 2,500 metres; *Archotermopsis*, found in Himalayas; *Hodotermes* species, serious pests of African grasslands.
4. Family Rhinotermitidae (subterranean termites)
 - Lives under damp conditions; *Reticulitermes*, widely distributed in North America and other temperate and subtemperate regions and a serious pest; *Coptotermes*, a serious pest in tropical and subtropical regions.
 - 158 living, 13 fossil species
5. Family Serritermitidae
 - One living species in South America; specialized family evolved from Rhinotermitidae.
6. Family Termitidae (higher termites)
 - Largest termite family (about 75 percent of all termites),
 - 1,413 living,
 - 3 fossil species;
 - 4 subfamilies variable in morphology, social organization, and nesting habits.(Kumar Krishna)

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Bees

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Bees are essentially sphecoid wasps that began eating pollen about 80-100 million years ago. For this reason, bees are often called simply Apidae by some taxonomists, but their biologies suggest there are too many differences among them to be contained in a single family. So, therefore, the two long-tongued bee groups are known as Apidae and Megachilidae, while the four short-tongued bee groups are called Halictidae, Andrenidae, Colletidae and Melittidae. There are about 20,000 valid names and about 95 percent of bee species have nothing to do with honey or colonies (with queens and workers, and drones). Bees are generally solitary, seasonal, and lay eggs in one or more nests, and then die. Their larvae may develop over a few weeks to several months or even years, and the adults sometimes visit flowers of a narrow range of plant taxa, or may visit many diverse flowers (and other resources) throughout the year. About 20 percent are parasites, mostly of other bees.

In the tropics, there are fewer species of bees than in much of the warm and dry temperate zone (Mediterranean climates). Moreover, there is a strong shift in dominance from solitary to eusocial species. Especially important in the lowland rain forests are honey bees (Apidae; Asia & Africa only) and stingless bees (Meliponinae). Other families are represented but less important; they are better represented in disturbed habitats and dry forest types.

Eusocial colonies (those with reproductives and a sterile worker caste) function as a single super-organism. The reason for their importance in lowland rain forest most probably lies in the pattern of resource distribution. In the lowland rain forest, flowers, and other resources such as honey dew and resins, are often rare and unpredictable in space and time. Moreover, bees are central point foragers (ie returning to a nest), hence are restricted in their ability to range over the forest. Having large numbers of foragers employing a scout-and-recruit strategy is an efficient way to locate and capitalise on rare, unpredictable resources. Moreover, the colony's ability to store resources enables it to even out temporal fluctuations in resource abundance. The ubiquitous presence of these bees and their abundance at flowers makes them important pollinators. In Sri Lanka there are two species of honey bee and two stingless bees, but in some forests in Borneo there can be as many as four species of honey bee and 27 species of stingless bee living sympatrically.

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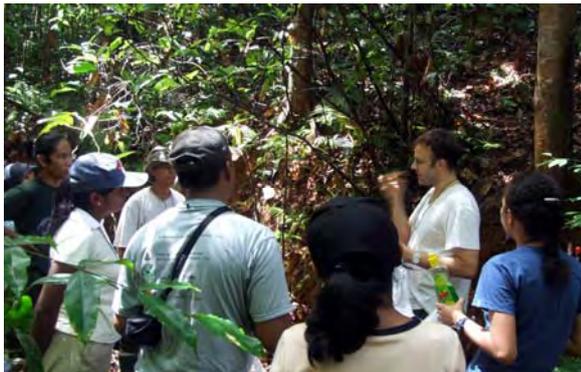
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Learning various insect-sampling methods and setting up insect traps in the field.



Demonstration of insect-pinning by Dave Lohman and Nihara Gunawardene.



Students working on their insect collection and presenting their trophy.



Students presenting their own research projects.

Birds

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Birds are from reptilian ancestor probably in the Mesozoic era about 150 to 200 million years ago, the reptilian origin is represented by reptilian scales and ovipary eggs formed similar to reptiles eggs. All the forms in Aves share following characteristics: feathers, lack of teeth and the only vertebrate group that does not produce live young (Vivipary). Birds show “Bipedalism” which is important to development of flight; forelimb specialized for flight; fusion and reduction of bones; pneumatic bones; physiologically high metabolic rates form adaptations to flight.

The avian fossils clearly indicate that birds evolved during the late Mesozoic era. Thomas Huxley described many similarities between *Archaeopteryx* and small Coelurosaurian dinosaurs; and postulated that possible bird ancestor was coelurosaurs. However the first human reference to birds can be seen in Paleolithic cave paintings. Although evolution is a continuous process, rapid genetic material changes result in genetic variations, genetic isolation and speciation. The genetic drift gradually creates a unique gene pool within isolated populations and reproductively isolated populations may form separate species.

So that all the species tend to have relationships with their environment and forms ecology of the local environment. Most species have their own ecological niche, a singular strategy to obtain food among the other species. Closely related species develop such distinct physical and behavioural differences and they may not genetically resemble each other (divergent evolution). On the other hand, unrelated bird species in widely separated geographic areas often evolved with similar ecological roles and detail resemblance to their anatomical structure (convergent evolution).

The early classification system was based on morphological systematic and the most recent biochemical systematic classification of birds listed 9,672 species living birds, belonging to 23 orders and 141 families. The largest known order is the Passeriformes with approximately 5,700 species.

Southeast Asia encompasses several zoogeographic regions rich in species diversity. Sri Lanka is one of the countries, which is rich in avifauna and including 482 species and 25 restricted range species.

Some aspects of the mixed species bird flocks and bird migration, with special reference to Sri Lanka, will be further discussed in the lecture.

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Herpetological Studies

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Amphibians are divided into three groups or orders: Urodeles (newts and salamanders), Gymnophionans (caecilians), and Anurans (frogs and toads). Some of the major differences that separate them from the other vertebrates include, a body covered with generally thin and moist skin, lack of protective outer layer such as scales, feathers or hairs; soft toes with no claws; a two-chambered heart in the larval stage and a three-chambered heart in adults; external fertilization of eggs; and the process of metamorphosis.

Reptiles are divided into four orders: Testudines (turtles and tortoises), Crocodylia (crocodiles, alligators, and gavials), Rhyncocephala (tuataaras) and Squamata (lizards, amphibinians, and snakes). The reptile anatomy is more advanced than the amphibian's. It has a body covered by waterproof skin with scales or osteoderms (bony skin plates), lack of skin glands; toes with claws; three-chambered heart in adults (four-chambered for crocodilians); internal fertilization, oviparity (egg laying) and viviparity (live-bearing).

Reptiles and amphibians are highly diverse in Sri Lanka with many endemics, but many are under considerable threat. Many species are important to the ecology of their habitats, acting as both prey and predators, and a decline in numbers of them maybe a sign of environmental pollution, habitat lost, or hunting.

Inventory and monitoring techniques for reptiles and amphibians are needed for the rapid surveys. I propose to demonstrate general collecting, visual encounter surveys (VES) and systematic sampling surveys (SSS). General collecting is used to investigate species richness in various habitats and methods such as sighting, listening, and sign collecting are employed. In SSS the target is to record 100 specimens for each habitat type. This technique is useful for the comparison of species richness between habitats. And VES is used to survey species richness and relative abundant in a constant period of time. Details of these techniques will be explained further in the full lecture and field practice.

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Vertebrate Sampling Methods

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Wildlife biologists, ecologists and natural resource managers have extended the effort to determine population parameters, such as population size or survival rate to quantify the occurrence, distribution, habitat relationships and population trends for conservation planning. Several methods adapted to estimate animal density or relative abundance of a closed population, which remain effectively unchanged during the investigation, have been developed. Counting the number of individuals or their signs (sound or droppings ect.) within a plot (quadrates or strips) forms the basis for direct estimates of density or relative abundance for many vertebrates such as birds, marine and land mammals, reptiles, and plants.

The sampling units such as lines and points have been used for detectability-based density estimates that can be varied at multiple temporal scales. It may be possible to count animals from a suitable vantage point or while moving along transect, but the count can only be converted to a density estimate if the area scanned can be estimated. This approach is often difficult to undertake for two reasons. Firstly, it may not be possible to estimate accurately the area scanned. Secondly, all of the animals present may not have been spotted.

Distancing sampling method (an extended version of plot sampling) has been developed to eliminate these problems by fitting a detection function to the observed distances from a selected line or point to the animals. The detection function determines by various models a density estimator using the DISTANCE program and enables one to estimate the proportion of objects missed by the survey. Thus the worker does not require accurately mapping out or defining the sampling area or may not expect to detect all the animals within a transect or point.

Hence, the distance sampling method is particularly appropriate for the estimation of population density for animals (birds, primates) living at low density in difficult to traverse habitats like tropical rain forests and also can be applied for data, collected non-visually. Several other methods, for example mark-recapture method that broadly used for measure survival rates of open biological populations, have been developed to use with distance sampling method. However, distance-sampling method is more effective on dispersed populations than populations aggregated at certain locations or extremely rare species.

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Twenty Questions

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This is an exercise in scientific thinking and the development of appropriate questions for investigation. Participants will go into the forest with instructions to observe the forest and come up with 20 questions of interest. Then working in groups of three, the participants will discuss each question and gradually focusing on the more interesting ones. Each group will develop these questions into testable scientific hypotheses. Finally, selecting just one question each group will propose a suitable project to test of the idea and examine it in a one-day field study. These projects will be written up for the course report and presented orally at the end of the course.



The very early birding session with Prof. Kotagama *et al.*



Students discussing and working on their group projects.



Practical of DISTANCE sampling, led by Chaminda.



Kelum teaching herpetofauna-sampling methods.



Students and resource staff relaxing at the end of first session of the course. The hectic but fun excursion trip follows.

Royal Botanic Gardens, Peradeniya

Siril Wijesunbara

Royal Botanic Gardens, Peradeniya, Sri Lanka

The Royal Botanic Gardens, Peradeniya was established by the British in 1821. It is responsible for almost all major plant introductions for economic and environmental development in this country. Activities that followed resulted in the development of economic and plantation crops, emergence of important state departments, such as Department of Agriculture, and institutions for the development of Plantation Crops, such as Tea and Rubber.

Royal Botanic Gardens, Peradeniya occupy a horse-shoe-shaped peninsula round which flows the chief river of Sri Lanka, the Mahaweli. The main entrance is from the Colombo road, about 4 miles from Kandy. The total area is 147 acres containing about 4,500 species. The mean elevation above sea level is about 1,600 ft. It has a yearly turn out of 1.4 million visitors, of which more than 200,000 are from overseas and about 200,000 are school children.

National Herbarium of Royal Botanic Gardens is the major plant repository involved in the authentication of flora of Sri Lanka. At present the Herbarium houses over 130,000 herbarium specimens. Earliest collections are more than 150 years old and are maintained according to international standards. The botanists at the herbarium are involved in taxonomic and ecological research activities related to ex-situ conservation of Sri Lankan flora.

Pioneering work on floriculture in Sri Lanka was done at the Royal Botanic Gardens in the late 1960s and many people were trained on the subject. This led to an organized cut-flower industry bringing a large amount of foreign exchange to this country. Research carried out in the floriculture laboratories in the gardens today are in the areas of variety development, agronomy, plant protection and post harvest handling.

In addition to displaying a diverse collection of floricultural crops, the garden staff conducts education and training programmes to a wide array of individuals, ranging from students to commercial growers. Such training programmes are an essential part of developing the floriculture industry in Sri Lanka, leading to greater income generation and employment opportunities. Over 15,000 individuals are trained annually in the production of cut flowers, such as Orchids, Anthuriums and other ornamental plants, landscaping, and garden design, plant conservation etc. Hundreds of individuals have also been trained during the past few years, on tissue culture of Anthuriums and Orchids. Numerous training programmes on herbarium techniques, plant identification and ex-situ conservation are conducted at the National Herbarium.

Royal Botanic Gardens, Peradeniya has a satellite garden devoted to conservation of medicinal plants at Ganewatte in the North Western Province. That 56 acre garden contains over 500 medicinal plant species.

Royal Botanic Gardens, Peradeniya, considered as one of the few classic botanic gardens in the world, is perhaps the finest of its kind in South Asia.

Further Reading

Department of Agriculture, Sri Lanka. <http://www.agridept.gov.lk/>

Elephant Ecology

R. Sukumar

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As the largest terrestrial consumer of plants, it is natural that the elephant would make a significant impact on vegetation, and that the ecology of plant communities is closely linked to the ecology of the elephant population in a region. In this lecture, I shall cover three aspects of this ecology:

- a. Feeding ecology of elephants: Although elephants feed on a large number of species and plant parts, certain botanical families predominate in their diets. Field observational studies supplemented with carbon isotopic studies of bone collagen have shown the importance of browse versus grass in the diets of elephants across a rainfall gradient. These have shown that overall browsing is more important than grazing for elephant populations.
- b. Role of elephants in seed dispersal: As a megaherbivore, it is likely that plants with large fruits and/or large seeds are dispersed by elephants. I shall examine the actual evidence for such dispersal syndromes from the limited data available from studies in Asia and Africa.
- c. Impact of elephants on vegetation: Elephants have the potential to make significant changes to vegetational structure through their feeding habits as well as actions such as pushing over trees that may be also dictated by social needs. There has been much debate on the role of elephants in converting woodlands to grasslands and causing "undesirable" changes to the ecosystem. I present the evidence from both African and Asian studies for such change, and discuss a model for considering elephant-woodland dynamics across a rainfall gradient.

The talk will be illustrated with examples from our studies in southern India, including the 50-ha Mudumalai Forest Dynamics Plot where applicable.

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Primate Behaviour and Ecology

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The objective of this lecture is briefly to outline: (a) the history primates, their rich phylogeny and diversity, with a special focus on the primates of Sri Lanka; (b) the ecological niche separation among four species of sympatric primates, for example, as manifest at Polonnaruwa; (c) the evolution of social organization and behavior as reflected by these species; and (d) issues of conservation.

The anatomical, behavioral, and ecological history of primates, like that of other placental mammals, can be traced back to the end of the age of reptiles. Several evolutionary trends are typical of primates, including adaptations for arboreal life, such as grasping hands, opposable thumbs, binocular depth perception and visual acuity. These developments were accompanied by a reduction of the sense of smell and numbers of teeth, and the expansion of the cerebral cortex.

The Order Primates first was represented worldwide in the tropical and subtropical continents (except Australia) by only the Suborder Prosimii or “pre-monkeys” (*e.g.*, lemurs, tarsiers, lorises). These ancestral types gave rise to and were largely replaced by the more efficient Suborder Anthropoidea, or the “true monkeys and apes”, represented in the New World by the ceboids (*e.g.*, marmosets, spider, cebus, and howler monkeys), and in the Old World by the cercopithecoidea (*e.g.*, baboons, guenons, macaques, colobus, langurs) and hominoids (apes and man). The prosimian stock flourished in their ancient ways, however, on the island of Madagascar where they were insulated from replacement by modern anthropoids. Primates living today are represented by a diversity of body forms and life-styles among about 234 species.

The island of Sri Lanka, a biodiversity “hotspot,” boasts 4 or 5 species of non-human primates among 13 different subspecies. As is true for most mammals of Sri Lanka, the primate subspecies diversification reflects differences in adaptations to contrasts in climate and vegetation along geographic lines. The species include a generalist - the Toque macaque, two leaf-eating monkeys - the Gray or Hanuman langur and the Purple-faced langur, and a prosimian - the Slender loris (possibly two species). The four species are found sharing the same semi-evergreen forest habitat at Polonnaruwa, where these primates have been studied more or less continuously for nearly four decades. Taken together, these four species manifest a microcosm of socio-ecological relationships that is typical for much of the primate fauna, particularly that of the Old World.

Different anatomical, ecological and behavioral niche adaptations of the four primate species contribute to their peaceful co-existence at Polonnaruwa. For example, the macaque eats mainly fruits, leaf shoots, flowers and insects but cannot digest mature leaves. The two leaf-eating monkeys, on the other hand, have special gut adaptations with symbiotic bacteria in the foregut that allow these langurs to digest mature leaves (cellulose) and resist chemical plant defences. The two langur species, in turn, differ in the details of their diet. The loris is nocturnal and feeds on insects, small prey and fruit. Niche diversification and sympatry among these four species is a two-way effect.

The social organization of the four species also differs markedly and falls along a gradient of increasing complexity where each species' social life reflects a distinct step in the evolution of primate society – recapitulating phylogeny. Competition for limiting food resources, within and among species, had been a driving force underlying the selection for increased cooperation among primate individuals of the same species, and so the sophistication of social communication and behavioral strategies.

Scientific knowledge is a prerequisite to conservation success and it clearly points to the necessity for the protection of natural forest habitats that are suitable to sustain primate populations. This means lush and fairly diverse forests with the availability of year-round free water. Unfortunately, in Sri Lanka, most protected areas are in arid zones where primates are either few or absent altogether. The political and economic challenges to conservation action for primates are steep, and building public appreciation and support are necessary first steps.

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Niche Partitioning: The Comparative Ecology and Behavior of Three Species of Sympatric Primates at Polonnaruwa

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Introduction and rationale: The four species of primate at Polonnaruwa are: the Toque macaque (*Macaca sinica sinica*), the Gray or Hanuman langur (*Semnopithecus entellus thersites*), the Purple-faced langur (*Trachypithecus vetulus philbricki*), and the Slender loris (*Loris tardigradus nordicus*). These four species share the same dry evergreen forest habitat at our study site at Polonnaruwa, in north-central Sri Lanka. They differ anatomically, their living spaces overlap completely, their diets overlap partially, and there is some overt competition among them for limiting resources. Their sociological relationships are fairly typical of primate assemblages elsewhere in the world; therefore, knowledge about these species' niche adaptations provides an insight to primate phenotypic radiation.

Objective: We wish to investigate the similarities and differences in these species' niche adaptations. Also, is there evidence that humans may impact the ecological relations among these primates? How might we manage these primates for successful conservation?

Specific aims: We will focus on the ecology and behavior of only the three diurnal primate species, the macaque and the two species of langur. The slender loris is active at night and not easily observed. Student will be trained in observation and recording methods to collect data on the following aspects of behavior and ecology: Home range use, activity budget, forest layer use, diet, and interspecific relations. Under the guidance of experienced monkey observers, students will record their observations in the field, then collate and summarize their observations in tables and charts. They will present their results and conclusions for discussion among the group.

Procedure and Schedule:

05:30	Breakfast
06:00 to 07:00	Lecture instruction on field methods
07:00 to 11:30	Plant identification, geographical orientation and data collection
11:30 to 13:00	Lunch break
13:00 to 15:00	Data summary
15:00 to 16:00	Data presentation and discussion.
17:30	Evening lecture (Lecture #2)

Rationale and Methods of Data Recording and Analysis:

Working Teams: Students are divided into teams of up to 5 persons that will be assigned a social group of one of the three target monkey species. Team members will be assigned different tasks, 1-2 members will navigate and chart the movements of their monkey group, the other team members will be assigned a focal animal for behavioral and ecological observation.

Focal Animal Identification: Individual monkeys are distinguished by their natural markings, especially among the macaques and Gray langurs. Students are provided with monkey identification cards. Animals are identified to at least to general age and sex, such as adult female, adult male, etc. Students will focus on one or more adult females of the assigned focal groups and species, and individual identification is not always necessary.

Home Range:

(a) Navigation & charting in the field: Observers are provided with maps indicating the geographical features of the area where they will observe the monkeys. The maps are overlain with grids of either 100 X 100 m (hectare) or 50 X 50 m. Navigators indicate the times and movements of the monkeys on these maps. They also indicate the locations of important feeding and resting places as well as the locations of encounters with other groups of the same or different primate species.

(b) Data analysis: Home range data charted on the field maps are translated onto a check sheet indicating the number of minutes that each grid square (hectare or quarter hectare) was used by the monkeys and the major events occurring at these locations. We wish to know the total area (number of grids) the different social groups and species used and the distances traveled during the period of observation. As the end product of this analysis we seek a map indicating the proportional distribution of time across the home range and an identification and location of relevant resources and events.

Behavior and Activity Budget:

(a) Rationale: Behavior is defined simply as movement. Observers of primates are usually confronted by a bewildering array of different behaviors that cannot all be recorded easily. We simplify our task by concentrating on those behaviors that are most relevant to our hypotheses or inquiry. Thus, behaviors fall into two major categories: discrete acts of short duration (walk, hit, scream, etc.) and behavioral states. The latter are behaviors that continue more or less uninterrupted for long periods of time, e.g., sleeping, traveling, and

are mutually exclusive. Behavioral states are composed of a series of discrete acts but they are related to one another by their overall effect. Behavioral states are of interest, in particular as rough proxies of where and how individuals invest their energies. For example, an individual that spends its entire day foraging (seeking food) is probably more energetically stressed than one who feeds briefly but then sleeps most of the day. Activity budgets reflect an individual's quality of life. One would expect them to vary according to the age, gender, reproductive state, diet and resource distribution and availability, among others. The following are definitions of some states:

- Resting (R): not moving in sitting or lying position but alert
- Sleeping (S): resting still with eyes closed
- Grooming (G): using the hands and mouth to clean and comb through the fur of a social partner
- Foraging (F): all those behaviors that are related to the search for and consumption of food. This category has the most diverse and extensive repertoire of discrete act.
- Moving (M): walking or running from one place to another for short distances and not related to foraging or traveling.
- Traveling (T): walking or running over a long distance in synchrony with other group members as a compact group, as when going from a sleeping site to a distant feeding site.

(b) Field recording: Activity states are recorded approximately at one minute intervals, normally sampled for a few seconds at the middle of each minute of observation. Forest layer use and food item intake, if applicable, are recorded simultaneously.

(c) Data Analysis: The total number of minutes observed in each activity state are summed and displayed as proportions of time in each state for each focal animal.

Forest Layer Use:

(a) Rationale: Primates are anatomically and behaviorally specialized for different degrees of arboreal and/or terrestrial locomotion. In addition, the type and availability of food items differ by forest stratum. Differences in forest layer use can influence social organization and groups size.

(b) Field recording: All activity states are recorded as to the location of the activity, for example F1 is foraging on the ground layer, F2 is foraging in the trees subcanopy, S3 is sleeping in the canopy or emergent layer. Data are summarized according to the sum of active (F, M, T, P) and inactive states (S, R, G) by forest layer.

(c) Data Analysis: we seek a chart of where the distribution of foraging and other states by forest layer for each species.

Diet:

(a) Rationale: The quality of the diet can influence survival, growth and reproduction, and species differ in their ability to process different foods.

(b) Field recording: For each minute of observation of foraging, we indicate (a) the species of plant consumed, (b) the specific plant part consumed (leaf, flower, fruit, resin,) and (c) its state of development: Leaf (leaf shoot, young leaf, mature leaf); Fruit (green fruit, ripe fruit, subpart of fruit if applicable), and flower (Flower bud or mature flower). Student observers will be assisted in plant species identification.

(c) Data analysis: Data are summarized in a tabulation, where each different food or plant species and part eaten is listed once and the number of minutes devoted to its consumption are indicated. Data are further collapsed according to the distribution of foraging durations devoted to different plant items (*e.g.*, leaf bud, ripe fruit) regardless of plant species.

Inter-specific Relations: The navigator keeps a track of interactions of his group with others of the same or other species, in particular with reference to group supplantations, for example as often occurs at contested fruit trees. Any other behavior noted between species, such as social grooming, is also recorded. These are recorded as simple brief descriptive notes.

Data Analysis:

The manner of summarizing data from field records has been described above. The purpose of these charts, tabulations and maps is for comparison among different species.

Group Discussion:

Each team will present their particular results and conclusions to the group for discussion.

Raising Sons and Daughters in Macaque Society

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Toque macaques are typical polygynous mammals with exceptional adaptations for parental care and cooperation among social partners as traits to maximize their Darwinian fitness. The object of the lecture is briefly to (a) outline the life-history challenges facing macaques, (b) gender differences in achieving fitness, and (c) discrimination by control individuals (*e.g.*, mothers) in the allocation of resources to offspring of different sex in a manner that serves to maximize the reproductive success of mothers and other relatives.

Macaque populations in an undisturbed natural habitat tend to be at equilibrium with the carrying capacity of their environment, such that the net population growth is zero. This means that, on average, each individual replaces itself only once per generation. As many more individual are born than can ever hope to survive under these conditions, mortality is high. Individuals that are survived by more than one of their own offspring in the breeding cohort will have achieved this at the expense of competitors. Competition for food

is a basic fact of life for macaques. It is manifest in many ways and has a direct effect on the efficiency with which macaques garner food, the quality of food they ingest, and the amount of time (or energy) that they expend in achieving their daily needs. Success in food competition is a strong determinant of a female's growth, survival and reproductive success. To enhance their success females have evolved cooperative matrilineal (social groups) that serve as tools for competition among groups in the community at large.

Females never leave their natal group but share the group's limited resources for life. Males, on the other hand, disperse at adolescence and thus do not pose a long-term threat to their matrilineal larder. Therefore, the greatest long-term threat to a mother's daughter (*i.e.*, her own reproductive success) is the survival of unrelated infant females that may compete with her own daughter for food. Aggression from control females against such competing young females is therefore high and they die at greater rates than do male peers.

Adult males generally dominate females and take priority in food competition. In contrast to females, the greatest obstacle to reproductive success is not food but other males who compete for mates. In addition, males face the life threatening obstacles involved in mandatory dispersal (to avoid fitness loss through inbreeding). Male survival and reproductive success rest, at least in part, on the development of large body size and fighting ability.

Mothers (and other relatives) promote the potential reproductive success of young male relatives by fostering their growth to large body size before they disperse from their natal group; such males are tolerated more than female peers in food competition with matrilineal relatives. These gender differences in the allocation of limiting resources by sex represents only a difference in the scheduling of benefits, as males and females during their lifetime, benefit equally from their relatives per generation. Females benefit from their matrilineal larder throughout their lives, whereas males receive their entire allotment before dispersal at adolescence. Fisher's theory on sex allocation is supported, and the same phenomenon would be expected in all polygynous mammals where food competition is a determinant of female fitness and sexual dimorphism is the product of sexual selection.

Further Reading

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Horton Plains

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Horton Plains is Sri Lanka's only high-altitude national park. It nestles between the island's second and third highest mountains, Kirigalpotta (2,390 m) and Totupolakanda (2,360 m), which lie to the west and north-east of the plains, respectively. Situated approximately 2,100 m above sea level, the 32 km² national park comprises rolling grasslands set within tropical montane cloud forest. The area was named after Sir Robert Horton, Governor of Sri Lanka from 1831–1837, following a meeting that took place on the plains between him and the *ratè mahatteya* (chieftain) of Sabaragamuwa in 1836. Another name associated with the plains is that of Thomas Farr, a British tea planter and sportsman resident at North Cove Estate at the south-west corner of the plains in the early 1900s. Over the years, Farr's hunting cabin (now Farr Inn) developed from a rude hunting shelter to a lodge for the trout fishing club; introduced in the 1880s, trout still persist in the park's streams. In 1999, Farr Inn was acquired by the Department of Wildlife Conservation for use as a visitor centre.

Despite a century of hunting and fishing, the landscape of the Horton Plains remained largely intact until 1961, when the government decided to convert part of the grasslands into a potato farm under the Department of Agriculture. This scheme was eventually abandoned owing to pressure from conservationists, but not before irreparable harm had been done. When the potato cultivators left, their abandoned fields were rapidly colonised by exotic species, including fodder grasses, that are now impossible to eradicate (these nevertheless support a thriving population of Sambar deer). The cultivators also left behind a large number of unsightly buildings on either side of the road; the terraces cut for potato farming are still visible even from space.

In 1969, Hortons Plains was declared a nature reserve. Finally, on 16 March 1988 it was declared a national park. In addition to its scenic beauty and biodiversity, Horton Plains is also important as an archaeological site: stone tools associated with prehistoric inhabitants of Sri Lanka have been reported from several sites close to the river by Dr. S. Deraniyagala. Although these have not yet been dated, similar tools at Batadomba Cave, near Kuruwita, have been dated to 28,500 years before present.

Recent studies of buried pollen by Prof. R. Premathilake show that the present-day Horton Plains vegetation stabilized as recently as 9,000 years ago, at the end of the last Ice Age; the grasslands date to about 24,000 years before present, just before the peak of the last Ice Age. These data suggest that on-going global climate change could bring about significant changes in Horton Plains vegetation (indeed, the rapid increase in rhododendrons seen in the grasslands in recent years may signal a change in the forest-grassland balance). Interestingly, these pollen studies led also to the discovery of evidence of cereal (oats and barley) cultivation on Horton Plains as long as 13,000 years ago, the earliest evidence of agriculture in southern Asia.

Despite its small area, Horton Plains is the habitat of a rich and unique montane flora. A study led by the late Prof. S. Balasubramaniam showed that about half of all woody plants occurring here are endemic to Sri Lanka, many others being shared only with the montane forests of southern India (*e.g.*, the Nilgiri Hills). Several other species such as the dwarf bamboo, *Arundinaria densifolia*, abundant in exposed marshy areas, are found nowhere outside Horton Plains. Likewise, about half of Sri Lanka's endemic birds (the park's bird inventory totals about 90 species) occur here. All groups of vertebrate animals have distinctive species on the plains,

some of them extremely rare (e.g., the mountain loris, *Loris tardigradus nycticiboides*, known only from two specimens). All three freshwater-crab species occurring here are endemic to Sri Lanka (two are found nowhere else), as are all eight species of frogs. The three species of ‘garden lizards’ found on the plains too, are endemic, including the horned lizard, *Ceratophora stoddartii*. The park also contains representatives of several endemic genera including the live-bearing lizard *Cophotis ceylanica*, the shrimp *Lancaris singhalensis*, the spider *Wanniyala agrabopath*, the mouse, *Srilankamys ohiensis* and the shrew *Feroculus feroculus*.

The unique biodiversity of Horton Plains is threatened by the spread of alien invasive species, pollution and climate change. Some 50 species of invasive plants have become established through cultivation in the gardens of Farr Inn and Anderson Lodge, and as a result of potato farming. With upwards of 150,000 visitors annually, pollution from vehicle exhausts is clearly having an impact on the flora (as is evident from the disappearance of ‘beard lichens’, *Usnea*, from trees on the sides of motorable roads and the busier footpaths). The widespread dieback of canopy trees observed during the past 30 years could be the result of acid rain. Such dieback stands go on to provide exposed territory ideal for colonisation by alien species in the very heart of the forest. Together with montane habitats worldwide, Horton Plains will also be affected by global climate warming, with lowland species migrating upwards and highland species — which have nowhere ‘upwards’ left to go — facing extinction. Climate change will also entail phenological impacts, affecting the times at which plants flower and animals reproduce. Finally, despite precautions, fire poses a significant threat to this fragile habitat. A sizeable extent of forest on the right bank of the Belihul Oya, between Old Chimney Pool and Slabrock Falls, destroyed by fire in February 1989, is showing no signs of recovery as at 2006; it is now colonised by bracken (the fern *Pteridium aquilinum*) and the aggressively-invasive Mexican weed *Eupatorium riparium*.

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Colourful memories and enriching experiences from the excursions; For detailed accounts, see reports written by the students in section “Excursion Reports”, pp. 40-48.

An Introduction to R

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Increasingly, ecologists are using the free software 'R' for their statistical needs, from basic data summaries to complex analyses. R is an object-based programming language optimized for statistics. It is the open-source implementation of the S language developed at AT&T Bell Laboratories. Among its strengths are the ability to construct complicated, repeatable analyses from raw text data to publishable graphics. There are many contributed packages (libraries) that can be imported to extend the analyses. R distributions, packages and documentation can be found at <<http://cran.r-project.org>>.

In this lecture and practical, I will introduce R, beginning with installation on a typical Windows system. R is command-line driven rather than point-and-click, and this requires some users to shift their approach to software use. Commands (*i.e.*, program statements) are typed or pasted into the terminal window (or R console). Complete scripts can be imported and run, and interactive sessions can be saved for later editing and re-running.

We will cover basic language structure (functions and assignments), the basic objects of data (vectors, matrices, data frames) and indexing. We will then move to basic data summaries (means, variance, etc), tabulation, and introduce some of the graphics routines (histograms, x-y plots). Importing data and exporting graphics will be discussed. Next I will introduce simple statistical tests (t-test, Wilcoxon test), and basic linear models. The final two sections will be demonstrations introducing more complex analyses: randomization methods, and community analysis (ordination, diversity curves, etc.).

The whole class will follow an R-script that can be 'played back' at any time by the students.

The student exercises will then take the form of simple statistical analyses after the Basic Statistics lecture by Richard Corlett. These analyses will be implemented in R.

Further Reading

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Venables *et al.* 2006. An introduction to R. <http://CRAN.R-project.org/>.

Statistics

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The availability of user-friendly statistical packages has made statistics too easy: it is no longer necessary to know what you are doing or why. One aim of this session, therefore, is to make the statistical analysis of ecological data as difficult as it should be, by making you aware of issues that the packages don't always mention. I will also illustrate the range of statistical techniques available for the analysis of standard ecological datasets. The topics covered will probably include: hypotheses and null hypotheses; differences and trends; statistical significance; significance tests; data types; parametric and nonparametric tests; one-tailed and two-tailed tests; testing for differences; testing for trends; confounding effects; observations vs. experiments; non-independence and pseudo-replication.

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Tropical Forests Compared

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Tropical forests are variable on all spatial scales, but I will concentrate on the broadest – biogeographical regions – and consider only lowland evergreen rain forests. There are five major rain forest regions: the Neotropics (S. & C. America); Africa (C. & W. Africa); Asia (SE Asia and various outliers); New Guinea (and Australia); and Madagascar. Rain forests in these five regions are similar because the laws of physics are the same, but they differ because they contain different organisms, and many key processes are under biological control, including seed dispersal, predation, herbivory and decomposition. The major biological differences between regions result largely from the interaction between phylogeny, plate tectonics, and past climates and sea levels. Most modern rain forests are on fragments of the Mesozoic southern supercontinent of Gondwana, which drifted apart during the Cretaceous and early Tertiary. The fragments were widely separated during the period when most rain forest genera and many families evolved. Barriers between the major

fragments have generally declined over the last 20 million years, but the absence of rain forest connections between the regions has maintained much of their distinctiveness.

The Neotropical rain forests are the most extensive, the most diverse for plants, birds, butterflies and many other groups, and in many ways the most distinctive. The rain forest vertebrate fauna includes: groups of possible Gondwanic origin that radiated in South America during the long period of isolation (*e.g.*, sloths, anteaters, suboscine passerines); groups that arrived during the period of isolation (*e.g.*, primates, caviomorph rodents); and groups that arrived only after the Panama land bridge connected South America with the north 3 million years ago (*e.g.*, carnivores, deer, squirrels). The most distinctive botanical feature is the abundance and diversity of epiphytes in the Bromeliaceae.

African rain forests were once (*ca* 30 million years ago) as extensive, diverse and distinctive as those of the Neotropics, but intermittent connections to Eurasia since the Miocene have reduced their distinctiveness and the drying of the continent has reduced their diversity and extent. Today they are mostly drier, lower, more open, and less diverse than the other major regions. Most major families of plants and animals are shared with Asian rain forests, but very few species. The most distinctive feature of Southeast Asian rain forests are the everwet climate, the dominance of dipterocarps and – probably related to both of these – the supra-annual pattern of community-level mass flowering and mast fruiting. This results in an irregular alternation of brief “feasts” and prolonged “famines” for animals dependent on flowers, fruits or seeds.

New Guinea and Australia were joined during Pleistocene low sea levels but have never been connected to Asia, so the contrast across Wallace’s Line is sharp, despite the relative proximity of the two regions. Rain forest covered much of northern Australia in the early to middle Miocene, but has since become restricted to a tiny area in the northeast by drying. Rain forest in New Guinea, in contrast, largely occupies land that was uplifted above sea level only 10-15 million years ago. The lowland rain forest flora of New Guinea is largely Asian, while the vertebrate fauna is largely non-Asian. Rats and bats are the only native placental mammals. Marsupials fill the mammalian herbivore, frugivore and small carnivore niches, but there are no large mammalian carnivores. The bird fauna includes some Asian groups and several endemic families, such as the birds of paradise.

Madagascar has been isolated for 90 million years by a deep ocean barrier. The entire non-flying mammal fauna of 101 species has resulted from only 4 colonization events: an ancestral lemur *ca* 65 million years ago, an ancestral carnivore *ca* 20 million years ago, an ancestral insectivore, and an ancestral rodent. Other groups show the same pattern: very few colonization events followed by adaptive radiation into a wide range of habitats and niches. Many groups are absent, such as woodpeckers and grazing mammals, and mass extinctions of large vertebrates followed the arrival of the first humans *ca* 2000 years ago.

What are the consequences of these differences? In theory, convergent evolution could ensure that niches are filled from whatever lineages are available, but, although there are clear examples of convergent evolution in some groups (*e.g.*, flycatching birds), convergence is incomplete in others (*e.g.*, frugivores and browsers). Non-convergence is most obvious for Madagascar and New Guinea, where many vertebrate niches appear to be unfilled, but there are also striking examples from the three largest and most diverse regions (*e.g.*, leaf-cutter ants are confined to the Neotropics). Do these differences in the organisms present have any consequences for community function? The lack of comparable measurements between sites with matched physical environments makes this question almost impossible to answer at present.

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Frugivory and Seed Dispersal

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Adult plants are fixed in space for their whole lives. However, movement is essential at two points in the life cycle – during sexual reproduction (*i.e.*, pollination) and during the dispersal of offspring (*i.e.*, seeds) away from the parent plant. Seed dispersal has two potential benefits for the offspring: it gets the seed away from the immediate surroundings of the mother plant, where competition with both parent and siblings is greatest and pests and pathogens are concentrated; and it increases the chance of the seed getting to a suitable site for germination, establishment and growth.

Dispersal by wind depends on the aerodynamic properties of the dispersal unit (seed or fruit), the height at which it is released, and the wind speed during its fall. Seeds will be dispersed further if they fall slowly, from a great height, or in strong winds. The terminal velocity of a seed is strongly correlated with its wing loading (weight per unit area), which can be decreased by wings, plumes etc. In tropical rain forests, wind dispersal below the canopy is only practical for the smallest of seeds (*e.g.*, orchids) and spores, but it is quite common among emergent and upper canopy trees and climbers, and also pioneers of open sites. Most tropical forest plants are dispersed by animals. Ants are important mostly in the secondary dispersal of small seeds that were initially dispersed by vertebrates, although some plants produce seeds or fruits that are targeted directly at ants. Seed dispersal by vertebrates may take place externally or internally, but

internal dispersal is most important by far in tropical forests. Internal dispersal requires that the seeds are packaged in nutritious tissues and are advertised.

Dispersal relationships in tropical forests are extremely diverse. In the tropical Asia, most species of forest birds and mammals eat at least some fruit, and specialized frugivores range in size from 5 g flowerpeckers to 1.5 kg flying foxes, 2-3 kg hornbills and 70 kg orangutans. These frugivores differ not only in diet and size, but also in locomotory and sensory capabilities, fruit and seed handling techniques, digestive physiologies, gut passage times and ranging behaviors. Most animals that eat fruits are capable of dispersing some seeds, but the consequences for a plant's fitness of its fruit being eaten by different animals vary greatly. Fruits, too, vary tremendously in phenology, size, morphology and chemistry, and thus also in their potential contribution to animal fitness. The number of possible pairs of plants and frugivores is enormous, but fruit-frugivore relationships in tropical forests are structured in a variety of ways, so only a small subset of the possible interactions actually occurs.

When fruit and frugivore coincide in space and time, frugivores are more likely to be attracted to fruits that signal their ripeness by colour or odour cues tuned to their particular sensory capabilities, and may overlook fruits that do not. Different crop sizes and degrees of ripening synchrony may also attract different types of frugivores. Fruit and seed size interact with the size, gape width and oral processing capabilities of frugivores. Frugivores also differ in their ability to reach fruits displayed in different positions relative to potential perches, while mechanical barriers to the fruit rewards will restrict access to animals with the necessary strength and/or skill to overcome them. The nutritional content of the fruit pulp will interact with the digestive capabilities of the consumer, while the non-nutrient chemical content could potentially narrow the range of consumers. Discrete plant guilds are most obvious among species dispersed largely by primates, by fruit bats, and by terrestrial mammals. The lengths of the fruit lists compiled for well-studied animal species suggest a general lack of specialization among frugivores, but when the quantity of each fruit species consumed is taken into account, there is much less overlap in diet between animal species. The most important dispersal agents in tropical Asian forests are a few families of birds (Megalaimidae, Bucerotidae, Columbidae, Pycnonotidae, plus some species from a wide range of other families) and mammals (Pteropodidae, Cercopithecinae, Hylobatidae, Viverridae, plus some large terrestrial herbivores and some scatter-hoarding rodents).

Post-dispersal processes, such as seed predation, may effectively decouple patterns of plant regeneration from patterns of seed dispersal, making it very difficult to assess the conservation consequences of frugivore losses. Although dispersal relationships may be less specialized than those for pollination, the animals that disperse seeds are, in general, much larger than the animals that pollinate flowers. This makes them more vulnerable to both forest fragmentation and direct exploitation. Complete failures of dispersal mutualisms may be rare so far, but changes in the composition and spatial pattern of the seed rain must already be widespread. In the longer term, this will inevitably lead to the erosion of plant diversity.

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Conservation Biology - Effects of Small Population Size

Priya Davidar
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The global loss of natural ecosystems and biodiversity has led to the loss and fragmentation of habitats. Tropical forests are rich in biodiversity and loss of these forests will lead to the extinction of many species. Species that were found in a large area are now being restricted to small areas due to loss of habitats. Thus once large and continuous populations have now become small, isolated populations. Therefore conservation genetics addresses the issue of how to maintain small populations without loss of genetic diversity and inbreeding depression. This has led to the concept of Minimum Viable Population (MVP) size.

What is a Minimum Viable Population? Shaffer (1981) defined the term MVP as "Minimum Viable Population for any species in given habitat is the smallest isolated population having a 99 percent chance of remaining extant (surviving) for 1000 years despite genetic, environmental and demographic stochasticities and natural catastrophes". This definition allows a quantitative estimate of population size to ensure long term survival.

- To accurately estimate MVP, it is necessary to do a detailed demographic study of the population and analysis of its environment.
- Once MVP has been established the minimum dynamic area (MDA) has to be estimated.
- Study of home ranges of each species, *e.g.*, to protect grizzly bears in Canada, the size of the protected areas has to be about 49,000 for 50 individuals and 2,420,000 km² for 1000 individuals.

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Invasive Species

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An invasive alien species (IAS) is defined as an alien species whose establishment and spread threaten ecosystems, habitats or species with economic or environmental harm. IAS are now recognized as one of the greatest biological threats to our planet's ecological and economic well-being. The impacts of IAS are immense, insidious, and often irreversible. It has been well documented that IAS have resulted in massive and rapid losses of biodiversity, especially in island ecosystems. Hundreds of species extinctions have been caused by IAS. Therefore, the direct ecological cost of IAS is the irretrievable loss of native species and habitats. In addition, the direct economic costs of IAS run into many billions of dollars annually, as control costs related to some IAS which function as weeds, pests and pathogens of crops, livestock and forest plantations. A vast number of IAS occur in the Asian region. Invasive alien plants such as Water Hyacinth (*Eichhornia crassipes*), Salvinia (*Salvinia molesta*), Giant mimosa (*Mimosa pigra*) and Lantana (*Lantana camara*) have established themselves in freshwater and terrestrial ecosystems throughout Asia. Among invasive alien animals, mollusc species such as the Giant African Snail (*Lissachatina fulica*) and the Golden Apple Snail (*Pomacea canaliculata*) have spread in many parts of the Asian region, causing immense economic damage to agricultural crops.

The introduction of plant and animal species beyond their natural range is closely linked to the history of civilization. Colonization in particular led to massive transoceanic movements and exposed ecological systems and native species to new stresses and threats. Establishment of an alien species that may become invasive could result either from intentional introductions for use in biological production systems (*e.g.*, agriculture, forestry and fisheries) or through accidental introductions by pathways involving transport, trade, travel or tourism. While many IAS have been introduced deliberately into different parts of Asia for economic and aesthetic purposes, several others have entered accidentally. At present, the major pathways for introduction of IAS in the Asian region include aquaculture development, the horticultural trade, and the ornamental fish trade.

IAS are found in all taxonomic groups; they include introduced viruses, fungi, algae, mosses, ferns, higher plants, invertebrates and vertebrates. In general, IAS can take advantage of disturbances to colonize or expand their populations. It is known that about 1-2 percent of all introduced species are likely to become invasive. While all ecosystems can be invaded, some are more vulnerable than others. Ecosystems particularly vulnerable to IAS include ones that are geographically or evolutionarily isolated (islands, lakes, mountains etc.), degraded and stressed ecosystems, and agricultural systems. In general, the conditions that favour the establishment and spread of IAS include the availability of empty or unutilized niches that occur naturally or created by habitat destruction/degradation, absence of natural enemies and diseases, intrinsic factors of IAS such as high reproduction and dispersal capabilities, and ability of IAS to tolerate sub-optimal levels of resources. The major impacts of IAS on native biodiversity includes direct exploitation or destruction of species (carnivorous IAS), displacement of native species by being superior competitors for resources, and genetic contamination through hybridization with native species.

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Plant Diversity in Forests: Negative Density Dependence

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The high diversity of tropical tree communities poses a challenge to classical theories of species coexistence in species rich plant communities. These classical theories proposed that all coexisting species possess unique responses to their biotic and abiotic environments that are manifested as differential niche occupancy. However, extending this theory to species-rich tropical tree communities requires us to identify up to approximately 300 unique ecological niches per ha for the woody plants >10 cm diameter. Theoretical and empirical studies have failed to support such a diversity of life histories among tropical forest trees.

One alternative mechanism for the coexistence of highly diverse tropical tree communities proposes that rare species escape from host specific natural enemies and therefore enjoy a recruitment advantage. The so-called Janzen-Connell hypothesis predicts that

seed or seedling survivorship is a negative function of adult or juvenile density. Such negative density- or frequency-dependent interactions may be pervasive in tropical forests.

However, the importance of negative density dependent interactions for seedling recruitment have been poorly explored in the lowland dipterocarp forests of South and Southeast Asia. One possible reason for this is that the reproductive ecology of dipterocarp forests is driven by irregular, supra-annual masting events during which plants in many families, including members of the dominant family of trees, the Dipterocarpaceae, flower gregariously during a general flowering event and then fruit simultaneously over a short period but only once every 5-9 years. This pattern of reproductive phenology, known as masting, results in a highly episodic pattern of dipterocarp seedling recruitment and generates transient, high-density cohorts of dipterocarp seedlings in the forest understorey at irregular intervals.

The evolutionary drivers of masting in dipterocarp forests are poorly understood. One possibility is that masting is an evolutionary response to abundant seed predators that feed on the fruits of dipterocarps and other species. If all species fruit simultaneously then populations of seed predators may be unable to consume the entire crop of seeds, thereby inducing selection for interspecific aggregation of fruit production. The predator satiation hypothesis predicts that, at certain spatial scales, the probability that an individual seed or seedling avoids predation is a positive function of the amount of food available to seed predators during a mast event. Therefore the Janzen-Connell hypothesis and the seed predator satiation hypothesis predict opposite functional relationships of seed and seedling survival to conspecific density.

The aim of this practical exercise will be to quantify the relative strength of positive and negative density dependent dipterocarp seedling survival. We will exploit a network of existing seedling plots established on the Sinharaja 25-ha Forest Dynamics Plot (FDP) to test these competing hypotheses using 24-month seedling survival following a masting event in August 2004. The timetable for the day will include a preliminary lecture to provide an overview of the mechanisms maintaining tree species richness in tropical forests and the reproductive ecology of dipterocarps, a practical exercise on the FDP involving a re-census of the seedling plots, a data analysis exercise based at the field station to analyse the data using the program R, and a discussion and synthesis session to report back on our findings.

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Richard Corlett and Cam Webb teaching basic statistics with the mighty 'R'!

Students having fun during the intense seedling ecology session with David Burslem, and tea break at the field station.



Frugivory and seed dispersal by Richard Corlett. Students sorting fruits and seeds according to their ecology, morphology, abundance, and potential dispersal methods. Check out the 'loot' on the tables!

Phylogenetic Methods

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Understanding local biodiversity involves asking questions about species habitat and niche choice (autecology), variation in species richness (diversity studies), and variation in species composition (floristics and faunistics). In studies of species composition we are interested in detecting non-random patterns in the identity of species that can live together, usually in the context of assembly from some local or regional species pool. Much classic work in community ecology has been done on the distribution of traits (*e.g.*, body sizes, feeding modes) in communities, testing theories about the maintenance of species composition. However, the full set of morphological and physiological characters are seldom, if ever, known for every possible organism in a community, and identifying the character axes most important in interactions can be difficult. Much information about similarities and differences among organisms is encoded in their phylogenetic relationships, and it is fruitful to ask questions about the phylogenetic structure of local communities: are taxa that co-occur more or less related than expected by chance. For instance, if key characters have evolved in a phylogenetically conservative fashion, and communities are structured by the action of habitat filters on these characters, then we should expect to see co-occurring taxa to be more closely related than expected by chance. This approach is a modern spin on the analysis of species-per-genus ratios. However, traditional ranks have serious drawbacks in community analysis, foremost being the non-equivalence (*e.g.*, in age) of different groups at the same rank. With the advent of increasingly broad coverage of taxa subjected to molecular phylogenetic analysis, and supertree construction methods, analyses of phylogenetic structure can be conducted even if the taxa involved have never been included in a phylogenetic systematic analysis.

I will review classic approaches and findings of species-per-genus analyses, discuss the creation of phylogenies for community members (introducing the software tool, *PhyloMatic*), null models for community assembly from a regional species pool, and measuring and testing community phylogenetic structure using the *PhyloCom* software application. I will demonstrate the use of these tools with data from tropical rain forest tree communities. I will also introduce the further use of phylogenies in: (i) modelling seedling dynamics; (ii) assessing the influence of host-sharing by pathogens in communities; and (iii) biogeographic analyses at larger scales. I will also discuss the measurement of niche parameters from GIS-based species distribution analysis, and how these parameters can be optimized on a phylogeny to understand the evolution of ecological character and possibly to detect the evolutionary effect of historical species interactions.

In our practical exercise, we will test the hypothesis that taxa occurring in more physiologically demanding environments should be more closely related than expected by chance species assembly. In small groups, we will walk around the Sinharaja Forest Dynamics Plot and locate a spatial sample (of *ca* 0.05 ha) in a 'stressful, demanding' habitat, and one in a less demanding habitat. An example of the former would be seasonally inundated flat areas, and of the latter possibly well-drained but not drought-prone slopes. Having noted the location of these habitats, we will return to the lab, extract the species lists for these habitats (using 'R'), create a supertree-based phylogeny for the tree species in the Sinharaja plot (using *PhyloMatic*), and use the '*PhyloCom*' software to assess the phylogenetic structure of taxa in these subplots. We will interpret the results in the light of a discussion on the physiology of trees and the nature of homoplasy in the evolution of ecological characters.

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Evolutionary Philosophy

Shawn Lum,
National Institute of Education, Singapore

The plant population ecologist John Harper once referred to Chapter 3 of Darwin's *On the Origin of Species* as one of the greatest ecological treatises ever written. What was the basis for Harper's assertion? To find out, this session will begin with a review of the basic tenets of Darwinian evolution. We will then try to see how an evolutionary approach could be incorporated into ecological studies.

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Molecular Ecology

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Molecular ecology is a broad field that has elements of evolutionary biology, population genetics and, as the term suggests, ecology. We will start by learning what kinds of work are generally placed under the umbrella of “molecular ecology” and read through a couple of studies as examples of molecular ecology research. Following the introductory activity, we will go to the field to plan possible ecological studies that could benefit from the addition of molecular-based techniques.

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Fig Biology: An Intricate Interaction

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Figs (*Ficus*, Moraceae) are important plants in lowland tropical rain forests. Over approximately 50-80 million years they have co-evolved with fig wasps (Agaoninae, Agaonidae, Chalcidoidea) in an intricate mutualism. The fig inflorescence is a closed urn-shaped receptacle lined with tiny uni-ovular flowers. Female fig wasps enter the inflorescence through a tiny bract covered entrance, losing their wings in the process, and pollinate the flowers inside. Simultaneously, the fig wasps attempt to oviposit on some ovules. Ovules that receive a wasp egg form a gall and the fig wasp larva feeds on the gall tissue. Pollinated ovules missed by the wasps develop into seeds normally. The fig wasp is thus a seed predator – pollinator, and well illustrates the fact that mutualisms are perhaps best understood as mutual exploitation. After approximately one month the adult fig wasp offspring emerge. The wingless males emerge first and mate with the gall-enclosed females. The females then emerge and collect pollen, either passively or by actively filling pollen pockets on the mesothorax. Meanwhile, the male wasps cut a tunnel through the fig wall, which the female wasps use to escape from the fig. The adult female wasps live only 1-3 days, and thus must locate a receptive fig within this brief lifespan to reproduce. However, many fig species occur at low densities and only a small proportion of individuals are receptive at any point in time. Thus, in their search for trees with receptive inflorescences the pollinators of these figs disperse further than is known for any other pollinator (> 10 km). They achieve by flying above the canopy and using the wind. However, there is diversity in the dispersal ecology of fig wasps, and other species fly much shorter distances.

A few days after the emergence of the fig wasps the fig inflorescence softens and ripens into a fruit (pseudo-carp) that is eaten by a variety of vertebrate seed dispersers. Over 1200 species of vertebrate feed on figs worldwide and year-round availability of fig fruit makes figs a critical component in the diet of many species, especially at times of the year when few other fruit are available.

The monoecious system described above is the ancestral system in figs, but in Asia there are also many dioecious figs in which the sexual roles are separated. On female trees the fig wasp enters the inflorescence and pollinates the flowers, but fails to lay its eggs because the styles are too long and too thin. It, therefore, dies without reproducing. It can be considered a deceit pollination system. On male trees the flowers are modified to receive a wasp egg and only wasps and pollen are produced; the male role of the fig.

The alignment of the reproductive interests of the fig wasp with delivery of the fig's pollen has led to an incredibly efficient pollination system. The fig - fig wasp interaction has often been used as a model system to investigate co-evolution and other aspects of evolutionary theory, such as sex ratio theory (Local Mate Competition), the evolution of virulence, co-adaptation and co-speciation.

In addition to pollinating wasps there exists in most fig species a diverse community of non-pollinating wasp. Some species enter the fig at the receptive stage like the pollinators, but the majority of species lay their eggs by piercing the wall of the inflorescence with a very long ovipositor. Species have diverse ecological roles and include ovule galls (*i.e.*, competitors of the pollinators) and galls that use the tissue of the inflorescence wall, inquiline (gall parasites), and parasitoids.

Practical:-

How is the fig – fig wasp system evolutionarily stable? Why don't the pollinators eat all the seeds? Or why don't non-pollinating wasps destroy all the seeds and pollinators?

We will investigate the impact of different wasp species on the reproductive success of the host fig (if possible across 2 or more species of fig) to address these questions.

We will collect the following basic data:-

male and # female flowers

seeds

bladders

pollinator males and females

males and females of each non-pollinating wasp species

Using multivariate regression we will investigate the impact of each factor on seed and female pollinator production.

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Pollination

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When it comes to breeding plants have a problem. They can't move (at least not very far). The flowering or seed plants thus exploit animals, including bees, flies, wasps and beetles, butterflies, bats, birds or other vertebrates (occasionally shrimps and other weird things) to move their genes for them. However, they must pay for these services. In tropical forests, where the nearest conspecific may be kilometres away, the problem is particularly acute and plants invest a substantial proportion ($\approx 3\%$?) of their net primary production on pollination. Food, synchrony and deception are the key factors. Different cues trigger innate responses in pollinators to colors and odors. These cues are reinforced by the plants, which provide a particular kind of reward, usually carbohydrates and protein. As illustrated by primitive angiosperms today, flowering plants have probably co-evolved with pollinators since they emerged in the mid Cretaceous. However, individual pairwise interactions are rarely old, as the movements of the continental plates and climatic fluctuations have led to large turnovers in biotas. For example, the Asian Giant Honey bee (*Apis dorsata*) is one of the most important pollinators throughout this region and has been foraging in these forests for approximately 40 million years. A majority of the plant species it pollinates, however, have only been around since the India subcontinent offloaded its cargo on to the Asia continent about 20 million years ago. Ecologically plant-pollinator interactions represent the full spectrum of possibilities from extreme specialisation to highly generalist. Moreover, interactions are rarely symmetrical. Plants may interact with relatively small number of potential pollinators, but pollinators often forage on a wide variety of floral resources. Interactions also vary substantially from place to place or from one year to the next. Most pollination niches are, therefore, loosely defined.

Plants and their pollinators share their ecological discourse with a variety of 'floral parasites' who usurp the resources of the hard-won pollinator-plant relationships. The pollinators of one plant may often be the parasites (or at best commensal) of another. Understanding the roles of different visitors, thus, requires careful observation, backed up where possible by controlled experiments.

Pollination is vastly inefficient. Plants produce enormous amounts of pollen, and usually also huge numbers of ovules. However, maternal plants (those making the seeds and fruit) are choosy about which ovules they allow to mature; bud, flower, and immature fruit abscission are common. This enables plants to sample a large number of genetic combinations, but be selective about

where they put their resources, as pollen and ovules are cheap by comparison to seeds. On the other hand, after pollination there are 'aggressive' seeds demanding nutrients and maternal resources.

As indicated in the excellent pollination biology text by Kearns and Inouye, there are three general areas of pollination biology. The first concerns interactions between animals and the reproductive structures of plants – flower visitation. The second concerns which pollen germinates on the stigma and fertilizes the ovule, and the third concerns the growth and survival of the offspring resulting from pollination. In field studies, particularly those of short duration, we examine the details in interactions but remain ignorant of the absolute result of pollen transfer and flower visitation.

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Shawn Lum conducting practical on molecular ecology. Big 'grant money' will be awarded to the best research proposals!



Students examining fig fruits (pseudocarp). Counting figs can be tedious, but the results are interesting!



Modern phylogenetic methods by Cam Webb (top right), and students choosing quadrats to test relatedness of tree community with 'Phylocom' software.



Rhett Harrison teaching fig biology.

Seedling Ecology

Mark Ashton
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Understanding the regeneration dynamic as a basis for restoration and sustainable management of forests: We foresee that upland forests in humid regions of the world, after two centuries of dramatic decline and degradation, will become critical resources for the sustenance of global services (water, climate amelioration, recreation) and products (genetic reservoirs of new products, specialty timber and nontimber products) demanded by society. Our research concentrates on the ecological adaptations by which trees of various species of these complex forest types become established naturally after disturbances that make vacancies in the growing space. The kind of knowledge gained is a key part of the basis for developing silviculture that will sustain and augment the various forest values of the future.

The importance of big scale comparisons: The regeneration period is a critical window of time during which the future composition and development of the forest is largely determined. It is also the period during which the silviculturist has the most opportunity to restore and guide forest growth. Our research has focused on understanding the most important biological and physical processes governing regeneration of species-rich moist forests. The majority of our research has been centered for over twenty years at field sites in the Asian tropical wet-evergreen forest (mixed-dipterocarp) of Sri Lanka. Sites were selected to develop common methodological protocols that would enable a better understanding of the differences and similarities of regeneration within a major forest biome - the Asian Mixed Dipterocarp Forest.

Long-term experimental rationale and framework: Building the basics: Cladistic groups (at the genus level in particular) are largely the level at which species differentiation occurs in tree species-rich forests such as those of the Asian moist tropics. Co-occurring species within a genus may differ in value and the products that they yield, as well as in their spatial and temporal role in biodiverse plant assemblages. We have chosen to study a series of co-occurring species that are of the same cladistic group (and often of the same successional status), because their similar morphology and growth adaptations facilitate examination of differences. Identifying these differences and their variations can provide a better understanding of evolving species specialization in relation to environment. This, in turn, provides the ecological information necessary for restoration and sustainable management of moist tree species-rich forests.

Applying this knowledge to silviculture: Our work has immediate application for the development and testing of regeneration methods in natural forests. We have long-term plots monitoring regeneration performance in experimental canopy openings that are intended to test hypotheses concerning forest resilience in relation to disturbance and site productivity. We have used the information gleaned from seedling regeneration ecology to start a series of sequential studies with collaborators on site reforestation. Much of this information has been summarized in two seminal textbooks on silviculture and agroforestry.

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Tropical Forest Restoration

Mark Ashton
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Twenty years of experimental work, chiefly in Sri Lanka and Panama, have provided the basis for the development of a framework for tropical rain forest restoration. This framework uses seven ecological principles for understanding the integrity of tropical rain forest dynamics. These principles are: (i) site productivity inherently changes across landscapes at differing scales driven primarily by soil water availability and soil nutrition; (ii) disturbances are variable in severity, type and extent across topography; (iii) disturbances provide the simultaneous initiation and/or release of a new forest stand; (iv) disturbances are non-lethal to the groundstory vegetation; (v) guild diversity (habitat diversity) is largely dependent upon "advance regeneration"; (vi) the majority of "advance regeneration" species

are site restricted; and (vii) tree canopy stratification is based on both “static” and “dynamic” processes. These principles are applied to determine effects of two rain forest degradation processes that have been characterized as chronic (continuous detrimental impacts) and acute (one-time impacts). Chronic impacts are sub-lethal and can be divided into those that affect forest structure and composition from the bottom up and those that are top down. Acute impacts can be divided into those that are lethal to forest structure and those that transcend structure and affect inherent site function.

Restoration pathways are suggested that range from low to high input silvicultural techniques that match differing levels of degradation. In order of management intensity these are: (i) simple prevention of disturbance to promote release of rain forest succession; (ii) site specific enrichment planting protocols for late-seral tree and shrub species; (iii) sequential amelioration of arrested fern and grasslands by use of plantation analogs of old-field pine, to facilitate secondary succession of rain forest and plantings of late-seral site-restricted tree species; and (iv) site stabilization, establishment and release of successional compatible mixed-species plantations. I summarize with a synthesis of restoration techniques used for native species reforestation.

Tropical Forest Silviculture/Regeneration

Mark Ashton
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Sustainable forest management first requires a social platform of stability in property rights, and interest in long term land investment. I will first discuss these issues in relation to South and Southeast Asia. Then, using general ecological principles for rain forest management I will summarize application to the development of silvicultural systems across complex intra and inter stand scale gradients within mixed dipterocarp forest (MDF) of the Sinharaja region, Sri Lanka. Examples will be given of irregular and uniform shelter woods with different use of reserves and age-class structures to accommodate a variety of social values. Such systems will be compared to the widescale practice of selective logging. An example of a midslope MDF silvicultural treatment will illustrate complementary products and services within a single stand and over a silvicultural cycle. A financial analysis will be used to compare stacked values through Net Present Value analysis of the MDF stand with a similar stand converted and cultivated for tea. Tea has been used for comparison because it is the one product that has the highest and best use on private land in the region.

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Independent Student Projects

Rhett D. Harrison
Research Institute for Humanity and Nature, Japan



Mark Ashton talking about forest restoration, using experiments conducted in pine plantation as examples.



An animated Mark Ashton telling stories of tea plantation and home garden.



Students and staff chilling out at the top of Mt. Moulawella after a long hike.



The 'rich developers' presenting their ideas on managing and utilising land resources in sustainable manner.



Students working hard on their independent projects and presenting their findings at the end of the course.



All rest and relax at the Ranweli Ecotourist resort, before bidding farewell to IFBC-2006 and Sri Lanka.

EXCURSION REPORTS

Perahera Festival at Kandy, 7 August 2006

Harvey John D. Garcia, Cynthia Hong-Wa, and Simon Jiun-Nan Huang

THE WAY TO KANDY

A PART OF THE INTERNATIONAL FIELD BIOLOGY COURSE 2006, other than the interesting scientific lectures and practicals, and the adventurous fieldwork, was the excursions. This served as a portal to the culture of Sri Lanka and enabled us to partake of the tremendous diversity of environments it has to offer. The first stop of this excursion was the hill capital of Kandy.

We left Sinharaja and its majestic wet forest early in the morning of 7 August 2006, traveling the winding roads of Sri Lanka. This was the first noticeable character of this island country; apparently there are few straight roads. Our first pit stop was Ratnapura Rest House, a historic old colonial building that doubled as a quaint restaurant atop a hill serving a most sumptuous breakfast.

We arrived at Kandy at about 3 o'clock in the afternoon and stayed at the Hotel Casamara. Some participants got some shut-eye but most preferred to walk around the fascinating streets of Kandy and hunt for bargains. Before the Perahera some lady participants dressed up in a Sari, an exquisite textile draped around the body, to grace the event. The actual Esala Perahera parade started at the gates of the Temple of the Tooth. Thanks to our hosts, we were able to get some of the limited seats at the Queens court, near the start of the procession.

A BRIEF HISTORY

The Perahera, the most splendid ceremony in Sri Lanka, takes place every August for two weeks in the city of Kandy. Through its current manifestation, the Perahera reveals a folklore that is full of significance and with a deep respect for tradition. The origin of Perahera dates back to the fourth century when the Tooth Relic of the Buddha was brought to Sri Lanka. In the 13th or 14th century, King Megavanna decreed that the Tooth Relic of the Buddha, which was also the symbol of sovereignty, should be brought out for a public homage in a perahera (procession) once a year. This ritual was reaffirmed in the 18th century during the reign of King Kirthi Sri Rajasinha of Kandy. The actual meaning of the Kandy Perahera has transcended the centuries. The ritual is marked by the procession of four major devalas. First, the Natha devala opens the ceremony, and then comes the procession from the temple of Vishnu, followed by the devalas of Skanka and Pattini. The beauty of the Perahera, which is perhaps one of the most spectacular pageants in Southeast Asia, has made Kandy a principal tourist attraction.

SPECTACLE OF THE PARADE

The Perahera started with the cracking of whips followed by dancers that twirling flaming batons. Kandyans participating in the parade were of all ages, from child flame dancers that melodiously danced to old men beating parade music with their "Bera" (drums). The climax of the flame dance was the Kandyans that performed on 8-ft stilts continually twirling a ring of fire!

Other dancers wore metals jackets, fascinating headdresses and jingling bells (Fig. 1). There were also disk tossers that whirled ceramic disks in the air using a long bow, catching them

by hand on the way down. The music of "Bera" and "Horana" (flutes) was infectious to the point that you want to join the parade. Although the ethnic dances are fantastic, the Perahera is most famous for the dressed elephants that parade through the streets in lighted costumes almost covering their entire bodies and carrying men in costumes with effigies symbolizing kings and generals. In between the dancers, acrobats and elephants were religious representatives carrying the colors of their monastery.



FIGURE 1. The flamboyantly dressed dancers perform their best movement all night long



FIGURE 2. Brilliantly decorated elephants parading the tooth relics

The climax of the event was when the effigy of the tooth relic was paraded atop of a stunning elephant (Fig. 2). From our vantage point, Sri Lankans and tourists alike were captivated by the whole event which was as amazingly spiritual, as it was a grandiose festival. We left our stands at about half past ten, overwhelmed and grateful that we were able to experience this part of Sri Lankan culture. Our faces were flushed from the heat of the copra used to light the parade, and our hearts were a flame from the warmth of the smiling Kandyans in the parade.

Visit to Minneriya National Park, 8 August 2006

Nurfazliza bt. Kamarulbahrin and Raghunandan K. L.

MINNERIYA NATIONAL PARK LOCATED NEAR POLONNARUWA in the north central province. The park is dominated by the Minneriya tank, a reservoir 249 km² in extent. The forest surrounding the reservoir is the home for many species of flora and fauna that benefit from increased availability of water. It is especially important for wild elephants (*Elephas maximus*).

On the afternoon of 8 August, we arrived at the park. We were warmly welcomed by Mr. Chitrasena, the officer in-charge, while Dr. R. Sukumar, an expert on elephants briefed us on the behaviour of elephants and the observations to be made in the field. About 97 percent of male elephants in Sri Lanka do not have tusks; as opposed to India where a majority of male elephants have tusk. This has resulted in a more even sex ratio in Sri Lanka as compared to India. In Sri Lanka the ratio is one male to three females, while in India it is approximated 1:20, as a result of ivory poaching.



A herd of elephants near Minneriya reservoir

The identification characters of male and female elephants were explained to us. For males, the rear view looks like a 'V' shape, while in females it is a 'W' shape. Usually, adult male elephants are solitary and female elephants will be in a family group. One can estimate age by height. The calf at birth will be 3 ft, by 1 yr 4 ft, and 2 yr 5 ft (juveniles). At 15 yr in age a female will be 7 ft and a male will be 8 ft in height. Normally, male elephants have a faster growth rate compared with females. Musculature development is better in male elephants and forehead is smoother, whereas in females it is tipped. Elephants at the Minneriya National Park congregate during the dry season, when water in the reservoir has receded. During this season there is an abundance of fresh grass with >10 percent protein is high in the vicinity of reservoir. However, nutrients available in this grass are lower compared with woody species inside forest. Elephants also congregate to socialize and for mating. Male elephants in 'musk' are called 'makahanas' and can be very aggressive. This can be recognized from a weeping gland on the temple. During this time, risk of charging or attack is higher.



'Makahana' in search of female in estrous



A solitary 'makahana'



Female elephant with its calf

As we moved into the park we came across several herds and identified the sexes and ages of the elephants. When we arrived at the reservoir area we observed one huge solitary male moving towards the herds that were grazing on the grasses near the reservoir. Here was a herd of 15 elephants out of which five were juveniles. The makahana visited this herd in search of a female in estrous. Later we had an opportunity to see a large herd close by, with approximately 39 adult elephants and four juveniles around 1-2 yr old. The solitary makahana was moving from one herd to other smelling the urine of the female elephants. Male elephants in 'musk' use this to test for females in estrous.

We saw nearly 200 elephants with 50 juveniles in the park. While the observing elephants in the reservoir and surrounding area, we saw many interesting birds and there was big herd of wild buffalos in the reservoir.

On the way back, we witnessed a herd of elephants charging towards one of our vehicles. It was amazing experience to observe the behavior and habits of wild elephants. We were grateful for the opportunity to observe the harmony of the elephant's world at Minneriya National Park.

Primate Ecology and Behavior at Polonnaruwa Ruins, 10 August 2006

Agung Sedayu, Siriya Sripanomyom, and Yoshiko Yazawa

POLONNARUWA RUINS AND THE SURROUNDING DRY EVERGREEN FORESTS are an important habitat for four co-existing primates, including Slender Loris, Toque Macaque, Hanuman Langur and Purple-faced Langur. We visited the area on 10 August 2006 and were given practical exercise on primate behavioral observation by Dr. W. P. J. Dittus, who has been studying these primates for over twenty years. The objective of the practical was to record home range use, activity budget, forest layer use, diet, and interspecific interaction.

We were divided into six groups with two groups following each species. Each student followed a focal individual, which were all previously habituated by Dr. Dittus and his research assistances (Fig. 1). We followed the primates for approximately five hours. We calculated home range use, activity budget, forest layer use, diet, and interspecific interactions were summarized the field practical. Finally, we had a nice conclusion at Dr. Dittus's house by the Polonnaruwa Tank, playing cricket before nightfall.



FIGURE 1. Taking notes of focal primates behavior.

From the practical, we found that the three diurnal primate species interact, but each species showed niche partitioning in their activity budget, food preference and forest layer use. Toque Macaque (*Macaca sinica*) was the most active among the three species, consumed widest range of food items, including garbage, and occupied ground layer of the forest most of the time (Fig. 2). Hanuman Langur (*Semnopithecus entellus*) allocated its time almost equally between active and inactive states; diet constituted mostly of ripe fruits and mixture of young leaf and mature leaf,

and it occupied all strata of forest evenly. Purple-faced Langur (*Trachypithecus vetulus*) was more inactive during the day, spent most time in the emergent layer and canopy of the forest, and fed mostly on young leaves. It was evident that even though there was partially overlap in activities, forest layer occupancy and food items, the three primates showed distinctive niche partitioning, thus minimizing their interspecific competition.



FIGURE 2. Activity budget of *M. sinica*, mostly on the ground.

For the beginners who are inexperienced with primate behavior observation, this field practical was a really hard work, especially with the Toque Macaque when the focal individual stays in the troop and continued foraging. We had to record behaviors at one minute intervals. Overall work requires patience and perseverance, also keen eyes to identify details of what the primates are doing and what they are eating at the different canopy layers. Dr. Dittus' long-term research has been extremely valuable in raising our knowledge and understanding of the way primates behave toward their environment, including their competitors which is a prerequisite for facilitating effective conservation plan development.

The Ancient City of Polonnaruwa, 10 August 2006

Vijay Palavai and Lindsay Banin

THE RUINS OF THE MEDIEVAL CAPITAL CITY, POLONNARUWA, lie in the north central Province of Sri Lanka, covering an area of approximately 122 ha. The oldest structures date back to the 11th century, decreasing in age to the first quarter of the 13th century AD. The city owes its diversity in architecture to the complex history of Sinhalese and Indian occupation. In the 1980's the ruins of Polonnaruwa were dedicated the 66th World Heritage Site. Beyond the city ruins, the landscape of the region is dotted with reservoirs of varying size that supported the local populations and sustained a strong agrarian economy in the area. The largest of the tanks is a result of the amalgamation of three smaller tanks, known as the Sea of Parakrama (or Parakrama Samudra) after King Parakramabahu I who commissioned the work.

Archeological evidence suggests that early inhabitation of the area dates back to the second century BC. In the first millennium AD, Polonnaruwa (known then as kandavuru-nuvara, or the 'camp city') served as a fortified outpost to protect the older city of Anuradhapura because of its optimal location near river crossings. By the 10th century, King Rajaraja I had invaded and established Chola rule in Anuradhapura and Polonnaruwa, which was subsequently renamed Jananatha Mangalam. Hindu monuments proliferate from this occupation, and a further Indian occupation in the 13th century.

The Sinhalese regained control of the city under the rule of King Vijayabahu I in 1055, resulting in the resurgence of Buddhism and its associated architecture. In particular, Vijayabahu encouraged a new influx of monks from Burma and went to great efforts to establish and restore buildings housing monastic activities. He also commissioned the oldest of the Tooth Relic temples, Atadage.

Vijayabahu's reign ended in 1110, and was followed by an unsettled period, with several contenders competing for the throne, until the commencement of Parakramabahu I's industrious rule in 1153. The impressive ruins of Parakramabahu's palace can be seen. Two stories have been conserved, but some estimate that in its intact state, it would have stood seven stories high. Gaps in the brick wall indicate where huge beams would have formed the structure of the building, and the original plasterwork can still be seen on many areas of the brickwork. It has been suggested that the series of small rooms on the ground floor served as guardrooms and storerooms and that the second floor would have housed the King's family. The audience hall of Parakramabahu, situated a little to the west of the palace, is a classic example of an ancient royal council chamber.

Parakramabahu was also responsible for the building of the monastic university, Alahana Parivena, to the north of the city. The university site extends over eighty hectares. The Lankatilaka image house occupies a central position in the complex, and is one of the most impressive of the edifices at Polonnaruwa. The immense brick building houses a 40-ft Bhudda statue and the best conserved walls at the entrance of the building give an idea of the intact height of the building. The external walls are decorated with Hindu-influenced stucco architectural models. Rankot Vehera "the Golden Pinnacle" is the largest stupa in Polonnaruwa, built in the tradition of the Mahavihara stupas of early Anuradhapura. The stupa rests on a square paved platform surrounded by a wide sand path and provided with entrances at the cardinal points and roadways leading to them. The northern

monastery (Uttarama) encompasses the Galvihara, colossal depictions of Bhudda cut from rock and in the various poses (Fig. 1): the seated meditation pose; seated Bhudda surrounded by paintings of deities and flanked by Brahma and Vishnu; the final passing away of Bhudda and; a controversial depiction of a standing Bhudda. Some argue that the latter depicts Ananda, the attendant of the Bhudda, in a lamenting pose, mourning the Bhudda's death. Others contend that this figure also depicts Bhudda displaying sympathy for suffering or the Bhuddas still period after Enlightenment when he spent seven days gazing at the tree under which he became Bhudda.

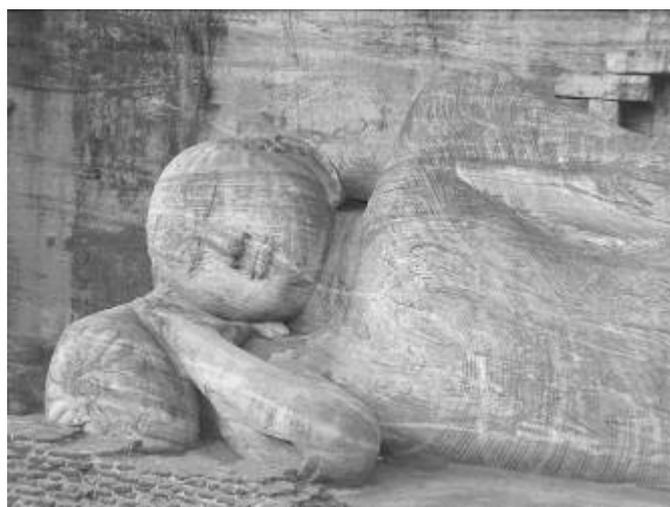


FIGURE 1. Bhudda image at Galvihara.

Nissankamalla (12th century) followed in the foot-steps of Parakramabahu and embellished the city with a variety of monuments, the vestiges of which exhibit even today the grandeur that was Polonnaruwa. The most obvious example is Vatadage, a circular stupa surrounded by four seated Bhudda images and a series of terraces, which is particularly ornate (Fig. 2). Another inspired architectural achievement of King Nissankamalla is the royal council chamber, with inscriptions on the pillars indicating the seats allocated to each minister, and the Lion Throne of Nissankamalla. The Nissankalatamandapa is a unique structure, with pillars simulating a lotus stalk with the flower as the capital. An inscription attributes this charming edifice to Nissankamalla, and relates how the king used to listen to recitals of the Buddhist scriptures there. Hatadage, another tooth relic temple built during his time, encompasses a standing statue on the ground floor and the tooth relic would have been enshrined on the upper floor. King Nissankamalla also had a keen appreciation of nature and commissioned an inscription (known as Prethidanamandaya), encouraging others to think in a similar way. Some important recreational sites also came out of the period of his reign. The Dipuyyana or Promontory Garden of Nissankamalla is located between the citadel and the lake. The ruins of two baths, one for swimming and the other a shallow pool, are particularly interesting.



FIGURE 2. The Vatadage.

In the 13th century, Polonnaruwa came under Indian control with Pandyan King Kulasekaran (1273-1293). He was responsible for the building of Siva Devale (shrine) No. 1, dedicated to Siva, the god of dance. The most notable feature is the centre-piece of the inner sanctum - the symbolic stonework of lingum and yoni. Lingum is the phallus or male symbol which is encapsulated by yoni, a pit representing the female, fertility and energy respectively. This is one of the many ruins of temples reflecting typical South Indian architecture.

The above discussion refers only to a selection of the extensive ruins which make Polonnaruwa well worthy of its conservation status. The site is particularly interesting and valuable because of its unique blend of Sinhalese and Indian architectural influence, reflecting the legacy of two intertwining cultures.

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Journey to the Ancient Tanks of Sri Lanka

Chun Liang Liu, Ruthairat Songchan, and Ruliyana Susanti

DURING THE SIX DAYS EXCURSION, WE ENJOY THE BEAUTY OF SEVERAL TANKS in Kandy and Polonnaruwa districts. First, we visit Kandy Lake, this is a small tank located near Sri Dalada Maligawa Temple in the middle of Kandy city. Second, we visited Minneriya tank (Fig. 1A, B), a reservoir in Minneriya National Park, Polonnaruwa district and support for a variety of waterfowl, elephant and other wild animals, besides of being immerse socio-economic value. Minneriya tank was created by the famous tank builder and monk-baiter Mahasena. Next on our agenda were Giritale and Parakrama Samudra tanks at Polonnaruwa (Fig. 1C, D). Actually these two tanks form one big tank joined by a narrow neck, and we enjoy their beauty from the two different parts of the tank.

In Sri Lanka, there are more than 12,000 small tanks scattered throughout the dry zone. The existence of tanks is highly linked with dry zone community. Climate in the dry zone, which has a long period of drought altering with brief monsoonal deluges, made the use of irrigation, based on the storage of water, necessary for the regular cultivation of wet fields.

The small tank system has contributed to food production and environmental conservation with a multitude of social benefits to the villagers. These tanks form a series of water bodies along small water courses in cascading systems. They

have been designed so that water is repeatedly put into use to counteract irregularities of rainfall, non availability of large catchment areas and the difficulty in constructing large reservoirs. The water supplies of tanks are from rainfall and catchments runoff. This system is closely related with the farming system in the dry zone area, characterized by crop cultivation under water stress conditions, the "gangoda" (home garden), "chena" (shifting cultivation) and "welyaya" (lowland).

It was interesting to explore the history of tanks or wewas in Sinhalese. First, we have to go back to the earliest day of Sinhalese settlement in the third century BC, when the first farmers dammed rivers and stored water in small village reservoirs. Sri Lanka's kings then began to take an active role in the construction of the irrigation schemes, leading to the creation of the three tanks which now surround Anuradhapura. The first major irrigation works were undertaken in the reign of Vasabha (65-110), who is said to have created twelve irrigation canals and eleven tanks, the largest with a circumference of three kilometers. Soon afterwards, Sinhalese engineers mastered the technology which allowed water in tanks to be stored until needed, then released through sluice gates and channeled through canals to distant fields.



FIGURE 1. (A) Elephants at Minneriya tank, Polonnaruwa. (B) A cormorant at Minneriya tank, Polonnaruwa. (C) Sunset at Giritale tank, Polonnaruwa. (D) Enjoying ourselves at Giritale tank, Polonnaruwa

The first giant reservoirs were constructed in reign of Mahasena (274-301), who oversaw the construction of some sixteen major tanks, including the vast Minneriya tank, and Dhatusena (455-473), who constructed Jaya Ganga canals that are almost 90 km long and maintain a subtle gradient of six inches to a mile, delivering water to Anuradhapura from the huge Kalawewa tank. Further tanks and canals were built during to the reigns of Moggallana II (513-551), whose Padaviya tank in the northern Vavuniya district was the largest ever constructed in ancient Sri Lanka, and Aggabodhi II (604-614), who was responsible for the tank at Giritale, amongst other works. Large new irrigation projects in the Anuradhapura region virtually ceased after the seventh century, and although the simple maintenance of the tanks and canals already built must have been a huge task, the entire system appears to have worked smoothly for the next three centuries until the final collapse of Anuradhapura in the year 993.

The construction of large-scale irrigation works became a defining feature of these Sinhalese civilizations: the maintenance of such massive hydraulic feats required skilled engineering and a highly evolved bureaucracy and also encouraged the development of centralized control and a hierarchical social structure. The captured waters allowed a second rice crop to be grown each year, as well as additional vegetables and pulses, all of which supported much higher population densities than would otherwise have been the case. The surplus agricultural produce created by large-scale irrigation and the taxes raised from the system were major sources of royal revenue, allowing expansive building works at home and military campaigns overseas. Parakramabahu I, who famously declared that “not one drop of water must flow into the ocean without serving the purpose of man”, oversaw the

creation of the vast Parakrama Samudra tank at Polonnaruwa, one of the last but finest monuments to Sinhalese irrigation.

Behind the beauty and benefit of tanks, there are some concerns about the future existence of tanks. Good management systems, clear policies and sustainable utilization of tanks are required.

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Royal Botanic Gardens Peradeniya, 11 August 2006

Harsha K. Sathischandra, Kanistha Husjumnong, and Shirley Xiaobi Dong

AFTER THE GLORIOUS VISIT TO POLONNARUWA, we arrived at Peradeniya Botanical Gardens on 11 August 2006. As we entered the Royal Botanical Gardens from its main gate, we were all enthralled on seeing the picturesque landscape. Mr. Danasekara, the deputy director for the Royal Botanical Gardens, warmly welcomed us and accompanied us to the different sections of the garden, introducing several of its components.



Great variety of orchids at the Orchid House

The Royal Botanic Gardens date as far back as 1371 when King Wickramabahu III ascended the throne and kept court at Peradeniya near the Mahaweli river. Later, in the reign of King Kirti Sri from 1747 - 1780, King Rajadhi Rajasinghe resided therein, where a temporary residence was erected for him. A vihare and dagaba were built in the reign of King Wimala Dhamma and improved by Kind Rajadhi Rajasinghe, but were destroyed by the English when they occupied Kandy in 1815. The famous historical battle of Gannoruwa (1685) between Rajasinghe II and the Portuguese was fought on the Northern side

of the river just across from the gardens. A priest resided here on until the Gardens were formed by Mr. Alexandar Moon in 1821, six years after the final conquest of the Kandyan Kingdom.

The setting-up of the Gardens was initiated by clearing the south west portion of the garden, where western fruits and vegetables were grown., Later, exotic crops such as coffee, tea, nutmeg, rubber and cinchona, all of which later became important to the island's economy, were introduced. Since its establishment, successive superintendents made great efforts to bring the garden to the presence status.

Today the garden covers almost 150 acres and with a bewildering variety of local and foreign tree species. There are around ten thousand trees in the garden, which are categorized in to distinct sections such as the orchid house, spice garden, Japanese garden, Royal palm garden, Great Circle and so on. The northern half of the gardens has an altogether wilder quality and the trees here are home to enormous population of fruit bats, which form squabbling clusters in the branches overhead. Following the bank of the Mahavali Gaga one often sees troupes of Macaque monkeys.



Lush greenery at the Peradeniya Royal Botanical Gardens

The final part of our tour was a visit to the National Herbarium, which has a marvelous collection of watercolour illustrations Sri Lankan ferns, shrubs, and trees, and most of countries plant specimens are stored here. Our knowledge was refreshed during the visit. Royal Botanic Gardens ultimate goals are research and interpretation, of the native floral diversity, conservation, and tourism.

Trekking at Horton Plains, 12 August 2006

Dwi Tyaningsih Adriyanti, Inoka Manori Ambagahaduwa, and Min Sheng Khoo

AFTER THE VISIT TO PERADENIYA BOTANICAL GARDEN ON 11 AUGUST, the group traveled to Ohiya for an overnight stay. The arduous six-hour car-ride up the winding, bumpy road was considered worthwhile as we were to visit Horton Plains the next morning. At the lodge, we were treated with a sumptuous dinner, and some of us took a walk around the railway town of Ohiya to enjoy cool evening breeze. Fortunately, we were back to the lodge early enough to avoid contact with some unexpected (and semi-naked) visitors from the Sri Lankan Navy trainees, who disturbed the sleep of a few male participants by asking for clothes!

Nevertheless, the visit to Horton Plains was still a very enjoyable one. Horton Plains is a large (more than 3000 ha), high elevation (ranges from 1800 m to 2300 m) plateau, with fascinating landscapes and interesting assemblages of flora and fauna. Two main ecosystems are found on this highest plateau of Sri Lanka. Upper montane rainforests covers the rolling hills and upper slopes of Horton Plains, while an equal extent of grasslands are seen in the valley and lower slopes. These ecosystems are vital as the watershed for several tributaries that feed major rivers like Mahaweli, Kelani, and Walawe.

We were guided by Dr. Hashendra Kathriarachchi, one of the course observers and also a biologist who are very familiar with the natural history of Horton Plains. From the entrance, we walked along a 9-km circular track that leads around the Plains. The path first cut through rolling open grasslands dotted with tussock or clump grass and brilliant red flowers of *Rhododendron* bushes. Some of the grasslands were potato farms back in the 1950's. These areas are now represented as patches of carpet grass.



Unique aquatic and grassland habitats found along the stream

Dissecting the grasslands are numerous meandering streams and pools, which provide unique aquatic habitat to many interesting water plants. The pink flowers of *Ketatiya (Aponogeton jacobsenii)* were often seen sticking out above the water like a string of fish eggs, while the Dwarf Bamboo (*Arundinaria densifolia*) grows gregariously along the streamside. This endemic bamboo is the smallest in Sri Lanka and apparently the young leaves are eaten by Sambur deers (*Cervus unicolor*). These deer were seen from the bus before we entered the park, but not

along the track. However, footprints of these animals were seen on the muddy track.

At many points along the track we were able to see clear profile of the grassland soil. The topmost layer is generally black because of the accumulation of humus. This layer, due to its high organic content, is also most susceptible to the fires that frequent these grasslands. It is understood that such fire would sometimes spread underground within this layer and reemerge at a quite distant site from the origin!



Trekking the misty and undulating terrain of Horton Plains

The montane forest of Horton Plains is interesting in its own right. Unlike most other montane forests in Asia, where trees of the family Fagaceae (Oak and Chestnut) contribute most to the floristic composition, the forest here is dominated by Lauraceae and Myrtaceae (mainly *Syzygium* spp.). Also, the transition from grassland to forest is so abrupt that one would imagine someone has just cut away trees along the forest fringe. This, however, may be an indication that the forest does not colonize the grasslands.

Along the forest fringe, patches of the forests were seen dead but standing. Some were killed by grassland fire mentioned above, as charred tree trunks were evident among them, while some by unknown reasons. Changing weather patterns, contrasting temperatures, clearing of the forests on the lower slopes and a reduction in the water table are said to be possible causes of such phenomenon, which termed 'Forest Die Back', but nothing has been established conclusively.

Soon after we entered the forest, we were able to hear the sound of Baker's falls clearly. The view at the falls was simply breath-taking that most of us became so engrossed in taking pictures, without paying much attention to our guide! However, the small and slippery platform beside the falls has no railing, and that worried us when we tried to pack onto that platform for taking group photos. Fortunately nothing bad happened because we held so tightly together (as we love each other that much)!

The Big and Small World's Ends were the next highlights after Baker's falls. From these points, one can, supposedly, look down a sheer drop of about 2000 m to the lowlands. But, we were too late to enjoy the stupendous scenery, as mist that built up

after late morning obscured the view. Nevertheless we still enjoyed ourselves with plenty of photo-taking and snacks. The sea of cloud is simply an amazing view from the World's Ends, and we were quite tempted to jump onto it as if it was a comfortable bed (especially after a tiring walk and filling food).

The tranquility of the countryside along our return journey was greatly disturbed by groups of youngsters who were shouting and singing. We chose to stay quiet and pardon their ignorance. The increasingly heavy rain further decreased the ambient temperature and adding to the discomfort of our exhausted bodies. Nevertheless, we were soon out of the park and found ourselves on the way back to the lodge, and then Sinharaja.

The visit, despite short, gave us a good understanding on the montane ecosystems of Horton Plains, and was simply an enjoyable and unforgettable experience! The beautiful image of green grassy hills, punctuated with wind-battered vegetation and sparkling water bodies, will be on the back of our memory for a long time.

GROUP PROJECTS

Composition of Insect Communities in the Domatia of *Humboldtia laurifolia* (Fabaceae) along an Elevation Gradient

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ABSTRACT

The interaction between *Humboldtia laurifolia* and the insect communities occupying the domatia was studied. The association was sampled at three different elevations of Sinharaja rain forest, Sri Lanka. Different species were present in the domatia at different elevations. Moreover, the level of herbivory decreased with increasing elevation. *Humboldtia laurifolia* is largely restricted to ridges.

Key words: *Humboldtia laurifolia*; domatia; ants; earthworm.

THE INTERACTIONS BETWEEN PLANTS AND HERBIVORES are key determinants of community structure worldwide. Their role is particularly important in lowland tropical rain forests where rates of herbivory are higher, plants are better defended chemically and physically, and herbivores have more specialized diets (Coley 1998). Most plant-herbivore studies have demonstrated that young leaves are preferred over mature leaves, and that the majority of lifetime damage occurs during the first month after opening (Aide 1993). Plants inhabited by ants (myrmecophytes) have evolved in a diversity of tropical plant lineages (Davies *et al.* 2001). Certain interactions between ants and plants can be classified as mutualisms, with benefit accruing to both members. The plant provides a source of energy, either as solid food or as nectar, and sometimes a domicile, such as a hollow stem (or a stem capable of being made hollow by the ants) or hollow stipular thorns. A number of plants throughout the world have entered into facultative or obligate mutualistic relationships with ants, taking advantage of the insect's ability to protect its territory by repelling the intruders. The plants have evolved numerous methods to domicile the ants, and provide food supply throughout the year or at temporary nectaries. The ants provide the plant with defense against herbivory and vine overgrowth (Risch *et al.* 1981). Ants may be obligate and restricted to one part of the plant, or a single species may attract many generalist ant species (Krombein 1999).

Humboldtia laurifolia (Fabaceae) is a common understorey tree in lowland and upland forests of Sri Lanka. However, it is distributed most frequently along ridges. It is a myrmecophyte, but also attracts a diversity of other animal life to its domatia. The internodes in *Humboldtia laurifolia* are inflated, hollow cavities that provide nesting sites for ant colonies. In addition to collapse of the central pith against the inner walls of the cavity, a slit like opening develops at the top of the hollow internodes, which allows access for any organism small enough to fit through. The tree also has numerous extra floral nectaries. In this mutualistic arrangement some of the ant species protect the foliage and flower buds from herbivory. The internodes not occupied by the ant colonies may nest solitary or sub-social wasps and bees, as well as other invertebrates (Krombein 1999).

In this study we hypothesized that: (1) the species composition of domatia inhabitants changes along an elevation

gradient; and (2) the level of herbivory would vary with different domatia inhabitants and decrease with increasing elevation.

METHODS

We sampled *Humboldtia laurifolia* at various elevations at Sinharaja forest. Similar sized plants were selected for sampling. Three samples each of older and younger domatia were sampled for presence of organisms on the same plant. The domatia were removed and carefully opened longitudinally from the internodes entrance. Care was taken to cut open the hollow internodes chamber without damaging the organisms inside. The cut internodes were collected in vials of alcohol for identification of the contents in laboratory. The percent herbivory on younger and older leaves were also recorded. In addition, stem diameter, height and elevation of the plants were noted. Ten samples were sampled at three different elevations.

The data were analyzed using R 2.3.1. The results were tested with Welch Two Sample t-test to compare the abundance of different species in the domatia, and herbivory along the elevation gradient was analyzed using linear regression.

RESULTS

A total of 90 samples were collected at different elevations. The number of species inhabiting domatia was highest in the younger domatia along the ridge. We found four species of ants, an earthworm, and a beetle larva nesting the domatia on the ridge.

TABLE 1. *Species recorded in domatia of Humboldtia laurifolia along elevation.*

Elevation (m)	Species in domatia
490-505	<i>Tapinoma</i> (Sub-family: Dolichordine),
516-520	<i>Tapinoma</i> (Sub-family: Dolichordine), <i>Camponodus</i> sp
562-564	<i>Camponotus</i> sp.1, <i>Camponotus</i> sp.2, <i>Camponotus</i> sp.3, (Order: Formicidae), Beetle larvae (Order: Coleoptera), earthworm

The abundance of inhabitants in domatia was compared using Welch two-sample t-test, and was found to be marginally significant. ($P = 0.07231$). There was a significant decrease in herbivory with increasing elevation (Fig. 1).

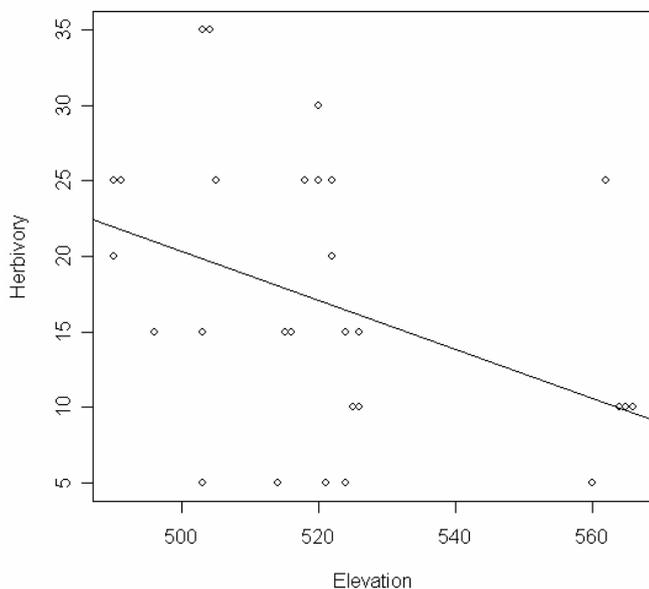


FIGURE 1. Linear regression between elevation and herbivory (Linear model R-squared: 0.1436, $P = 0.02220$).

DISCUSSION

There was a clear relationship between the elevation and herbivory in *Humboldtia laurifolia*. Herbivory on the leaves was higher on plants from slope sites, when compared with plants on the ridge. The domatia inhabitants also changed with elevation, with an increase in the number of species, particularly ant species, occupying domatia of plants from ridge sites.

Herbivory damage was also higher on younger leaves. Coley (1998) has shown that, in contrast to the temperate zone, most of the herbivory in the tropics occurs on the ephemeral young leaves (>70%), which requires herbivores to have finely tuned to host finding abilities. The decrease in herbivory found on the ridge may be explained by the fact that the domatia are occupied by different ant species. This suggests that *Humboldtia laurifolia*'s restricted distribution may be a consequence of the variable outcome of the interaction with its domatia inhabitants.

ACKNOWLEDGMENTS

We would like to extend heartfelt thanks to Dr. Rhett Harrison and Dr. David Lohman, for their advice and encouragement. We are thankful to Mr. Tennakkon for assisting in field. Thank you also Ms. Nihara for identification of species.

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Determinants of the Distribution of Water Striders in Different Stream Microhabitats

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ABSTRACT

Water striders are insects living on the surface of water, and they have adaptations to this specialized environment. Our objective was to test whether the body size of water striders was related to stream microhabitat. Two line-transects with three sampling points over 150 m were made for collection in different streams. All water striders found at each sampling point were collected. We measured the length of body and legs. Our results show that Water striders living in faster current were significantly larger than those living in slow current microhabitats.

Key words: water striders; Gerridae; Veliidae; microhabitat.

WATER STRIDERS OR POND SKATERS ARE INSECTS WITH A SPECIALIZED LIFE STYLE. They live on the surface film of water (Hill & Abang, 2005). All water striders are members of the order Hemiptera, and there are three families of insect known as water striders: Gerridae, the true water striders; Veliidae, broad-shouldered water striders and Hydrometridae; the water measurers (Carver *et al.* 1991; Castner 2004).

Water striders have adaptations to the specialized environment. Gerridae have long legs and are slender, and the middle leg originates closer to the hind leg than to the front leg. Veliidae have shorter legs, the proximal half of body is wider than the tapering distal half, and the front tarsi have a cleft with claws arising before the tips. Hydrometridae have long slender bodies and legs, a long slender head, that is equal in length to the thorax, and bulging eyes that arise from sides of head.

The objective of this study was to test whether the body shape of water striders is related to stream microhabitats. Our hypothesis was that bigger water striders would be found in faster water, because they should be better able to move over the current.

METHODS

STUDY SITE.—This experiment was conducted in two small streams located near the field station at Sinharaja World Heritage Site, Sri Lanka. The first stream was a rocky stream, while the other had a sandy substrate at the bottom.

METHODS.—A line-transect with three sampling points over 150 m was establish in each stream. Paired collections from fast and slow moving water were made at each point. The distance between each sampling point was 50 m. All water striders found at each sampling point were collected using dip nets, preserved in 95% alcohol and brought to the laboratory for measurement. The parameters measured were length of the body and the three legs on the right side of body. Data were analyzed using R.

RESULTS

From this study we were able to collect six species of Gerridae and one species of Veliidae (Fig. 1).

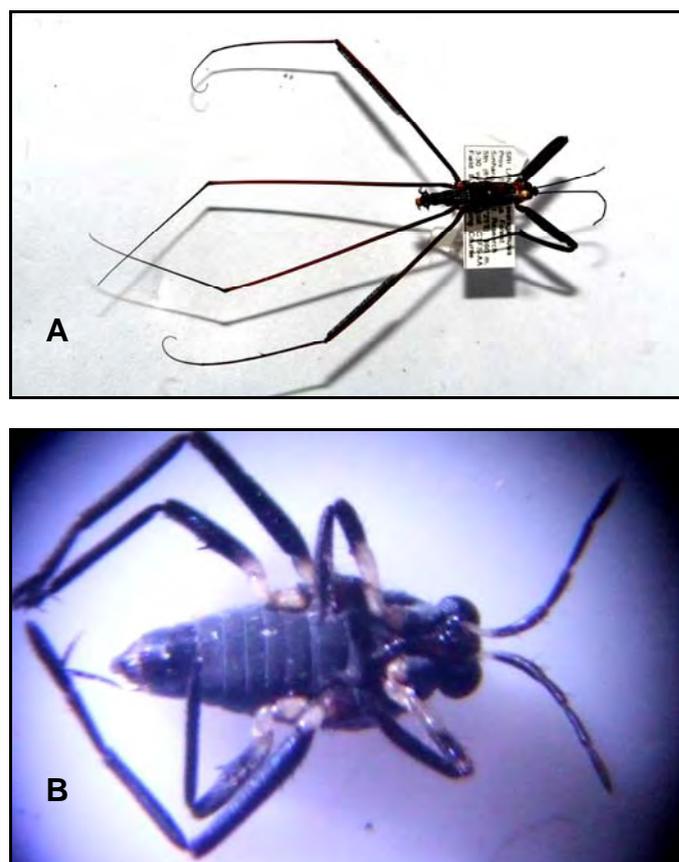


FIGURE 1. Water striders found in fast and slow current (A) Gerridae and (B) Veliidae.

We compared the body size of water striders in different habitats (Table 1). Wilcox test showed a significant association between body size and habitat ($W=1726$, $P < 0.001$).

TABLE 1. *Summary of measurement of water strider data and habitat.*

Habitat	Mean Body length	SD	Number of sample
Fast water	0.886	0.718	50
Slow water	0.352	0.162	45

Result from the cluster analysis incorporating all the body measurements (Fig. 2) illustrates that two groups separate according to the body size. First group was the “Slow” group consists of small sized of water striders, while second group is the “Fast” group consisting of larger individuals.

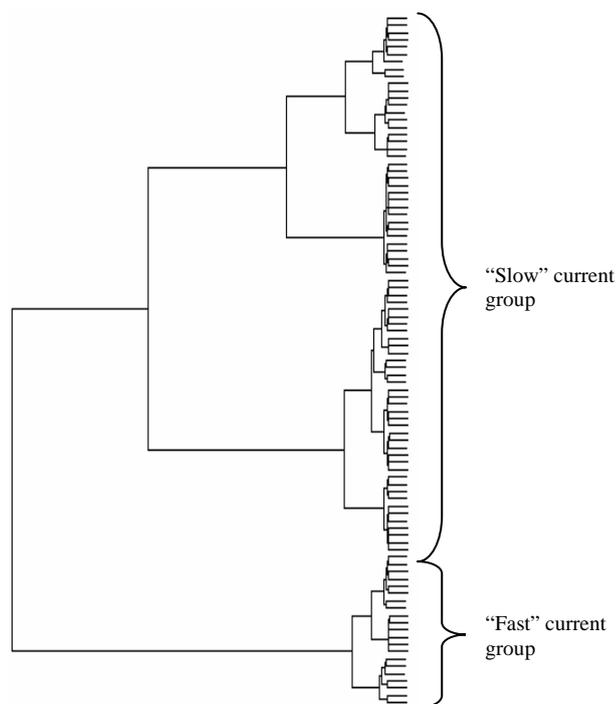


FIGURE 2. Cluster tree based on body size of different microhabitat.

DISCUSSION

The differences in body size of water striders living in fast and slow current are perhaps related with the ability to move over the water. In this study we found that the same species with different body sized occupied different microhabitats. This suggests water striders develop their ability to adapt to faster currents as they grow.

The result from this study supported our hypothesis, but because we did not have information on the behavior or life history of water striders, we are not able to explain the mechanism fully. Future study with more observations on the

morphology and behavioral ecology would help explain this phenomenon.

ACKNOWLEDGMENTS

We would like to say our deepest gratitude to Dr. R. D. Harrison, Prof. Nimal & Savi Gunatileke, Dr. Cam Webb, Ms. Luan, and all technicians, for all your help to us while finishing this project. Sincerely thank for all our friends on this field course.

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Relationship between Pitcher Size and Prey Size in *Nepenthes distillatoria* (Nepenthaceae)

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ABSTRACT

Nepenthes distillatoria is an endemic species occurring in Sinharaja Forest. The size of the pitchers varies greatly suggesting that they target different kinds of insect. We investigated the relationship between the size of the pitcher and the size of insect prey, and the relationship between the pitcher size and height above the ground. From thirty samples, pitcher size varied from 7.2 mm to 38.2 mm diameter (mean 26.4 ± 10.0 mm). The prey in pitchers varied from the smallest at 3 mm in length to 36 mm (mean 9.7 ± 0.8 mm). The height above the ground of pitchers varied from 0 cm – 160.5 cm (mean 36.2 ± 43.8 cm). Smaller pitchers and larger pitchers were found on the ground or at lower levels, while the medium sized pitchers tended to occupy all levels. Maximum body length of prey was positively correlated with pitcher size. The results supported our hypothesis, that larger pitchers catch the bigger prey.

PITCHER PLANTS (*NEPENTHES*) OCCUR IN THE MOIST EASTERN TROPICS from Madagascar and Seychelles, to northern Australia and New Guinea, and all the way down to the Caroline Islands. In Sri Lanka, including Sinharaja Forest Reserve, only a single endemic species, *Nepenthes distillatoria*, occurs. *Nepenthes* prefers exposed habitats, on nutrient poor soils and occur from 0 m to 3400 m above sea level. The occurrence of *Nepenthes* in these habitats is attributed to its carnivorous habit (Adam *et al.* 1992). *Nepenthes distillatoria*, as in other species of *Nepenthes*, lures insects by means of glandular secretions at the base of the pitcher and the bright pitcher and rim color. The prey are subsequently digested by enzymes in the pitcher and absorbed to fulfill the nutritional needs of the plant (Amaratunga 1987).

In *N. distillatoria*, the size of the pitchers varies greatly suggesting that different pitchers target different kinds of insect. We investigated the relationship between the size of the pitcher and the size of insect prey, and the relationship between the pitcher size and the height above the ground.

MATERIALS AND METHODS

This study was conducted at the field research station, Sinharaja Forest Reserve. The pitchers sampled were located along the former logging trails. Data collection was conducted on 6 August 2006. Thirty different pitchers of *N. distillatoria* were selected. The width, height above the ground and volume of each pitcher were measured. Insect prey in the pitchers were collected and subsequently measured for maximum body length in the laboratory.

The relationship between size (width) of pitcher and pitcher's height above ground and between size (width) of pitcher and maximum body length of prey were examined using R (2.3.1).

RESULTS

From thirty sampled pitcher size varied from 7.2 mm diameter to 38.2 mm diameter (mean 26.4 ± 10.0 mm). The prey in pitchers varied in size from the smallest, an ant, at 3 mm in length to a stick insect at 36 mm (mean 9.7 ± 0.8 mm). The height of pitchers varied from 0 cm to 160.5 cm (mean 36.2 ± 43.8 cm) above the ground. Smaller pitchers and larger pitchers were found on the ground or at lower levels, while the medium pitchers tended to occupy different heights above the ground (Fig. 1). Maximum body length of prey was positively correlated with size (width) of pitchers ($R^2 = 0.49$; $P < 0.0001$) (Fig. 2).

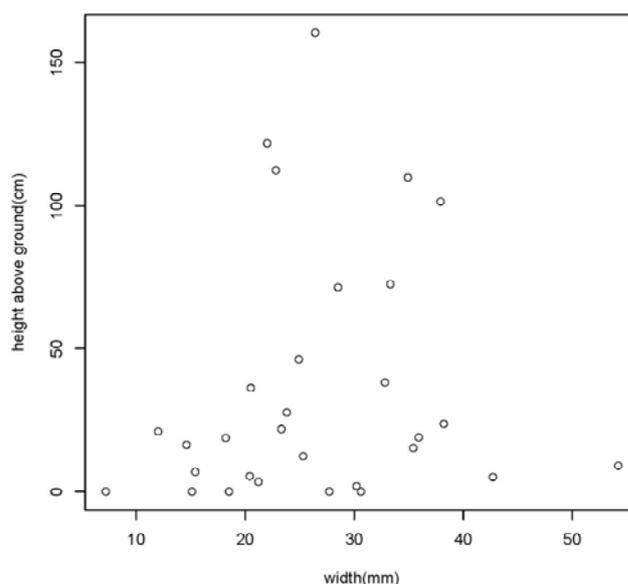


FIGURE 1. Relationship between pitcher width and height above the ground in *Nepenthes distillatoria*.

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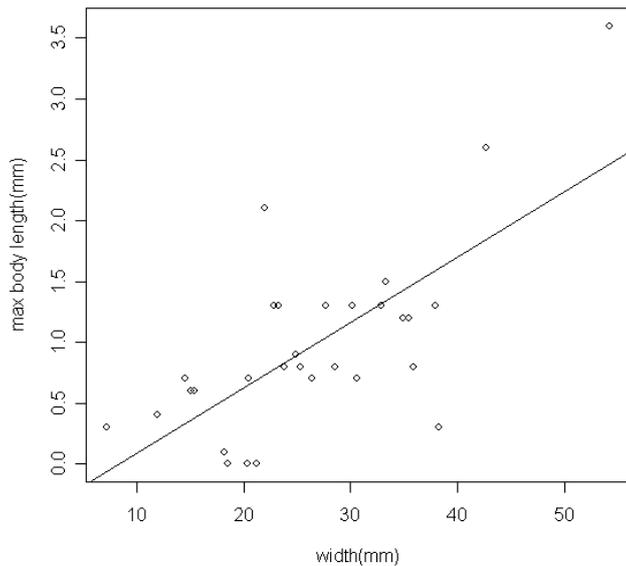


FIGURE 2. Relationship between pitcher width and prey maximum body length in *Nepenthes distillatoria*.

DISCUSSION

It is expected that the bigger pitchers would occur on the ground due to their weight when full of liquid. However, the fact that most of the smaller pitchers were also found on the ground was a surprise. The smallest pitchers may target terrestrial prey, but this requires further testing. The other interesting thing found in this study was the very large variation in pitcher size in *Nepenthes distillatoria*. For example, in the same area where two individuals occurred just 5 m apart, we found the smallest pitcher was only 7.2 mm in diameter, compared to a neighbor at 21.2 mm in diameter.

The largest prey found was a stick insect (Order Phasmatodea) at 3.6 cm in length, and was inside the biggest pitcher sampled. Phasmatodea are herbivorous insects. Thus, the nectar lures secreted the pitchers are effective even for larger herbivorous insects. We observed ants feeding on nectar at the pitchers. Thus these extra floral nectaries may be part of ant-plant mutualism for plant defense or a pitcher lure that the ants have usurped.

ACKNOWLEDGMENTS

We would like to express our sincere gratitude to Dr. Rhett D. Harrison, Dr. David Lohman and Ms Luan Keng Wang for their advice and supervision. We wish to give our sincere thanks to Dr. I. A. U. Nimal and Dr. C. V. Savi Gunatilleke, all resource staff for their encouragement and help. Thank you also to all our friends who had helped and encouraged us throughout the course.

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What Factors Affect the Abundance of Leeches (*Haemadipsa zeylanica*) on Forest Trails?

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ABSTRACT

Along with the diversity of fauna, Sinharaja has an intriguing abundance of land leeches, *Haemadipsa zeylanica*. This phenomenon could be due to high rainfall and the abundance of mammals in the forest. This study was aimed to understand the abundance of leeches along two forest trails, which show different degree of human utilization. The weather was very hot and dry on the day we collected data, and hence our observations were fewer than expected. However, the trail with greater numbers of visitors had fewer leeches. Possibly visitors carry leeches away. There were no significant correlations between body temperature, trail temperature, trail humidity as well as light intensity and the abundance of leeches, probably as a result of the poor sample size.

SINHARAJA WORLD HERITAGE SITE, LOCATED IN THE SOUTH-WEST LOWLAND WET ZONE OF SRI LANKA, has a high diversity of flora and fauna, of which many are endemic to the island (Bambaradeniya *et al.* 2006). Along with the richness of fauna, Sinharaja has an intriguing abundance of land leeches, *Haemadipsa zeylanica* (Baker 1937). This phenomenon could be due to high rainfall and the abundance of mammals (*e.g.*, wild boar, barking deer, and mouse-deer) in the forest. Despite their high abundance and the inconvenience caused to forest visitors, little study had been made of these animals.

hypothesized that people with a higher body temperature would be more attractive to leeches.

MATERIALS AND METHODS

This study was carried out near the Forest Research Station at Sinharaja. Two forest trails of different degree of human usage were selected. Trail A, which leads to the CTFS Forest Dynamic Plot, is narrower and less utilized than trail B, which leads to the Giant Nawada tree, a frequent tourist destination. Hundred meter point transects were laid out along both trails, and six points were marked out along each transect at an interval of 20 m.



FIGURE 1. Without proper protection, one of the participants became victim to the Sinharajan leeches.

In this study, we aimed to understand the abundance of leeches along two forest trails, which show different degrees of human utilization. We hypothesized that there should be more leeches found on the trail with more human usage, as the leeches are attracted to human visitors. Also, we investigated if there was any preference of leeches for different human subjects. Baker (1937) noted that if a petrol lantern was put on the ground during the night, it would attract leeches. We assumed that leeches are attracted to the heat emitted by the petrol lantern. Therefore, we

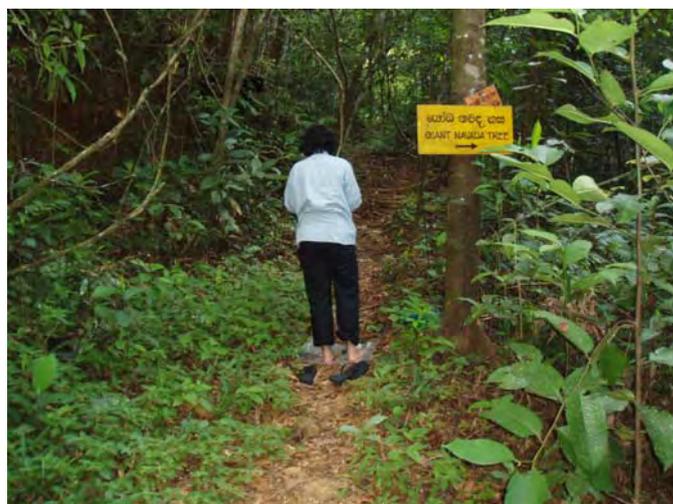


FIGURE 2. One of the 'leech-bait', Dwi, working on Trail A

Three human observers were used as 'leech-bait' in this study. Each subject walked the transects twice, and stood on a 0.5 m x 0.5 m clear polythene sheet for five minutes at each sampling point. All leeches observed moving towards the observer were counted, and the time for each leech to reach the polythene sheet was recorded. Body temperature of the observers, as well as light

intensity, humidity, ambient temperature and average crawling speed of the leeches were also recorded.

R 2.3.1 was used to analyze the results, by using Wilcoxon test and Generalized Linear Model.

RESULTS

Wilcoxon rank sum test with continuity correction indicated a significant difference the numbers of leeches observed on each trail ($W = 568.5$, $P = 0.02939$; Table 1).

There was no significant correlation between body temperatures and leech abundance (Table 2). Likewise, there were no significant correlations between the leech abundance and the three environmental variables recorded (Table 3).

TABLE 1. *Difference in leech abundance between trail A and trail B (N = 30 per trail), W = 568.5, P = 0.02939.*

Trail	Abundance	Mean
A	18	0.6
B	3	0.1

TABLE 2. *Mean leeches per sample point in relation to observers' body temperature; Linear Model, estimate of coefficients = 1.924, P = 0.3368.*

Trail	Observer	Mean body temperature (°F)	Mean leeches per sighting
A	Dwi (N=9)	96.07	0.22
	Inoka (N=9)	97.48	0.56
	Ming (N=12)	96.09	0.67
B	Dwi (N=9)	94.87	0.00
	Inoka (N=9)	97.43	0.22
	Ming (N=12)	96.43	0.33

TABLE 3. *Correlations between number of leeches and human/environmental factors (Generalized Linear Model, family = Poisson)*

Factor	Estimate of coefficients	Standard error	z value	p-value
Body temperature	0.2410	0.1987	1.213	0.225
Trail temperature	-0.5257	0.5336	-0.985	0.324
Trail humidity	-0.0492	0.1053	-0.467	0.640
Light intensity	0.0005	0.0005	1.011	0.312

DISCUSSION

It was unfortunately a very hot day when this study was conducted, which resulted in very few sightings of leeches. However we still found significantly more leeches on lesser used trail, which was contrary to our prediction. This may be due to the fact that visitors carry leeches away. There were no significant correlations between body temperature, trail temperature, trail humidity as well as light intensity and the abundance of leeches, probably due to our small sample sizes, resulting from the dry conditions. Therefore, we have to reject our hypothesis that humans with higher body temperature are more attractive to leeches.

ACKNOWLEDGMENTS

We would like to express our gratitude to CTFS-AA for organizing and facilitating this field course, especially to R. D. Harrison and other teaching staff for their kind support and useful suggestion. Thanks to all friends who helped and gave fun throughout the course.

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Does Leaf Anatomy Explain Distribution Patterns in *Mesua ferrea* and *Mesua nagassarium* (Clusiaceae) in Sinharaja Rain Forest, Sri Lanka?

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ABSTRACT

Two related species, *Mesua ferrea* and *Mesua nagassarium* show distinct spatial patterning in Sinharaja rain forest, Sri Lanka. *Mesua nagassarium* occupies ridge tops and upper slopes, whilst *Mesua ferrea* is found on low lying land close to streams. One proposed explanation for this apparent pattern is that trees on the upper slopes are more subject to periodic water stress. We tested whether leaf anatomical traits support this hypothesis. Leaves were sampled from a range of size classes for each species at two heights in the tree crown. Leaf area and specific leaf area (SLA) were measured, and stomatal density and size characterised. *Mesua nagassarium* leaves were found to be much smaller in area and stomatal density was lower than the leaves of *M. ferrea*, but SLA was significantly lower for *M. nagassarium* and stomata size did not apparently vary between the species. These results provide mixed evidence in support of *M. nagassarium* leaves being better adapted to drought. Therefore, it is not possible to conclude that the spatial distribution in the two species is the result of *M. nagassarium* being better adapted, with respect to leaf anatomy, to cope with periodic drought.

Key words: leaf; anatomy; adaptation; drought; *Mesua nagassarium*; *Mesua ferrea*; spatial distribution; niche differentiation.

SINHARAJA RAIN FOREST HAS STRONG RELIEF and it has been observed that a number of species show preferences as to their topographic position. These observations have been qualified by the mapping of all trees ≥ 1 cm in a 25-ha plot. In particular, *Mesua ferrea* and *M. nagassarium*, display distinct habitat preferences. The species' local distributions overlap very little, with *M. ferrea* confined to low-elevation valley locations while *M. nagassarium* occupies higher topographic positions (Gunatilleke *et al.* 2004). Soil texture covaries with topography, such that soils on upper slope positions are much sandier in texture than the clayey soils found on lower slopes near water courses. One proposed hypothesis to explain the spatial pattern recorded is that individuals on the upper slopes are subject to periodic drought. Although the annual precipitation is high, averaging at over 5000 mm/yr, and there is no notable dry season, the forest can still be subject to short periods without rainfall. On the upper slopes drought is exacerbated by the freely draining, shallower soils (Gunatilleke *et al.* 2004). Differences in plant anatomical adaptations may explain the habitat preferences, as plant physiology (associated to anatomy) in part determines its propensity to survive in a given habitat (Turner 2001).

There are a number of key traits one might expect to observe if a plant is adapted to withstand water stress. Typically, in water stressed environments, leaves are smaller to enhance cooling as a result of greater air turbulence around each leaf, which reduces the necessity for water loss through transpirative cooling. Leaves tend to be thicker, often with thick or waxy cutaneous layer. Stomata are often deep-set and density and size are reduced to further minimise transpiration losses (Ashton & Berlyn 1992). If some of these traits are apparent in *M. nagassarium* and not *M. ferrea*, this may explain the distinct differentiation in habitat preference. The hypothesis we wish to test is that leaves of *M. nagassarium* display evidence of adaptation to water stress, including leaf size, thickness and stomatal characteristics that is not represented in *M. ferrea*.

METHODS

Mesua ferrea and *M. nagassarium* occupy different slope positions in the Sinharaja rain forest. Individuals were identified within two 30 m x 30 m survey areas, located at downslope and upslope positions to capture individuals from both species as they do not coexist. Light environments were observed to be reasonably similar between the two environments. A total of 200 leaves were sampled. For each species, leaf specimens were taken from five individuals within three sizes, as determined by diameter at breast height (DBH). The three size classes were: 1-4 cm DBH, 5-9 cm DBH, and 10-14 cm DBH. For the first size class, crowns were very shallow and so leaves were sampled at only one height. For the two larger size classes, leaves were sampled using a pruner or tree climber at two heights; the first at the bottom of the crown and the second at the middle of the crown. A visual estimate of the height of sampling was recorded. To reduce size variation associated to leaf age and position, the first four mature leaves from the apex were sampled. Leaves were taken from the upslope side of the tree. This controlled for some effects of varying light availability associated to slope.

Leaf areas were calculated and leaves were weighed. From these measurements, specific leaf area (SLA) was calculated (weight/area). The effect of species on SLA was investigated using a Generalized Linear Model (GLM). Measurement height and tree diameter were included in the model. A Wilcoxon Rank Sum test was used to confirm results as errors were not normally distributed.

Leaf undersides were examined under the microscope to make a comparison of stomatal density. To control for area, a constant field of view was maintained and number of stomata were counted. To compare stomata size, photographs were taken through the microscope using constant magnification and field of view.

RESULTS

Leaves of both species are lanceolate in shape, with an entire margin and pinnate venation. The most readily observable difference is that of area. *Mesua nagassarium* leaves are much smaller than *M. ferrea* leaves (Fig. 1).

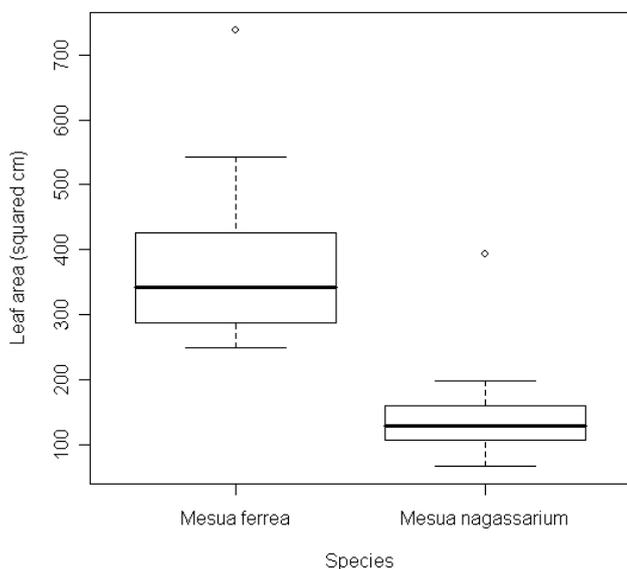


FIGURE 1. Comparison of leaf area of *Mesua ferrea* and *Mesua nagassarium*.

A GLM analysis was performed to investigate SLA as a function of species, tree diameter and measurement height. At the 5% significance level, any effect of height was deemed to be due to chance ($P = 0.3234$). The effect of diameter was marginally significant ($P = 0.0462$), while the effect of species on SLA was highly significant ($P = 3.69 \times 10^{-10}$) such that leaves of *M. nagassarium* are thinner than those of *M. ferrea*. A Shapiro-Wilk test was used to test normality of errors of the model and the errors were found to be significantly different from normal ($P = 0.001139$). A Wilcoxon Rank Sum test was performed to check the findings of the GLM, and the rank means of SLA for the two species were again found to be significantly different ($P = 2.527 \times 10^{-11}$).

Leaves of both species were examined under the microscope. The limited sample size did not permit any statistical analyses, but Fig. 2 shows the general observations of the investigation. The circles demarcate the stomata and it can be seen that *M. nagassarium* leaves have fewer stomata than those of *M. ferrea*. No difference in stomata size could readily be observed. Leaf cross-sections also demonstrated that *M. ferrea* leaves had a much thicker cuticle than *M. nagassarium* specimens.

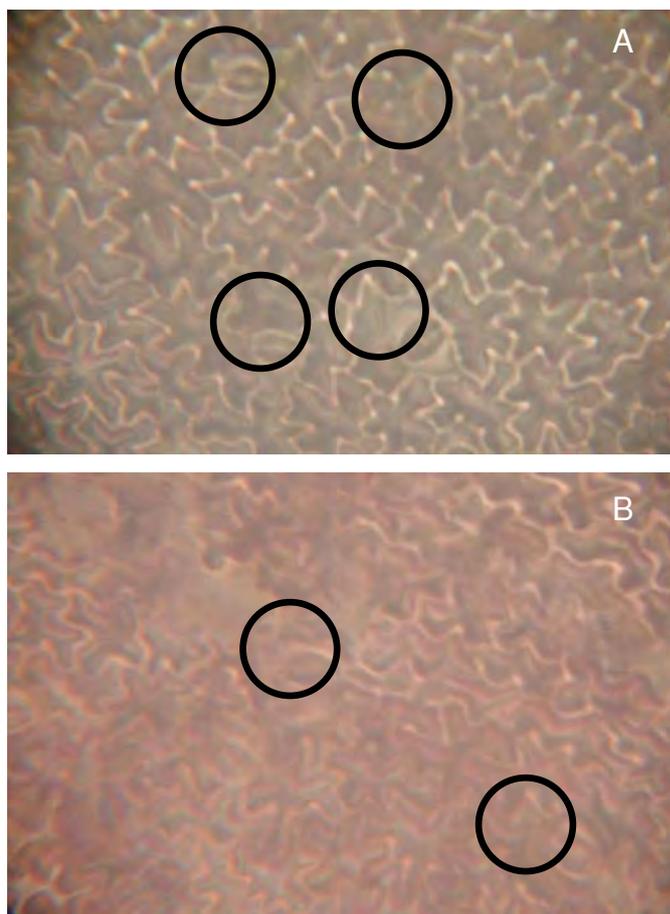


FIGURE 2. (A) Stomata of *Mesua ferrea* leaf. (B) Stomata of *Mesua nagassarium* leaf.

DISCUSSION

In both species, there was no significant trend in specific leaf area with canopy position. There was, however, a significant, positive effect of tree diameter on SLA, which may be the result of leaves thickening with tree age.

As predicted by our hypothesis, *M. nagassarium* displayed some characteristics of adaptation to drought when compared to *M. ferrea*. Firstly, the leaves of *M. nagassarium* were smaller and had fewer stomata than *M. ferrea* leaves. However, stomata were not clearly different in size between the two species. Contrary to our predictions, *M. nagassarium* leaves were significantly thinner than *M. ferrea*, as indicated by the SLA analyses. The expectation, based on previous plant physiological studies, is that leaves should be thicker in the more drought adapted species (Turner 2001). In this respect, our hypothesis that *M. nagassarium* leaves are better adapted to drought was not conclusive. Furthermore, *M. ferrea* has a much thicker cuticle than *M. nagassarium* whereas you might reasonably expect this difference to be in the other direction if *M. nagassarium* leaves were displaying adaptation to water stress. Clearly, there is not enough evidence to accept or reject the hypothesis that *M. nagassarium* leaves display more adaptation to water stress. It would be interesting to examine the change in leaf morphology in the field over a topographical gradient, particularly at locations where the species coexist (though these zones are limited). It would also be useful to apply controlled treatments of water availability to investigate the potential for phenotypic plasticity in

each species. Some studies of leaf processes, such as photosynthetic and transpiration rates, would enhance morphological comparisons (Ashton & Berlyn 1992). Finally, leaves are not the only organs of the plant that determine its success in different environments. For example, root design or below- versus above-ground allocation may explain the niche differentiation between sites.

ACKNOWLEDGMENTS

We wish to thank the organizers of the CTFS International Field Biology Course 2006 for the opportunity to study in the Sinharaja forest, for their support and input on the project. We would also like to extend special thanks to Ratnayke and Januke for their effort in the field and to Savi Gunatilleke for aiding us with the microscope work.

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Variation in Pitcher Size and Prey Items in *Nepenthes distillatoria* (Nepenthaceae) between Two Microhabitats at Sinharaja, Sri Lanka

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ABSTRACT

Nepenthes distillatoria is the only species of pitcher plant in Sinharaja. The diameter and length of pitcher were found to depend on habitat, suggesting that environmental factors cause a difference in pitcher allometry between habitats. We investigated whether this was related to prey capture.

Key words: *Nepenthes distillatoria*; pitcher plant; environmental factors.

PITCHER PLANTS LOCALLY KNOWN AS “BANDURA”, family Nepenthaceae, are creepers on shrubs and small trees. The leaf tip is modified to form an elongated sac (a pitcher) filled with liquid, which traps and digests mostly insect prey. Secretion glands inside the pitcher produce the fluids and enzymes that drown and digest the trapped insects. The plant obtains its protein by this method.

Nepenthes are restricted to the tropical areas of the world. (Adam *et al.* 1992). Sinharaja has only one species of pitcher plant *Nepenthes distillatoria* L. (Forestry Extension & Education Division, 2002). There is a large variation in pitcher morphology, even within sunny or shady microhabitats, and little is understood of the factors causing this variation. We therefore examined the major environmental factors affecting pitcher morphology in both sunny and shady microhabitats.

METHODS

STUDY SITE.—Our study site was at Sinharaja World Heritage Site, Sri Lanka. Field work was conducted on 6 August 2006.

FIELD COLLECTION.—Thirty mature pitchers were collected from two microhabitats - sunny and shady areas. The environmental conditions, such as percent crown cover, soil character and forest

type, were noted. The preys in the pitchers were identified in the laboratory. The length and diameter of all pitchers were measured.

DATA ANALYSIS.—Student’s T test was used to compare the length and diameter, between the two microhabitats.

RESULTS

PREY FOUND IN THE PITCHERS.—We collected prey from the pitchers in sunny and shady areas (Table 1). In both habitats, the majority of prey was ants (>90% of prey). In the sunny area, we found a slug. In the shady area we also found bees and spiders.

There was no significant difference in prey abundance between habitats.

DIAMETER OF PITCHERS.—The difference in the diameter of pitchers between sunny and shady area was significant (Fig. 1, $t = -6.2562$, $df = 51.57$, $P < 0.0001$).

LENGTH OF PITCHERS.—The difference of length of pitchers between sunny and shady area was significant (Fig. 2, $t = -4.6557$, $df = 52.64$, $P < 0.0001$).

TABLE 1. *Prey in pitchers.*

	Number of individuals	
	Sunny	Shady
Insecta		
Coleoptera	Family Histeridae (beetles) = 3	Family Histeridae (beetles) = 6 Family Curculionidae = 2
Hymenoptera	Suborder Apocrita (ants) Family Formicidae = 260	Sub Order Apocrita (ants), Family Formicidae = 240 Sub Order Apocrita (bees), Family Mutillidae = 4
Others	Mollusca (slug) = 1	Class Arachnida, Family Heteropodidae (spiders) = 2

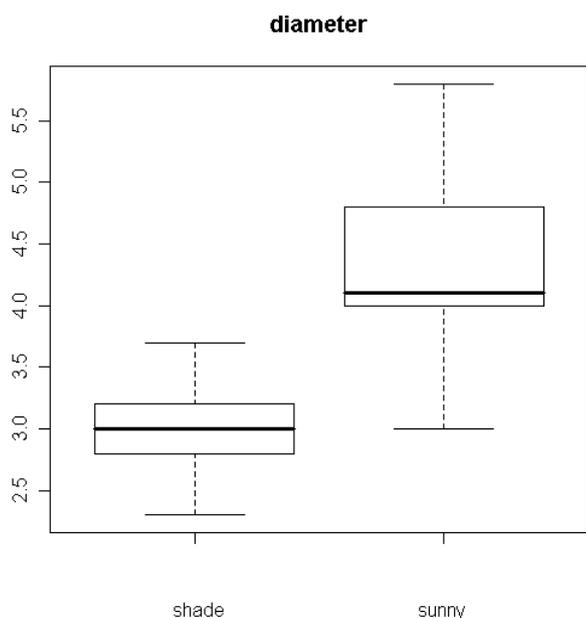


FIGURE 1. Boxplot of pitcher diameter (cm) of *Nepenthes distillatoria* in sunny and shady habitats at Sinharaja.

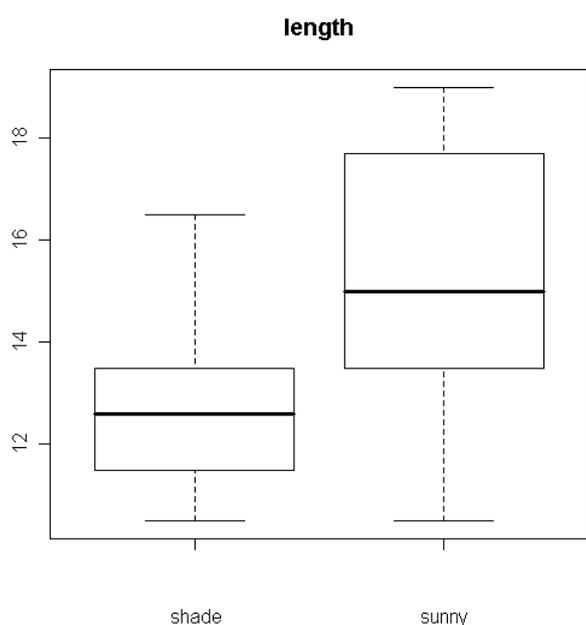


FIGURE 2. Boxplot of pitcher length (cm) of *Nepenthes distillatoria* in sunny and shady habitats at Sinharaja.

DISCUSSION

Most prey were ants (>90%) in both habitats because ants feeding on nectarines around the pitcher rim often fall into the fluid. There was no significant difference in prey abundance between habitats. (Table 1). Both the diameter and length of the pitchers increased in sunny areas so we conclude this difference in pitcher size resulted from increased light intensity. In the future, one could test other environmental factors that might affect pitcher size, such as soil nutrients and humidity. However, as there was no significant difference in prey abundance or type, we conclude this change in pitcher size was not related to prey capture.

ACKNOWLEDGMENTS

We would like to extend our heartfelt gratitude to all resource staff who gave their time to advice our group. Also thank you to CTFS-AA for the chance to join the International Biology Field Course 2006.

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Web Structure and Efficiency of Prey Capture in *Nephila maculata* (Tetragnathidae)

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ABSTRACT

A web building spider such as *Nephila maculata* relies on its web to capture prey for its sustenance. Although it is expected that the size of the web is correlated to the size of the spider, we were interested in knowing whether the spider size, and therefore the web size, is a factor determining the success of the prey capture. Our objectives were to confirm the positive relationship between spider size and web size and to assess the effects of different variables, such as interstrand distance or web height, on the prey capture. Regression analyses were carried out and the results showed that web size varied positively with spider size, while prey size was inversely correlated to web height. The distance between the strands did not show significant correlation with prey size. The majority of prey belonged to the order Coleoptera, suggesting that the efficiency of the prey capture depends not only on the spider characteristics, but also on the biology of the prey. Most Coleoptera fly near ground level.

Key words: *Nephila maculata*; spider size; web size; prey capture efficiency.

SPIDERS, WITH A CURRENT 5,000 DESCRIBED SPECIES, are one of the most diverse arthropod groups, and are widespread and abundant in many terrestrial habitats. Spiders play an important role in terrestrial ecosystem as both prey and predators. *Nephila maculata* (Tetragnathidae), an orb-web spider, has a wide distribution occurring from Asia to Africa (Hill & Abang 2005). In Sinharaja, it is a common species. The female is bigger than the male and its size ranges from 1 cm to 4 cm from juvenile to adult stage. It has a colorful and bright body pattern that functions to attract pollinator species, an adaptation that enhances its ability to capture prey. Prey capture is also highly dependent on web site, web size and stochastic effects. In this study, we addressed the question of whether the prey capture efficiency is positively correlated with spider size, and whether web height influences the success of prey capture. Our hypotheses were that there would be a positive relationship between web structure and spider size, and that prey size and abundance would depend on web size and web height.



FIGURE 1. A *Nephila maculata* on its web.

METHODS

STUDY SITE.—The study was done at Sinharaja World Heritage Site, a rain forest in southwest of Sri Lanka, on 6 August 2006. The sample areas were distributed along the road to the field station. Shrubs, the edges of tea plantations, and forest edge habitats were sampled.

Individual spiders were identified and measured for body length (anterior tip of head to posterior tip of abdomen) using Vernier calipers. The height of the web was taken from the center of the web. Using a tape, web diameter was measured four times at 90° intervals and the mean was calculated. The mean strand spacing was taken at mid level from center of the web to the edge. This was done by taking a digital photograph of the web against a diameter tape. The strand length was measured using PHOTO IMPACT ver. 8, ten measurements were taken and the mean strand spacing was calculated. The sampling area was then tagged for prey observation.

Prey observation involved visiting the webs every hour to check for prey. This was done because *N. maculata* disposes of the remains of its prey after feeding. If there were prey present, they were identified and prey length was taken. In cases where there were no measurable prey present indicators such as wings, head and other chitinous parts were considered as presence of a prey.

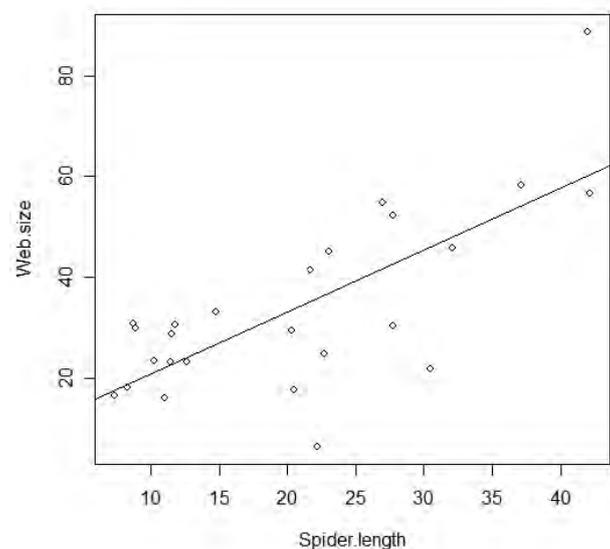
All statistical analyses were executed with the R program. Response variables were tested for normality with the Shapiro-Wilk statistic. Relationships between spider size considered as the predictor variable and other parameters such as web size, inter-strand distance were assessed. Web size and the height of the web were also predicted to affect the number and especially the size of the prey. Regression analyses were performed with the generalized linear model procedure.

RESULTS

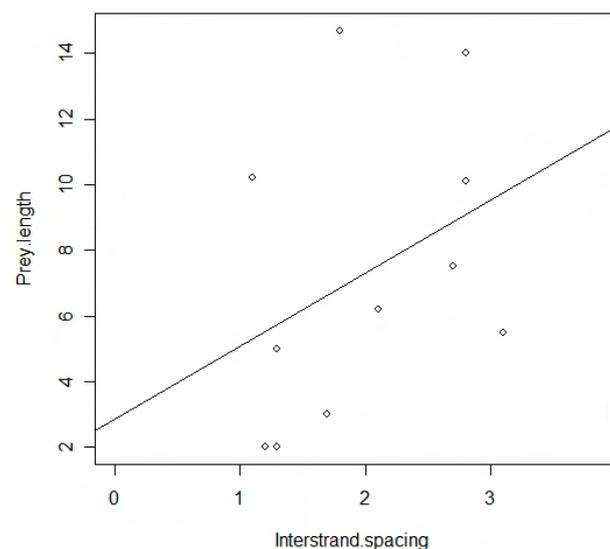
Prey found on the spider web belonged to four insect orders. Over half identified individuals were Coleoptera (Table 1).

The relationship between spider size and web size showed a significant positive correlation (Fig. 2A). Although the relationship between strand spacing and prey length tended to display a positive correlation, this relationship was not significant (Fig. 2B).

Prey size was also found to be negatively correlated with the height of the web (Fig. 3A). Relationship between web size and number of prey was tested but the result was not significant (Fig. 3B).



A

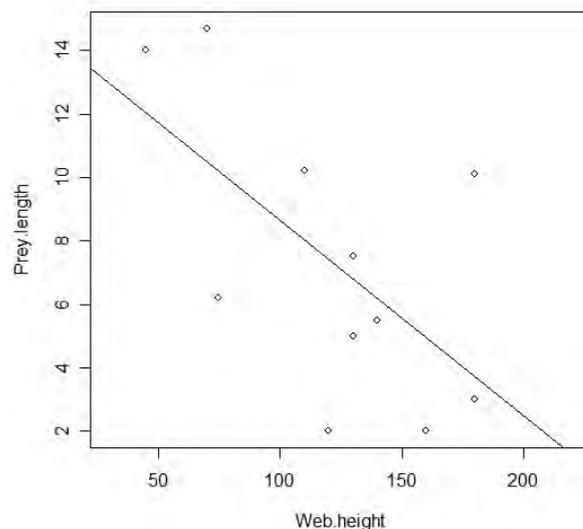


B

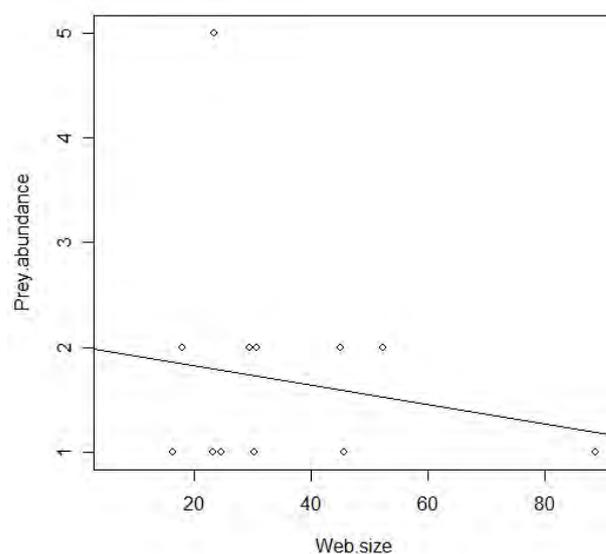
FIGURE 2. Relationship between: A) spider length and web size (adjusted $r^2 = 0.508$, $P < 0.0001$); B) interstrand spacing and prey length (adjusted $r^2 = 0.04$, $P = 0.259$).

TABLE 1. *Insect prey found on spider web.*

Order	Number
Coleoptera	6
Diptera	1
Hemiptera	2
Lepidoptera	2
Unidentified	6



A



B

FIGURE 3. Regression analysis for: A) web height and prey size (adjusted $r^2 = 0.303$, $P = 0.045$); B) web size and prey number (adjusted $r^2 = -0.061$, $P = 0.591$).

DISCUSSION

Our results show that big spiders tend to have larger webs, possibly to increase prey capture efficiency. However, neither the number of prey captured nor prey size increased with web size, suggesting that strategically large webs were not more efficient than smaller ones. This may be because they become too obvious to potential prey. However, the height of the web seems to be a factor in prey capture efficiency. Most preys were found at medium heights, between 70 cm and 180 cm. In summary, the success of prey capture in *N. maculata* was found to be maximized only at mid-level webs for all variables tested.

Coleoptera constituted the majority of prey. There are about 300,000 species of described beetles species in the world. They occur in almost all habitats and are found at high density especially inside the forest. Most species are phytophagous and saprophagous, which may explain their abundance just above ground and their frequency in spider webs.

ACKNOWLEDGMENTS

We would like to thank Rhett Harrison and David Lohman for their comments on the subject. We are also grateful to all those who contributed to the success of this course.

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INDEPENDENT PROJECTS

Role of Habitat and Diversity in Determining the Susceptibility of Primary Forest at Sinharaja World Heritage Site, Sri Lanka to Invasion by *Clidemia hirta* (Melastomataceae)

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ABSTRACT

Clidemia hirta is a highly invasive shrub at Sinharaja. We studied the abundance of *C. hirta* in relation to eight different topographical microhabitats, the light environment, and the diversity of other plant species in Sinharaja's undisturbed lowland evergreen forest. Our results indicate that the abundance of *C. hirta* was highly correlated with topological microhabitat, positively associated with the amount of light, and inversely correlated with diversity of other species. The highest abundance of *C. hirta* occurred in valley habitats. This habitat has high light availability, as a result of wind-blown tree falls, and moist soil. The negative association with diversity is consistent with theoretical predictions that more diverse communities should be more resilient to invasion.

Key words: *Clidemia hirta*; abundance; invasive shrub; undisturbed lowland evergreen forest; Sinharaja World Heritage Site.

THE GREAT MAJORITY OF EXOTIC SPECIES, species occurring outside of their natural ranges due to human activity, do not become established in the place to which they are introduced, because the new environment is not suitable to their needs. However, a certain percentage of species do establish themselves in their new homes, and some become invasive species; that is, they increase in abundance at expense of native species. These exotic species may displace native species through competition for limiting resources (Wilcove *et al.* 1998; Primack 2000). Invasion by exotic species to the detriment of native species is a further threat to degraded and fragmentation rain forests. So far exotic species have been a problem mainly only on oceanic islands in the tropics (Primack & Corlett 2005). The isolation of island habitats encourages the development of unique assemblages of endemic species, but it also leaves those species particularly vulnerable to better adapted, and more aggressive invading species. Moreover, island species often have no natural immunities to mainland diseases. When exotic species are introduced to the island, they frequently carry pathogens or parasites that, though relatively harmless to the carrier, can devastate native populations.

Why are some exotic species so easily able to invade and dominate new habitats displacing native species? One reason is the absence of their natural predators and parasites in the new habitat. Human activity may also create environmental conditions such as increased levels of soil disturbance, an increased incidence of fire, or enhanced light availability, to which exotic species often adapt more readily than native species. The highest concentrations of invasive exotics are often found in habitats that have been most altered by human activity (Primack 2000).

Clidemia hirta (L.) D. Don (Melastomataceae) is a Neotropical pioneer shrub that has invaded both undisturbed and secondary forests in the Old World (Rogers & Hartemink 2001; Primack & Corlett 2005). It has invaded both wet and dry regions of the tropics and sub-tropics. In Hawaii, *C. hirta* appears to be replacing endemic species that formerly dominated. It has also been found at Pasoh Forest Reserve, Malaysia, a continental site with primary forest, where there had been no previously recorded invasive plant or animal. Ground disturbance created by super-abundant wild pigs (*Sus scrofa*) appears to have played a major

role in the establishment of *C. hirta* in the tropical forest at Pasoh (Peters 2001). Relative growth rates were found to be significantly higher in gaps and gap edges than in the understorey, and no reproductive individuals were found in the understorey. As a result the population of *C. hirta* at Pasoh is confined almost exclusively to high light environments (Peters 2001).

We examined the factors affecting the susceptibility of primary rain forest at Sinharaja, Sri Lanka to invasion by *C. hirta*. We examined the hypotheses that the abundance of *C. hirta* is related to the topographical microhabitat and light environment (hypothesis 1), and negatively associated with the diversity of other plants (hypothesis 2).

MATERIALS AND METHODS

STUDY SITE.—Sinharaja is in the lowland wet zone of southwest Sri Lanka and extends from 6°21'–26'N and 80°–21'–34'E. The study site was located in the 25-ha Sinharaja Forest Dynamics Plot (FDP) (Gunatilleke *et al.* 2004).

We counted number of mature and immature *Clidemia* stems in 60 randomly selected 5 x 5 m quadrats. Quadrats were selected using a random number generator. We measured plant height of *Clidemia* individuals, stem diameter, and estimated the percentage canopy cover above the quadrat.

We extracted data on the topographical microhabitat and species abundances for each quadrat from the FDP dataset.

STATISTICAL ANALYSIS.—We used R 2.3.1 software package for analysis of our data. We used Generalized Linear Models with the number of *C. hirta* as the dependent variable and topographical microhabitat, percentage crown cover, and the abundance and diversity of other plants in the 5 x 5 m quadrat as the independent variables. We used a model with a Poisson distribution of the error term, as our data were count data.

RESULTS

There was a highly significant difference in the abundance of *C. hirta* across topographical microhabitats (Fig. 1). The abundance of *C. hirta* was also significantly associated with the abundance of other species (stem diameter at breast height (DBH) >1 cm) in the quadrates, and negatively associated with the percentage crown cover and species richness of stems >1 cm in the quadrate (Table 1). The results were broadly similar for the abundance of both mature and immature *C. hirta* stems. However, the distribution of immature *C. hirta* stems was more equitable across habitats, although topography was still highly predictive. Also, the abundance of immature *C. hirta* stems was not significantly associated with species richness.

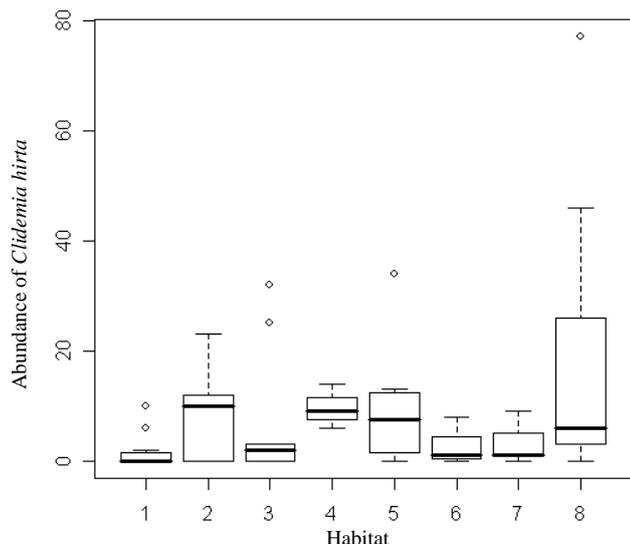


FIGURE 1. Abundance of *Clidemia hirta* in eight different habitats in Sinharaja Forest Dynamics Plot. 1= High Steep Spurs; 2= High Less Steep Spurs; 3= High Steep Gullies; 4= High Less Steep Gullies; 5= Low Steep Spurs; 6= Low Less Steep Spurs; 7= Low Steep Gullies; 8= Low Less Steep Gullies.

DISCUSSION

The abundance of *C. hirta* was significantly associated with topography, light conditions, the abundance of other species, and species richness. Densities were highest in the valleys, which are continually moist and have high light conditions as a result of many tree-falls. The abundance of mature *C. hirta* was negatively associated with species richness, but positively associated with the abundance of other plants, suggesting that the diversity of plant species imparts a resilience to invasion upon the community, at least at the scale of a 5 x 5 m quadrate. Theoretical studies have suggested that increases in species richness may imply a filling up of the available niche space, thereby reducing the possibilities for an invasive species to colonize. In our study, the distribution of immature *C. hirta* stems was not significantly associated with species richness, and was more even across topographic microhabitats, although the habitat term was still significant in the model. This is to be expected if the distribution of *C. hirta* is not dispersal limited but that the growth of *C. hirta* is site specific. Thus, it is further evidence that *C. hirta* is being competitively excluded as it grows from quadrates with a higher diversity of other species.

TABLE 1. Generalized Linear Model output for the abundance of mature *Clidemia hirta* stems as a factor of topographical microhabitat, percentage crown cover, abundance of other species (DBH > 1 cm), and species richness (DBH > 1 cm).

Habitat	Estimate	P
(Intercept) Topography – baseline		
High Steep Spurs	1.039499	0.003443 **
High Less Steep Spurs	1.602356	4.71e-08 ***
High Steep Gullies	1.233607	1.02e-05 ***
High Less Steep Gullies	1.738593	1.48e-08 ***
Low Steep Spurs	1.905315	2.05e-13 ***
Low Less Steep Spurs	0.690032	0.033621 *
Low Steep Gullies	0.697699	0.045531 *
Low Less Steep Gullies	2.555858	< 2e-16 ***
Percentage crown cover	-0.014383	1.22e-07 ***
Abundance of other species	0.042254	5.32e-12 ***
Species richness	-0.058365	7.39e-05 ***

Our results indicate that *C. hirta* has successfully invaded the primary forest at Sinharaja. However, while widespread, *C. hirta* is largely restricted to particular microhabitats within the primary forest, particularly valleys with a high rate of tree fall. Moreover, quadrates with a high diversity of other species were resilient to invasion. These results are important for the conservation of other ecosystems threatened by invasive species. It supports theoretical predictions that highly diverse, intact habitats should be more resilient to invasion. The best conservation strategy to prevent colonization by invasives should therefore be simply to protect the natural communities and maintain high species richness.

We recommend an extended study at Sinharaja to examine whether *C. hirta* is still increasing in abundance, and whether any native plants are threatened as a result.

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We would like to express our sincere gratitude to Dr. Rhett D. Harrison and Dr. Campbell O. Webb for their encouragement. Our appreciation also goes to Prof. C. V. S. Gunatilleke and Prof. N. Gunatilleke for hosting the course. We wish to give our sincere thanks to our colleagues for their care and support throughout the making of this.

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Effect of Land-Use on Spider (Araneae) Community Structure

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ABSTRACT

The effect of four different land-use types on the composition of spider (Araneae) communities was investigated at the Sinharaja World Heritage site, Sri Lanka. Overall we collected nine families and 49 morpho-species of spider. Salticidae occurred at all sites and was most abundant at the village marsh. Species dominance (Simpson Index) was similar among different land-use types. The Shannon Diversity Index ($H' = 2.607$) was highest in village. The similarity indices between land-use types were low. The abundance of spiders was highest in marsh areas.

Key words: spider; Araneae; biodiversity; wetland.

SPIDERS (ARANEAE) ARE EVERYWHERE. There are about forty thousand described species. Spiders are defined into different guilds, according to habitat and spacial distribution, in the ecosystem, as the complex roles of spiders in ecosystems become apparent. They are important predators and also prey to other animals. The abundance of spiders can reflect the biomass and biodiversity of particular area. Around the village, the landscape is fragmented into different land-use types (*e.g.*, Tea farm, palm plantation, marsh, and village area), and has experienced different histories of land-use.

Freshwater wetland is defined as any area covered by shallow fresh water for at least part of the annual cycle. Wetland soils are, therefore, saturated with water continually or for part of the year. The productivity and the community composition of the wetland are dependent on the period of inundation. Marshland, as with other types of wetland, can be important components of the landscape and maintain water resources (*e.g.*, stream and river flow, and ground water). Marshlands include many organisms, including mammals, fishes, insects, plants, and also spiders. In Sri Lanka marshes are often not natural. About a decade ago, for economical reasons, farmers abandoned their paddy fields. Today, these abandoned paddy fields have become wetlands, usually marshes, and are found dotted around the village and forest.

This study attempted to investigate the relationship between biodiversity and different land-use types by examining the diversity of spiders. We compared the diversity, abundance and guild structure of spiders in four types of land-use: forest, village, forest marsh, and village marsh.

MATERIALS AND METHODS

STUDY AREA.—The study was conducted at Sinharaja World Heritage site, Sri Lanka. Sinharaja is a rain forest in South-west Sri Lanka that receives >5000 mm of rain annually, and is aseasonal. Two sample sites, secondary forest and forest marsh were located near the boundary of the rain forest reserve, and two sample sites, village and village marsh, were located near the Kudawa Forest Bungalow.

DATA COLLECTION AND ANALYSIS.—We used sweep nets to collect spiders in the four different land-use types over one day from 23

to 24 August 2006. At each site, we made thirty replicate collections, and every replication had ten sweeps. In the secondary forest and the village sites, we sampled spiders along roadside. In the forest marsh and village marsh, we walked down to the marsh sampling spiders. The spiders were brought back to the laboratory for classification. We identified families (Ken 1998) and assigned specimens to morpho-species, as far as possible.

Shannon Diversity Index, species richness, individual abundance and community similarity were calculated for each site using R program (version 2.3.1) Vegan package.

RESULTS

A total of 1200 individual spiders were collected from 118 sweep net replications in the four different land-use types (Table 1). We identified nine families overall and 49 morpho-species.

Species richness was high at three sites; forest, village, and forest marsh (Table 2). All the diversity indices were highest for the village site. The marsh near the village had the lowest diversity. Evenness index (Pielou e) in the village was also the highest ($e = 0.940$).

DISCUSSION

The diversity of spiders was not very different in the four land-use types. However, we found the diversity of spiders in the village and the forest higher than in the marsh sites, especially Tetragnathidae. We suggested that maybe because there was a more complex spacial structure in the forest and village. However, comparing the dominance of two families, Tetragnathidae and Oxyopidae, among four land-use types, we also found the foliage runners and orb web builders were the dominant guilds to live in the forest and village. We found the species richness and abundance in village was much lower than the species richness in the forest. Local people had several plantations, such as tea farms, palm farms, and houses and roadside effects cause different levels of disturbance to the environment of village. However, diversity of spiders was higher in the village, which probably results from the diversity of microhabitats.

TABLE 1. *Spiders in the different land-use types at Sinharaja, Sri Lanka.*

Taxon (Number of Family)	Guild	Forest	Village	Forest marsh	Village marsh	Total individual
Oxyopidae (2)	Foliage runner	2 (2)	1 (3)	1 (75)	1 (337)	417
Salticidae (14)	Foliage runner	5 (25)	3 (7)	5 (35)	8 (48)	115
Thomisidae (4)	Foliage runner	4 (5)	0	1 (41)	1 (6)	55
Lycosidae (9)	Ground runner	0	0	2 (21)	1 (2)	23
Araneidae (9)	Orb web builder	4 (5)	2 (3)	3 (7)	1 (1)	18
Tetragnathidae (7)	Orb web builder	2 (2)	2 (6)	4 (241)	5 (263)	513
Linyphiidae (6)	Space web builder	1 (1)	3 (8)	3 (15)	2 (9)	33
Theridiidae (2)	Space web builder	4 (5)	3 (6)	0	0	11
Unknown (3)	Unknown	2 (17)	1 (1)	1 (5)	1 (1)	24

TABLE 2. *Comparison of species richness, dominance, diversity and evenness in the different land-use types at Sinharaja, Sri Lanka.*

Land-use types	Number of species	Dominance (Simpson Index)	Diversity (Shannon Index)	Evenness (Pielou <i>e</i>)
Forest	20	0.829	2.289	0.764
Village	16	0.915	2.607	0.940
Forest marsh	20	0.747	1.899	0.634
Village marsh	20	0.602	1.262	0.421

The number of spiders in both marshes was much higher than other two land-use types, with some very dominant species and guilds. We suggested that the ecological and spacial structure in marshes was limited and resulted in this low diversity, but the availability of water supported high productivity, and thus a large abundance of spiders.

Finally, we believe that using only sweep nets method is not enough to sample all guilds of spiders. We lacked collections of ground-dwelling spiders which may have biased our analyses. Despite this, we found the abundance of spiders to be very high in the marshes. It indicated marshes are not simply abandoned areas, but important repositories for biodiversity. We should place more attention on these kinds of habitats for conservation.

ACKNOWLEDGMENTS

We would like to express our sincere gratitude to Dr. Rhett Harrison, Dr. Campbell O. Webb, and Luan Keng for their encouragement. Our appreciation also goes to Dr. Nimal Gunatilleke and Dr. Savi Gunatilleke for hosting the course. And we wish to thank Mr. Saranjan and our colleagues, especially Woody for their help in their field to help us conduct this study.

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Comparing Seedling and Adult Tree Densities in Three Species of *Shorea* (Dipterocarpaceae)

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ABSTRACT

Three *Shorea* species in Sinharaja rain forest show evidence of niche differentiation. *Shorea cordifolia*, *S. disticha* and *S. trapezifolia* have distinct spatial distributions within a 25-ha plot. It is unclear at which stage new recruits of the three *Shorea* species are excluded from the locations where adult populations are sparse or absent. Seedling densities and heights were measured at 38 sites within a 6 ha area encompassing a range of habitats. Results showed that seedling distributions were strongly determined by habitat, and therefore matched the distribution of older trees. We conclude that habitat specialisation is governed either by seed dispersal or niche differentiation at a very early developmental stage, rather than post-establishment seedling mortality.

Key words: seedling; *Shorea*; habitat preference; niche differentiation.

THE FACTORS THAT STRUCTURE SPECIES-RICH COMMUNITIES remain a source of contention in ecological research. The spatial distributions of individual species have been used to find evidence in support of two opposing ideas, suggesting that: (1) species are distributed at random within the limits of dispersal, as suggested by null models of diversity (*e.g.*, Hubbell 1997); and (2) species' distributions are determined by local environmental conditions and that niche differentiation drives local spatial distribution patterns (Russo *et al.* 2005; Brown *et al.* 1999). Support for the latter concept is often found in highly heterogeneous environments (Potts *et al.* 2004). Such niche differentiation is believed to exist between *Shorea* species in the Sinharaja rain forest because species' distributions are highly patterned in accordance with topography and its covariates and in relation to their life-history strategies (Ashton 1995). *Shorea disticha* and *S. cordifolia* are members of the Beraliya group, and are medium heavy, hardwood species with large edible fruits and supra-annual flowering (Gunatilleke *et al.* 2004). Conversely, *S. trapezifolia* belongs to the Thiniya-Duna group, where member species have some traits associated to pioneer species, for instance, softer wood, non-edible fruits, and they bloom annually. Further support for niche differentiation comes from observed physiological differences between *Shorea* seedlings under different environmental

treatments (Ashton 1995). For example, in low-light conditions, *Shorea trapezifolia* allocated the lowest proportion of dry mass to roots, suggesting it is light loving and may suffer from periodic water stress (Ashton 1995). Understanding the processes by which habitat associations are maintained could help us understand the controls on species distributions and diversity.

In 1993, CTFS and the University of Peradeniya established a 25-ha forest dynamics plot (FDP) at Sinharaja, Sri Lanka and mapped all trees ≥ 1 cm. Trees belonging to the genus *Shorea* are abundant, constituting 20.8% of basal area in the FDP (Gunatilleke & Gunatilleke 2004), but there is a distinct spatial patterning in the species' distributions. The FDP relief is dominated by a central valley. Elevation ranges from 430 m above sea level in the valley to 575 m on the steep, rocky, southwest facing slope and 505 m on the gentler, northeast facing slope. At a glance, it appears that the species distributions are aspect driven. However, soil water availability is clearly related to topography and soil structural properties vary between the shallower and steeper slopes (Daws; Gunatilleke pers. comm.). *Shorea disticha* and *S. cordifolia* are restricted to the steeper, rocky slopes, while *S. trapezifolia* is water- and light-loving, and favours the gentler slopes and valley areas (Fig. 1A, B & C).

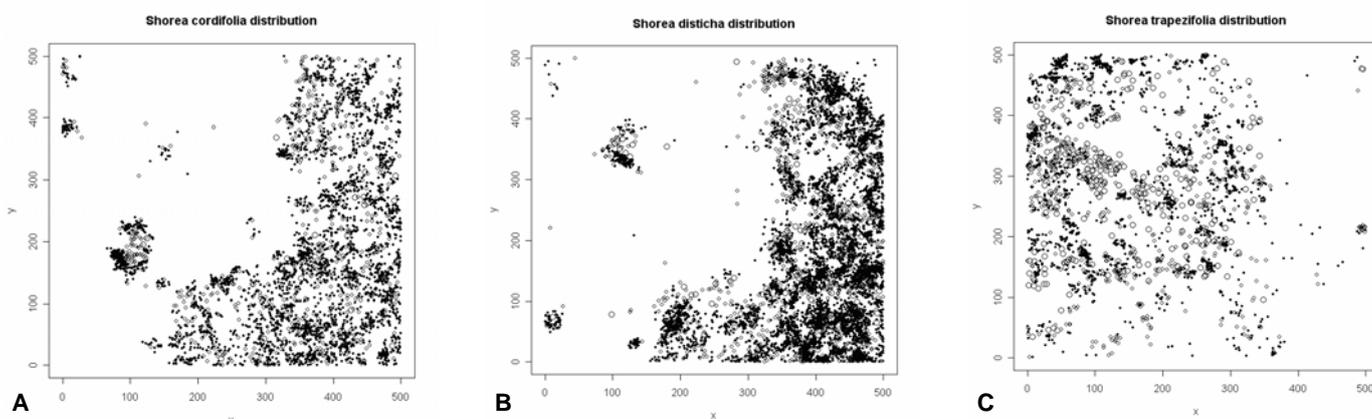


FIGURE 1. Distribution of three *Shorea* species in the Sinharaja Forest Dynamics Plot, Sri Lanka.

In this study, we aimed to identify at which stage new recruits of the three *Shorea* species are excluded from the locations where adult populations are sparse or absent. The hypotheses we considered are that: (1) seedlings are absent and either seeds are failing to disperse, germinate or establish; or (2) seedlings are being excluded at the post-establishment seedling stage as a result of unsuitable abiotic conditions or biotic interactions.

MATERIALS AND METHODS

We quantified seedling abundance and individual height for three species, *S. cordifolia*, *S. disticha* and *S. trapezifolia*, in 2 x 2 m seedling plots on both sides of the central valley in the Sinharaja FDP. In the north-western portion of the plot, the area on each side of the river is approximately equivalent, so we delimited a sample area of 6 ha that encompassed the whole width of the plot (500 m) to give maximum variation in topography. The FDP is divided into 20 x 20 m sub-plots. Our sample area was made up of 150 sub-plots, and from these we randomly selected 38 sub-plots, stratified by three habitat classes (ridge, slope and valley) and the two aspects. Two extra sub-plots were selected so that valley-within-slope habitats were also sampled. The seedling plots were placed at the centre of the selected sub-plots. Numbers of seedling individuals of the three target species and their heights were recorded.

A wide-angle, black and white photograph was taken vertically, 1.3 m from the ground, at each seedling plot to quantify canopy openness. Canopy openness was taken as the number of pixels where brightness was greater than 0.6 (where brightness ranges between 0 and 1.0). This threshold was selected by examining frequency distributions of pixel brightness; typically, there was a peak in brightness at approximately 0.9, representing the brightest (sky) pixels, but to incorporate other less bright pixels that still represent gap, the threshold was reduced to 0.6.

We used adult tree density as the measure of species 'presence', with which we compared seedling abundance. Adults were defined as all stems greater than 330 mm diameter at breast height (DBH) in the 60 x 60 m catchment area surrounding each seedling plot. As tree sizes were similar across species, the same size threshold was applied for all species. Given that the species have relatively heavy, gravity or wind dispersed fruits, a 60 x 60 m catchment area was deemed a suitable scale.

Stepwise analyses of covariance (GLM) were performed using a Poisson error distribution, to examine the relationships

between light, adult density and habitat on seedling abundance.

It was not possible to examine any change in seedling height with distance from adult distributional range because seedlings were rarely found outside of the parent distributional range. Size-frequency distributions of each species were examined.

RESULTS

For all species, adult density was not a significant determinant of seedling abundance and the terms were subsequently removed to simplify the models. Significant terms ($P \geq 0.05$) and explanatory power of the models are discussed for each species.

SHOREA CORDIFOLIA.—With other variables controlled for, canopy openness did not have a significant effect on the abundance of *S. cordifolia* seedlings. Seedling abundance was higher on the slope habitat than on valley and ridge habitats, and this association was significant in the model (Table 1). Thirty-nine percent of the variation in seedling abundance of *S. cordifolia* was explained by the model presented in Table 1.

SHOREA DISTICHA.—The GLM indicated that there was a significant negative relationship between light and seedling abundance. Habitat was also a significant determinant of seedling abundance. Valley sites had fewer individuals than slope and ridge sites, and seedlings were most abundant on ridges sites. The model explained forty-two percent of variation in seedling abundance.

SHOREA TRAPEZIFOLIA.—The relationship between canopy openness and seedling abundance was highly significant but the slope was negligible showing little causative effect (Table 1). The effects of the valley and ridge habitats on seedling abundance were not significantly different, but the positive association between slope habitat and seedling abundance was significantly different from the other habitats. Only ten percent of the variation in seedling abundance was explained by the model.

Seedling size-frequency distributions across the species were similar in shape, characterized by many small individuals and very few larger individuals (Fig. 2). There were a few larger individuals of *S. disticha*. However, there was a much higher overall abundance of *S. trapezifolia* seedlings in plots where they were dominant compared to seedling plots where the other two species were dominant.

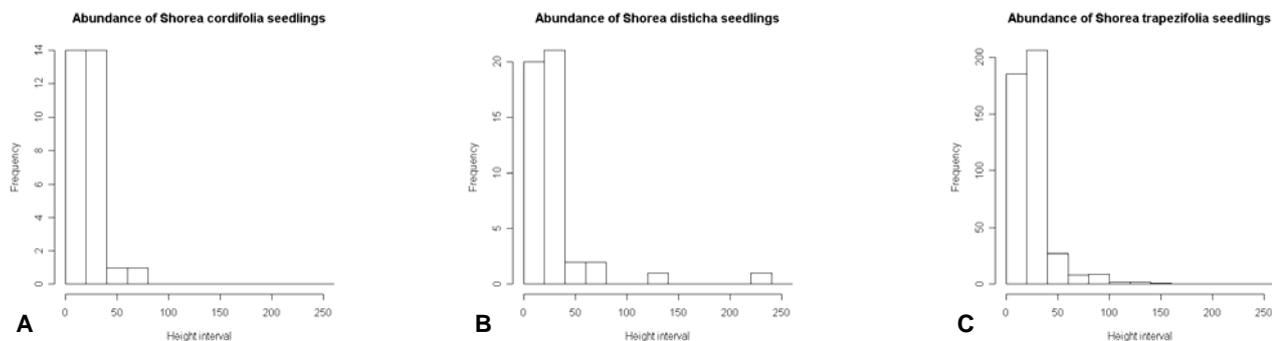


FIGURE 2. Size-frequency distributions of seedlings for the three *Shorea* species at Sinharaja.

TABLE 1. Results of GLM analyses conducted for the abundance of seedlings of three *Shorea* species in the Sinharaja Forest Dynamics Plot

	Estimate	P
<i>Shorea cordifolia</i>		
Habitat		
Ridge vs Slope	-3.176e+00	0.00182 **
Ridge vs Valley	2.517e-01	0.85883
Valley vs Slope	-3.427e+00	0.000793
Canopy openness	1.228e-06	0.810298
<i>Shorea disticha</i>		
Habitat		
Ridge vs Slope	1.204e+00	0.000193
Ridge vs Valley	2.818e+00	0.000115
Valley vs Slope	-1.614e+00	0.033318 *
Canopy openness	-2.652e-05	1.27e-08
<i>Shorea trapezifolia</i>		
Habitat		
Ridge vs Slope	-5.661e-01	5.35e-06 ***
Ridge vs Valley	-1.440e-01	0.289
Valley vs Slope	-4.221e-01	0.000200 ***
Canopy openness	-1.031e-05	5.5e-13

DISCUSSION

Local coexistence of species was more common between *S. cordifolia* and *S. disticha* than the coexistence of either with *S. trapezifolia*. The results of the statistical models showed that seedlings had strong habitat preferences, which matched those of the trees ≥ 1 cm DBH, as shown by the distribution maps. Models showed that adult tree density was not a significant determinant of seedling abundance though this is likely to be because the effect of habitat accounted for the same variation in seedling abundance as would adult tree density. *Shorea disticha* seedlings were most strongly associated to ridge habitats, though the adult distribution extends downslope. *Shorea cordifolia* seedlings were associated to slope habitats. More surprisingly, model results showed that the *S. trapezifolia* association with valley sites was not significantly different from ridge sites, and that *S. trapezifolia* are more closely associated to slope sites. It is likely that this results from the fact that a number of valley plots were dominated by dense communities of pioneer species, excluding all *Shorea* seedlings.

Non-significant relationships or a lack of effect of light were surprising as higher light environments are typically favourable to seedling establishment and growth. This may reflect shade-tolerance in *Shorea* species or the fact that a high proportion of seedlings establish under the parent tree where light conditions are nevertheless less than favourable. Furthermore, the method used to quantify light availability may not accurately represent the light reaching the forest floor, and thus confounded results.

Model explanatory power was moderately high for *S. disticha* and *S. cordifolia*, but much lower for *S. trapezifolia*. High spatial and temporal heterogeneity may conceal patterns, especially given small plot sizes. A number of sources of

variation have not been accounted for, for instance: surrounding low-growing vegetation, soil nutrients and moisture availability, seedling predation and stochastic events. As a result, there is a large proportion of unexplained variation in seedling abundance.

Size-frequency distributions of seedlings showed that *S. trapezifolia* seedlings were most abundant overall. This may reflect a reproductive strategy closer to that of a pioneer than the other *Shorea* species. *Shorea trapezifolia* is known to bloom annually and during fieldwork we observed a large number of fruits, so it is possible that the high abundance was temporary and reflected recruitment from this recent fruiting event.

In summary, the three *Shorea* species we studied displayed some evidence of habitat specialisation at the seedling stage as seedlings failed to establish outside of the parent distribution. Therefore we favour the arguments that spatial distribution patterns are being maintained by either a failure to establish where environmental conditions are limiting, where the species does not have competitive advantage, or because of dispersal limitation rather than as a result of post-establishment seedling mortality.

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Community Organization in Flower-Visiting Butterflies

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ABSTRACT

Butterfly-flower interactions offer a great potential to understand the evolutionary relationships among plants and pollinators. In this study butterfly proboscis length was found to be significantly correlated with corolla length. As the corolla length increased, the length of the proboscis is also considerably increased irrespective of butterfly body size. This trend may be explained as a possible adaptation to the availability of food resources.

Key words: pollination; flower; butterfly; corolla; proboscis; coevolution; adaptation.

THE COMMUNITY ORGANIZATION WITHIN THE PLANT-POLLINATOR ASSEMBLAGES is a complex phenomenon that requires critical investigation to understand with respect to evolutionary patterns. Plants have developed different flower syndromes to suit different pollinating agents thereby increasing their reproductive success. Similarly, the pollinators have evolved in response to flower morphology (Wiebel 1979). The present study aimed to investigate plant-pollinator interactions at a finer scale, focusing on just butterflies and butterfly-pollinated plants. I examined the hypotheses that the plants have developed different flower morphologies to attract certain butterflies and that butterfly body size and length of proboscis varies in relation to flower morphology.

METHODS

This study was conducted in the buffer zone of Sinharaja rain forest, Sri Lanka. Sinharaja is known for its diverse plant and animal communities. It receives a mean annual rainfall of > 5000 mm from both south-west and north-east monsoons. Sinharaja has no dry season and the temperature ranges from 27-28°C with relatively constant day length.

A total of six plant species in bloom over the study period (21 – 24 August) were selected. Flowers were collected from each plant species to measure morphometry. Colour, strength of

floral odour, and type of fragrance were quantified as perceived by the observer. Length and width of the corolla were measured using vernier calipers. Butterfly species that visited the flowers were recorded and a representative of the species collected. Butterfly visitation rate (number of visits per hour) and foraging time (minutes per hour) were recorded. Body length, wingspan and length of proboscis were measured using vernier calipers. Linear model regression and correlation was performed using R version 2.3.1.

RESULTS

A total of 14 butterfly species were recorded visiting all six plant species. The visitation rate and foraging time of each butterfly species are given in Appendix 1. Corolla length in *Mussaenda frondosa* was significantly longer than that of the other five plant species (Table 1). All flowers were axial and had fragrant flowers, but varied in colour, length and width (Table 1).

Proboscis length varied considerably among the butterfly species, irrespective of body size and wingspan (Fig. 1A & 1B). However, the correlation between proboscis length and corolla length is positive and highly significant ($r = 2.2 \times 10^{-16}$, $df = 75$, $P < 0.001$). The proboscis length and corolla length plotted on a logarithmic scale is given in Fig. 2.

TABLE 1. *Morphological characters of the flowers of six species observed*

Plant species	Family	Colour*	Smell*	Length	Width
<i>Hedyotis fruticosa</i>	Rubiaceae	White	Strong	5.51	5.1
<i>Emelia sp.</i>	Asteraceae	Pink	Moderate	8.9	0.6
<i>Lantana camara</i>	Verbenaceae	Orange	Strong	9.23	5.6
<i>Mussaenda frondosa</i>	Rubiaceae	Orange	Moderate	32.13	16.71
<i>Eupatorium sp.</i>	Asteraceae	Yellow	Moderate	3.7	1.94
<i>Elaeocarpus amoenus</i>	Elaeocarpaceae	White	Strong	6.7	7.24

* Human Perceived

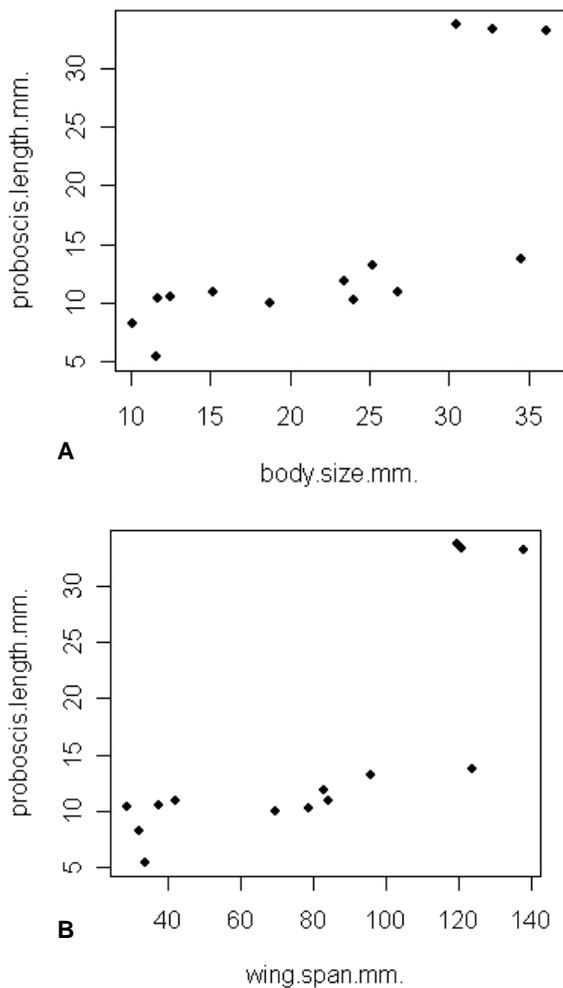


FIGURE 1. (A) Proboscis length plotted against body size and (B) wingspan of butterflies visiting flowers at Sinharaja.

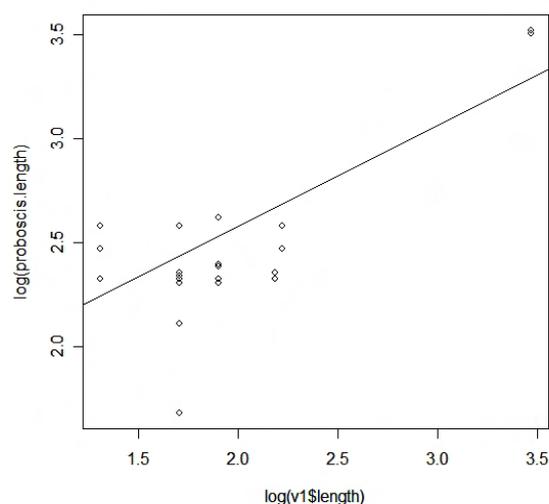


FIGURE 2. Relationship between proboscis length and corolla length for six butterfly visited flowers at Sinharaja.

DISCUSSION

Butterfly-flower interactions offer great potential to understand the evolutionary relationships between plants and pollinators. Flower characters like colour and smell showed only slight variation among plant species. However, these were human perceived variables, and hence the assessment may not be appropriate. Scent compounds do serve as a signal to attract pollinating butterflies and may have evolved in conjunction with the sensory capabilities of butterflies as a specific group of pollinators (Andersson *et al.* 2002).

The most important finding of this study was the significant relationship between the proboscis length and corolla length (Fig. 3). Proboscis length was not correlated with either body size or wingspan among butterfly species. Butterflies that visited *Mussaenda frondosa* had a long proboscis, while those visited *Elaeocarpus amoenus*, for example, varied greatly in wingspan and body size but had a moderate proboscis length. The most likely explanation for this trend is adaptation to host plant morphology (Novotny *et al.* 1999, Sota *et al.* 1997), possibly a product of coevolution between plants and their pollinators. Long term study could further elucidate niche partitioning among butterfly species.

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APPENDIX 1. *Species of butterfly pollinated plants observed over four days at Sinharaja World Heritage Site, Sri Lanka, the butterfly species observed visiting their flowers, their visitation rates and foraging time*

Plant	Butterfly	Family	Visitation rate	Foraging Time (sec)
<i>Hedyotis fruticosa</i>	<i>Eurema blanda</i>	Pieridae	10	143
	<i>Species Unknown</i>	Hesperiidae	1	18
	<i>Ypthima ceyloniica</i>	Satyridae	4	25
	<i>Cupha eymanthis placida</i>	Nymphalidae	2	23
	<i>Graphium agamemnon menides</i>	Papilionidae	5	109
	<i>Caleta decidia</i>	Lycaenidae	1	12
	<i>Ideopsiss similes</i>	Danidae	2	21
<i>Emelia sp.</i>	<i>Eurema blanda</i>	Pieridae	4	24
	<i>Ideopsiss similes</i>	Danidae	2	17
<i>Lantana camara</i>	<i>Graphium sarpedon teredon</i>	Papilionidae	2	40
	<i>Graphium agamemnon menides</i>	Papilionidae	1	15
<i>Eupatorium sp.</i>	<i>Graphium sarpedon teredon</i>	Papilionidae	3	17
	<i>Graphium agamemnon menides</i>	Papilionidae	17	637
	<i>Ideopsiss similes</i>	Danidae	1	4
<i>Mussaenda frondosa</i>	<i>Papilio helenus mooreanus</i>	Papilionidae	6	32
	<i>Papilio polymnestor</i>	Papilionidae	3	11
	<i>Hypolimnys bolina</i>	Danidae	2	7
<i>Elaeocarpus amoenus</i>	<i>Idea iasonia</i>	Papilionidae	2	11
	<i>Eurema andorsoni</i>	Pieridae	3	142
	<i>Ideopsiss similes</i>	Danidae	2	6
	<i>Cupha erymanthis placida</i>	Nymphalidae	4	43
	<i>Cirrochroa thais lanka</i>	Nymphalidae	3	39

Variation in Ant Defense on *Macaranga indica* (Euphorbiaceae) in Different Size Classes and Habitats

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ABSTRACT

The interaction between ants and *Macaranga indica* was studied in three different habitats (logged area, forest edge and primary forest). I examined the percentage of herbivory on *Macaranga indica* of different size classes and the number of ants per leaf. My study showed a positive relationship between height of tree and the percentage of leaves with herbivory damage. There was also a positive relationship between the number of ants per leaf and herbivory damage. Comparison of herbivory percentage among habitats found no significant differences. Nine species of ants were recorded during the observation.

Key words: *Macaranga*; mutualism; ant; herbivory.

MYRMECOPHYTES ARE A GROUP OF PLANTS WITH A SYMBIOTIC RELATIONSHIP WITH ANTS. Some interactions between ants and plants can be classified as mutualisms, with benefit accruing to both members. The plant provides a source of energy, either as solid food or as nectar, and sometimes a domicile such as a hollow stem (or a stem capable of being made hollow by the ants) or hollow stipular thorns. The ants provide the plant with defense against herbivory and/or vine overgrowth (Risch & Rickson 1981).

Macaranga is a genus consisting of mainly pioneer tree species with its center of diversity in New Guinea and Borneo. It includes many myrmecophytic species. (Whitmore 1969, 1975; Fiala *et al.* 1989). In Malaysia (Peninsular and Borneo), 23 of the 52 *Macaranga* species are myrmecophytes, and provide domatia for their symbiotic ants, but all species provide food bodies (called Beccarian bodies) on the undersides of the leaves or the stipules (Fiala & Maschwitz 1991, 1992). Most of the ant species that are symbiotic with *Macaranga* belong to the genus *Crematogaster* (Formicidae: Myrmicinae). The ants defend their host plant against herbivores and competitors (Fiala *et al.* 1989) and both plants and their symbiotic ants depend on each other for their survival.

In this study, I examined the herbivory on *Macaranga indica* at Sinharaja, Sri Lanka for different size classes in three different habitats. My hypotheses were ants' defense is more important for juvenile stages than mature stages of *Macaranga indica* and herbivory at the forest edge is higher than in logged areas and primary forest.

METHODS

STUDY SITES.—Field observations were carried out around the Field Research Station, Sinharaja. Three habitats were selected for these studies; forest edge, logged forest and primary forest.

SAMPLING.—Fifteen trees of *Macaranga indica* in different size classes were selected from each of the three different habitats (total = 135 trees). All trees were measured for height and percentage herbivory. For herbivory measurements, roughly five percent of the total number of leaves was removed. On each leaf, the number of feeding marks made by herbivores was counted and the leaf area was measured. Damaged leaf area and total leaf area were counted using graph paper. Ant aggressiveness was recorded. I disturbed the plants by shaking a branch. I considered aggressiveness to be high when ants tried to attack the disturbance, medium when the ants investigated the disturbance, and

low when ants did not respond. All ants were collected for identification.

DATA ANALYSIS.—To obtain normally distributed data, herbivory percentage was log transformed. All analyses were done using R 2.3.1 software.

RESULTS

EFFECTS OF PLANT SIZE ON HERBIVORY.—All samples of *Macaranga indica* were subjected to considerable herbivore. Figure 1 shows clearly a significant increase in herbivory with tree size ($F_{1,43} = 36.07, P < 0.0001$).

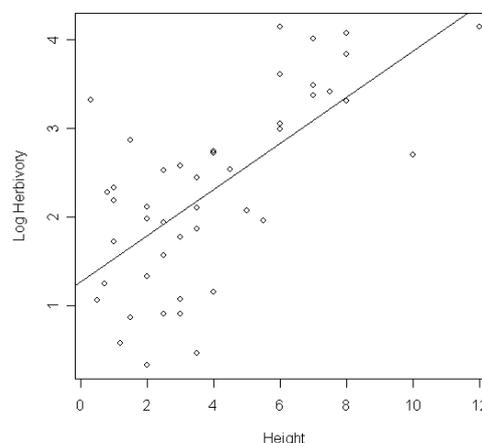


FIGURE 1. Plot of log herbivory percentage against tree height for *Macaranga indica*.

EFFECTS OF ANT ABUNDANCE ON HERBIVORY.—There was a positive relationship between the number of ants per leaf and percentage herbivory ($S = 10169.73, P = 0.02681$; Fig. 1), contrary to expectations.

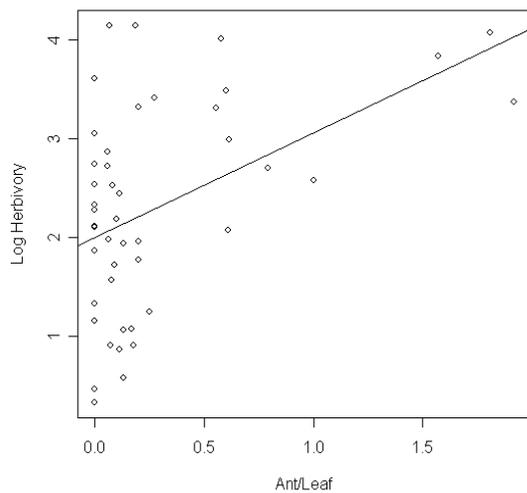


FIGURE 2. Plot of number of ants per leaf with against log herbivory percentage.

COMPARISON OF HERBIVORY BETWEEN HABITATS.—Percentage of herbivory varied between habitats. Figure 3 shows that there were no significant differences in the level of herbivory between habitats.

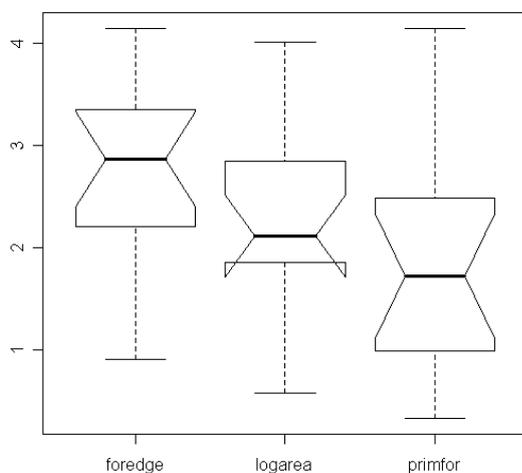


FIGURE 3. Comparison of habitat with herbivory percentage.

PRESENCE OF ANT SPECIES IN THREE DIFFERENT HABITATS.—Ants that were found in the *Macaranga indica* during observation were collected for identification. Nine species were recorded during the observation period (Fig. 4). *Technomyrmex albipes* was the only species found in all habitats.

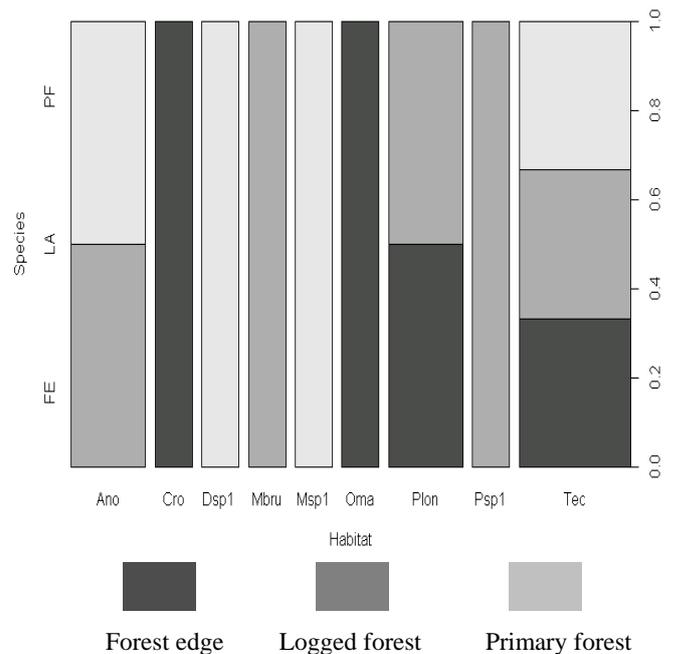


FIGURE 4. Presence of ants in three different habitats. Ano: *Anoplolepis gracifilus*; Cre: *Crematogaster sp 1*; Dsp1: *Dolichoderus sp1*; Mbru: *Myrmecaria brunnea*; Msp1: *Myrmecaria sp*; Oma: *Oecophylla smaragdina*; Plon: *Paratrechinas longicornis*; Psp1: *Paratrechinas sp1*; Tec: *Technomyrmex albipes*.

DISCUSSION

The study demonstrated a significant increase in herbivory percentage with increasing tree height. An increase in size indicates an increase in the number of the leaves on the plant and therefore a larger resource patch size for herbivores, potentially able to sustain larger populations.

The results indicated a positive correlation between the abundance of ants per leaf and herbivory. This was contrary to my original hypothesis that there would be less herbivory with increasing numbers of ants on the leaves. This may be a result of the species of ants present on *Macaranga indica*. All five species found on *Macaranga indica* are ants associated with disturbed areas, and therefore could be categorized as generalist or opportunistic foragers (N. R. Gunawardene, pers. comm.).

In this study, there was no significant difference in herbivory among habitats. This may be due to similarity of the habitats.

I recommend furthering this study by comparison with other *Macaranga* species to understand the mutualism interactions of particular ants with *Macaranga* species. I would like to further my study to look on nectar ingredients that might differ with other *Macaranga* species and attract different level of protection provided by different ant species.

ACKNOWLEDGMENTS

My deepest thanks goes to Dr. Rhett Harrison, Dr. Campbell Webb, Drs. Savi and Nimal Gunatilleke, Ms. Luan Keng Wang, Ms. Nihara Gunawardene, all participants and resource staff of the CTFS-AA International Field Biological Course 2006, Sri Lanka.

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Study of Willingness of Farmers to Convert Existing Tea Cultivation System to More Eco-Friendly Analog Forestry System

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ABSTRACT

The existing tea cultivation system surrounding the natural rain forest in Sri Lanka is a big threat for the conservation of biodiversity. The tea cultivation system has become unviable economically and environmentally. Inappropriate agricultural practices are the main reason. Analog forestry can be a viable alternative to the existing tea farming system. Analog forestry is one of the traditional farming systems that mimics structurally and functionally the natural forest ecosystem. This study was aimed to assess the willingness of tea farmers to change their present agricultural practices to an analog forestry system. The study area was Pitakele village situated in buffer zone of Sinharaja world heritage site. Twenty farmers were interviewed through questionnaire surveys and informal interviews. Level of income and level of willingness had a significant positive correlation.

Key words: analog forestry; agro-ecosystem; buffer zone; serial succession.

SRI LANKA LIKE MUCH OF THE DEVELOPING WORLD IS AT AN IMPORTANT STAGE of redefining village development policies to contend with the increasing threats to biodiversity. One endangered area in Asia is the Sinharaja forest, despite its designation as a UNESCO world heritage site (de Zoysa & Simon 1999).

The need for subsistence and income among a rapidly increasing local population has spurred encroachment for cultivation of tea. The emergence of tea as a lucrative small holder crop has transformed the village economy in the Sinharaja buffer zone and has attracted new immigrants to the area (de Zoysa & Simon 1999). The present tea cultivation system that is practiced in buffer zone is a big threat. Soil erosion, land slides, flooding, soil pollution, and water quality deterioration are the major environmental problems that follow tea cultivation. Fragmentation and isolation of biological reserves, which causes disturbances to animal dispersal and gene flow between highly protected core conservation areas and human dominated transitional unprotected areas is another important environmental issue (Wijesooriya & Gunathilaka 2003).

The environmental and economical viability of present tea farming sector has degraded, because of the marginalization of land. Modern agricultural techniques that are used in the present tea farming system are main cause for these problems.

During the classical period, the village community used the neighboring forest environment in a more sustainable, long-term system of cultivation and extraction (Kariyawasam 1996). They used appropriate traditional technologies for their farming activities.

The traditional home garden system called in Sinhala *Hela gewatta* (*Hela* = Sinhala *Gewatta* = Home garden) is one good example. The application of ecological and cultural principles in this farming system to modify the existing tea farming system may be a viable solution.

Analog forestry is a man-made agricultural ecosystem that is analogous to the natural forest in ecological function and vegetation structure. This farming system is developed through a serial succession of tree crops.

This study assessed the willingness of farmers to change their present tea (*Camelia sinensis*) cultivation system to more environmentally friendly analog forestry system.

I hypothesized that the willingness of farmers to change their present tea cultivation would depend on the area of land they possessed, their level of awareness to cultural practices in their cultivation and the cost of production of fresh tea leaf.

MATERIALS AND METHODS

STUDY SITES.—Pitakele village is situated about one kilometer from Kudawa Forest Office, Sinharaja. It is one of the more ancient villages, dating back to the times of the Sinhalese kings several centuries ago. Pitakele is located in the western buffer zone of the Sinharaja World Heritage Site, and abuts the conservation area on one side and a forest reserve on the other. The village comprises 31 families. Most of the people living in the village are tea farmers. They previously practiced rice cultivation but this was recently given up due to problems of wild animals feeding on the crops.

DATA COLLECTION AND ANALYSIS.—Twenty tea farmers were interviewed through questionnaire surveys. In addition, informal interviews were conducted with five knowledgeable key persons in village about the traditional agricultural practices they followed before converting farm lands to tea cultivation, and their opinions of the present changes. All the data recorded in questionnaires were analyzed using R statistical software package.

Hypotheses of the research were, there is (1) a positive correlation between willingness of farmers and negative changes of tea yield with the time, (2) willingness is increased with increasing level of awareness, (3) if the cost of tea production is high willingness is high and (4) willingness is increased with increase of level of awareness.

RESULTS

Stepwise multiple regression tests using all variables found that three variables remained after applying removal of non-significant effects. These were level of education, age of the tea crop, and the predicted income change for switching to analog forestry (Table 1). The cost of production and level of awareness were non-significant in the model.

TABLE 1. Variables of the model that are significant correlation with willingness.

Variable	Correlation	P value
Level of education	- ve	0.035
Age of crop	+ ve	0.008
Income Changes	- ve	0.015

DISCUSSION

Level of education (formal and informal) was highly correlated with willingness of farmers to change their present tea cultivation practices because farmer with good education have more understanding about the negative impacts of present cultivation practices, like the application of insecticide, fungicide and chemical fertilizer than low educated ones. The high cost of production for fresh tea leaves is strongly responsible for the level of income, so low income groups prefer alternatives that reduce the cost of production. Hence, they showed high willingness than high-income group. Farmers with relatively old plantations obtain lower yields. They also need to bear the future cost for re-planting and re-habilitation of marginal land. So this group of farmers is also willing to apply cost effective alternatives to the present cultivation system.

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Tree Species Diversity and Phylogeny along an Elevational Gradient in the Sinharaja Rain Forest, Sri Lanka

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ABSTRACT

Species diversity along an elevation gradient is often expected to display either a monotonic decrease or a hump-shaped pattern. Here we assessed the pattern of tree diversity along a gradient from 324 m to 741 m elevation in the Sinharaja rain forest in Sri Lanka. Phylogenetic patterns among the species were also assessed in order to understand ecological affinity between species. Our results showed that species diversity (Fisher's α) decreased with increasing elevation. Area effect, that is the reduction of available area at higher elevation, is the simplest explanation for this pattern, but other factors might also intervene. Species composition was also found to vary from the low elevation to the uppermost site. However, the phylogenetic analysis did not meet our expectation that communities at the top of the mountain should be more phylogenetically clustered.

Key words: species diversity; elevation; phylogeny; Sinharaja.

PATTERNS OF SPECIES RICHNESS HAVE LONG BEEN A CENTRAL TOPIC IN COMMUNITY ECOLOGY and have been documented for different environmental variables. The most popular of these patterns are the species-area relationship (Rosenzweig 1995) in which the number of species is assumed to increase with area, as well as the thoroughly documented latitudinal pattern of species diversity, depicting an increase of species number from the poles towards the equator (Rahbek & Graves 2001). Another frequently documented ecological pattern is the relationship between species richness and elevation. The altitudinal gradients are often suggested to be a reflection of the latitudinal gradients, as they display an increase of species richness from the top of mountains toward the lowlands (Rohde 1992). However, empirical studies in a variety of habitats and taxa show that two patterns emerge. The most predicted is the monotonic decrease in species diversity with increasing elevation (Stevens 1992), but a hump-shaped relationship, with peak in richness at mid-elevations, proves to be the most common (Rahbek 1995).

Basic information about composition and abundance of species within the Sinharaja Forest Dynamics Plot (FDP) is available (Gunatilleke *et al.* 2004). Our objectives were to understand patterns of species diversity over an expanded altitudinal gradient and to compare phylogenetic patterns of ecological adaptation. We expected a monotonic decrease pattern to be displayed owing to the scarcity of suitable habitats at higher elevation, which was dominated by rocky areas. We also hypothesized that there would be greater phylogenetic clustering at the top of the mountain, since the more extreme conditions would be expected to act as an environmental filter to colonization of the summit habitat.

MATERIALS AND METHODS

STUDY SITE.—The study was conducted at Sinharaja World Heritage Site in southwestern Sri Lanka (6°21–26'N, 80°21–34'E).

SAMPLING.—Eleven 5 x 10 m plots were set up in primary forest along an elevational gradient from 324 m to 741 m, starting close to Murakele Bungalow and continuing to the top of Mount Moulawella. Elevation at each plot was recorded with a GPS

(Garmin Etrex Vista). We identified and recorded every tree species whose diameter at breast height (DBH) was in the range 1 ~ 5 cm. Trees larger than 5 cm in DBH were excluded from this study because sampling the leaves was difficult and hence identification not possible.

In addition, we compared our results with data from the 25-ha Sinharaja long-term Forest Dynamics Plot (FDP) (6°24'N, 80°24'E), which represents a greater intensity of sampling over a shorter elevation gradient (424 m – 575 m).

DATA ANALYSES.—We used the software R 2.3.1 (R Development Core Team 2006) to analyze data and plot graphs. For diversity comparisons, we applied the vegan package (Oksanen *et al.* 2006) to calculate Fisher's alpha. The relationship between the diversity index and elevation was investigated by linear regression. We then examined the phylogenetic structure of the community using the software Phylocom 3.40 (Webb *et al.* 2006) with the null hypothesis that the pattern is random across the altitudinal gradient. The net relatedness index (NRI) and nearest taxon index (NTI), which respectively quantify the overall proximity of taxa on a phylogenetic tree and the amount of close terminal taxa represented, were used to assess the phylogenetic patterns. Phylogenetic clustering is indicated by high positive NRI and NTI, while negative values reflect evenness (Webb *et al.* 2002). Significance was assessed at a p-value of 0.05. We generated a tree representing the species from the most extreme plots (324 m and 741 m a.s.l.) using TreeView 1.6.6 (Page 2001). The phylogeny of the species is based on the ordinal classification of angiosperms (APG 1998, 2003) and the pool of species used to construct the tree is presented in Appendix 1.

RESULTS

In the 11 plots of 5 x 10 m established along an elevational gradient in Sinharaja, we recorded a total of 78 species, in 53 genera and 30 families. All taxa were identified to species level. The most species-rich families were Anacardiaceae, Clusiaceae, Euphorbiaceae and Myrtaceae, each with a total number of seven species (Table 1). In terms of tree abundance, eight species

dominated, with *Shorea affinis*, represented by a total of 40 individuals, the most abundant (Table 2).

TABLE 1. The most species-rich families found in 11 plots from 324 m to 741 m elevation at Sinharaja

Family	Genera	Species	Species to Family ratio	
			324 m	741 m
Euphorbiaceae	6	7	3:1	2:1
Rubiaceae	6	6	2:1	-
Lauraceae	5	6	2:1	1:1
Anacardiaceae	3	7	1:1	-
Clusiaceae	3	7	2:1	1:1
Dipterocarpaceae	3	3	-	3:1
Melastomataceae	2	4	-	2:1
Sapindaceae	2	2	2:1	-
Ebenaceae	1	3	-	-
Myrtaceae	1	7	4:1	-
Sapotaceae	1	4	2:1	-

TABLE 2. Dominant tree species in terms of individual abundance found in 11 plots from 324 m to 741 m elevation at Sinharaja

Species	Abundance	Altitudinal range (m a.s.l.)
<i>Palaquium twaitesii</i>	10	324 – 700
<i>Cryptocarya wightiana</i>	12	324 – 741
<i>Garcinia hermonii</i>	18	361 – 700
<i>Aporusa lanceolata</i>	21	324 – 660
<i>Palaquium petiolare</i>	23	419 – 700
<i>Humboldtia laurifolia</i>	28	452 – 741
<i>Mesua ferrea</i>	36	578 – 660
<i>Shorea affinis</i>	40	619 – 741

The distribution of plant families along the altitudinal gradient is illustrated in Fig. 1. Some families had a large elevational range, while others were restricted to a smaller range. Euphorbiaceae was found across the total gradient, whereas Dipterocarpaceae was mainly distributed in the upper range, and Myrtaceae occupied the lower elevations. It should be noted that the species to family ratio was low at higher elevation and high at low elevations (Table 1). Conversely, abundance of individuals per species increases with increasing elevation (Table 2).

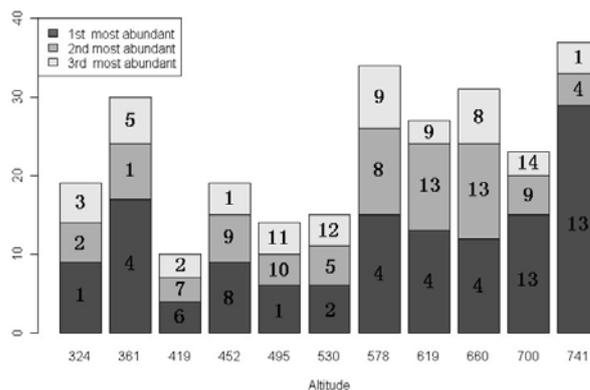


FIGURE 1. The most abundant families in terms of number of individual trees in every plot. Numbers refer to family. 1: Euphorbiaceae; 2: Lauraceae; 3: Myrtaceae; 4: Clusiaceae; 5: Rubiaceae; 6: Ebenaceae; 7: Bombacaceae; 8: Sapotaceae; 9: Fabaceae; 10: Ochnaceae; 11: Theaceae; 12: Symplocaceae; 13: Dipterocarpaceae; 14: Myristicaceae.

Pattern of species diversity along the altitudinal gradient was clearly a monotonic decrease in diversity with increasing altitude (adjusted $r^2 = 0.546$, $P < 0.0001$) (Fig. 2). Fisher's α varied from 21.084 to 4.464. The number of species recorded decreased from twenty-one at 324 m to eleven at the top of Mount Moulawella, and data from the small plots alone was consistent with that from the expanded dataset including the FDP data. Species that were common at low elevation included *Aporusa lanceolata*, *Cryptocarya wightiana*, *Ostodes zeylanica* and *Semecarpus walkeri*, while the high elevation was dominated by *Shorea affinis*, *Stemonoporus canaliculatus* and *Humboldtia laurifolia*.

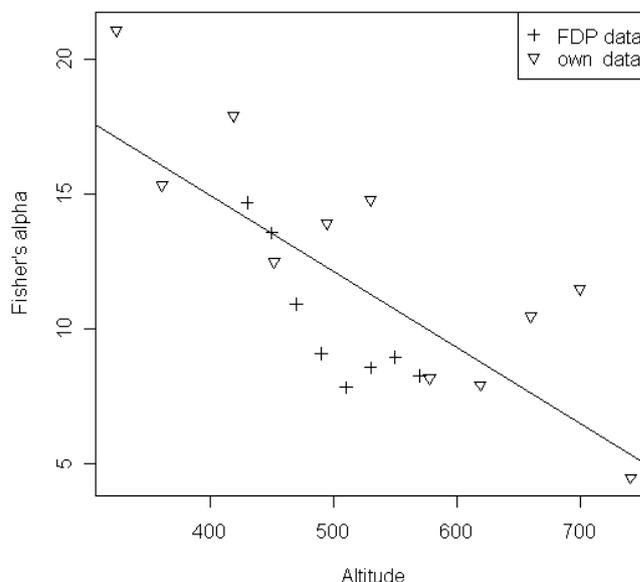


FIGURE 2. Pattern of species diversity along an elevational gradient at Sinharaja, including 11 small (5 x 5 m) plots and data from the large-scale Forest Dynamics Plot. Fisher's α (adjusted $r^2 = 0.546$; $P < 0.0001$).

We also looked at the phylogenetic species composition along the elevation gradient. We observed that the composition varied with altitude, and several species occurring at lower elevation were rarely found at the highest elevation. Only two species were found at both lowest and highest elevations (Fig. 3). We expected an even phylogenetic distribution at lower elevation narrowing down to a clustered distribution at the top of the mountain. However, the analyses showed that the difference of NRI from the expectations of the null hypothesis was not significant at either low elevation (NRI = 0.693, $P = 0.239$) or high elevation (NRI = 1.156, $P = 0.122$). In contrast, NTI (=

2.196) was greater than expected by chance alone ($P = 0.013$) at low elevation, while it was marginally significantly greater than expected at high elevation (NTI = 1.737, $P = 0.052$).

We cannot therefore reject our null hypothesis that the phylogenetic pattern of species assemblage is random along the altitudinal gradient. However, the higher NTI at both low and high elevations indicates that species occurring in the same habitat tend to be closer to each other than would be expected by chance; suggesting that habitat-filtering affects community assembly at all elevations.

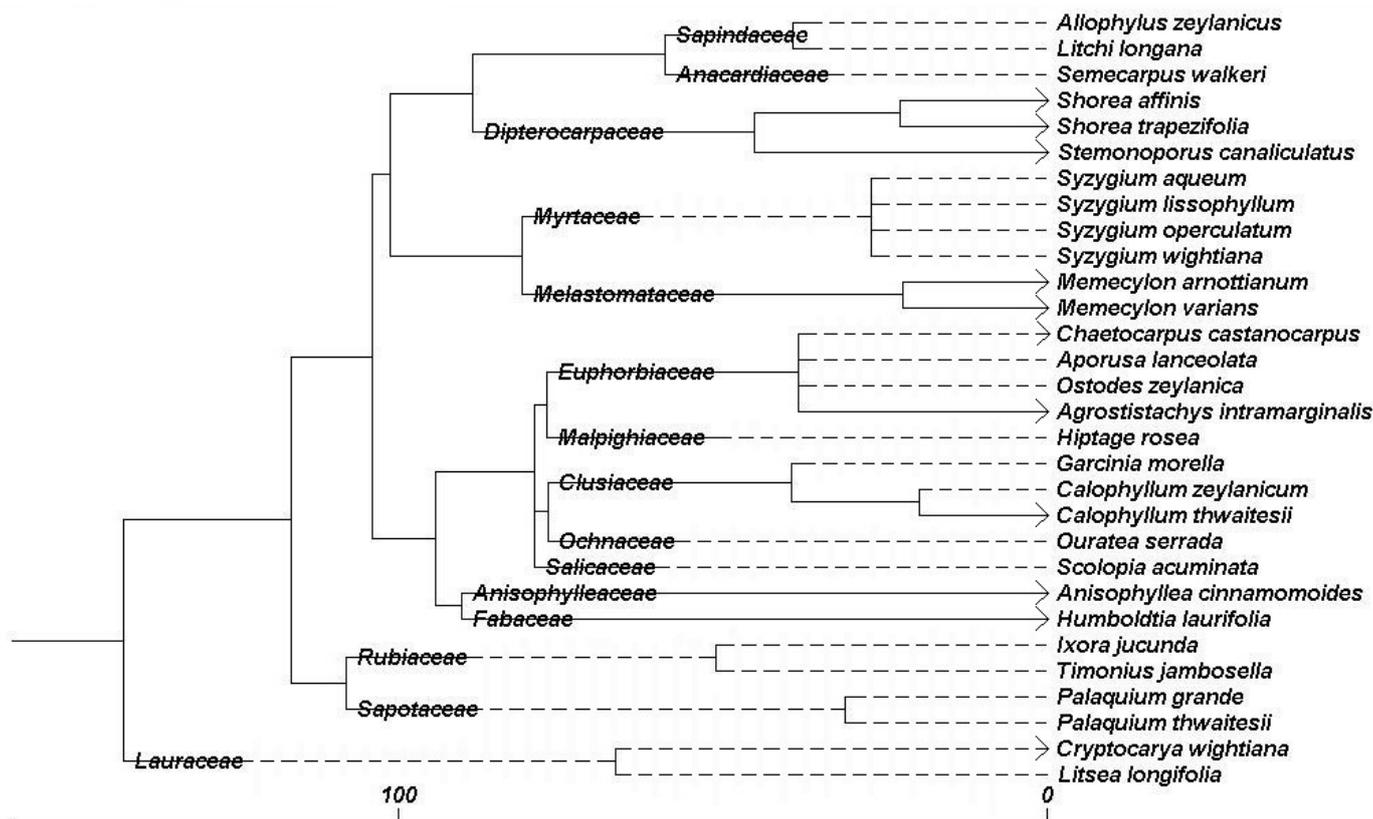


FIGURE 3. Species phylogenetic composition at low elevation (324 m) and high elevation (741 m) in Sinharaja. Dashed lines indicate present at low elevation only; arrows indicate present at high elevation only; and dashed lines with arrow indicate present at both low and high elevations).

DISCUSSION

As expected, the altitudinal pattern we got for the Sinharaja rain forest was a monotonic decrease in diversity with increasing altitude. Although, the suggested causes of variation in species richness along elevation are climatic, ecological, geographic and historical events, only ecological and geographic features are likely to play a substantial role in the pattern observed at this much localized scale. More specifically, area may potentially account for the monotonic decrease found in Sinharaja. Indeed, available area for species establishment is constrained by the existence of an upper limit that is itself dominated by non-suitable rocky habitats in Mount Moulawella. Other environmental factors are more or less homogenous along the elevational gradient we measured and are not expected to generate much habitat heterogeneity.

Decrease in species richness may also be explained by the larger elevational range of some species of Clusiaceae (*Mesua ferrea*), Dipterocarpaceae (*Shorea affinis*), Fabaceae (*Humboldtia laurifolia*) and Euphorbiaceae (*Aporosa lanceolata*) (Fig. 1; Table 2), but more importantly by the existence of more niches at low elevation than at the top. Indeed, the coexistence of more species at lower altitudes indicates a niche differentiation probably resulting from past competitions or evolutionary processes. Kluge *et al.* (2006) pointed out that the altitudinal patterns in species diversity might be taxon-dependent, as they might also depend on the variables used. In our case, variables other than elevation were not tested. However, other factors such as humidity, temperature, soil nutrients did not vary greatly along the gradient we surveyed, as well as in Sinharaja in general (Gunatilleke *et al.* 2004 and reference therein). The uniformity of environmental conditions may explain the extended range of

some species. Interestingly, *Mesua ferrea*, one of the most abundant species, was found at mid-elevation from 578 m to 660 m, whereas it is reported to occur only at lower elevation in the Sinharaja Forest Dynamics Plot (430 to 520 m) (Gunatilleke *et al.* 2004). This study thus showed that *Mesua ferrea* had a larger altitudinal range than has been previously reported. Nevertheless, the high density of *Mesua* and *Shorea* at higher elevation we found agrees with the results of Gunatilleke *et al.* (2004).

The ecological processes of community assemblage should be reflected in the phylogenetic composition. Species that are closely related are expected to be either ecologically distinct as a result of niche divergence or, in contrast, colonizing the same habitat owing to shared ability to respond to the ecological conditions. Our result showing clumping (higher NTI than expected by chance) is consistent with other studies (see Webb 2000) and indicates that the local assemblage is dominated by related taxa (Fig. 3) and that environmental filtering is the major force influencing the community assembly at all elevations. We expected, but did not find a higher degree of clustering at high elevations, although this may be due to the fact that we sampled only a small pool of species. It suggests that species interactions, mainly competition for a limiting resource, are a driving force in structuring the community.

Difference in species composition at lower and higher elevations also reflects the fact that other factors might contribute to the pattern. Particularly, the difference in species composition might be the result of interplay of environmental factors such as soil types and water-table depth. Studies show that in general there is a negative correlation between species richness and water-table depth, leading to some species being site specialists as the case of the Myrtaceae species found only at low elevation, perhaps due to intolerance to water stress. Species to family ratio has been used to evaluate the importance of competition and ecological processes in determining assemblage composition (Gotelli & Colwell 2001). Lower species to family ratio at higher elevation indicates stronger competition in the summit, where the groundwater is deeper, and corroborates the lower NTI (low phenotypic similarity).

Understanding of the spatial patterns in species richness and the mechanisms behind these patterns constitute a requisite for conservation biology. The altitudinal gradient is one of the most prevalent patterns, but also very controversial, in the study of community structure. Although, our study encompasses a relatively small altitudinal range, it showed that once again the monotonic decrease in species diversity competes with the hump-shaped pattern. Diversity in Sinharaja rain forest is higher in lower elevation forests. The causes of such a pattern are not well understood and should be explored further.

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APPENDIX 1: <i>Species pool used to generate the phylogenetic tree</i>		
Family	Genus	Species
Anacardiaceae	<i>Semecarpus</i>	<i>walkeri</i>
Anisophylleaceae	<i>Anisophyllea</i>	<i>cinnamomoides</i>
Dipterocarpaceae	<i>Shorea</i>	<i>affinis</i>
Dipterocarpaceae	<i>Shorea</i>	<i>trapezifolia</i>
Dipterocarpaceae	<i>Stemonoporus</i>	<i>canaliculatus</i>
Euphorbiaceae	<i>Agrostistachys</i>	<i>intramarginalis</i>
Euphorbiaceae	<i>Aporusa</i>	<i>lanceolata</i>
Euphorbiaceae	<i>Chaetocarpus</i>	<i>castanocarpus</i>
Euphorbiaceae	<i>Ostodes</i>	<i>zeylanica</i>
Salicaceae	<i>Scolopia</i>	<i>acuminata</i>
Clusiaceae	<i>Calophyllum</i>	<i>zeylanicum</i>
Clusiaceae	<i>Calophyllum</i>	<i>thwaitesii</i>
Clusiaceae	<i>Garcinia</i>	<i>morella</i>
Lauraceae	<i>Cryptocarya</i>	<i>wightiana</i>
Lauraceae	<i>Litsea</i>	<i>longifolia</i>
Fabaceae	<i>Humboldtia</i>	<i>laurifolia</i>
Malpighiaceae	<i>Hiptage</i>	<i>rosea</i>
Melastomataceae	<i>Memecylon</i>	<i>arnottianum</i>
Melastomataceae	<i>Memecylon</i>	<i>varians</i>
Myrtaceae	<i>Syzygium</i>	<i>aqueum</i>
Myrtaceae	<i>Syzygium</i>	<i>lissophyllum</i>
Myrtaceae	<i>Syzygium</i>	<i>operculatum</i>
Myrtaceae	<i>Syzygium</i>	<i>wightiana</i>
Ochnaceae	<i>Ochna</i>	<i>serrata</i>
Rubiaceae	<i>Ixora</i>	<i>jucunda</i>
Rubiaceae	<i>Timonius</i>	<i>jambosella</i>
Sapindaceae	<i>Allophylus</i>	<i>zeylanicus</i>
Sapindaceae	<i>Litchi</i>	<i>longana</i>
Sapotaceae	<i>Palaquium</i>	<i>grande</i>
Sapotaceae	<i>Palaquium</i>	<i>thwaitesii</i>

Does the Large White Sepal of *Mussaenda frondosa* (Rubiaceae) Attract More Flower Visitors?

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ABSTRACT

For flowering plants to increase the pollination success is very important. *Mussaenda frondosa* is abundant in tropical areas, especially in disturbed sites and secondary forest edges. *Mussaenda frondosa* produce small orange flowers usually with several enlarged white sepals in one inflorescence. The goal of this study was to confirm whether the function of the enlarged white sepal is to attract flower visitors. In field observation, the butterfly *Papilio helenus mooreanus* was the main flower visitor of *M. frondosa*. Our results showed that a large tree attracts more flower visitors than smaller trees. The main flower visitor *P. helenus mooreanus* flew directly to *M. frondosa*, and ignored other nearby flowering plants. Even though there was no direct evidence to support that the white sepals function to attract flower visitors, we suggest that the white sepal is a distinct visual signal to attract flower visitors from the long distance.

Key words: *Mussaenda frondosa*; flower visitor; pollination; attract device.

FOR PLANTS, IT IS NECESSARY TO DISPERSE MALE GAMETES from one individual to another conspecific to achieve sexual reproduction (Turner 2001). In flowering plants, many plants rely on flower visitors to carry pollen from flower to flower since pollen is mobile but not motile. Therefore, how to attract more flower visitors to visit flowers and carry pollen to another conspecific is the most important problem facing flowering plants. Many flowering plants have large, conspicuous and colorful flowers that give off a strong odor to attract their pollinators. Plants use different devices to attract their pollinators and increase the pollination success. In tropical areas, *Mussaenda frondosa* (Rubiaceae) is a unique case – the white sepal is large compared to the small orange flower. Borges *et al.* (2003) showed that the white sepal absorbs ultraviolet light and removal of white sepal caused a significant decrease in fruit set. They suggested that the white sepal was an important visual signal for flower visitors.

In this study, we investigated whether the enlarged white sepal attracts flower visitors and whether increasing sepal number attracted more flower visitors. If the white sepal is an important visual signal for flower visitors, the rate of visitation should increase relative to the white sepal number.

METHODS AND METHODS

STUDY SPECIES.—*Mussaenda frondosa* is a scandent shrub with hirsute branchlets distributed in the secondary forests in Sri Lanka and south India (Dassanayaka & Clayton 1998). In Sinharaja, *M. frondosa* grows in scrub and roadside particularly.

Its inflorescence has small brilliant orange flowers with several conspicuously enlarged white sepals.

STUDY SITE.—The study was conducted from August 21 to 24 in the Sinharaja Forest, a National Heritage Wilderness Area, an International Man and Biosphere Reserve and a Natural World Heritage Site, Sri Lanka.

TREES SAMPLING.—For 30 individual trees, the number of branchlets, white sepals, flowers and fruits on one shoot were counted, tree height and width were measured, and 5-10 shoots were collected. The number of flowers, buds and fruits were counted for each collected shoot in the laboratory. The sepals of each individual were removed from the collected shoots and put on a 10 cm x 10 cm paper and were photographed with a Nikon D70s DSLR camera. By overlaying the images of sepal by grids in PhotoImpact 8, the sepals' areas were measured.

VISITATION EXPERIMENT.—The tubular flowers of *Mussaenda frondosa* are probably pollinated by moths or butterflies. We expected that the large white sepal might play an important role in the pollination. To compare visitors and visitation rate between big and small trees, two different sized trees were observed. To confirm the function of large white sepal, three treatments were performed for similar sized small trees: (1) flower removal; (2) sepal removal; (3) sepal attachment. The flower and sepal number of controls and treatments are showed in Table 1. The visitation observation was conducted from 0900 h. to 1100 h. Flower visitors were recorded for 4 h in total on 23 and 24 August 2006.

TABLE 1. *The flower and sepal number of control and treatments.*

	Control		Treatment		
	Big tree	Small tree	Flower removal	Sepal removal	Sepal attach
Flower number	63	26	0	15	0
Sepal number	337	130	42	0	35

STATISTICAL ANALYSIS.—Allometric relationships among tree height, tree width, branchlet number, flower number, sepal number and fruit number were shown by application of standardized major axis estimation (SMA). Allometric relationships between two variables of biological interest are known widely. In general, linear regression, or ordinary least squares regression is applied to obtain the allometric relationship. Residuals are estimated in only the Y dimension by using linear regression, while they are estimated in both X and Y dimensions by using standardized major axis estimation. Standardized major axis estimation were performed with (S)MATR.

In the observation data including visitor number and visitation rate, the best-fitted generalized linear model (GLM), with a Poisson error distribution, was selected with the lowest AIC to confirm which parameters strongly affect visitor number or visitation rate.

RESULTS

TREE SAMPLING.—Allometric relationships between sepal number, flower number and fruit number, and tree size (height times width), were significant, while fruit number per inflorescence and mean sepal area does not correlate significantly with tree size (Table 2).

TABLE 2. Allometric relationships for sepal number, fruit number, fruit number per inflorescence, flower number, mean sepal area and tree size. (***: $P < 0.001$; NS: no significance).

logx-logy	Individual No.	Slope	Intercept	R^2
Sepal no.-size	30	1.12	-1.116	0.422 ***
Fruit no.-size	30	0.861	-0.678	0.364 ***
Fruit no. per inflorescence-size	18	-0.916	1.177	0.011 NS
Flower no-size	28	0.943	0.042	0.321 ***
Mean sepal area-size	30	-5.62	8.626	0.001 NS

Table 3. The total visitor number and visitation events between different trees and treatments, treatment 1: flower removal; treatment 2: sepal removal; treatment 3: sepal attachment for *Ficus sp.* leaves.

	Control (Big)	Control (Small)	Flower removal	Sepal removal	Sepal attachment
Visitors number	32	3	4	1	2
Visitation number	232	4	4	1	2

TABLE 4. The results of the model selection on GLM by using AIC.

	Estimate		Deviance	
	Intercept	Tree size	Null deviance	Residual deviance
Visitor number	3.47	-2.55	63.49	2.13
Visitation number	1.98	-1.89	68.37	0.21

VISITATION EXPERIMENT.—In our flower visitation experiment, 32 flower visitors belonging to three species: *Papilio helenus mooreanus*, *P. polymnestor* and *Hypolimnus bolina* were observed. The visitor number and visiting events of each treatment are shown in Table 3. Two hundred and forty-three visitation events in 4 h over two days were observed. All flower visitors visited the big tree and a total of 232 visiting events occurred on the big tree.

The results of model selections for visitation rate and visitor number are shown in Table 4. For the visitor data, four parameters including tree size, and flower removal, sepal removal and sepal attachment treatments, were added first. As the result of the model selection, the best-fitted model with the lowest AIC had only one parameter, tree size. This indicates that the three treatments had no effect to the visitor number and only tree size is related to it strongly.

For the visitation data, four parameters were added first. Because the visitation number depends on the visitor number, the visitor number was inserted to the model as the offset term. As the result of the model selection, the best-fitted model had only one parameter, tree size. This indicates that three treatments had no effect on visitation rate and only tree size is related to it strongly.

DISCUSSION

The sepal number, flower number and fruit number have significant correlations with tree size. Bigger trees have more shoots, and hence more inflorescences. Mean sepal area was not correlated with tree size, indicating that the energy investment to produce white sepal of *Mussaenda frondosa* is not different between small and big trees. The fruit number per inflorescence also did not change with tree size. This result indicates that the fruit set did not differ between small and big tree. Therefore, we can suggest that the reproduction success is not different between small and big trees.

In our observations, three butterfly species were recorded as flower visitors. Among 32 observed flower visitors only three individuals belong to two butterfly species; *P. polymnestor* and *Hypolimnys bolina*. This indicates *P. helenus mooreanus* is the main flower visitor of *M. frondosa*. The main visitor *P. helenus mooreanus* always flew directly to *M. frondosa* trees despite the presence of other flowering trees. These results suggest that *M. frondosa* relies on a small number of particular visitor species for pollination.

In visitation experiments, both visitor number and visitation rate were related with only tree size (Table 4). This indicates that both visitor number and visitation rate were not different among three treatments, but they were different between big and small trees.

In the sepal removal treatment, we attached extra flowers to the treatments, but only one pollinator was recorded. Although the number of flower visitation events to treatments was small, we believe that the enlarged white sepal may play a role for flower visitors to locate trees from a distance. First, when flower visitors are far away from *M. frondosa* tree, the large white sepals make the tree distinct. Flower visitors may easily recognize their feeding tree from the complex forest environment background. The other function of white sepals may be to emphasize the flowers location within a tree to increase the visitation efficiency of flower visitors.

Unfortunately, no direct evidence can support that the sepals serve as a attract device for pollinators. The pollinator visitation data was collected for only total 4 h in two observation days and was evidently not enough to obtain efficient data for analysis. We were prevented from collecting more data because of heavy rain storms during the study period.

We suggest that more data from visitation experiment is needed to understand the function of white sepal.

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Role of Calyx Coloration in the Attraction of Pollinators in *Elaeocarpus* (Elaeocarpaceae)

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ABSTRACT

Elaeocarpus serratus and *Elaeocarpus amoenus* have similar shape and pattern of flower, but different calyx coloration and flower odor. *Elaeocarpus serratus* has pale olive green calyx, while *E. amoenus* is red. We studied both species to examine whether different calyx coloration attracts different pollinators. The study was conducted in Sinharaja World Heritage Site, Sri Lanka, during 21-24 August 2006. We conducted direct observation at five individual trees and a calyx removal experiment. Due to heavy rain, all *E. serratus* tree lost their flowers during the study period, which made it impossible to observe this species. For *E. amoenus*, the result from direct observation showed that thirty-one species from three orders of invertebrate (*Lepidoptera* 19 species, *Diptera* 6 species and *Hymenoptera* 6 species) and one species of bird visited the flowers. There were no differences in visitor composition between four different periods of observation ($\chi^2 = 6.011$, $df = 9$, $P = 0.7388$). In the calyx removal experiment, we found no difference in visitation between treatment and controls ($\chi^2 = 3.0177$, $df = 2$, $P = 0.2212$). Hence, we were not able to show an effect of calyx coloration in *E. amoenus* on pollinator attraction nor were there differences in time period of visitation. This might be caused by the small sample size in the experiment.

Key words: *Elaeocarpus*; pollinator; Sinharaja; calyx coloration.

ELAEOCARPUS IS A GENUS CONSISTING OF 60 SPECIES distributed from Madagascar to Indo-Malaysia, North Australia and the Pacific. In Sri Lanka there are seven species of *Elaeocarpus*, of these four are endemic. These endemic species are *Elaeocarpus coriaceus*, *E. montanus*, *E. subvillosus*, *E. glandulifer* (Dassanayake *et al.* 1995). All species of this genus have similar characters in the shape and design of the flower, but there are some differences in color of sepals and fragrance. Flower color has been interpreted as an adaptation by which the flower attracts or guides pollinators, while floral fragrance is also a potential agent to attract pollinators and act as a mechanism to be selectively attractive to different species (Kearn and Inouye 1993). Regarding this importance of color and fragrance, we were interested to investigate this phenomenon in closely related *Elaeocarpus* species.

The objective of this study was to examine the function of calyx color and the odor of flowers in attracting visitors, to two *Elaeocarpus* species; *Elaeocarpus serratus* and *Elaeocarpus amoenus*. *Elaeocarpus serratus* has a white corolla and calyx, while *E. amoenus* has a white corolla with red calyx. Both species commonly occupy open areas and forest edges. We hypothesized that white and red calyx and different odors of the two *Elaeocarpus* species would attract different pollinators.

METHODS

This study was conducted on 21 to 24 August 2006 at Sinharaja, World Heritage Site, Sri Lanka. A lowland rain forest with over 5000 mm rainfall annually and no regular dry season. Two species of *Elaeocarpus* were selected for the study; *Elaeocarpus serratus* and *E. amoenus*. We observed all possible visitors that visited the flowers from 0700 h until 1600 h, and collected them using a sweep net for identification. Five individual trees were observed for this study. For each *Elaeocarpus* species, on three twigs with 100 flowers we removed the calyx and flower buds with the flowers in tact. Three other twigs were used as controls (Fig. 1). These twigs were placed at 1-1.5 m above the ground in different trees and arranged in lines with 2 m space between

twigs. Observations were conducted from 1000 h until 1400 h. All visitors were recorded and collected.



FIGURE 1. Experimental flower (A) flower without calyx and bud, and (B) control flower.

TABLE 1. *List of characters found in flowers of Elaeocarpus serratus and Elaeocarpus amoenus.*

Character	<i>E. serratus</i>	<i>E. amoenus</i>
Color of petiole	Pale green	Red
Color of calyx	Pale olive green	Red
Number of calyx	5	5
Length of sepal	4-6 mm	4 mm
Color of corolla	White	White
Number of corolla	5	5
Length of petal	4-5 mm	5-6 mm
Color of anther	Slightly black	White
Number of stamen	18-30	25-35
Anthesis time	Late afternoon (1500 h - evening)	Morning (0900 h -1100 h)
Strong fragrant	Late afternoon	Morning
Visiting time	Evening	Morning
Type of visitor	Moth	Butterfly, moth, bee, wasps, fly, ant

DATA ANALYSIS.—To examine whether there are differences between visitors coming in different time periods of a day, we used Chi-square analysis. Chi-square was used to examine the differences between visitors coming in the treatment and control flowers. Binomial test was used for overall abundance of visitors coming to the treatment and control twigs.

RESULTS

From the observation and study of flowers, we found some distinct differences between *Elaeocarpus serratus* and *Elaeocarpus amoenus* flowers (Table 1, Fig. 1).

In *E. amoenus* trees, we made three days of observation and found thirty-one species of invertebrate and one species of bird visiting the flowers. The largest group within the invertebrates was Lepidoptera with nineteen species, Diptera with six species, and Hymenoptera with six species. The only bird found visiting the tree was a Sri Lanka White-eye, from the Order Passeriformes (Appendix 1). On the experimental twigs, we observed three insect orders visiting, comprised of one species of Coleoptera, four species of Diptera and six species of Hymenoptera (Appendix 1).

There were no differences for types of visitor over the day (Table 2, $\chi^2 = 6.011$, $df = 9$, and $P = 0.7388$).

TABLE 2. *Number of visitor to the Elaeocarpus amoenus trees in four time periods.*

Order	0700 h - 0900 h	0900 h - 1200 h	1200 h - 1400 h	1400 h - 1600 h
Diptera	3	2	3	4
Hymenoptera	2	4	5	3
Lepidoptera	10	15	11	10
Passeriformes	1	0	0	0

Very few visitors were observed at our experimental set up, and there were no differences between visitors that came to the treatment flowers and the controls ($\chi^2 = 3.0177$, $df = 2$, $P = 0.2212$). The numbers of visitors from each order visiting the experiment twigs are presented in Table 3.

TABLE 3. *Number of visitors from different orders to the experimental twigs*

Order	1030 h -1200 h		1200 h -1400 h	
	Control	Remove	Control	Remove
Coleoptera	0	1	0	0
Diptera	4	1	1	0
Hymenoptera	4	3	2	2

DISCUSSION

Elaeocarpus serratus and *Elaeocarpus amoenus* have different floral characteristics that may be related with the target visitor. From our preliminary observations on *E. serratus*, we observed that the flowers tended to expand to maximum size in the late afternoon, and hence are most likely adapted to night pollinators. *Elaeocarpus amoenus* appeared to be adapted to day pollination. We found many visitors from morning until evening. The flowers have a red calyx and secrete strong fragrance from around 0900 h to 1100 h. Butterflies are the dominant visitors and elsewhere are reported to be attracted to flowers with orange or red colors (Momose *et al.* 1998, d'Abbrera 1998). Fragrance is associated with nectar and the opening periods of flowers suitable for attracting insects (Roubik 1989). We suggest that the main pollinators for *E. amoenus* may be butterflies. These insects spent a longer time visiting flowers, among the other visitors we observed, and were the most frequent visitors.

Our experiment did not demonstrate an effect of calyx removal in *E. amoenus* on visitation frequency or taxonomic composition of visitors. This is seemingly due to the small number of observations in our experiment.

Beside butterflies we often found ants and drosophilids visiting flowers both in the trees and the experiments. These two insects were probably not pollinators. Moreover, we had one sighting of a bird; Sri Lanka White-eye (*Zosterops ceylonensis*) visiting the flowers. This bird has been widely reported as a flower visitor not as a pollinator (Corlett 2004).

From the observations we found different sizes of butterfly, some of them visiting the flowers the whole day. Two smaller sized butterflies known as Yellow Grass butterflies (*Eurema blanda sithetana* and *Eurema andersonii orristoni*) visited the

entire day. *Eurema blanda* is a commonly occurring butterfly but *E. andersonii* is less common as it is only present from April to September (d'Abrera 1998). Larger sized butterflies that visited the flowers the whole day were the Paper butterfly (*Idea iasonia*) endemic to Sri Lanka and the Clipper butterfly (*Pantheros sylvia cyaneus*). The smaller and larger butterflies had different behaviors in collecting nectar. Smaller butterflies were usually found hanging upside down below the flower taking nectar, while larger butterflies usually sat above the flower stalk and extended their proboscis down and round to reach the flower.

In the experiments both treatment and controls attracted many species of ants very quickly in less than 5 min after we put the twigs on tree trunks. Drosophilids were a common and tiny visitor which visited both calyx removals and controls, but they evidenced different behavior when visiting treatments or controls. For calyx removals they went from top of flowers and moved quickly straight into the flowers, but in control flowers they stayed on the calyx for very long time before going into the flowers. Surprisingly, we got one record of a bee that visited both calyx removals and controls but first visited at control flowers and spent quite a long time feeding before leaving to visit calyx removal flowers nearby and spent a very short time on the flowers.

Our results were compromised by the small sample size and short time period of observation, and unfortunately the heavy rain. Further study with bigger sample size and longer observation is suggested. While we cannot say that the differences in calyx coloration attract different pollinators, there appears to be differences between pollinators and pollination periods for the two species of *Elaeocarpus*.

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APPENDIX 1. *Species found in Elaeocarpus amoenus trees** = *species found in treatment and control flowers*

Order	Family	Species
Coleoptera	Cossoninae	Cossoninae sp. 1*
Diptera	Undetermined	Diptera sp. 1*
Diptera	Undetermined	Diptera sp. 2*
Diptera	Undetermined	Diptera sp. 3*
Diptera	Undetermined	Diptera sp. 4*
Diptera	Drosophilidae	<i>Drosophila</i> sp. 1
Diptera	Drosophilidae	<i>Drosophila</i> sp. 2
Diptera	Tabanidae	Tabanidae sp. 1
Diptera	Tabanidae	Tabanidae sp. 2
Diptera	Tabanidae	Tabanidae sp.3
Diptera	Tabanidae	Tabanidae sp.4
Hymenoptera	Undetermined	Hymenoptera sp. 1
Hymenoptera	Undetermined	Hymenoptera sp. 2
Hymenoptera	Apoidea	<i>Megachile</i> sp. 2*
Hymenoptera	Apoidea	<i>Trigona</i> sp.1*
Hymenoptera	Formicidae	<i>Polyrachis</i> sp. 1
Hymenoptera	Formicidae	<i>Polyrachis</i> sp. 2
Hymenoptera	Formicidae	<i>Myrmecaria brunnea</i> (sp. complex)*
Hymenoptera	Formicidae	<i>Pheiole</i> sp. 1*
Hymenoptera	Formicidae	<i>Technomyrmex albipes</i> *
Hymenoptera	Megachilidae	<i>Megachile lanata</i>
Hymenoptera	Pompilidae	<i>Turneromyia</i> sp. 1
Lepidoptera	Undetermined	Lepidoptera sp. 1
Lepidoptera	Undetermined	Lepidoptera sp. 2
Lepidoptera	Undetermined	Lepidoptera sp. 3
Lepidoptera	Undetermined	Lepidoptera sp. 4
Lepidoptera	Undetermined	Lepidoptera sp. 5
Lepidoptera	Undetermined	Lepidoptera sp. 6
Lepidoptera	Undetermined	Lepidoptera sp. 7
Lepidoptera	Arctiidae	Arctiinae sp.1
Lepidoptera	Danaidea	<i>Idea iasonia</i>
Lepidoptera	Danaidea	<i>Ideopsis similes</i>
Lepidoptera	Lycaenidae	<i>Arhopala</i> sp. 1
Lepidoptera	Lycaenidae	<i>Jamides bochus</i>
Lepidoptera	Nymphalidae	<i>Cirrochoa lanka</i>
Lepidoptera	Nymphalidae	<i>Cupha erymanthis</i>
Lepidoptera	Nymphalidae	<i>Moduza procris calidosa</i>
Lepidoptera	Nymphalidae	<i>Pantheros sylvia cyaneus</i>
Lepidoptera	Papilionidae	<i>Graphium sarpedon</i>
Lepidoptera	Pieridae	<i>Eurema andersonii orristoni</i>
Lepidoptera	Pieridae	<i>Eurema blanda sithetana</i>
Passeriformes	Zosteropidae	<i>Zosterops ceylonensis</i>

Pollination and Fruit Set in *Schumacheria castaneifolia* (Dilleniaceae) in Forest Gaps and Edge Habitats

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ABSTRACT

This study examines the pollinators visiting *Schumacheria castaneifolia*, a small sized light demanding understorey tree. The study was conducted in Sinharaja rain forest at three sites one disturbed patch and other two undisturbed patches. We made direct observations for pollinators and also recorded for fruit and seed set in the trees. There was no significant difference in the visitation rates of pollinators between sites, which may be due to small number of observations. But it was marginally significant in one of the forest patch. There was no significant difference in fruit set between the sites.

Key words: *Schumacheria castaneifolia*; pollinators; fruit set; *Nomia* sp.

ANIMAL-POLLINATED FLOWERS HAVE EVOLVED VARIOUS REWARDS AND ATTRACTANTS to entice pollinators, and thus promote pollen transport. Whereas nectar and pollen are the most common rewards, a diversity of other materials, including floral tissues offered as brood sites for pollinators in some plant groups (Ashton *et al* 1997). Reproductive failure in plant species can often be attributed to either pollination limitation, where there is insufficient movement of viable pollen between flowers (e.g., because of an absence of pollinators), or to resource limitation, where insufficient resources (such as water or nutrients) are available to allow maximum fruit set to take place (Bierzychudek 1981; Stephenson, 1981), or to both.

Successful sexual reproduction in animal-pollinated species depends to a large extent on the behaviour of flower visitors (Conner *et al.* 1995; Harder & Barrett 1993; Pellmyr & Thompson 1996; Thostesen & Olesen 1996; Webb & Bawa 1983). The number of visits a plant receives and the number of pollen grains deposited per visit affect female reproductive success through seed set (the proportion of ovules fertilized) and male reproductive success through pollen export (the number of ovules fertilized by pollen grains from that plant) (Burd 1994).

Schumacheria castaneifolia, is endemic to Sri Lanka and is usually found in rain forest in gaps and on the fringes. It is an understorey tree that normally grows to around eight to ten meters in height. Its prominent identification characteristics are smooth, brownish bark, inflorescences produced terminally in spreading panicles, numerous yellowish sessile flowers with nectar present at the base of the ovaries, indehiscent fruits containing three ovules, and covered with a membranous aril base.

Schumacheria castaneifolia is found in both forest gaps and edge environments. We hypothesized that the pollination environment, specifically the types of flower visitors, their abundance, and efficiency as pollinators, would be different in these two habitats. Hence, in this study we addressed the question: Is pollination quality is better in forest gaps or in edge habitats? We postulated that forest gaps sites would be closer to diverse forest habitat, and therefore to a greater diversity of potential pollinators. Hence, we proposed three hypotheses for investigation: (1) *Schumacheria castaneifolia* should receive more flower visitors in forest gaps than in edge environments; (2) flower visitors in forest gaps will be better quality pollinators;

and hence (3) there will be higher fruit and seed set in forest gaps than on the edge.

MATERIALS AND METHODS

STUDY SITE.—The present study was conducted at Sinharaja World Heritage Site, which is relatively undisturbed lowland rain forest in Sri Lanka. It is a significant part of the Western Ghats and Sri Lanka biodiversity hotspot.

The study was conducted at three sites in the Sinharaja forest, two disturbed areas (buffer zone and Mulawella trek trail: edge habitat) and one undisturbed area (near the research station: forest gaps).

Four to five trees together in a clump (< 5 m distance between trees) and three solitary trees (> 30 m distance between trees) at a distance from clump were selected at each site for observations of insect visitation. The same trees were used to count fruit and seed set.

The flowers opened in early morning and remained open for one day. The trees were observed for pollinators from 0600 h to 1100 h and we recorded the number of pollen visitors in 30-min intervals. The number of inflorescences per branch, number of flowers per inflorescence, fruit set per inflorescence and the number of fruit and seed aborted per inflorescence were recorded. The nearest neighbor distance of each tree was also recorded.

DATA ANALYSIS.—The data was analysed using R 2.3.1. The results were examined using a Generalized Linear Model based on a Poisson distribution, with the number of pollinators and pollinator visits as dependent variables. For fruit and seed set, since these are proportions a Generalized Linear Model with binomial distribution was used.

RESULTS

We saw four species visiting the flowers of *S. castaneifolia*; a large bee, *Nomia* sp. (Halictidae), a beetle, and an ant (*Camponotus* sp.). We also saw a wasp hunting on leaves and flowers. However, we only saw pollen loads on *Nomia* sp. and the beetle, and thus considered these to be the major pollinators. No pollen

was found on other insects. The insect visitation was high from 0830 h to 1030 h. Pollinators were not observed visiting flowers in evening. *Nomia* sp. had highest number of visits when compared to other insects, which were negligible. There was no significant difference in the number of pollinators visiting the flowers in the three areas.

The number of flowers visited per visit made by the pollinators was not significantly different between the two edge sites, but was significantly higher at the research station.

There was no significant difference in fruit set between the three sites.

DISCUSSION

This study documents the pollinator visitation, number of pollinators, and fruit set in three sites at Sinharaja. Pollinators collected nectar from the flowers. Pollinator's preferred undisturbed patch as they could feed quickly and availability of flowers in this patch was more. In the present study we saw only two species of pollinator.

Fruit set showed no significant difference between the three sites. We suggest this indicates flowers are pollinated very quickly. The greater number of flowers visited per visit at the forest site probably reflects consumption of the nectar thus forcing insects to search more flowers to find nectar. The high fruit set at all sites indicates the efficiency of the pollinators and contrary to our predictions that pollination is not more limiting in the edge habitats.

ACKNOWLEDGMENTS

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Distribution of Terrestrial Pteridophytes with respect to Topography and Light Exposure in Tropical Rain Forest

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ABSTRACT

Terrestrial Pteridophytes community in the Sinharaja Forest Dynamics Plot was studied to understand the relationship of topography and light with species composition. The survey documented 12 species of Pteridophytes from nine families. Results showed that some species were related to their topological feature, which is valley, while others did not.

Key words: light intensity; Pteridophytes; terrestrial; topographical gradient; Sinharaja.

TROPICAL RAIN FORESTS ARE EXCEPTIONALLY RICH IN PTERIDOPHYTES (FERNS). A small area like Bukit Timah in Singapore was recorded to harbor a fern flora as diverse as 65 species from various families (Corlett 1990), which forms vary from trees and shrubs (5 spp.), climbers (7 spp.), herbs (29 spp.) to epi/hemi-phytes (26 spp.). For the whole island of Sri Lanka, the almost-published *Revised Handbook to the Flora of Ceylon* (Shaffer-Fehre *in review*) recorded 30 families of ferns and fern allies, which ranged variably in the life form and habitat occupation, from aquatic ferns (Marsileaceae, Azollaceae) to epiphytic ferns (Vittariaceae).

Terrestrial Pteridophytes are abundant in the understorey, but their roles in the dynamics of the tropical forests are of little understanding. Existing works on ferns are mostly taxonomic rather than ecological, leaving *terra incognita* in the ecological aspects of forest ferns.

Plants living along topographical gradient experience soil moisture regimes. For example in Sarawak, *Dryobalanops aromatica* was significantly more abundant on convex and steep slopes in contrast to its close relative, *D. lanceolata* (Itoh *et al.* 2003), a condition that might also apply to Pteridophytes communities.

Generally, ferns prefer moist environment, and some species show this preference very pronouncedly, such as all members of *Angiopteris*, which are always found under close canopy cover, often near streams (Holttum 1966). In Sinharaja, the simple fronded tree fern *Cyathea sinuata* seems to live always near streams, showing its fondness of high moisture and becomes scarce with increasing elevation which has lower moisture (*pers. obs.*).

Pteridophytes differ in their tolerance to sunlight exposure. The terrestrial forest ferns in the Sinharaja Forest Dynamics Plot are mostly categorized as shade-ferns, living under close canopy. Whenever there is disturbance, causing a gap to occur between canopies, the Pteridophytes composition changes, sun-ferns thrive. Big gap as the logging trail will be invaded exclusively by *Dicranopteris linearis*. This sun-fern species provides protection to land erosion, but also a nuisance to foresters, for it prevents the seedling regenerations, unless some efforts to restore the vegetation condition are introduced (Holttum 1959-1982; Cohen *et al.* 1995). Small natural gap inside the forest can be occupied by sun-ferns or tolerant shade-fern species.

It is important to understand how the Pteridophytes respond to different environmental factors as part of the whole understanding toward tropical rain forest dynamics. Terrestrial ferns

are of great interest since this type of ferns along with the seedlings forms a special community in forest floor.

This research aims to understand the relationship between the compositions of Pteridophytes community with the topographical gradient and the contrast in light intensity caused by natural gap inside the permanent Forest Dynamics Plot (FDP) in Sinharaja, Sri Lanka. At different types of topological features and different natural light exposures, Pteridophytes species within the FDP would be sampled to understand such relationship.

MATERIALS AND METHODS

In the FDP, natural gaps in different topographical features, namely ridges, mid-slopes and valleys were surveyed. The middle point of each natural gap is appointed the observation point, and said as open area with direct sun exposure. Another point under the canopy, approximately 15 meter adjacent to the open area point was also set as a contrasting point, and assigned as shaded area. The latter must also occupies a similar topographic feature to the former.

I set a total of 89 points throughout the FDP. In each point, four Pteridophytes individual closest to the center of the point were recorded. I recorded some habitat variables such as the topological features and the light exposure. Sloping areas with rivulet were assigned as valleys rather than slopes. Specimens of unknown species are taken for latter identification using Shaffer-Fehre (*in review*), Holttum (1966, 1959-1982), Hovenkamp (1998), Nooteboom (1998), Saunders (1998), Lafferrier (1998), Kato (1998), Zhang & Nooteboom (1998) and Boonkerd & Pollawatn (2000). The taxonomic classification follows Shaffer-Fehre (*in review*).

To make a throughout analysis between the fern species to light intensity and the topographical feature, I employed ordination technique using metaMDS. The similarities between groups of sampling unit were tested using ANOSIM. To test the probability of some four common species to occupy certain topographical gradient in the study area, I tested the data set using chi-square test. The whole analyses were done with R version 2.3.1.

RESULTS

The survey documented 12 species from nine families of terrestrial ferns and fern allies inside the Sinharaja Forest Dynamics Plot; much less than the total 30 families of the fern flora of Sri Lanka (Shaffer-Fehre *in review*), or 70 species from 18 families of Pteridophytes ranging from aquatic to epiphytic life forms in Kanneliya MAB Reserve at a recent survey by Ranil *et al.* (2004) in an over six months survey (Table 1). Twelve species collected in this survey represents only lowland forest fern flora (where the study area is situated), excluding the epiphytes.

TABLE 1: List of Pteridophyte species in Forest Dynamics Plot, Sinharaja (12 species from eight fern and one fern allies families)

Family	Species
Blechnaceae	<i>Blechnum orientale</i>
Cyatheaceae	<i>Cyathea sinuata</i>
	<i>Cyathea hookeri</i>
	<i>Cyathea crinita</i>
Dryopteridaceae	<i>Tectaria paradoxa</i>
	<i>Tectaria decurrens</i>
Dennstaedtiaceae	<i>Lindsaea caudata</i>
Oleandraceae	<i>Nephrolepis bisserata</i>
Polypodiaceae	<i>Microsorium punctatum</i>
Selaginellaceae	<i>Selaginella cochleata</i>
Thelypteridaceae	<i>cf. Metathelypteris flaccida</i>
Woodsiaceae	<i>Athyrium cumingianum</i>

The ordination technique to plot all the data parameters showed that light exposures (“lightopen” and “lightshaded”) are relatively grouped around the 0 of both ordination axes (NMDS1 and NMDS2) (Fig. 1), showing that this light condition played small part in determining the Pteridophytes flora of the area, as opposed to what topography showed.

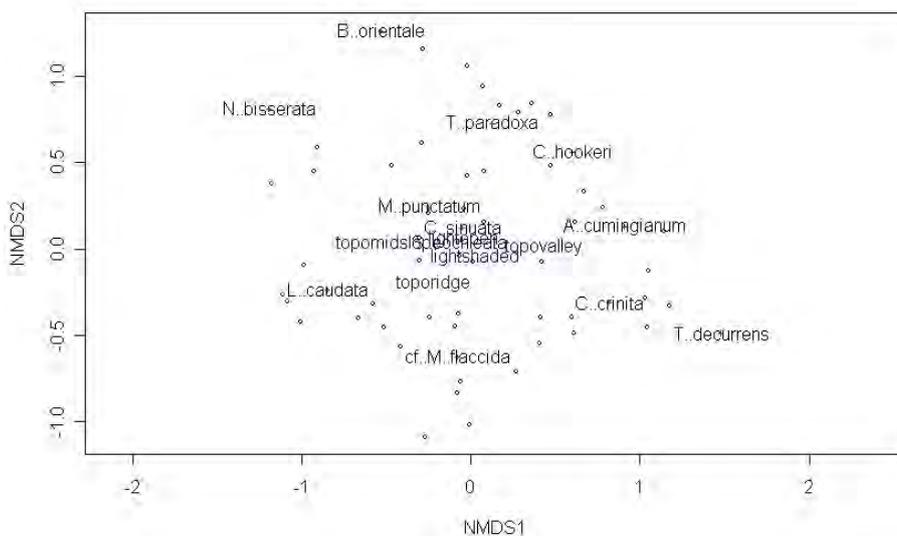


FIGURE 1. Ordination of the Pteridophyte species against the topographical features and light exposure (Method = Non-metric Multi-Dimensional Scaling).

Analysis of the similarities between topological gradient (Fig. 2) showed that the dissimilarity value was biggest between groups of topographical features than within each topographical feature.

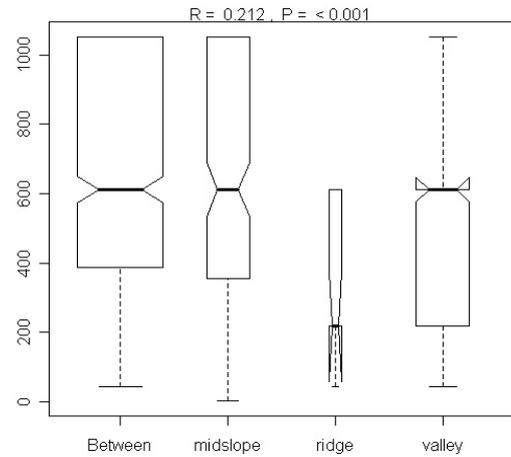


FIGURE 2. Boxplot of similarities between topographical gradients.

Analysis on more commonly found species in the study area (Table 2) showed that two species (*Lindsaea caudata* and *Cyathea crinita*) tended to occupy certain topological gradient ($P < 0.005$) while the other two species, *Tectaria paradoxa* and *cf. Metathelypteris flaccida* tended to occur in all three topological gradients.

TABLE 2. Chi-square tests on four common Pteridophytes species in different topological gradients

Species	χ^2	df	P-value
<i>Tectaria paradoxa</i>	0.5255	2	0.769
<i>Lindsaea caudata</i>	20.9962	2	2.759e-05
<i>cf. Metathelypteris flaccida</i>	8.3591	2	0.01531
<i>Cyathea crinita</i>	21.2181	2	2.469e-05

DISCUSSION

Figure 1 showed that some species of Pteridophytes, like *Blechnum orientale*, *Nephrolepis bisserata*, *Lindsaea caudata* and *Tectaria deccurens* occupied distinctive habitat of their own, and most unlikely to coexist with each other. This habitat preference was influenced by topography more than light. As seen in Fig. 1, the light exposures were plotted toward the 0 along both NMDS1 and NMDS2 axes. Each species had its own preference relative to light exposure and topography. *Blechnum orientale* and *N. bisserata* are known as sun-ferns, commonly found on the big opening (Holtum 1966, Shaffer-Fehre *in review*). Places where the two species were found are big landslide places which were not occupied by *Clidemia hirta*.

Tectaria deccurens was always found in the valleys where rivulets are frequent. This species really shows its affinity toward wet condition, and probably can not withstand drought as exposed by mid-slopes and ridges.

Conversely, *Lindsaea caudata* tended to “avoid” valleys. This species probably had developed certain physiological specialty to withstand drought, thus specialized in colonizing emptier niches in drier areas of the forest such as mid-slopes, which are avoided by other wet-loving Pteridophytes species.

Chi-square test on four common species (Table 2) confirmed the previous analysis, showing the probability of *Lindsaea caudata* and *Cyathea crinita* to occupy certain topological gradient is highly significant ($P < 0.005$), with the former tending to prefer the mid-slope while the latter the valley. The other two species, *Tectaria paradoxa* and cf. *Metathelypteris flaccida* tended to distribute in all three topological gradients.

Cyathea crinita seemed suited in the valley and best adapted to ever wet condition. This species, with its tree habit, is the only fern species growing in a valley gap rapidly colonized by *Clidemia hirta* and *Strobilanthes* sp. Some “sporelings” of *C. crinita* are observed as the only fern species waiting under the weedy shade of *Clidemia hirta* and *Strobilanthes* sp. to shoot up when the future gap is introduced.

In the Fig. 2, test using ANOSIM showed that the compositional dissimilarities between groups were indeed greater than those within the groups, showing that topography units are significantly different in their species composition. This is also confirming the previous analyses in testing the way Pteridophytes species distributed in certain type of forest are influenced by abiotic factors, as topography and light which are discussed here.

In the future it is important to include other Pteridophytes life forms such as the epiphytes, since they probably have greater degree of diversity and might also play important role in tropical rain forest ecology. A bigger sampling size and sampling area must be done to capture the more realistic composition and distribution of Pteridophytes in Sinharaja

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Use of Benthic Macro-Invertebrates to Assess Stream Water Quality in Disturbed and Undisturbed Watersheds

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ABSTRACT

Benthic macro invertebrates are the most widely used group of organisms to assess the river and stream health. I collected benthic samples from six streams, three streams were in disturbed watershed areas and three streams in undisturbed forest areas. From each stream two samples were collected and the macro invertebrate community was analyzed. The Family Biotic Index (FBI) was calculated for each sampling site. FBI value did not show significant difference between upstream reaches and downstream reaches of the same stream. Whereas FBI mean values of watershed disturbed and undisturbed forest streams were significant different ($P < 0.0001$). Thus watershed undisturbed streams have excellent water quality and in watershed disturbed streams water quality vary from good condition to fair condition according to Hilsenhoff (1988) criteria.

Key words: Benthic macro invertebrates; water quality; family biotic index.

BENTHIC MACRO INVERTEBRATES ARE THE MOST WIDELY USED GROUP OF ORGANISMS in recent years to assess the river and stream health. (Resh & Jackson 1993). Benthic macro invertebrate are used to assess water quality for various reasons. First, they are found everywhere, include different taxa, and vary widely in their sensitivities to pollutants and to various perturbations. Therefore, it is probable that most types of disturbance will change the macro invertebrate community composition in a stream. Secondly, macro invertebrates occupy a central role in the ecology of rivers and form key links in the aquatic food chain. Their diversity and abundance are therefore crucial to maintaining a balanced, functioning and healthy ecosystem. Thirdly, benthic macro invertebrates are generally sedentary and have life cycles ranging from a few weeks to a few years. Thus, their communities recover only slowly if damaged by a disturbance event (Chessmen 1995). Taxonomic richness and composition of benthic macro invertebrates is often affected by small to medium scale factors, such as water temperature, shade, riffle depth, channel slope, substrate, water conductivity, removal of riparian vegetation, and water shed habitat (Collier 1995).

Sinharaja's tropical rain forest is over 11,187 ha in extent and provides the headwaters for two major rivers namely 'Kalu Ganga' and 'Gin Ganga'. A large number of streams originate from the deep forest and drain through valleys to feed the main stream. In the buffer zones various anthropogenic activities have taken place that might have caused stream deterioration., Housing, conversion of riparian vegetation and watershed into tea lands, which leads to soil erosion and silting, exposure of streams to light, agricultural fertilizers, and pesticides runoff, and household waste draining directly to streams, may all cause stream deterioration. The objective of this study was to investigate the water quality in stream of buffer zone areas and in the forest by sampling their macro invertebrate faunas.

MATERIALS AND METHODS

At total of six streams were assessed, representing three forest streams and three buffer zone streams. From each stream, two samples were collected, representing upstream and downstream localities. A total of twelve samples were taken. The sample sites of streams were similar in substrate composition (cobbles, gravels and leaf litter), current velocity (moderate), depth, but different in watershed habitat. Buffer zones watersheds had human habitations and tea plantations. Forest streams were surrounded by

forest with dense canopy cover. Standardized samples were obtained from each site. Samples were taken using an aquatic D-shaped net with 0.25 mm mesh. The substratum was disturbed to dislodge benthic organisms while holding the collecting net downstream of the disturbed area. Stones were moved, overturned, and scrubbed by kicking with the feet and rubbing with the hands. A total of 5 m length for each site was sampled. Samples were preserved immediately in 70% ethanol and brought to the laboratory for identification. All macro invertebrate specimens were examined under stereomicroscope and identified to morphospecies and family using available keys and text books. The Family Biotic Index (FBI) was calculated according to Hilsenhoff tolerance score system. The FBI was obtained for the each site by multiplying number of individuals of a family with the tolerance score assign to the family, and the total sum of scores divided by the total number of individuals in the sample recorded. Data were analyzed using R 2.3.1. The water quality of sample sites was compared using Hilsenhoff (1988) criteria for water quality assessment based on the FBI (Table 1).

TABLE 1. *Water Quality Based On Family Biotic Index (FBI) Hilsenhoff (1988)*

FBI	Water Quality
0.00 – 3.75	Excellent
3.76 – 4.25	Very Good
4.26 – 5.00	Good
5.01 – 5.75	Fair
5.76 – 6.50	Fairly Poor
6.51 – 7.25	Poor
7.26 – 10.00	Very Poor

RESULTS

Overall nineteen families of benthic organisms were recorded. The FBI values varied from 3.01 to 5.85. According to linear modeling there was no significant difference ($P = 0.2829$) between FBI values in upstream and downstream reaches of the same stream. Whereas, there was a highly significant difference ($P < 0.0001$; Fig. 1) in FBI values in forest and buffer zone streams. Macro invertebrate family composition for the sites was

measured using Jaccard Index [$C_j = a / (a+b+c)$] and cluster analysis performed (Fig. 2).

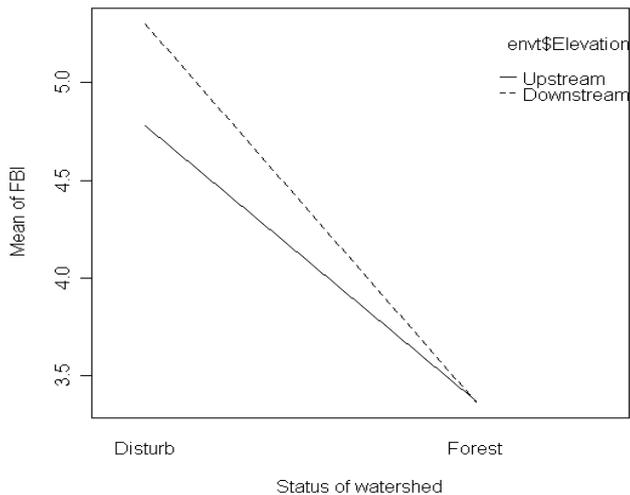


FIGURE 1. An interaction plot of mean Family Biotic Index (FBI) values for forest and buffer zone streams at Sinharaja.

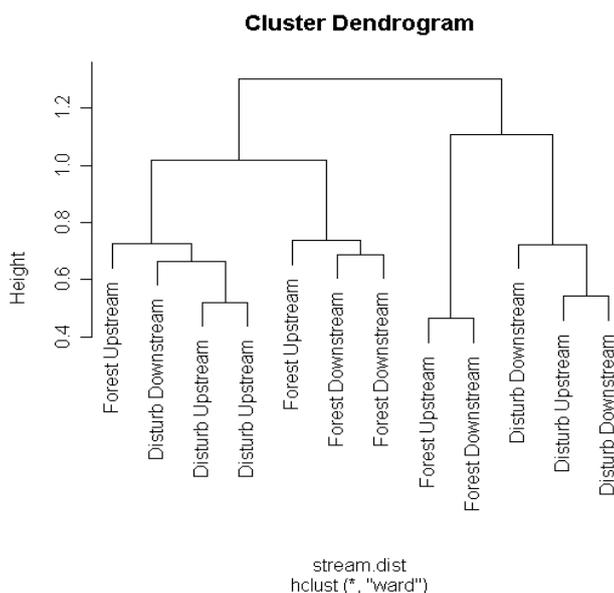


FIGURE 2. Dendrogram of benthic macro invertebrate community composition clustered according to Jaccard Index in forest and buffer zone streams.

DISCUSSION

Mean FBI was below 3.5 in forest streams and increased up to 5.85 in buffer zone streams, but there was no significant difference in mean FBI values from upstream to downstream reaches of the same stream. According to Hilsenhoff (1988) criteria the undisturbed streams are in excellent water quality (FBI < 3.75) whereas disturbed are streams water quality vary from good quality to fair condition (FBI = 5.75–4.26). From the cluster analysis it is evident that there is not much difference in

taxonomic composition of benthic macro invertebrates in upstream reaches and down stream reaches of the same stream as these are often paired together in the cladogram. At second level, macro invertebrate community composition in forest streams varies from buffer zone streams. It is evident that anthropogenic activities in the buffer zone have caused stream deterioration. Further research has to be carried out to find exact reasons for water quality deterioration and the changes in macro-invertebrate community composition.

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Gall Diversity and Host Specificity in the Rain Forest of Sinharaja, Sri Lanka

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ABSTRACT

Interactions between plants and herbivory insects are common in the rain forest. Such interactions have often resulted in high selection pressure, and consequently, high specificity between animals and the plants they utilized. Diversity and specificity of galls on their plant hosts were studied in the rain forest of Sinharaja. Of 17 tree species sampled, 14 species were found infected by a total of 25 gall morphotypes. Four species from genus *Shorea* section *Doona* (Dipterocarpaceae) share certain gall morphotypes. Number of gall morphotypes per tree genus was found to be positively related with the number of tree species per genus. These results suggested that the relationship is not monospecific and galls are likely to infect related species. The number of gall morphotypes may be a direct function of plant diversity. Similar morphological phenotypes and defense mechanisms in closely related plant species are likely to be the main explanations for host transfer among gall morphotypes.

Key words: congeneric infection; galls; herbivory insects; specificity.

THE FOREST OF SINHARAJA HARBORS A DIVERSE ARRAY OF PLANT SPECIES, which provide a wide range of resources for other organisms. This also provides a great opportunity to study various plant-animal interactions, such as herbivory and pollination, and the mechanisms that drive co-evolution, and maintain the balance of such relationships.

All plants in the forest have to deal with various challenges in the battle of survival, and the most severe of those may be from herbivorous insects. As a result, plants produce various defence mechanisms, which include physical barriers and organic chemical compounds. This in turn leads to the diversification and specialisation of herbivorous insects, many of which utilize only a limited range of plant species, where different guilds of herbivores have overcome their host plant defences (Futuyma, 1998).

One such relationship can be seen between gall-inducing insects and their host plants. Galls are abnormal growth of plant tissues, inside which juvenile stages of the gall-inducing insects shelter and feed. The gall is a response of the plant to chemical stimuli secreted by the insects, mostly of the orders Hymenoptera, Diptera and Coleoptera. Its shape and location are often characteristic of the plant and insect species involved (Norris, 1991). In the forest of Sinharaja, such phenomenon is so common that sometimes whole plant individuals or local populations are infected by galls.

Few studies have been done on the gall-inducers and their host plants, except in the case of fig (*Ficus* spp.) and their species-specific fig wasps (Hymenoptera: Chalcidoidea) (Compton *et al.* 1996; Kerdelhué *et al.* 2000). The unique, enclosed structure of fig syconium performs a remarkable selection pressure on their pollinator fig wasps, making the relationship strict and obligated. Nonetheless, gall-formation on the exposed vegetative parts (*e.g.*, leaves, buds, stems or roots) is expected to be less host-specific. Low host specificity of herbivorous insects has been shown by Novotny *et al.* (2002) in the tropical lowland forest of New Guinea.

Host specificity is difficult to measure unless the entire guilds of herbivorous groups as well as host plant groups are sampled (Novotny *et al.* 2002). In this study, I attempt to examine the specificity of gall morphology on four important tree families in Sinharaja forests. Clusiaceae, Dilleniaceae, Dipterocarpaceae and Euphorbiaceae were chosen as the focal groups, for their significant abundance and number of congeneric species (*Shorea* spp.) (Gunatilleke *et al.* 2004).

I assumed that gall morphology is galler-specific, *i.e.*, structurally similar galls on different but related tree species are thought to be the extended phenotypes of the same gall-inducing insect, instead of reflecting similarity in the host trees galled (Stone and Schönrogge, 2003). My hypothesis was that gall induction on vegetative structures is less host-specific and therefore same gall morphotype is to be observed on different but closely related trees (*e.g.*, *Shorea* spp.).

METHODS

FIELDWORK.—On 21-23 August 2006, I sampled gall-infected individuals along the forest trails near Sinharaja Research Center. Trails at different elevation and habitats were included, so that as many habitat specialists as possible (Gunatilleke *et al.* 2004) could be encountered. I first determined the family of every sapling and understory tree shorter than 5 m within sight, and inspected the targeted plants for galls. The galls were then collected for morphotype classification. Only tree species with more than 10 individuals inspected were included in the analysis.

ANALYSES.—To classify the galls, I described their position, shape, color and size (Appendix 1), as well as numbered the gall morphotypes to facilitate analysis. Then, I summarized and compiled the number of gall morphotypes per tree species/genus, number of gall-types shared between congeners, and number of tree species per genus. Also, total number of tree species per genus within the region of Sinharaja was determined (Gunatilleke *et al.* 2004, pers. comm. C. V. S. Gunatilleke). Data were fitted on Generalized Linear Model (GLM) based on Poisson distribution of errors. Analyses were performed on R 2.3.1 (R Development Core Team, 2005).

RESULTS

Of a total of 17 tree species observed, 14 were found to be infected by 25 gall morphotypes (Table 1; for example see Fig. 1). Three species were not infected, while eight species were infected by more than one type of gall. Four species of *Shorea* were found to have shared gall-types, with the degree of gall-types shared ranging between 33 percent - 100 percent.

TABLE 1. *Host trees with galls and galls' specificity*

Host tree	Number of gall morphotype	Number of gall morphotype shared	Percentage of gall morphotype shared
<i>Mesua ferrea</i>	0	0	0
<i>Mesua nagasarium</i>	0	0	0
<i>Calophyllum thwaitesii</i>	1	0	0
<i>Garcinia hermonii</i>	2	0	0
<i>Dillenia triquetra</i>	1	0	0
<i>Shcumacheria castaneifolia</i>	3	0	0
<i>Agrostistachys intramarginalis</i>	1	0	0
<i>Aporusa sp.</i>	2	0	0
<i>Chaetocarpus coriaceus</i>	2	0	0
<i>Shorea affinis</i>	1	0	0
<i>Shorea cordifolia</i>	4	4	100
<i>Shorea disticha</i>	4	4	100
<i>Shorea megistophylla</i>	3	1	33
<i>Shorea stipularis</i>	1	0	0
<i>Shorea trapezifolia</i>	1	0	0
<i>Shorea worthingtonii</i>	7	5	71
<i>Hopea jucunda</i>	0	0	0

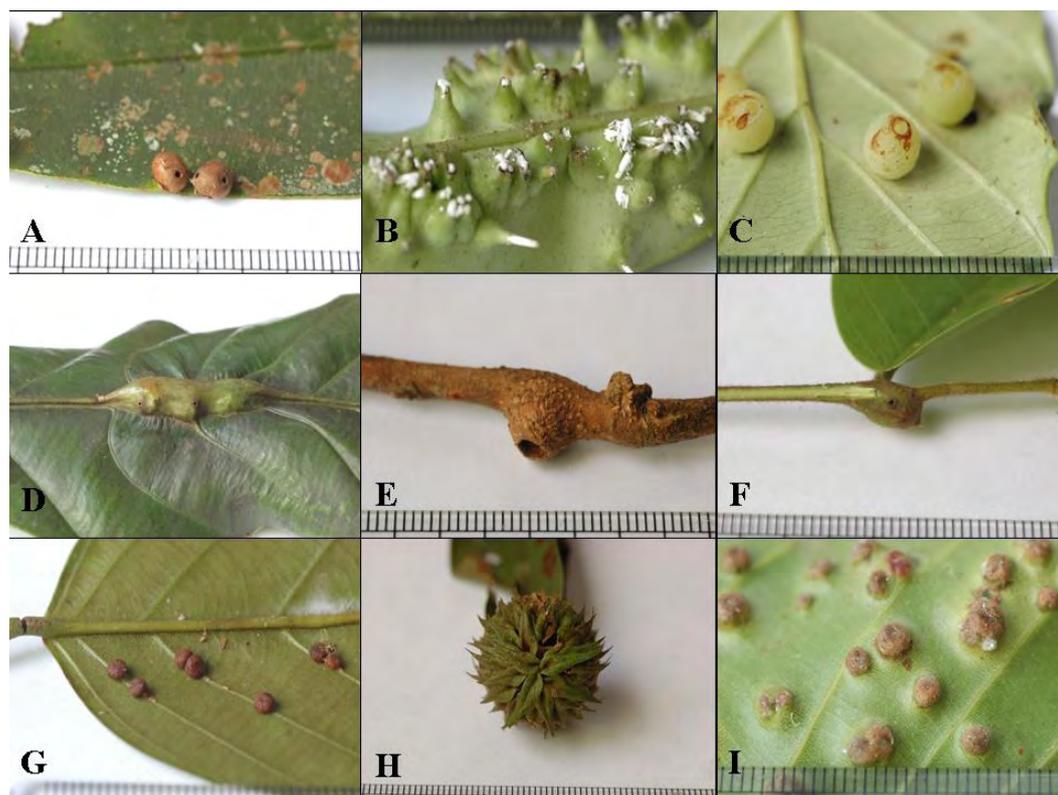


FIGURE 1. Diversity of gall morphotype: (A) Type 1 on *Calophyllum thwaitesii*; (B) Type 3 on *Garcinia hermonii*; (C) Type 4 on *Dillenia triquetra*; (D) Type 8 on *Agrostistachys intramarginalis*; (E) Type 11 on *Chaetocarpus coriaceus*; (F) Type 22 on *Shorea stipularis*; (G) Type 14 on *S. cordifolia*, *S. disticha* and *S. worthingtonii*; (H) Type 17 on *S. cordifolia* and *S. worthingtonii*; (I) Type 20 on *S. megistophylla*.

A significant positive correlation was found between the total number of galls per genus and number of tree species sampled (GLM, family = Poisson; Estimate = 0.38 ± 0.07 , $df = 8$, $p < 0.0001$), as well as and the number of tree species in a genus at Sinharaja (GLM, family = Poisson; Estimate = 0.42 ± 0.08 , $df = 8$, $p < 0.0001$).

However, the average number of gall types per congeneric species was not significantly associated with the number of tree species sampled (GLM, family = Poisson; Estimate = 0.005 ± 0.15 , $df = 8$, $p = 0.97$); nor with the number of tree species in a genus at Sinharaja (GLM, family = Poisson; Estimate = 0.06 ± 0.13 , $df = 8$, $p = 0.66$) (Table 2).

TABLE 2. Number of gall-types and number of species per tree genus in the Sinharaja area

Genera	Gall morphotypes	Tree species sampled	Species per genus
<i>Mesua</i>	0	2	2
<i>Calophyllum</i>	1	1	3
<i>Garcinia</i>	2	1	4
<i>Dillenia</i>	1	1	3
<i>Shcumacheria</i>	3	1	1
<i>Agrostistachys</i>	1	1	2
<i>Aporusa</i>	2	1	5
<i>Chaetocarpus</i>	2	1	3
<i>Shorea</i>	13	7	8
<i>Hopea</i>	0	1	2

DISCUSSION

My results show that there were more gall morphotypes than their host species in the forest. This may simply reflect the fact that number of insect species is much superior to the number of tree species (751,000 insect species vs. 170,000 dicotyledonous angiosperm species; Wilson 1999). The much shorter and rapid life cycle of herbivorous insects, coupled with higher mutation rate, could also have facilitated the speed of their evolution, which helps them overcome various plant defences, and thus radiate on their hosts.

Trees that are abundant but not infected by galls (e.g., *Mesua* spp.) probably have special defence against gall-inducing insects. This could be also due to sampling artifact. Since this study sampled only understory trees, galls of these abundant trees could have preference for the mature ontogenic stage of their hosts and could be found in the canopy of these trees (Fonseca *et al.* 2006).

Gall morphotypes were found to be shared by congeneric tree species but restricted to within their respective genera. This fits the initial prediction that gall making insects are not species-specific, and that closely related tree species are more likely to share gall morphotypes than less closely related species. Interestingly, all four *Shorea* spp. that shared gall morphotypes are from section *Doona* and are dominant species in the forest canopy. The high cross infection among the understory trees of these *Shorea* may be a result of similar morphological phenotypes and defense mechanisms (Futuyma 1998). Once a gall-inducing insect was specialized to gall on one particular *Shorea*, it should not be difficult to infect closely related species.

My result also showed that the species-rich genera had more gall morphotypes. Cospeciation of gallers and their host plants

may be one mechanism to such increase in gall diversity. For gall-inducing insects radiating parallel with their host plants, a species-rich genus definitely provides more opportunity for host-shift (i.e., cross-infection) and subsequent speciation than a species-poor genus.

Due to time constraint, this study focuses only on certain plant groups and limited class size within the local forest community at Sinharaja. This is probably too limited to describe the overall pattern of interaction and co-evolution between plants and gall-making insects. Such study could be improved further by expanding the sampling to a complete herbivory guild or size class of trees, as well as by including more plant taxa with a wider range of species richness. Instead of looking at the morphology of galls, the biology and phylogeny of gall insects should be also investigated. Genetic analysis will definitely serve as a useful tool to compare the lineages of both herbivore and plants; especially in case the herbivores are difficult to rear out.

Nevertheless, this study has shown that by examining gall morphology, we have learned something about the diversity of gall morphotype in the Sinharaja rain forest and observed interesting patterns in the relationship between gall-inducing insects and their host plants.

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APPENDIX 1: *Classification and description of galls*

Morphotype	Hosts	Position	Shape	Color	Width (mm)	Height (mm)
1	<i>Calophyllum thwaitesii</i>	lamina	globular	brown	2-3	2-3
2	<i>Garcinia hermonii</i>	lamina	warty, subtendly foveolate	green/grey-brown	2	1
3	<i>Garcinia hermonii</i>	lamina	conical with acicular point	green/black	3-6	2-5
4	<i>Dillenia triquetra</i>	lamina	globular with punctated apex	green/dark-brown	5-8	5-8
5	<i>Shcumacheria castaneifolia</i>	twig	irregular swell	green	10	20
6	<i>Shcumacheria castaneifolia</i>	lamina	adpressedly pustular	green	3-6	1
7	<i>Shcumacheria castaneifolia</i>	apical bud	swell	dark	7	10
8	<i>Agrostistachys intramarginalis</i>	midrib	swell	green	7-10	15-20
9	<i>Aporusa sp.</i>	lamina	conical with a deflexed caudated point	green/yellow-brown	4-6	5-8
10	<i>Aporusa sp.</i>	lamina	urceolate/adpressedly columnar	green/red-brown	1	2
11	<i>Chaetocarpus coriaceus</i>	twig	hemisphere with foveolated apex	red-brown	6	4
12	<i>Chaetocarpus coriaceus</i>	lamina	conical-hemisphere	green/red-brown	5-6	2-4
13	<i>Shorea affinis</i>	lamina/midrib	warty	yellow/grey-brown	2-4	1-3
14	<i>Shorea cordifolia, S. disticha, S. worthingtonii</i>	midrib/nerves	globular, glomerated	chocolate	2-3	2-3
15	<i>Shorea cordifolia, S. disticha, S. worthingtonii</i>	lamina	warty	red-brown	3-4	1
16	<i>Shorea cordifolia, S. megistophylla</i>	midrib	globular	chocolate	8-14	6-10
17	<i>Shorea cordifolia, S. worthingtonii</i>	apical bud	urchin-like, cluster of numerous scale leaves	green	15-20	15-20
18	<i>Shorea disticha, S. worthingtonii</i>	lamina	hemisphere, cracking	yellow-brown	4-7	3-5
19	<i>Shorea disticha, S. worthingtonii</i>	lamina	warty/disciform	orange-brown	2	1
20	<i>Shorea megistophylla</i>	lamina	tubularly warty	grey-brown	3-5	3-4
21	<i>Shorea megistophylla</i>	twig	globular	purple/black	4-5	4-5
22	<i>Shorea trapezifolia</i>	twig	swell, pisiform	green/brown	7	10
23	<i>Shorea worthingtonii</i>	twig	pocky	brown	3-4	?
24	<i>Shorea stipularis</i>	twig	swell, pisiform	brown	5-7	8-10
25	<i>Shorea worthingtonii</i>	lamina/midrib	pustular	yellow	8-15	4-6

The Interaction between Ants and Rattans: Is It Mutualistic?

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ABSTRACT

I studied the diversity and functionality of the relationship between ants and rattans in Sinharaja World Heritage Site. Out of 83 individuals of five species of rattan (*Calamus zeylanicus* Becc., *C. ovoideus* Thw. Ex Trim., *C. thwaitseii* Becc., *C. digitatus* Becc. and *C. sp. A.*) I collected 9 species of ants from 8 genera, representatives of subfamilies: Myrmicinae, Formicinae, Ponerinae and Dalicordinae. I observed that there is an uneven distribution of species of ants among different rattan. Where *C. zeylanicus* is more diverse, *Anoplolepis* and *Technomyrmex* are the most abundant group of ants. Based on a disturbance experiment and leaf damage analysis, I found that aggression has a negative relationship with food investment and herbivory has a strong positive relationship with shelter benefits.

Key words: *Calamus*; ants; mutualism.

ANTS PLAY AN IMPORTANT ROLE IN THE ECOSYSTEM as seed dispersers and insect predators. They are key players in important insect-plant mutualisms that have resulted in co-evolution between some host plants and their ant dwellers (Dejean *et al.* 1997; Garcia *et al.* 1995; Thomas 1988). Some rattan species in the genera *Daemonorops* and *Korthalsia* are known to harbor ants. A preliminary survey of *Calamus* species revealed that there were assemblages of ants in the rachis of some species present at Sinharaja World Heritage Site.

In this study I addressed the questions: Is there specificity in the relationship between different ant species and *Calamus* spp., and what is the occurrence and functionality of this relationship? To answer these questions I proposed four hypotheses:

H_{A1}: Diversity of ant species differs in different rattan species,

H_{A2}: Higher investment of rattan species in ant shelter benefits positively correlates to increase in ant aggression,

H_{A3}: Higher investment of rattan species in ant food benefits positively correlates to increase in ant aggression and;

H_{A4}: Increased aggression in ants positively correlates to a decrease in rattan leaf damage due to herbivory.

METHODOLOGY

I sampled rattan species in from two areas where rattans were abundant; natural forest edge areas, and within a pine plantation. I selected sample plants based on their accessibility for study. For each individual, I measured diameter at 2 m above ground, and the percentage herbivory. I quantified whole plant percentage herbivory, as the average of four leaf damage percentages from two basal and top leaves.

If there was an indication of ant presence, I applied physical disturbance to the rattan by tapping the stem close to the probable nest (approximately 40 cm away) for 1 min, and counted the number of ants that investigated the disturbance over a 10-sec period. Thereafter I proceeded with an intensive search for ants on the rattan. I collected ants using two sizes of pooter. Identification of the ant species was through experts and references.

I measured the food benefit provided to the ants by presence or absence of food materials and by the behavior of foragers. Shelter benefits were assessed from the presence or

absence of occupied mud houses, leaf sheaths, and rachis, with larvae, winged individuals, or assemblage of ≥ 20 individuals. I used R 2.3.1 for my statistical analysis.

RESULTS

I sampled a total of 83 individuals of rattan belonging to 5 species, *Calamus zeylanicus* Becc. *C. ovoideus* Thw. Ex Trim., *C. thwaitseii* Becc., *C. digitatus* Becc. and *C. sp. A.*, and 12 species of ants from 8 genera, representing the subfamilies; Myrmicinae (*Phidole*, *Tetramorium*,) Formicinae (*Anoplolepis*, *Camponotus*, *Paratrechina*, *Polyrachis*), Ponerinae (*Pachycondyla*), and Dalicordinae (*Technomyrmex*) (Fig. 1). Nine species of ants were found in the forest, including *Anoplolepis*, *Camponotus sp.1*, *Camponotus sp. 2*, *Camponotus sp. 3*, *Pachycondyla*, *Paratrechina*, *Pheidole*, *Tetramorium* and *Technomyrmex*. Three species were found in the *Pinus* plantation composed of *Technomyrmex*, *Pheidole* and *Polyrachis*.

I fitted my data on Generalized Linear Model based on Poisson distribution of errors. I set the significance level at $P < 0.01$. I found that food benefits, shelter benefits, and habitat all had significant effect on ant aggression. Across all samples, I found that food benefits were negatively associated with aggression ($z = -10.371$, $P = < 2e-16$, $df = 75$), while shelter benefits strongly positively associated with aggression ($z = 15.974$, $P = < 2e-16$, $df = 75$). Also, ants in the *Pinus* habitat were significant more aggressive than the natural forest ($z = 22.007$, $P = < 2e-16$, $df = 75$).

I also tested the same variables for a dominant rattan species, *C. zeylanicus* and found a similar pattern to that across all *Calamus* spp. Furthermore, I tested the same relationship of aggression as a function of food and shelter for two ant species that were most abundant in all my sampling. Both species followed the same pattern, with *Anoplolepis* (shelter benefits: $z = 5.574$, $P = 2.49e-08$, $df = 18$) and *Technomyrmex* (food and shelter benefits respectively, $z = -3.750$, $P = 0.000177$, $df = 12$; $z = 5.062$, $P = 4.15e-07$, $df = 12$)

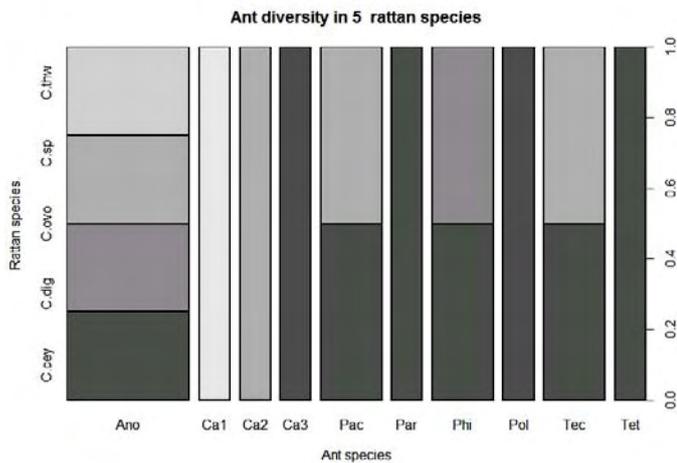


FIGURE 1. Ant diversity in five *Calamus* species, *C. cey* (*Calamus zeylanicus* Becc.) *C. ovo* (*C. ovoideus*), *C. thw* (*C. thwaitseii*), *C. dig* (*C. digitatus*) and *C. sp.*, *Ano* (*Anoplolepis*), *Ca1* (*Camponotus sp1*), *Ca1* (*Camponotus sp2*), *Ca1* (*Camponotus sp3*), *Pac* (*Pachycondyla*), *Par* (*Paratrachina*), *Phi* (*Pheidole*), *Pol* (*Polyrachis*), *Tet* (*Tetramorium*), *Tec* (*Technomyrmex*).

I tested leaf damage caused by herbivory as a function of aggression, presence of food benefits and difference in habitats. I found a strong negative relationship with aggression ($z = -6.101$, $P = 1.06e-09$, $df = 75$) and food ($z = -3.467$, $P = 0.000526$, $df = 75$).

There was a strong significant positive relationship with shelter ($z = 8.833$, $P < 2e-16$, $df = 75$), and pine habitat ($z = 6.518$, $P = 7.14e-11$, $df = 75$). I then tested herbivory as a function of aggression and habitat for a single species of rattan *C. zeylanicus* and found a similar pattern.

DISCUSSION

The pattern where food benefits had a significantly strong negative relationship with aggression while shelter benefits had a significantly strong positive relationship with aggression was observed on all *Calamus spp.*, solely for *Calamus zeylanicus*, and for the two species of dominant ant species tested. Herbivory, however, had a significant positive association with shelter and pine habitat across all rattan species and for *Calamus zeylanicus*.

I observed that those ants, such as *Technomyrmex*, that had the scale insects inside the rachis and mud house were the less aggressive. *Anoplolepis* which tend scale insects on the rachis usually moved away from a disturbance. The negative relationship between the level of ant aggression and food benefits provided by the rattan, based on my observations can be explained by the kind of food that they utilize in the rattan and the stability of the food resource. The most frequent food items was nectar exudate from scale insects that are fostered either on stems of the rattan, on underside of the spines, inside the rachis or inside the mud houses. Most scale insects outside a shelter were on or near the young shoots. I suggest that this can be attributed to the waxy substance covering the young shoot which the ants or the scale insect utilize. However, this type of food item in the rattan was not enough to cause the species to be much aggressive. I propose this following possible hypothesis: that there are lesser animals feeding on the rattan thus the lesser need to protect it (for

ants with shelter benefits without eggs or larvae and with food benefits); that the ant species most of which are tramp species tends to invest less in protecting their food resource and invest more in nomadic foraging; ants tends to invest more on the protecting shelter; food in the rattan is much opportunistic and unstable in nature compared to shelter which is readily available and more diverse.

The positive relationship for aggression and shelter can be attributed to the protection of the larvae and eggs. Mud house nests are common on older rattans. Whereas, young rattans with mud houses tended to have the nests either in between the spines, inside the rachis at mid level, or at the basal area. Based on my observation the highest level of aggressiveness tended to be the ants that have larvae in shelters at the rachis. I hypothesize that this is because of the lesser protective position compared to the other two.

Based on my sample, there are more ant species in the natural forest compared to the *Pinus* plantation. The large number of tramp species such as *Anoplolepis* and *Technomyrmex* in the *Pinus* area compared to the forested area where there was more or less even species abundance could suggest their higher tolerance to a monocrop environment. Although, this has to be tested with a larger sample for both types of habitats.

I did not perform any statistical analysis to test my first hypothesis due to a small and uneven sample size. However, based on my observations diversity in rattan can be attributed more to habitat rather than the rattan species concerned. Based on my observations and the statistical test I am rejecting my third hypothesis that higher investment of rattan species in ant food benefits positively correlates to increase in ant aggression; and accepting my second and fourth hypothesis which is higher investment of rattan species in ant shelter benefits positively correlates to increase in ant aggression and increased aggression in ants positively correlates to a decrease in rattan leaf damage due to herbivory.

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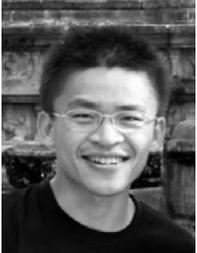
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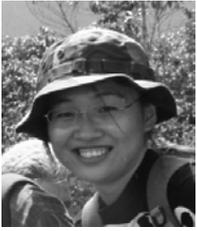
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IFBC-2006 in the News

STRI News

18 August 2006

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CTFS Field Biology Course

The Center for Tropical Forest Science - Arnold Arboretum (Harvard University) Asia program's annual field biology course was opened by Anura Sathurusinghe, Conservator of Forests, at Sinharaja World Heritage Site, Sri Lanka, on July 31.

Twenty-one graduate students from 11 countries are participating in the course that includes training in plant and animal systematics, population biology, plant-animal interactions, behavioral ecology, molecular ecology and evolutionary biology for a month.

Over 20 instructors from both international and local institutions, including STRI researchers, will participate in the course. In addition to the rain forest at Sinharaja, the participants will visit semi-deciduous and dry zone forests and wildlife preserves.

The course, organized by STRI research associate Rhett D Harrison, is hosted



by Nimal and Savi Gunetilleke from the University of Peradeniya and the Forest Department, Sri Lanka.

El curso anual de campo del Programa de Asia del Centro de Ciencias Forestales del Trópico - Arnold Arboretum (Harvard University) fue inaugurado por Anura Sathurusinghe, Conservador de Bosques, el 31 de julio en Sinharaja, sitio de Patrimonio Mundial en Sri Lanka.

Veintiún estudiantes graduados de 11 países participan en el curso que incluye sistemática de plantas y animales, biología de poblaciones, interacciones entre plantas y animales, ecología del comportamiento, ecología

molecular, y biología evolutiva durante un mes.

Más de 20 instructores, tanto locales como internacionales, incluyendo varios investigadores de STRI participan en el curso. Además de los bosques tropicales de Sinharaja, los participantes visitarán bosques de zonas semi-deciduas y secas, así como reservas de vida silvestre.

El curso, organizado por Rhett D. Harrison, investigador asociado a STRI, cuenta con el apoyo de Nimal y Savi Gunetilleke, Universidad de Peradeniya y del Departamento de Bosques de Sri Lanka.

Fernández-Marín awarded for best student paper

STRI postdoctoral fellow Hermógenes Fernández-Marín received the prize for the best student paper at the recent International Congress of the International Union for the Study of Social Insects in Washington DC. The paper, "The use of different antibiotic agents and the stability of mutualism in fungus-growing ants and their partners," was co-authored with Jess K. Zimmerman, Jacobus J. Boomsma, and William T. Wcislo.

El becario postdoctoral, Hermógenes Fernández-Marín, recibió el premio por el mejor artículo en el reciente Congreso internacional de la Unión Internacional para el Estudio de Insectos Sociales en Washington DC. El artículo, "El uso de agentes antibióticos diferentes y la estabilidad del mutualismo en hormigas que cultivan hongos y sus aliados" fue escrito junto con Jess K. Zimmerman, Jacobus J. Boomsma and William T. Wcislo.



fue escrito junto con Jess K. Zimmerman, Jacobus J. Boomsma and William T. Wcislo.