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Abstracts

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**I**  
**Lectures**



## Session 1

# Vascular Epiphytes in Forest Canopies

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## The life history of vascular epiphytes – does it differ from other perennials?

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Vascular epiphytes are mostly long-lived, herbaceous plants living in a habitat with high rates of disturbance and a high degree of abiotic stress. A thorough, quantitative analysis of their life history parameters, however, was not possible until now, simply due to lack of data. Thus, the relative importance of demographic processes such as growth, stasis, or sexual/vegetative reproduction in comparison to other perennials has been unclear. Now, using the considerable number of recently published and other, still unpublished, demographic studies of vascular epiphytes tentative, quantitative generalisations seem finally possible. Apart from long-term monitoring, the results of studies on population genetics provide additional insight. I will present these demographic data in the comprehensive context of Silvertown's triangle, which allows the comparison of epiphyte life history characteristics not only with those of perennial terrestrial herbs, but also with those of other life forms such as trees or short-lived annuals.

## Biogeography of vascular epiphytes in South-East of Brazil

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The aim of this work is to compare the species richness and ecological categories of vascular epiphytes in four forest formations in the State of São Paulo, south-east of Brazil. This work has been developed in association with the project “Diversity, Dynamics and Conservation of trees in forests in the State of São Paulo: studies in permanent plots” (BIOTA-FAPESP, 1999/09635-0) in four conservation areas (Parque Estadual Ilha do Cardoso, Parque Estadual Carlos Botelho, Estação Ecológica Caetetus, Estação Ecológica Assis), that represent the main forest formations in São Paulo (coastal plain rain forest, mountain rain forest, seasonal forest and woody savanna respectively). The floristic composition of all vascular plants growing without soil-stem contact (epiphytes, hemiepiphytes, hemiparasites and parasites) was studied in 10ha of each forest formation. The plants were collected using climbing techniques adapted from canopy studies and were identified through consultation with specialists, and in herbaria and specialized bibliographies. The results presented here are preliminary and are based on morph-species. Altogether, in the 40 ha sampled, 34 families of vascular plants and 242 species were registered. The families and species richness registered in the 10 ha of each forest formation was: coastal plain rain forest (26/149), mountain rain forest (27/141), seasonal forest (8/22) and woody savanna (5/16). The families with most species were Orchidaceae (89), Bromeliaceae (41), Polypodiaceae (18), Araceae (14) and Cactaceae (12), although their proportions, and indeed their presence, vary in total richness according to the type of forest formation. The richness of hemiparasites and hemiepiphytes were: coastal plain rain forest (2/16), mountain rain forest (1/17), seasonal forest (0/2) and woody savanna (1/1). Parasites were not registered. The genera that occurred in the four areas were *Tillandsia* (Bromeliaceae), *Microgramma*, *Polypodium* and *Pleopeltis* (Polypodiaceae). Orchidaceae were also present in the four forests, but with different genera. This study suggests that floristic expression of vascular epiphytes in tropical forests is considerable; even in the forests strongly influenced by rainfall seasonality, species of epiphytic plants can survive to water absence and they use different morph-physiologic strategies. In seasonal forests, exclusive families were not registered, though genera and species restricted to seasonal forests do exist. It is in the rainforests that forms of vascular epiphyte are expressed with most variety, with an great profusion of families and species. Hemiparasites have a low number of species, but hemi-epiphytes have a considerable presence, and the Araceae family contains most of its representations. Only three families and four genera were present in all forests and hence showed the plasticity to adapt to different climatic and environmental conditions. In summary, of the five richest families of epiphitic species sampled, it is Bromeliaceae and Cactaceae, both endemic to the Americas, which contribute to this impressive neotropical epiphytic richness, when compared to paleotropical epiphytism. (CAPES, FAEP - UNICAMP, Projeto Parcelas Permanentes / BIOTA - FAPESP).

## Andes versus Amazon – patterns of vascular epiphyte diversity on different spatial scales

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Montane rainforests of the Neotropics are generally considered to harbour the maximum of the world's vascular epiphyte diversity. In contrast, preliminary data from Neotropical lowland sites suggest that lowland rainforests especially in the supposedly homogenous Amazon basin are very poor in epiphytes. To test this hypothesis, we expanded the data base of so far exclusively Northern Amazonian studies with data from Western Amazonia (Tiputini Biodiversity Station, Ecuador, 0°38'S 76°09'W, 230m a.s.l., 650ha). Thus, we present an overview on Neotropical epiphyte diversity at different spatial scales, based on a biogeographic analysis of 0.1ha plot inventories as well as local and national checklists of vascular epiphytes. The main focus of our study is the dependence of epiphyte diversity and endemism on elevation and climatic factors.

Diversity patterns of vascular epiphytes and the influence of elevation and rainfall are strongly scale dependent. On local and national scale, both diversity and endemism of vascular epiphytes reach a maximum at mid elevations in Andean cloud forests. Accordingly, species turnover among montane sites exceeds that of lowland sites, but, surprisingly, the ratio between local diversity and diversity of corresponding 0.1 ha plots (as another measure for  $\alpha$ -diversity) is lower for montane than for lowland sites. Amount and seasonality of rainfall are the major determinants of epiphyte diversity for local inventories among lowland sites. In contrast, diversity of 0.1 ha plots is only weakly correlated with rainfall and not with elevation: The plot richest in epiphyte diversity and abundance is located in Western Amazonian Tiputini, with 9670 epiphytic individuals of 146 species and 24 families.

In conclusion, the epiphyte flora of Western Amazonian Tiputini shows an unexpectedly high alpha diversity and abundance. Thus, vascular epiphytes are not necessarily less abundant and diverse in Amazonian than in Andean forests. We discuss reasons for different diversity patterns at different spatial scales and the role of the Andean orogenesis as well as past and present rainfall patterns in the generation and maintenance of epiphyte diversity and endemism in the Neotropics. Furthermore, our results suggest that Western Amazonian forests play a crucial role in conservation of Amazonian plant diversity.

## Long-term changes in epiphyte assemblages – dynamics and underlying mechanisms

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Vascular epiphytes are a major component of many tropical forests. Their ecology has attracted much interest in recent years, and there is a rapidly growing body of information on population and community structure of vascular epiphytes. But our knowledge of long-term changes in populations and assemblages of vascular epiphytes is almost completely circumstantial. This scarcity of information contrasts sharply with an on-going global effort to document and analyse the long-term changes in populations of woody plants of tropical forests and motivated the present studies which follow the fate of the epiphyte assemblages in two different lowland forests over several years. I am going to talk about changes during five years in the epiphyte assemblage of the palm species *Socratea exorrhiza* in a Panamanian lowland forest. And further about eight years changes in an epiphyte assemblage in c. 1000 *Annona glabra* host trees growing on the shore line of Barro Colorado Island, Panama. Despite a purely descriptive approach of changes in these epiphyte assemblages I will also address underlying mechanisms for the structure and dynamics in the latter system.

## Litter decomposition within epiphytic Bird's Nest Ferns (*Asplenium* spp.) in a range of forest habitats in Sabah, Malaysia

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Litter decomposition is a major ecosystem processes that occur within forest canopies. Epiphytes, especially those that are specifically adapted to trap litterfall such as Bird's Nest Ferns (*Asplenium* spp.), are perhaps the major focus for litter decomposition within the canopy. However, there has been relatively little research on this key process within the canopy. Here we present data from a study of litter decomposition carried out at Danum Valley Field Centre, Sabah, Malaysia. Using the litterbag technique, litter decomposition was evaluated in paired canopy (within Bird's Nest Ferns) and forest floor sites. The experiment was carried out across three main habitats in Sabah, primary and selectively logged dipterocarp forest and oil palm plantation. Analysis shows distinct differences between the three forest types. Differences in litter decomposition between the canopy and forest floor were greatest within the oil palm plantations. The relative decomposition rates were also significantly lower in the oil palm plantations. To our knowledge this is the first study to compare canopy and forest floor decomposition rates within a range of habitats. This experiment is part of a larger project, in which we are developing the Bird's Nest Ferns as a model microcosm in which to investigate how biodiversity affects a range of ecosystem functions within the rainforest canopy.

## Spatiotemporal variation in population dynamics of epiphytic orchids

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The population dynamics of epiphytes is influenced by the three-dimensional space offered by their host-trees with strong gradients of light and nutrient availability and substrate stability. Nevertheless, demographic studies covering not only temporal but also spatial variability in epiphyte populations are still rare.

We studied populations of three epiphytic orchids (*Lycaste aromatica*, *Jacquiniella leucomelana* and *J. teretifolia*) in a Mexican humid montane forest using matrix population models. To account for spatiotemporal variation populations of each species were followed for three years on six trees located in four patches with an inter-patch distance of at least 50 m. Asymptotic population growth rates ( $\lambda$ ) varied between years in the *Jacquiniella* species, which are common also in more open or disturbed vegetation, but were always below unity in *L. aromatica* which is restricted to closed forests. Elasticity analysis of single year matrices showed that  $\lambda$  was most sensitive to changes in the survival of pre-reproductives or juveniles in the *Jacquiniella* species, and to survival of large reproductives in *L. aromatica*. Environmental stochasticity was accounted for by linking climate data with the population matrices. Stochastic population growth rates indicated that the population of *L. aromatica* is indeed declining and will be driven to the edge of extinction in this forest if the current climatic trend holds on.

If tropical mountain forests get drier as a consequence of climate change, as has been predicted and in part already observed, we expect many epiphytes to survive only in relatively protected positions within the habitats they occupy now, and to possibly colonize higher elevation sites if such forests are present in an area and if migration is fast enough.

## The ecology of vascular epiphytes on *Ficus crassiuscula* host trees in a Peruvian cloud forest

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The diversity, distribution and community dynamics of vascular epiphytes were investigated from three emergent *Ficus crassiuscula* host trees in a lower montane cloud forest at 2400 m a.s.l. in the Central Peruvian Yungas. Arborist climbing techniques were used to access all parts of host trees and all vascular epiphytic individuals were counted and identified within Johansson canopy zones. One tree was completely inventoried in all Johansson zones, while two others were only inventoried in the upper canopy (zones 4 and 5). For each clump of epiphyte plants, measurements of branch angle and diameter were recorded, and incident PAR was calculated using hemispherical images and above canopy PAR data. The single complete host tree revealed an unprecedented high vascular epiphytic diversity of 195 species with a concentration of individuals in the outer canopy. Within the upper canopy of the three host trees, the majority of species appeared to be stochastically distributed, with most species showing a medium degree of coexistence with other species. Branch angle and PAR did not appear to be a major determinant of epiphyte position within the upper canopy, but branch diameter was important for some species. PAR was heterogeneously distributed within the upper canopy, but almost all epiphyte anchorage sites had much reduced PAR levels relative to above the canopy. There was little turnover between the upper canopy floras of the three trees. The dominance/diversity curve of upper canopy species showed a very high proportion of the lowest abundance species, with a distinct lack of the declining tail seen in other biological community structures. This variation on typical community structure could be caused by an exceptionally high rate of epiphyte slumping, creating random establishment and mortality. A relatively high rate of slumping could be expected due to steep branch angles, smooth bark, high browser activity and emergent status (higher wind exposure).

## The response of epiphytes to anthropogenic disturbance of pine-oak forests in the highlands of Chiapas, Mexico

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I described the vascular epiphyte community on 35 oak trees in six trunk diameter classes in 16 stands of pine-oak forest that differed substantially in their degree of disturbance as indicated by structural characteristics of the forest such as basal area, height, density, and the frequency of coppice trees and evidence of logging, grazing and burning. Pine trees supported few epiphytes and were not sampled. All stands were situated within a c. 400 km<sup>2</sup> relatively flat area at c. 2200 m elevation in the vicinity of San Cristobal de Las Casas. The explainable variation between the stands was partitioned between environmental (altitude, forest structure, management) and spatial variables (longitude, latitude), using multivariate analysis. In total, 74 species of epiphytes were encountered. Bromeliads dominate at all sites in terms of their biomass. Estimated epiphyte biomass on the 35 oaks varied between 0.8 and 243 kg dry-weight and richness between 13 and 34 species. Not surprisingly, disturbance, measured as the proportion of coppice trees, had a negative effect on epiphyte biomass and species richness per ground surface area. Epiphyte biomass and richness on the remaining or re-grown trees, however, was also negatively correlated with the proportion of coppice trees; biomass: Pearson's  $r = -0.55$ ,  $P = 0.02$ , richness: Pearson's  $r = -0.75$ ,  $P = 0.001$ . This pattern was, moreover, sustained after corrections for differences in host-tree size were made. Nevertheless, epiphytes show resilience to disturbance if forests are selectively logged to spare big trees. Such remnant trees are essential for epiphytes that require the presence of accumulated suspended soil and they may also serve as nearby epiphyte seed sources for the re-growing trees, viewing the development of the epiphyte community from a dispersal assembly perspective. Anthropogenic disturbances also force a shift from mesic- to more drought tolerant species. Hence, disturbance exerts an influence on the regional distribution of epiphytes, but a similar amount of variation (20-30 %, depending on the used spatial descriptors) could entirely be attributed to the geographic position of the stands in the landscape, i.e. independent from the influence of environmental variables. Nearby sites are more similar in epiphytes than distant sites (Mantels  $r = 0.44$ ,  $P = 0.002$ ) and I postulate that this relates to properties of the seed supply, again in compliance with the dispersal assembly perspective. The trees in the pine-oak forests in the Highlands of Chiapas are being exploited for subsistence purposes and this vital function is not likely to change in the near future. For epiphyte conservation purposes, it is recommended to adopt a management of selective logging instead of cyclic clear-cutting and to spare large 'rescue' trees in particularly during logging. In addition, it is wise to try to attain a homogeneous distribution of epiphyte protective reserves within a uniform physiographic region.



## Session 2

# Fungi and Fungal Organisms in the Canopy

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## Plant parasitic microfungi in Western Panama

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A just starting project which focuses on the diversity of plant parasitic microfungi in Panama is presented. Panama is a small country in the Southern part of the Central American isthmus. With about 9.500 species of vascular plants currently known from Panama (Correa et al. 2004), it can be assumed that the diversity of plant parasitic microfungi is very high as well. Systematic positions of plant parasitic microfungi are mostly in the Ascomycota (Meliolales, Phyllachorales, Dothideales a.o.), the Fungi Imperfecti, as well as in the Rusts, Smuts, and some smaller orders of the Basidiomycota.

The area of investigation corresponds to the Western part of Panama, comprising the provinces of Chiriquí and Bocas del Toro. The area includes the more or less permanently wet Caribbean- and the seasonally dry Pacific side. The altitude ranges from 0 to 3.475 m and houses a large variety of habitats ranging from mangroves, littoral forest, lowland deciduous forest, gallery-forest, lowland rainforest, savannas, land cultivated and influenced by man in low and high altitudes (i.e. pastures and wasteland) to mountain rain forest, elfin forest and paramo-like vegetation at the higher altitudes. Among numerous niches in which plant parasitic microfungi occur, canopies and epiphytic plants (mainly members of Orchidaceae, Bromeliaceae, Araceae, and ferns) are particularly interesting.

The project is a joint project including Panamanian and German botanists, mycologists, and plant pathologists. Each investigator focuses on a certain systematic or ecological group of fungi. In the present talk we present some preliminary results, especially those resulting from a subproject on parasitic fungi on orchids in Western Panama. About 1.200 species of orchids are known from Panama, the majority of these are epiphytes. Relative to the publications on orchid mycorrhiza, parasitic orchid fungi in situ are a subject of neglect. By field work in Panama as well as morphological and systematical investigation we intend to fill this gap.

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## Foliicolous ascomycetes in the canopy of a lowland rainforest in the Orinoco Basin (Venezuela)

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Up to now information on diversity, species composition and habitat preferences of leaf-inhabiting fungi in the canopy is very fragmentary. This is applicable for tropical as well as temperate forests. An investigation of this ecological group of fungi in a rainforest representative for the wet Neotropics shall contribute to reduce this lack of knowledge. Foliicolous fungi were collected during rain and dry season in a height between 15 and 30 m in an area of 1,5 ha of an evergreen forest using a mobile crane system (Surumoni Crane Project). For an overview of fungal diversity more than 1000 leaves belonging to 33 angiosperm families were screened for fungi. Furthermore a comparative study for 25 of these families was carried out. It based on an investigation of 10 leaves per family with a macroscopical evidence of fungal colonization.

About 50 % of all screened leaves revealed sporulating fungal stages. 24 ascomycetous genera (mainly teleomorphs) of 14 families were identified. As on leaves in the understorey a wide range of fungal guilds were found in the canopy. Saprobic invaders of the cuticle (12 genera), parasites on leaves (7 genera), parasites on leaf-inhabiting fungi (4 genera) and fungi associated with insects and their excudates (1 genus) were detected. The most common fungi are cuticular invaders of the Micropeltidaceae and Brefeldiellaceae, the most common parasites are Meliolaceae. "Fly speck fungi" (Micropeltidaceae) were found on about 90 % of all investigated tree species. These fungi must be regarded as the most unspecific foliicolous colonists which may develop fruitbodies within less than 2 months in the study site.

The fungal colonization conclusively depends on physical surface and biochemical characters of the leaves and on climatic conditions. Plant families found with a high number of foliicolous ascomycetes are e.g. Annonaceae, Caesalpinaceae and Lauraceae. In contrast to this, Bignoniaceae, Cecropiaceae and Loranthaceae showed only a slight colonization. The number of fungal species and the frequency of mycelia decreased from the lower to the upper canopy due to unfavorable conditions concerning humidity and temperature.

Among others the results point out that foliicolous fungi possess a high diversity in the canopy of rainforests and are able to indicate specific leaf characters and microclimatic conditions.

## Environmental and host specificity of epifoliar fungal symbionts in two tropical rain forests

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The distribution, abundance, and ecological impact of plant-associated fungi in forest ecosystems depend on host range, distribution of hosts, and distribution of suitable environmental conditions. Here we use epifoliar fungi, a guild of common, obligate fungal symbionts of plants from tropical rain forests in Panama and Australia to evaluate the relative importance of host selectivity and environmental conditions on three-dimensional spatial patterns of tree-fungal symbioses. Using canopy-access cranes, we used systematic collections to evaluate the distributions of epifoliar fungi in the forest canopy and in the understory. More than 50 species of epifoliar fungi were encountered from over a thousand leaf samples. Epifoliar fungi were found on approximately two-thirds of all plant species, but plant species varied greatly in how commonly they supported epifoliar fungi. We found that most epifoliar fungi are host non-specialists, and that the most ecologically successful fungal species are found on a diversity of plant families. We found no support for adult canopy trees acting as reservoirs for symbionts to colonize nearby understory plants, nor evidence for strong density-dependent colonization. These results call into question basic assumptions of the Janzen-Connell hypothesis, where plant pathogens transmitted from parent trees to nearby offspring as applied to plant pathogens. Epifoliar fungi are generally more common in the dark understory than in the exposed forest canopy and were highly sensitive to environmental conditions, suggesting strong environmental control over the establishment and outcome of plant-fungal symbioses.

## Mycological investigations in a temperate forest canopy – the fungal side of the LAK-Project

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Despite more than 20 years of long term canopy research, mycological projects never played an important role in investigating forest canopies. Our studies, using a construction tower crane to gain access to the canopy of a mixed deciduous forest near Leipzig are the first of this kind to study fungi living in different niches in tree crowns.

In the years 2002 and 2003, dead wood was collected in the canopy at as many different locations as possible by removing the final 20 to 100 cm of twigs and branches to assess the diversity and ecology of wood decaying 'canopy fungi'.

We could identify 118 different fungi at species or generic level using morphological characters. Members of the Stereales were present with 37 species, 18 pyrenomycetous and 16 mitotic species were recorded. Among them many species are known or were predicted to be canopy specialists with minor competitive strength at ground level. Tree species differ concerning fungal richness and composition. *F. excelsior* and *A. pseudoplatanus* were least populated with 19 and 23 species in total whereas dead wood of *Q. robur* and *T. cordata* revealed the highest fungal diversity with 34 and 47 species identified. Many fungal species growing on bark or slightly decayed wood showed a distinct host specificity. Most of the species occurring in the canopy possessed adaptations to xerotolerance or xeroresistance. Additionally, their abundance and species composition varied in different canopy areas with respect to sampling height, substrate diameter and stage of decay.

In May 2005 studies on leaf inhabiting, endophytic fungi began applying molecular methods to identify fungal isolates. First results concerning diversity and habitat preferences in the LAK investigation plot are presented.

## Species richness and ecological characterization of myxomycete-like organisms in the canopy of a temperate deciduous forest

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**M**yxomycete-like organisms (MLO), with the plasmodial slime molds (Myxomycetes) as the best-known of the six taxonomic groups included, are an ecological guild of unicellular, predatory organisms. As their main evolutionary innovation, they form small fruit bodies out of an aggregation process which elevate over the water film covering the substrate to disperse dry, air-borne propagules. Using the moist chamber culture technique, a survey for this group was carried out in the canopy of the LAK study site, Leipzig.

From a total of 146 moist chamber cultures we made 386 records of 37 taxa, with 33 myxomycetes, 2 myxobacteria, one protostelid and the fruitbody-forming ciliate *Sorogena stoianovitchae*, the latter recorded for the first time from Europe. With 94 % of all cultures positive for MLO, this group of organisms is highly frequent in the investigated microhabitat consisting of 2-4 cm thick, white rotten twigs attached to living trees within 10 and 30 m height. A species accumulation curve indicated the sampled community to come close to species saturation, with 42-44 species to be expected in the investigated microhabitat. Non-metric multidimensional scaling (NMS) revealed pH and stage of decay to be the environmental factors determining species distribution. Diameter or position of the twigs in the canopy had no significant effects on species' occurrence, which may be explained by the sheltering effect of the mostly intact bark of the twigs.

*Arcyria cinerea* and *Perichaena depressa* as the most common species occupied 32 % and 29 % of all samples, respectively. Viewing the sampled twigs as habitat islands and a single spore to be sufficient to produce a fructification, a simulation programme assuming a random spore rain estimated an average of 0.4 and 0.35 spore hits necessary twig to explain the observed frequencies. This is matched by the potential productivity of the substratum, which would be sufficient for 12 or 68 spore hits per twig if the sampled twigs would be the only habitat for the species in the 1.2 ha crane plot.

These investigations show that the dispersal via air as the evolutionary innovation of MLO seems to be the key factor for their surprisingly high abundance in the canopy.

## Session 3

# Forest Canopies and Global Change

*Chair:*

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## Forest canopies and climate change: science, risk and law

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New canopy research is showing that raised concentrations of atmospheric CO<sub>2</sub> to levels expected in 50-70 years time, alters forest function. If canopy function is disrupted, biotic regulation across 45 million hectares of land could be affected with possibly negative feedbacks on the ability of this ecosystem to counter the effects of climate change. The role of biodiversity in mitigating climate change remains largely unknown, but a majority of the world's biodiversity resides in forest canopies, where it is likely to be severely impacted by climate change.

It is possible that the forest canopy is one of earth's most significant biotic regulators of earth's atmospheric conditions. Just like the human lung, it depends on the diffusion of gases across a convoluted boundary, which is highly vulnerable to an increasingly noxious atmosphere. How can we better assess the role of biodiversity in forest function and the interplay of processes between the canopy and the atmosphere? How can we better quantify and model the risks that potential disruption of these processes presents to humans? What is the probability that those responsible for creating those risks by contributing to, or not acting to mitigate against, the effects of greenhouse gas build up in the atmosphere, will be exposed to the threat of legal actions undertaken by those harmed by the impacts of climate change, to seek compensation?

This paper will present two case studies: The first on a Global Canopy Programme initiative to set up a network of "Whole Forest Observatories" in collaboration with the United Nations Environment Programme to address some of these issues. Observatories planned in Brazil, Ghana, Madagascar, India and Malaysia will combine studies of gas fluxes, biodiversity and ecosystem function at any one site using protocols developed over the last few years.

The second will report on attempts by the scientific community in Brazil and the UK to raise awareness amongst the business, legal and Governmental community about the importance of canopy / atmosphere interactions and the local and global risks arising from of climate change impacts on forest canopies in the Amazon.

## Biodiversity drives CO<sub>2</sub> effects in the canopy of a hundred year old deciduous forest

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**F**orest canopies are responsible for the build-up of nearly 90 % of the global biomass-carbon pool. How will forests respond to a steady increase of carbon supply? After four years of treatment I will attempt a resumé of the first ever study of a mature natural forest exposed to elevated CO<sub>2</sub>. Using the Swiss Canopy Crane we exposed 14 temperate deciduous trees of 30-35 m height (*Fagus*, *Quercus*, *Carpinus* etc.) to a 540 ppm atmosphere (twice pre-industrial). Elevated CO<sub>2</sub> caused remarkably rapid responses: by the end of the first season, nearly half of the emitted soil CO<sub>2</sub> originated from new carbon, nearly all of the micorrhizal fungi biomass was new carbon. Carbon signals in soil air reflected canopy gas exchange between two and seven days before, indicating a very rapid canopy-soil linkage. Leaf carbohydrates increased significantly. The growth of stems (treerings) was stimulated significantly in *Fagus* in the first year of treatment, but not in the other species. The *Fagus* signal disappeared in the following years, although the heatwave summer of 2003 produced a second positive CO<sub>2</sub> effect on growth. Stomatal responses to elevated CO<sub>2</sub> vary across taxa. Some species save water (*Carpinus*) and others do not (*Fagus*), inducing interesting interactions in the soil, which may result in long-term changes of species abundance. The overall 5-10 % reduction of canopy water loss and the resultant higher soil moisture have biological and hydrological implications. Changes in plant-animal interactions in the canopy are likely and have already been documented for a number of taxa. Depending on leaf quality changes which are tree species specific herbivory may become increased (*Carpinus*) or decreased (*Quercus*, *Fagus*). Clouding the forest canopy with a CO<sub>2</sub> atmosphere which carries a stable carbon isotope tracer, permits for the first time, to follow the carbon signal from the canopy to the root tips through a complete forest ecosystem. Over the four experimental years the canopy did not change in density (leaf area index, LAI) nor did the annual litter deposition and the contribution of various species to litter production change. After four years, the growth response to CO<sub>2</sub> vanished, water relations continued to be slightly affected, and the tissue quality differences are perpetuated. The overall responses are smaller than expected from work with small trees, and tree species differed in responses of most of the traits studied, which is likely to cause changes in species abundance in the long run.

**Biology & chemistry of rainforest canopies in Amazonia might be crucial for extra-amazonian continental water cycle as deduced from results of the large-scale biosphere-atmosphere experiment in Amazonia**

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The potential importance of the biosphere-atmosphere interactions in Amazonia for the global climate has been in the realm of great speculation for decades. The complexity of the fluxes and processes involved in this forest-atmosphere coupling has previously prevented the development of a clear understanding and a consequent predictability capacity in models attempting to capture the phenomena. With the outpouring of disciplinary and transdisciplinary results from the LBA experiment, many new potential mechanisms and scenarios started to emerge. In the first part of this paper we layout the integration of results of a hydrological catchment study in Central Amazonia with findings of ecophysiological work dealing with canopy emissions of VOCs, with other study showing VOCs forming cloud condensation nuclei in the atmosphere and the ensuing transport that is connected with the nucleation of clouds and formation of rain. In the second part we layout the South America atmospheric circulation that places the Amazon forest in the “headwaters” of water-vapor transport from the tropical Atlantic, across the basin and into the center south of the SA continent. This SA circulation and moisture transport from the Amazon is possibly responsible for significant part of the summers rains that fall on areas east of the Andes, including central, southeast and southern Brazil, northern Argentina, Paraguay and other areas. Global change scenarios that predict changing in global circulation with possible drying up of the Amazon, potentially determining its radical change from forest to savannah, are not the only foreseeable threat to this massive continental forest-atmosphere-water system. Deforestation alone, as it replaces dense forest canopies by grasses or agriculture, places the most predictable and serious impact to the canopy-atmosphere interactions, possibly affecting the continental water system. In light of the LBA findings and articulating with the integration we analyzed in this paper, we conclude with the exploration of a few scenarios linking the logic of canopy-atmosphere coupling with the measured and likely anthropogenic disturbances in course.

## Spatial patterns in the dynamics and physiology of Amazonian rainforests

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**W**e report on results of field surveys of the structure and dynamics of old-growth forests across the Amazon Basin, conducted as part of the RAINFOR project. Forests in western Amazonia are 2-3 times as productive and dynamic as forests in the east, and this variation appears to be driven by soil fertility rather than by climate. The increased dynamism in western Amazonia is associated with higher occurrence of lianas, palms and other low wood-density species. The reduction in wood density results in lower biomass than in central and eastern Amazonia. The spatial gradient in productivity does not appear to be driven by an increase in photosynthesis, but rather by a shift in the pattern of carbon allocation between leaves, stems and roots. There is a need for more detailed ecosystem process studies in western Amazonia, to parallel those carried out in Brazil within the LBA (Large-Scale Biosphere Atmosphere Experiment in Amazonia) programme.

## Climate change impacts on the forest canopies

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**F**orest canopies cover 26 % of the land surface of the earth. Where they occur, forest canopies can increase local rainfall by 6% and intercept up to 25% of precipitation. This habitat has a significant influence on the hydrology of over 45 million ha of land. The forest canopy is therefore an essential arena in which to address the impact of climate change and habitat disturbance on ecosystem function.

From the global change perspective, relevant functions that are important to observe at the canopy scale within different forest types around the world are the water-, energy-, carbon exchanges which are directly linked to increasing temperature, changes in drought frequency, and increasing carbon dioxide. The hydrological cycle is the integrated product of the climate and the biogeophysical aspects of the surface. The equatorial region is responsible for a major portion of the global precipitation. Therefore, the atmospheric water vapor above tropical rainforest regions is largely supplied by water evaporation from those forests. In dense tropical forests at least around 50 % of the precipitation is returned to the atmosphere in the shape of water vapor as a result of tree transpiration and interception. The canopy trees alone guarantee 70-80 % of the total transpiration. Thus, changes in the vegetation parameters and other surface properties (such as albedo and roughness) modify the water and energy fluxes from the surface to the atmosphere. It is clearly shown that the pasture or savanna is warmer during the day and cooler at night compared to a forest site. Measurements of the evapotranspiration over tropical forest, pasture and cerrado in Brazil show large spatial and temporal variability. In general, a pasture transpires about 50 % of an intact tropical forest during the dry season while during the rainy season the transpiration rates are almost of the same value.

But so far, no clear trends of decreasing precipitation above the Amazon basin as a consequence of deforestation have been explored neither an increase due to global warming during the last decades. One possibility may be related to precipitation changes in the Amazon associated with the warming of the tropical Atlantic (since 1975 less precipitation in the northern and enhanced precipitation in the southern Amazon basin). This apparently natural cycle could also be responsible for the carbon uptake by the Amazon forest during the last 15 years although some interannual variability has been computed associated to the El Niño impact in several years.

GCMs indicate that the total deforestation of the Amazon is likely to reduce the precipitation in that region by about 20-30 %. Unfortunately, GCM's are not well equipped to simulate partial deforestation as is in fact taking place in the Amazon. Instead, it is conceivable that a relatively small deforestation first enhances precipitation due to the development of a forest/pasture breeze that was observed in several regions, followed by a catastrophic decrease in precipitation. The crucial question is: how big should a patch be before precipitation begins to decrease?

## Arthropods, the canopy and atmospheric dynamics: vital connections?

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The link between climate, atmospheric carbon and the vegetative canopy is well established. Further, arthropods have been rhetorized as the ‘little things that run the world’, without to much demurrals on the part of the ecological community. This presentation emphasizes and underscores the logical connections inherent in these two generalizations. Changes in climate and carbon balance will impact directly upon arthropods in the canopy through developmental rates, changes in foliage availability and quality, life history timing, geographical range size, and through temperature mediated animal/animal interactions. Changes in the nature and health of the canopy arthropod assemblage will simultaneously affect the atmospheric regime above and within the canopy. The arthropod assemblage impacts upon standing crops and turnover of carbon within the forest at several different time scales. These impacts occur through the processes of pollination, predation, herbivory and decomposition. The importance of this ecosystematic web will be demonstrated using both classical and new data. If the central role of biodiversity in atmospheric homeostasis (or heterostasis for that matter) is, as I contend, clear, then the conservation and management of arthropod diversity in the canopy becomes of vital importance in defining human responses to actual or predicted climate change. Some of the international policy consequences of this will be discussed.

## Predicted impact of global change on forest arthropods

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**F**orests are key biodiversity habitats, with the canopy alone supporting a very high percentage of extant species globally. The two major aspects of global change – climate and disturbance, will heavily impact these complex ecosystems. Some climate models predict a drying out of tropical forests and a regime of summer droughts and wetter winters for temperate regions. We propose that the differences in structure and dynamics seen currently between arthropod communities at forest edges (where microclimates are more extreme) and those in the forest core may be used to predict climate change effects. For example, groups such as the Acarina, Coleoptera and Diptera show strong responses to edge proximity with some species exhibiting marked changes in density. In the Acarina ‘dry-adapted’ species were more abundant at the edge and wet-adapted species more abundant in the core. We discuss the implications of this research and review the predicted impact of global change on forest canopy arthropods.

## Epiphytes as indicators of climate change

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Epiphytes are known to respond very sensitively to environmental changes. In Europe and other temperate regions of the Northern Hemisphere, cryptogamic epiphytes (lichens, bryophytes) have frequently been used as bioindicators of air quality. Owing to the lack of a protective cuticle, solutions and gases may enter freely into the living tissues of these plants causing sensitive reactions of the epiphytic plants to small changes in the environment. By mapping and monitoring the frequency of epiphytic bryophyte and lichen species, changes in environmental conditions are assessed. Recently, the impact of global warming on epiphytes has been demonstrated in The Netherlands based on monitoring epiphytic lichen diversity over a period of 22 years, between 1979 and 2001 (Herk et al. 2002). During 1979-1995, epiphytic lichen diversity changed significantly in relation to decreases in air pollution levels. After 1995, when air pollution changes became insignificant, major changes in lichen diversity correlated significantly with a measured rise in air temperature. These results, together with observations of increased frequencies of subtropical bryophyte species in Germany (Frahm & Klaus 1997), provide first direct evidence of the impact of current global warming on epiphytes in temperate regions. In tropical regions, known for their high diversity of cryptogamic as well as vascular epiphytes, long-term monitoring studies have not yet been carried out. Nevertheless, evidence for the significance of epiphytes as indicators of global warming is arising from transplantation studies along temperature gradients, carried out in Costa Rica (Nadkarni & Solano 2002 and in prep.) and Bolivia (Jacome et al., in prep.). The results show the relevance of these experimental studies for unraveling the impact of global warming on biological organisms.

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## The effect of canopy type on the atmosphere

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Canopies influence the atmospheric composition and the climate by exchanging gases and reflecting radiation. The differences between canopies of different ecosystems is profound, enough to exert substantial shifts in local and regional climate when the land surface cover is altered, as in deforestation. In this review, an attempt is made to compile existing data from several international programmes. The effects include (i) removal and sometimes release of greenhouse gases (ii) release of volatile gases which participate in atmospheric chemistry (iii) reflection of solar radiation. Some authors have tried to incorporate these effects into models to predict the impact of deforestation on climate. To what extent have they included the most important effects? Finally, we focus on the importance of this debate to the Kyoto Protocol: if canopy changes during reforestation and deforestation have such broad effects, why does the Protocol consider only one aspect of them, namely, the exchange of greenhouse gases?

## Session 4

# Competition for Light in Forest Canopies

*Chair:*

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## Vertical attenuation of Photosynthetically Active Radiation (PAR) in forest canopies: average patterns, variation, and implications

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To understand how canopy light environments varied with forest type, developmental stage, disturbance intensity, and internal organization we made spatially intensive observations of the vertical transmittance of global Photosynthetically Active Radiation (PAR, 400-700 nm) in 18 different forests, usually under bright skies near solar noon. PAR transmittance was extremely variable within and between canopies but exhibited several patterns that were repeated among the stands. The frequency distribution of transmittance was non-Gaussian and had a shape that altered with height: the skewness changed from highly positive in the understory to very negative in the overstory. Thus, the mean was a poor representation of canopy light environments and the way it misrepresented those conditions changed with height. Also, the vertical change in the mean transmittance was not equivalent to the mean absorbance. In general, spatial variation was highest at canopy levels where the transmittance gradient was greatest. The shape of individual vertical profiles differed between forest types: in needle-leaved forests there was often an abrupt transition between bright and dark along an individual vertical profile, whereas in broadleaved forests, the transition was usually smoother. The transmittance at the forest floor and the vertical gradients of light depended not only on the total area of absorbing surfaces but also on its vertical distribution. Average profile shapes depended on the forest type, developmental stage, and disturbance regime. The pattern of the mean attenuation and its spatial variation were used to define vertical light environment zones: where reliably dark (“dim”) or bright (“bright”) or where variable in space and changing rapidly with height (“transition”). The limits of these zones differed among stands. In most canopies this transition zone was narrow and within the upper canopy; in some it extended over the majority of levels. The mean profile of attenuation was used to deduce some aspects of vertical structure by inverting the Beer-Lambert law. These results have implications for how canopy light environments are measured (variability can and must be accounted for), modeled (the specific patterns in the variation are critical), and managed (providing measures of growth potential and habitat variation).

## Robust segmentation routines for hemispherical photography under different radiation conditions

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**H**emispherical photography is a widely used method in the scientific area of forest ecology. Research of ecology in forest stands requested very detailed information about radiation, which can not be completely served by continuous working sensor systems. Hemispherical photography delivers additional data about canopy structure, leaf area index, leaf angle distributions, gap distribution and spatial distribution of radiation intensity. So far analogue technology is mainly used, which is limited by different factors as reproducibility and independence of data. The problem is the objectivity of the method, caused by exposure, film developing and mainly in the classification of the pixel with and without radiant objectives. The increasing use of digital technology solves some of the problems and offers additionally the possibility of multi-spectral image data. Hemispherical photography can be manifold used for ecology research. The main focus in the presented study is the spatial radiation distribution.

The study aims an improvement of reproducibility of the measurement results, which are taken under adversarial lighting conditions and an increase of precision in forest stands with less radiation. Existent segmentation routines will get an extension, used for segregation of relevant and not relevant radiant parts of the image. It is used high resolution digital cameras (Kodak DCS Pro 14n and Coolpix 950) and additionally optical filters. The multi-spectral image data are utilised for segmentation routine within the image analysis software programme OPTIMAS. The image analyses are extended through the integration of segmentation procedure and texture analysis of sub-pixel level. The validation of the results takes place with measurements with different approved methods, like PAR Sensors, Plant Canopy Analyzer and analogue hemispherical photography. The new algorithms are tested by long time field research and under different canopy structures.

The analogue technology based on the exposure of the photographs to the zenith luminance of an overcast sky. The digital technology enables heterogeneous sky conditions. Direct sun at the image let increase reflections and luminance in the crown of the trees. The classification of the hemispherical image does not show a uniform signature of the class sky. The reasons are differences in brightness from the middle of the image to the border and according to the azimuth stand of the sun as well as the dependence of the signature from the weather conditions cause problems. The spectrum of different exposure times and aperture gives different information at the image. Long exposure times give more information within the crown of a tree and short exposure times show more detailed small crown structures, likes branches and twigs.

The new digital technology enhanced the application and analysis possibilities of the hemispherical photography, but on the other hand causes new problems within the method. The detailed analysis of the digital images and the comparison with the existing system will show the accuracy and the rating of the system.

## Competitiveness and fitness of trees in a mixed temperate forest: the case study “Kranzberger Forst”

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At the research site “Kranzberger Forst” 40 km north of Munich canopy access is provided by a crane and a scaffolding consisting of three towers connected through platforms. In an interdisciplinary approach from the gene to the stand level international scientific teams aim on clarifying central mechanisms in plants how their competitive ability and fitness is regulated. The findings aboveground are proofed on consistency with results from the belowground “canopy” of the roots.

Especially, the following research aims are pursued: (1) Quantification of competitive interactions between adult beech and spruce trees as based on the involved resource fluxes; (2) Clarification of the associated resource allocation, employing experimental “free-air” ozone (O<sub>3</sub>) exposure within the canopy to facilitate the assessment of regulatory mechanisms and their responsiveness; (3) Determination of eco-physiologically meaningful threshold levels in the O<sub>3</sub> sensitivity of adult forest trees and mitigation of their carbon sink strength under enhanced, chronic O<sub>3</sub> exposure.

Broad-leaved beech (*Fagus sylvatica*) and the evergreen conifer spruce (*Picea abies*) are representing contrasting extremes in foliage type, growing season and crown structure in Central Europe. In our space-related approach it could be shown that the standing foliage mass per foliated volume around branches was higher in the sun compared to the shade branches of beech, whereas spruce was similarly efficient in its foliation of sun and shade branches. Overall, beech invested less foliage mass per branch volume than spruce. The C gain per volume was higher in sun branches, but did not differ between species. Respiratory and transpiratory costs, when expressed accordingly on a unit-volume basis, neither differed between species nor sun and shade branches. In beech and spruce, the proportion of foliage investments remained rather stable in the C balance of sun and shade branches, whereas respiratory costs were a major proportion, which distinctly increased towards the shade foliage. Hence, shade branches were costly structures to occupy space, achieving only low and even negative C balances, which conflicts with the claimed C autonomy of branches. Findings are viewed in relation to competitiveness, highlighting the significance of the standing foliage mass versus annual investments in foliage or branch volume increment. Doubling the background ozone concentrations continuously in the crowns of five adult trees of each species displayed a similar regulating “buffer” capacity of beech and spruce. Photosynthetic limitations and biochemical constraints on the cell and leaf level did not affect stem increments significantly, even after five years. It is concluded that competitiveness, expressed through space-related resource investments versus returns, has the potential of promoting the mechanistic understanding of plant-plant interactions.

## Beyond the visible application of infra-red thermography within micrometeorological and biophysical forest canopy research

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Within forests the differential heating of air and biomass leads to comprehensive variations in microclimate that in turn produce a spectrum of different living conditions for the flora and fauna. Furthermore, the thermodynamic stratification has an important impact on the turbulent fluxes of heat and water vapor. In this context, canopy temperature is a crucial parameter since it directly influences the sensible and latent heat transfer as well as photosynthesis. However, the accuracy of direct measurements with fine-wire thermocouples or thermistors for instance, is still restricted to the limited number of single-point measurements, whereas reliable spatially averaged values are mostly unavailable.

This paper explores some innovative applications of infra-red thermography within micrometeorological and ecophysiological forest canopy research. A high resolution radiometric camera system was utilized to determine daily dynamics of canopy temperature fields. Using the Wind River Canopy Crane facility in Washington, US, detailed investigations were carried out in the upper canopy of an old-growth Douglas-fir/western hemlock forest. Close-up views revealed significant differences in body temperature between the dwarf mistletoe *Arceuthobium tsugense* and its host *Tsuga heterophylla* on individual branches. Thus, transpiration rates of dwarf mistletoe plants may be much greater than of host tree foliage to maintain a supply of nutrients and carbohydrates even during drought. In general, the results suggest that infra-red thermography is a highly suitable application to observe and to analyze the environmental impact of micrometeorological and physiological factors on the complex process of evapotranspiration.

## **Retention of canopy closure in tropical rainforests: a simple yet effective strategy for mitigating adverse impacts of roads and other linear infrastructure corridors**

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**T**he Wet Tropics World Heritage Area (WTWHA) covers about 900000 ha and is located in northeastern Australia. Tropical rainforest is the dominant vegetation type and the area is considered a global biodiversity hotspot. The WTWHA contains 1427 km of roads and highways (608 ha) and 324 km of powerline clearings (1316 ha) which produce a multitude of environmental impacts on the natural heritage values of the area. Significant impacts include linear barrier effects on ground and tree dwelling fauna, abiotic and biotic edge effects that penetrate up to 200 m into the forest interior, conduit effects for weeds and feral animal species through provision of alien habitat and road kills. This paper provides an overview of a multi-disciplinary research project examining environmental impacts of roads and powerline clearings in tropical rainforest ecosystems. Topics to be discussed include: impacts of linear barriers on small- and medium-sized mammal movements in the canopy and understorey, edge effects caused by linear clearings and resultant impacts on forest microclimate and vegetation structure and floristics and mitigation strategies to minimise adverse impacts. A central theme in the research findings is that retention of canopy closure over linear clearings significantly reduces linear barrier effects for native fauna (ground and tree dwelling) and minimises microclimate differences along edges and the penetration of weeds and feral animals into the forest interior. In situations where canopy closure cannot be achieved, such as for major highways, engineering solutions including provision of fauna overpasses and underpasses and canopy road bridges are an effective but expensive alternative.

## Session 5

# Physiological, Biomechanical and Allometric Constraints on Tree Height

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## Biomechanical and allometric changes along latitude and elevation transects: are there general trends?

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**E**nvironmental variables that influence plant growth rates, morphology, and absolute size are known to vary as a function of latitude or elevation (e.g., ambient light intensity, annual precipitation, average temperature, and duration of the growing season). It is reasonable therefore to expect latitudinal and elevational gradients in productivity, plant architecture, and size. Surveys corroborate this expectation in terms of plant form and growth habit. For example, the frequency and number of broad-leaf evergreen species, on average, declines toward higher latitudes as do species with non-intermittent growth, non-articulated branching patterns, shoot dimorphism (plagio- and orthotropic growth), or tank-tree species (i.e., arborescent drought-deciduous stem succulents). Conversely, species evidencing cauliflory, aerial roots, extensive trunk buttressing, or epiphytic or liana growth habits are generally more frequent toward the tropics. Likewise, tree height, which influences ambient light levels within forested communities, tends to decrease with increasing elevation or sparse community densities (but not across similar habitats differing in latitude). The result is an increase in the diversity of plant architecture toward lower latitudes elevations with concomitant changes in the magnitude, type, and duration of static and dynamic loads shoots and roots must sustain. Nevertheless, the available evidence also indicates that many allometric (size-dependent) trends are insensitive to significant differences in latitude or elevation, or absolute size (as measured by height). Among these trends are the scaling of total basal cross-sectional area with respect to available space, the relationship between standing dry leaf mass and dry stem mass, and the scaling of dry above- with respect to below-ground mass. Collectively, these observations indicate that species certainly differ in terms of many important life-history traits, but that at a very basic level tree species manifest equally important invariant features.

## Limits to tree height: the effect of leaf arrangement and physiology

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**R**ecent research has provided strong support for the idea that tree height is usually limited by hydraulic considerations. However, it is still unclear why the tallest trees in the world are conifers, despite the fact that their wood has poorer hydraulic conductivity than that of angiosperms. Nor has it been explained why the tallest trees live in temperate areas which are dry enough to be subjected to periodic forest fires. This talk examines how leaf morphology and arrangement should affect the photosynthetic and hydraulic performance of trees, and so cast light on these apparent paradoxes.

## What happens after maximum crown size is reached? – Adaptive reiteration as a mechanism for crown maintenance

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When trees are increasing in size, extension rates of shoots are greater in the upper part of the crown than in the lower part of the crown. This has been attributed to the vertical gradient in light intensity. However, investigation of shoot extension of canopy trees at the Wind River Canopy Crane indicated that, after reaching a certain size, shoot extension decreases in all parts of the crown regardless of light intensity. This occurred for trees taller than 40 m in all canopy species suggesting that some common physical constraint may determine maximum crown size in this forest. We observed in 500-year-old *Pseudotsuga menziesii* trees that have reached maximum crown size that parts of the crown die back and are replaced by newly growing architectural units originating from epicormic buds. This process is referred to as adaptive proleptic reiteration because it occurs without external stimuli, such as trauma, and by formation of new apical meristems through the release of suppressed buds. In old *P. menziesii* trees, reiteration occurs at various spatial scales. Clusters of foliated shoots are reiterated through epicormic sprouting from shoot axes that are themselves still foliated. Large sections of branches are reiterated through epicormic sprouting from older branch axes that are up to 58 years old. Entire branches are reiterated through epicormic sprouting from the main stem. Other studies have observed that, in older *P. menziesii* trees, the main stem of the tree is reiterated as some branches form vertical axes creating “mini trees” within the mother tree. We hypothesized that adaptive proleptic reiteration is a mechanism of crown maintenance that enables trees to overcome growth limitations of existing apical meristems. The ability to reiterate various architectural units and maintain the crown may also contribute to increasing individual tree longevity.

Adaptive proleptic reiteration also occurs ubiquitously in another long-lived tree species, *Sequoia sempervirens*. This species is known to reach heights of 100 m or more and shows great plasticity in shoot and needle morphology from upper to lower crown. We found that in 100-m-tall *S. sempervirens* trees, the ratio of shoot silhouette area to needle surface area, a measure of needle display, decreased and shoot dry mass per shoot silhouette area, analogous to leaf mass per area, increased with increasing height in the crown. However, these and other morphological variables did not change in the top 20 m of the crown despite marked increase in light intensity. Other studies have found limitations to physiological properties with increasing height in *S. sempervirens*. Limitations to morphological and physiological plasticity may define maximum tree height in this species. When the growth of existing meristems is limited, adaptive reiteration may be an effective mechanism for producing new meristems in trees that have reached maximum crown size.

## Immediate and long-term effects of hurricane winds on subtropical forest structure

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**G**uánica Forest, Puerto Rico, is a subtropical dry forest characterized by short, slender trees, of which about 42 % are multiple-stemmed. This forest physiognomy is common in the Caribbean, but absent in continental dry forests of the Neotropics. Previous studies have shown that the structure of Guánica Forest cannot be explained by prior cutting episodes. After the passage of Hurricane Georges over our field sites in September 1998, we measured wind effects and sprout development on over 2000 stems in Guánica dry forest in Puerto Rico. Only 2 % of stems died and only 12.4 % of stems incurred structural damage. Damage was biased toward larger diameter stems. Stems that showed *no signs of wounding* produced 5.7 to 10.1 sprouts per stem after the hurricane, 3-6 times higher than pre-hurricane sprouting rates. More than three-quarters of the hurricane-induced sprouts originated within 40 cm of the ground. After 2 years, only about 13 % of these sprouts had died. We hypothesize that the hurricane caused prolonged vertical displacement of the stems which would increase the production of ethylene where bending was greatest – near root collars. Ethylene production has been shown to inhibit auxin transport in stems, leading to sprout development. The sprouting responses seen after Hurricane Georges may help explain Caribbean dry forest structure.

## Fresh perspectives on hydraulic and hydrostatic limitations to tree height and tree growth

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The “hydraulic limitation hypothesis” was proposed by Ryan and Yoder in 1997 as an explanation for the well-documented decline in height growth and productivity in aging forests. The hypothesis proposed that tree hydraulic resistance should increase in direct proportion to height, resulting in decreased canopy conductance, transpiration and carbon assimilation, and therefore decreased growth. There have been many counter-arguments to this hypothesis, including: 1) Multiple structural adjustments (such as increased diameter of xylem tracheids or vessels, and decreased leaf area/sapwood area ratios) compensate for increased tree size, maintaining the physiological activity of individual leaves; 2) Decreased water use by older forests in the early part of a growing season will result in greater moisture availability, and therefore greater carbon assimilation and growth, later in the season; 3) Physiological change in foliage of aging trees is regulated by genetic changes associated with age rather than by physical changes associated with size. Extensive research has subsequently shown that truth lies somewhere within these extremes. Laboratory studies have demonstrated that experimental manipulations of plant hydraulic resistance result in proportional changes in stomatal conductance; however, although field studies of many angiosperm and gymnosperm species show that hydraulic resistance increases as trees grow older and taller (as long as trees are growing in comparable environments, especially access to soil water), these results are not found universally, and even when they are, changes in hydraulic resistance and leaf physiology are not as great as one would predict from a strict interpretation of the hydraulic limitation hypothesis. Structural compensations do moderate the impact of height on hydraulic resistance, although not completely. Furthermore, there is evidence for ontogenetic change in leaf physiology as trees progress from maturity to old age, although age-related reductions in carbon assimilation (due to hydraulic limitation, ontogenetic changes, or any other cause) are not sufficient to wholly explain age-related declines in productivity. Recent research suggests additional mechanisms by which size may limit growth. Hydrostatic forces impact turgor in newly-expanding leaves, and this may be an important limitation to extension growth (leaf expansion and twig elongation) in tall trees. This talk will present a summary of key research and an updated view of limitation to age- and size-related changes in tree height and biomass growth.

## Architectural complexity versus cellular senescence: reconciling two alternative views on tree lifespan

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**C**arbon sequestration by forests usually declines after a peak at mid-age. Reduced growth in ‘old’ trees has been shown to be one of the main contributors to this decline, but explanations for this are debated. A first theory proposes that reduced growth after the start of the reproductive phase is caused by cellular senescence. A second set of theories has focussed on plant size and the role of an increased respiratory burden or excessive height. We report on experimental manipulations to separate the effects of size from those of age for four tree species of contrasting ecology. For all species, evidence indicated that size, not cellular senescence, accounts for the observed age-related decline in tree vigour. Since woody plants lack a marked separation of soma and germ line, these results support the disposable-soma theory of the evolution of senescence, by extending it to trees.

## Scaling of plant hydraulic architecture

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The design of a plant's hydraulic architecture must satisfy a number of limiting constraints: transport of water, nutrients, and hormones from roots to shoots; maintenance of a continuous water column while minimizing the risk of xylem cavitation (or embolism); and, provide structural support for the aboveground tissues. Although aspects of these constraints are well understood, less information exists regarding how the transport system is designed to simultaneously satisfy these demands. The analysis of a tree's hydraulic architecture could be greatly simplified if the design were easily scalable across a tree's developmental and height chronology. One reported mechanism to explain the limits on tree height contends that the conduits for water transport are designed to decouple hydraulic resistance from path length. Such a decoupling is possible given a limited range of quantitative forms of xylem conduit and branch tapering. In this study, we present direct empirical evidence of an ontogenetically stable hydraulic design in woody plants. Dimensions of over 8900 xylem conduits (vessels) from a ring-porous tree, *Fraxinus americana* (white ash), are analyzed over 12 meters in height and 18 years of growth. The tapering of vessel radii is shown to depend only on the distance from the distal end of the tree. We derive a quantitative prediction of how vessel radii should taper based on recent theoretical studies of the allometry of fractal branching networks (FBN), as applied to plant vascular systems. We show that the observed vessel tapering profile of *F. americana* agrees remarkably well with the FBN scaling prediction: vessel radii taper like distance from the distal end to the 1/4-power, independent of tree height or age. However, it is not clear how such a stable design satisfies the trade-off between maximizing hydraulic conductance and minimizing the risk of cavitation. Importantly, whatever optimality principle is at work regarding the hydraulic design of a plant's vascular network, a scaling framework exists that uncouples this design from the plant's developmental and growth history.

## Size dependency of water- and nitrogen-use in photosynthesis and hydraulic conductance of three *Acer* species with different maximum sizes

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**I**t is suggested that limitation on tree morphological and physiological functions becomes severer as they grow, because of increased hydraulic stress in drawing water from soil into their canopies. Trees vary greatly in size within species and among species, therefore, the adaptive responses to hydraulic stress might be different among species with different maximum sizes. The purpose of this study is to clarify size dependencies in photosynthetic and hydraulic properties of three *Acer* species with different maximum sizes. We used different sized open-grown trees (from saplings to mature trees) of two canopy species, *Acer mono* and *A. amoenum*, and one subcanopy species, *A. japonicum*. We measured maximum photosynthetic rate, leaf water potential and transpiration rate for each tree and compared size dependency in these traits among species. Maximum net assimilation rate per unit dry mass significantly decreased with increasing tree size in these *Acer* species. Stomatal conductance at maximum photosynthetic rate decreased with tree size in the *Acer* species, which suggests that these species reduce the loss of water in larger trees, at the expense of carbon assimilation. In contrast, leaf nitrogen concentration was significantly higher in large trees than in small trees in these species. Because leaf nitrogen content is strongly correlated with photosynthetic ability, the increase in nitrogen content with size should contribute to compensate for the size-related decline in stomatal conductance, which decreases net assimilation rate. As a result, area-based maximum net assimilation rate was not different with tree size in these *Acer* species. The extent of increase in leaf nitrogen content with size were higher in *A. mono* than *A. amoenum* and *A. japonicum*. *A. mono*, larger than the other two species, is expected to have higher photosynthetic demand because of evolutionary response to vertical gradient in light availability through the canopy. As for hydraulic properties, neither root-to-leaf hydraulic conductance nor minimum leaf water potential changed with tree size. The size independency in hydraulic conductance suggests that these species have some structural compensation for hydraulic conductance. Leaf nitrogen content and stomatal conductance represent nitrogen- and water-use in photosynthesis, respectively. The relationship between photosynthesis, nitrogen content and stomatal conductance were not different among species but different along with tree size. Although area-based maximum photosynthetic rate as well as the size-dependent increase in leaf nitrogen were higher in larger statured species, the relationship among these parameters suggests a functional convergence in the two resource use, nitrogen and water, in photosynthesis among these *Acer* species.

## **Community level relationships between tree height, sun-exposed crown and stem growth for Barro Colorado Island, Panama**

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The relationship between light and growth has been derived entirely from small trees and saplings, yet the highest rates of photosynthesis and greatest biomass in the forest come from upper canopy trees. For understory trees, increased height generally indicates greater access to light and faster stem growth. But for canopy trees, light limitations to growth have not been measured because of the difficulties in accessing the canopy to measure light interception and in obtaining sufficient sample sizes of large trees. We used digitized aerial stereo photographs of a large forest inventory plot to determine the relationships between long-term stem growth, tree height and sun-exposed crown area on a community level. We test several hypothesis for all trees and for the 12 most common canopy species: (1) sun-exposed crown area and shading by neighboring trees, both of which determine the amount of direct light to a crown, are more important than basal area in determining stem growth and (2) as trees reach the height asymptote of the forest, stem growth would switch from being controlled more by neighborhood shading to being driven by sun-exposed crown area.

From the digitized stereo photographs, we determined tree height and sun-exposed crown area of each tree in 9.6 ha of the Barro Colorado Island forest dynamics plot in Panama. In the field, the digitized crowns were linked to tagged stems, for which species identity and 20 year growth rates are available. To determine shading by neighbor trees, we took an average of the heights of surrounding trees weighted by their distance from the target tree.

For the whole forest, height showed a strong asymptote with diameter at a height of 40 m, but sun-exposed crown area had no asymptote with stem diameter and continued to increase throughout the diameter range of the forest. Preliminary analyses showed that for all trees together, sun-exposed crown area was important for explaining tree growth only for trees over 25 m in height. For individual species there was a large degree of variation in allometric and growth relationships. A greater number of species showed a strong relationship between sun-exposed crown area and stem growth than between basal area and stem growth. However, over 50 % of the species showed no relationship between growth and either sun-exposed crown area or basal area. For these species, the effect of the height of neighborhood trees may be important.

## Investigation into ecophysiology and increment of tree crowns

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**H**igher Crown transparency is not necessarily correlated with lower increment. In some cases, trees with more transparent crowns had higher stem diameter increments in 1.3 m height than others. The relation of assimilate allocation and crown architecture is largely unknown. In order to describe growth in separate parts of the crown of mature trees in closed canopies the phenology of length and diameter increment was related to meteorological parameters (like photosynthetic active radiation) in representative trees of *Fraxinus excelsior*, *Quercus robur* and *Tilia cordata* in a riparian forest near Leipzig. Changes in stem, twig, and shoot diameter were recorded with high temporal resolution. In addition, xylem sap flow and soil water potential were recorded. Length increment and leaf gas exchange of selected canopy shoots (sun and shade crown) were recorded periodically. Current and past shoot length and stem diameter increment was used to analyse competition between shoots within and between species. The results will be used to predict shoot, crown, and tree increment in diverse stands and to derive recommendations for their treatment. The largest part of diameter increment in 2003 was completed in a phase of sufficient water supply. Soil water availability began to fall at the end of June, after diameter increment had culminated. Shoot length increment was completed even earlier and was not limited by soil water availability. In extreme cases the shade crown can be more effective than the light crown. In the summer of 2003 net photosynthesis and stomatal conductance in the shade crown of a linden tree were higher than in the sun crown (measured at an irradiation of 1200  $\mu\text{mol}/\text{m}^2/\text{s}$ ). This was probably caused by higher drought stress in the sun crown as indicated by lower stomatal conductance. At the time of measurement air temperature was 28 °C and leaf surface temperature up to 39 °C. We conclude that in normal climatic conditions shoots in the shade crown have only low length and diameter increment. Also net photosynthesis is low. Further data analyses will give more insight into the importance of the shade crown for the tree as a whole.



## Session 6

# Floral Ecology, Reproductive Systems, Pollination and Seed Dispersal

*Chair:*

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## Is stratification of cerrado vegetation related to pollination and seed dispersal systems? Quantitative studies in a cerrado s.s. woodland in Brazil, and a comparison with Neotropical lowland rainforests

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**W**hole census studies on pollination and seed dispersal in the tropics are very rare to non-existent, especially with regard to stratification of a particular vegetation. A long-term study has been carried out in a one hectare plot (100 m x 100 m) of cerrado s.s. low-tree and scrub woodland in southern Brazil, which had a total woody plant cover of about 50 % and a tree canopy varying from 3 to 8 m height. All species in this hectare were examined with respect to growth and life forms, pollination, dispersal and phenology of flowering and fruiting.

The majority of the 301 angiosperms occurring in the plot were either bee pollinated (38 %) or showed a more generalist pollination (37 %); in addition, 13 % were anemophiles, 3 % cantharophiles, 2 % each ornithophiles, sphingo- and phalenophiles, and 1 % each chiropterophiles, psycho- and myiophiles. The species and their respective modes of pollination and seed dispersal were ordered to three height classes or vegetation layers, "tree-layer" (3 m and more), "scrub" (higher than 1 m, but lower than 3 m) and "ground layer" (below 1 m). Species pollinated by small bees, generalist insect-pollinated species, hummingbird-, fly-, butterfly- and wind-pollinated species were more common in the lower layers of the vegetation, large bee- and beetle-pollinated species were  $\pm$  evenly distributed among the three vegetation layers, and phalenophilous, sphingophilous and chiropterophilous species occurred in the taller scrub and canopy layers only. Studies in rainforests either do not consider different forest strata and only refer to the canopy (e.g. van Dulmen 2001), or the given pollination systems especially of the canopy and subcanopy, because of the difficulty of access, represent only a subset of the real existing systems (e.g. Bawa et al. 1985, Kress and Beach 1994). Pollination mode stratification in tropical rainforests supposedly is much more accentuated than in low and open cerrado woodlands. Considering the present state of knowledge, however, such differences are hardly discernable. Dispersal in cerrado is also to a certain extent related to the three strata. In the hectare 135 spp. (45 %) were zoochores, 88 (30 %) anemochores and 78 (25 %) were autochores. A comparison of the three height classes shows that the percentage of zoochorous species decreases with height, from the tree layer down to the ground layer. However, the total number of zoochorous species increases because of the much greater number of ground-layer species. Likewise, the percentage of anemochorous species, contrary to their total number, decreases in the ground layer. Their highest percentage is in the scrub, with the tree layer occupying an intermediate position. The autochores increase considerably in number of species and also in percentage from the tree to the ground layer, that is, as height diminishes. The preponderance of the anemochorous and autochorous dispersal modes (55 % of species) over zoochory (45 %) in the hectare, tells two stories, one that many species are able to disperse their diaspores without recourse to animals, and two, that for many other species, animals are nearly as important as dispersers.

With respect to the major dispersal modes, the cerrado appears to occupy a position intermediate between dry forests and moist rainforests. While dry forest woody plants are predominantly wind dispersed and/or have a lower representation of zoochory than cerrado, in rainforests, the woody species are predominantly zoochorous, with more than 90 % of trees and about 75 % of lianas exhibiting this dispersal mode (Levey et al. 1984,

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## Long-term flowering and fruiting patterns of canopy trees in the rainforest of Southern Western Ghats, India

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**T**ropical rainforest tree phenology is complex as several proximate and ultimate factors could be responsible for the evolution of such complexity. Understanding such complexities will require long term data on phenology which is often not available especially from Asian forests. Here we describe the flowering and fruiting patterns of tropical rainforest canopy trees at Kakachi a mid elevation forest in the southern Western Ghats of India. Over 600 individual trees from 76 species were marked in 1990 and followed monthly to determine flowering and fruiting individuals till 2004. As phenology was difficult to do from the ground we also set up observation platforms in the canopy. We present the results from 1990-1996 in this paper.

Community peaks in flowering generally occur twice in a year between January and May followed by a second peak between Aug and October. High proportion of species flower non-annually and some have flowered only once in the last 14 years. Flowering intensity varies between years for most of the species. Flowering duration varies from less than one month in many species to almost 2 months in others. Fruiting reaches a high in May and continues till end of October. A trough in fruiting is observed between November and February. A community wide high in fruiting occurred in 1993 and not after that. In Kakachi flowering and fruiting patterns are complex and variable in intensity. Keeping in view the relatively low diversity of the forest compared to lowland forests of neotropics and Malaysia and the non annual flowering of the species flowering and fruiting resources may be just optimal to the pollinators and frugivores in the area. Any manipulation of the species assemblage can possibly alter the flowering and fruiting stratification affecting pollinators and frugivores in the forests.

## Generative phenology of a complex mesophyll vine forest plant community in Northeast Queensland, Australia

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**I**n this study the flowering and fruiting phenology of 1 hectare of complex mesophyll rainforest are documented. The state of knowledge about the generative phenology of the lowland Australian tropical rain forests is relatively low. Investigations concerning single species, thus as *Ficus variegata* (Moraceae) were conducted by Spencer et al. (1996). Long-term and integrated studies of a complex mesophyll vine forest were carried out by Crome (1975) and Hopkins et al. (1989). Hopkins et al. were able to reveal distinct seasonal patterns of generative phenology: The main flowering phase was confined to September and October, the main fruiting phase to the period from October to April. An increase of fruiting species during this period was also found by Crome (1975). Different criteria can be combined within the classification of phenological patterns. Based on Newstrom et al. (1994) we take into account the duration, time, amplitude and synchrony as well as the frequency and regularity of the phenological events and try to analyse those focused on the community level. The main question of our research therefore is: What generative phenological patterns does the plant community show over a period of two years?

To answer this question we take into account all the different life-forms as well as strata. This enables us to describe the generative phenology of understorey plants (70 species, 40 families), trees (77 species, 33 families) and vines (60 species, 29 families) as well as to compare the phenologies of these different life-forms. All data are documented in a monthly rhythm. Herewith the amount of reproductive units (flower buds, flowers and fruit) is ascertained over a period of 24 months. The quantity of flowering and fruiting events of trees is found out by extrapolation of counted random samples. Additionally the flowering and fruiting syndromes are documented.

After 22 month of data collection our first preliminary results can be summarized in the following conclusions: **(1)** Flowering and fruiting activity could be documented for all months and life-forms. **(2)** Within one year the plant community clearly shows a phase of increased flowering activity during the wet season as well as fruiting activity confined to the end of the dryer month. **(3)** Major rainfall peaks during the wet season lead to a decrease in the flowering and fruiting events.

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## Birds and their flowers in understory and up, UP there in the canopy in a tropical rain forest, Southeastern Brazil

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Hummingbirds are considered the most important vertebrate pollinators in the neotropics. Other flower-visiting birds are often considered as parasites of the flower-hummingbird relation, not presenting the high degree of specialization for nectarivory as hummingbirds. Although ornithophilous flowers are very showy, displaying colorful floral parts or structures associated with the flowers or inflorescences, hummingbirds also visit non-ornithophilous flowers, which most of the time are not pollinated during nectar probing. In a two year study about floral resource availability for birds, especially hummingbirds, in the Atlantic rainforest in Southeastern Brazil, their activities and flower abundance were estimated in vertical stratification. Records were made every month, during line transects samplings along a path of 1500 m and accessing canopy with climbing equipment. Nectar volume and concentration were measured with microliters syringes and a hand-refractometer, respectively, from bagged flowers at the end of the morning. Bird species were registered during sightings and focal observations while visits to flowers. Hummingbird visits were recorded on 56 plant species; a few were also visited by other birds. Most species are epiphytes, and some are shrubs, lianas or trees. About 60 % of these species are pollinated by hummingbirds, from the others they steal or rob nectar. Flowers visited by hummingbirds are distributed over the year, which is important to maintain resident species, and most of this resource occurs in the understory, although in some months there are more flowers in the canopy. Nectar features are very variable among species: mean nectar volume ranging from 2 to 220  $\mu$ l, and mean nectar concentration from 3 to over 32 %. Among the hummingbirds, four species belong to subfamily Phaethornithinae and six to Trochilinae. Two resident species were recorded all over the vertical stratification, while other species occurred in only one stratum: understory or canopy. Trapliners were recorded visiting one flower species along its vertical distribution, carrying pollen between different strata. In the canopy two species were visited and pollinated by other birds besides hummingbirds. CAPES, CNPq, Biotá/FAPESP, Funcamp/Unicamp, TNC.

***Parkia pendula* (Willd.) Benth. ex Walp. (Mimosaceae):  
amount of nectar and gum and its importance for the mam-  
mal fauna of a Mata Atlântica fragment in Pernambuco,  
Brazil**

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**W**e present a brief overview of the observed feeding behavior of visiting mammals, and quantify the nectar and gum production of *Parkia pendula* trees of an Atlantic rainforest fragment in northeastern Brazil.

During our observations in 2003/04 we found *Phyllostomus discolor* to be the main pollinator (as many as 467 visits/capitulum/night). The smaller bat *Platyrrhinus lineatus* was less frequent but visited principally capitula which were not accessible for *P. discolor*, being therefore an important pollinator as well. *Glossophoga soricina* did not normally function as a pollinator since it ingested the nectar on the wing and did not touch the reproductive organs of the inflorescences. Additionally, several other arboreal mammals fed on *P. pendula*. Single individuals of *Caluromys philander* and *Nasua nasua* groups exploited nectar during the whole night. Unlike the other mammals, *Coendou prehensilis* did not feed on nectar but on capitula-buds. Although the only primate that occurs in the study area, *Callithrix jacchus*, was rarely observed during the observation-period, it nevertheless was seen to use *P. pendula* as well. Groups of this animal were observed to feed on nectar as well as on seedpod exudates and ripe seeds. This primate is supposed to be the primary disperser for *P. pendula* in the study area. Nectar production starts at dusk and ends at 02:00 A.M.. Total nectar production (capitulum/night) was  $9.63 \pm 5.02$  ml (mean  $\pm$ SD; n=8) summing up to 20.3 l nectar per tree per flowering period. Gum produced by one unripe pod was  $5.47 \pm 3.14$  g (mean  $\pm$ SD; n=30) fresh weight amounting to 18.4 kg gum per tree.

*P. pendula* produces enormous quantities of exudates (nectar and gum) and apparently attracts a large number of mammals which aid in pollination and seed dispersal. Several non-pollinating or non-dispersing mammals are attracted by these exudates, too. The seven observed mammals represent nearly 20 % of all registered mammal species of a nearby larger forest fragment. The widespread Neotropical tree *P. pendula* therefore is an important source of nourishment for the mammal fauna of the last Atlantic rainforest remnants in northeastern Brazil.

Research was carried out within the project "Disturbance, fragmentation, and regeneration of the Atlantic rainforest in the northeastern Brazilian state of Pernambuco" financed by BMBF (Project No.01 LB 0203) as part of the Mata Atlântica program.

**Herbivory and reproductive success: a case study of the influence of a rutelid scarab beetle on fruit set of *Sclerolobium densiflorum* Benth. (Caesalpinaceae) trees in Mata Atlântica rainforest fragments of Pernambuco, Brazil**

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**F**lowering, fruit set and reproductive success can be influenced by various biotic factors. In the present study a case of the destructive herbivorous activity of the beetle *Anomala* sp. at *Sclerolobium densiflorum* flowers is described. *Sclerolobium densiflorum* is a canopy tree species typical for secondary sites of lowland rainforests of Northeast Brazil. The species is self-incompatible and has flowers of up about 8 mm diameter, which are arranged in spikes. Pollen is the main resource and is presented by the filaments. Flowers are pollinated predominantly by small- to medium-sized bee species such as *Trigona* spp. or *Apis mellifera*. Flowering occurs between August and September. Due to the terminal position of the inflorescences at the branches, access to flowers by single rope climbing technique is rather difficult. In 2003, observations were made only during the day. All marked flowers showed severe herbivorous damage, especially of stamens, carpels and petals. The more rigid sepals usually were undamaged. Fruit set only occurred in bagged inflorescences, which however had holes that allowed visits by small insects. In 2003 no *Sclerolobium densiflorum* individual showed fruit set. In the 2004 flowering period during nocturnal observations, *Anomala* sp. could be detected causing the same damage observed the year before. It was observed to visit and feed only the floral organs of newly opened flowers. *Anomala* sp. approached the flowers between ten and thirty minutes after sunset and foraged up to five hours on the inflorescences, needing ca.  $24 \pm 10.5$  (mean, sd) minutes to destroy one flower. The density of *Anomala* sp. this year appeared to be much lower than the year before; many flowers remained undamaged. As a consequence, most trees flowering 2004 showed fruit set. In conclusion, it appears that *Anomala* sp. is one of the limiting factors for the reproductive success of *Sclerolobium densiflorum*. It is not clear if the low density of young individuals of *Sclerolobium densiflorum* can be explained by the activity of the beetle destroying flowers and reducing the reproductive success of this species.

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## Considering directionality in fruit dispersal models

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**D**espite the progress which has been achieved in modelling the seed dispersal of plants by “seed shadow models” the accuracy of the predictions made by those models still needs improvement, especially in regard to long distance dispersal. Seed shadow models describe the scatter of seeds around a mother tree by distance dependent probability density functions.

One prerequisite in recent parameterization techniques of seed shadow models is isotropy of the scatter around the mother tree. However, published data show non-isotropic features of that scatter. Non-isotropy - or directionality - is understood here as any relevant heterogeneity in seed density by azimuth directions in regard to the mother trees position.

In this talk we present a general approach to estimate directionality in seed dispersal data by implementing azimuth directions in seed shadow models. This leads to anisotropic models. This approach makes it possible to consider symmetrical anisotropic effects as well as non-symmetrical. Especially, elliptical models and an approach based on a generalization of the von Mises distribution are discussed. Further, we show that the total number of fruits or seeds for anisotropic models can be estimated unbiasedly. The proposed anisotropic models are tested for some seed dispersion datasets. It is shown that the predictions are improved in comparison with the results obtained by isotropic models.

## A comparison between two methods for measuring fruit production in a tropical forest

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**F**ruit and seed production patterns of plants are critical to understand function, structure and regeneration of forests. Several methods have been used to examine community-wide fruiting patterns; however, depending on the type of the study some methods are more suitable than others. We compared 6 month data derived simultaneously from fruit traps placed above the forest floor with systematic canopy-transect sampling in one hectare terra firme rain forest, in Colombian Amazonia. Our objective was to select the most suitable method for estimating fruiting at the canopy level, including fruiting of climbers and epiphytes. In four 50 x 50 m plots, the number of species bearing fruits and the amount of fruit mass were recorded monthly by both methods. Monthly variations derived from fruit traps were not correlated with the canopy-transect sampling estimates. Moreover, total and monthly number of fruiting species and fruit mass obtained from the canopy-transect sampling were markedly higher than fruit trap estimates. The canopy-transect sampling revealed more species and fruit mass of climbers and epiphytes (19 sp. and 18.52 kg ha<sup>-1</sup>) than the fruit traps (2 sp. and 7.92 kg ha<sup>-1</sup>). Since the fruit-trap method does not inform on the fruiting patterns occurring at the highest levels of the forest, it can be more appropriate for studies on fruit available for terrestrial frugivores, and on what is dispersed from longer distances. As the canopy-transect sampling provided both quantitative and qualitative information on the canopy fruit production, and each species contribution, it can be used for a broad variety of studies, particularly those aimed at measuring fruit availability for canopy frugivores such as birds and primates.

## Seed dispersal of epiphytic Bromeliads (Tillandsioideae) in Costa Rica

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The distributional patterns of epiphytes have often been described as clumped and patchy, and epiphytes often occur in only a small part of what seems suitable habitat. Studies to explain these patterns have mainly focused on ecophysiological factors, but these can in general only partly explain the observed distribution of epiphytes. Various studies have suggested that random colonisation processes (i.e. propagule supply) are the main determining factor in the distribution and community composition of epiphytes, but so far this remained virtually untested. The main objective of this study was to investigate the role of seed dispersal in colonization of secondary forest by bromeliads.

We investigated seed rain of five epiphytic bromeliad species (subfamily Tillandsioideae) in different successional forest stages of montane cloud forest in the Monteverde region of Costa Rica during the dry season. Seed traps were placed in each of three different forest types: young secondary, old secondary and mature forest, and were monitored at regular intervals. Trapped seed numbers per trap were related to the distance of the nearest dispersing bromeliad and to the abundance in the plots of each species. We hypothesised that the seeds of different species would be captured proportional to their abundance in the surrounding canopy, and that seed dispersal occurs on a local scale.

The numbers of trapped seeds per species were highly correlated with the numbers of reproductive individuals per species for the plots ( $r = 0.83$ ,  $p < 0.001$ ). The ANOVA's comparing seed rain between plots and forest types for the five species showed a significant difference between plots, but not between forest types. Since seed numbers reflect numbers of dispersing individuals, the variation in numbers of trapped seeds between replicate plots is likely a direct consequence of the patchy distribution of the species over the plots. A very large part of the seeds were trapped in the close vicinity of dispersing plants. In a distance analysis seed traps were divided in 4 categories of distance to the nearest dispersing bromeliad. As expected, the number of trapped seeds declined with distance from dispersing plants. The analysis revealed a significant difference in seeds per trap between the categories 1-5 m and 5-10 m. There were no significant differences between the categories  $< 1$  m and 1-5 m, or between 5-10 m and  $> 10$  m. This indicates that beyond a distance of 5 meters, the number of trapped seeds decreased sharply. Looking at the average numbers of seeds per trap for each category, more than 90 % of the seeds that were trapped within 20 meters (maximum distance of a trap to a dispersing plant) were found on traps within 5 meters of a dispersing bromeliad. Our results have shown that Tillandsioid seed dispersal occurs at a very local scale, and thus is an important limiting factor in colonisation processes.

## Genetic evidence that successful long distance seedling recruitment is commonplace in a vertebrate-dispersed Neotropical tree

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We used genetic markers to match seedlings to their maternal and paternal parents in a natural population of the dioecious Neotropical tree, *Simarouba amara* (Simaroubaceae) in a forest in Panama. Our objectives were to 1) measure dispersal by calculating distances of successful seedling recruitment in this species, whose seeds are dispersed by vertebrate frugivores and 2) to compare gene movement via seed and pollen. In our study, recruitment includes seed dispersal, germination and subsequent seedling establishment. We were particularly interested in documenting the frequency of long-distance recruitment events, defined operationally as recruitment occurring > 100 m from the maternal parent. Seeds arriving > 50 m (i.e. away from the canopy of the parent plant) have likely been moved there due to active dispersal by birds or primates and/or secondary dispersal by terrestrial vertebrates or ants. In our study, less than 10 % of seedlings were produced by the nearest reproductive female and long distance dispersal was frequent. Seventy-four percent of matched seedlings were dispersed > 100m. The mean dispersal distance for between established seedlings and their maternal parent =348 m (range 9.3-100.5 m). Gene movement via pollen was comparable to though slightly higher than that of seed, with a mean pollen dispersal distance =373.2 (range 1.4-1005.8 m). These findings are important in providing insights to long-standing questions in dispersal ecology.

## Flowering biology of four temperate tree species

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Leipzig's floodplain crane (LAK) is a construction crane on rails, which enables repetitive and non-destructive access to 1.6 ha of semi-natural broad leaf and species rich temperate forest. This study focuses on the flowering biology of the main tree species in the stand and reveals its complexity, as basis for other biological processes in the forest.

The flowering phenology, gender distribution and reproduction of ca. 150 trees of the species *Fraxinus excelsior* (ash), *Acer pseudoplatanus* (sycamore maple), *Tilia cordata* (lime) and *Acer platanoides* (Norway maple) were described in detail and often on the levels from inflorescence to whole stand over three years, and new insights into these processes and the connections between them were gained.

A common pattern of flowering unfolding within the single trees is bottom-up and inside outwards. This pattern prevails in early flowering trees (ash and Norway maple in April) and is partly expressed in later flowering trees. Superposed on this pattern is a tendency to earlier flowering toward south and east, which is differently expressed in the four tree species. The resulting gradualism of anthesis enables avoidance of some frost injury, as shown in different instances in ash.

All four species have peculiar sexual systems. *Fraxinus excelsior*, defined as polygamous, has individuals which range from pure male to pure female, with many intermediate forms. 59 % of the trees were male (half of which with negligible number of hermaphrodite flowers), 17 % female, and 11 % male biased, 13 % female biased hermaphrodites (warm weather correlated with more femaleness) the latter also produces the greatest yield in the stand.

*Acer* spp. are duodichogamous which means they undergo gender change two times during each flowering season, synchronous in all inflorescences. In *A. pseudoplatanus* the proterogynous trees have lower flower and fruit number per inflorescence but higher seed per fruit than the protandrous trees (median fruit number 6.5 vs. 10.9, median seed per carpel 0.8 vs. 0.2 in 14 and 30 trees respectively). This difference correlates with greater pollen loads on the stigmas, and represent two different allocation strategies. *Tilia cordata*, regarded a simple hermaphrodite species, is shown to be andromonoecious, and the appearance of male flowers is correlated with stronger florivory in lower parts of the crowns.

Among the flower visitors, thrips (*Taeniothrips inconsequens* in maple and *Thrips major* in lime) were very abundant in the inflorescences, whereas bees (*Andrena* spp. and *Bombus* spp.) were quite rare. Their abundance may put them in an intermediate pollinator role, abridging the gap between classical insect pollination through bees and wind pollination, which seems to be preferred by dominant temperate forest trees.



## Session 7

# Arthropods in Temperate and Tropical Forest Canopies - 1<sup>st</sup> Symposium

*Chair:*

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## Arboreal arthropod communities of primary and anthropogenically disturbed tropical and temperate forests: comparisons are worth the effort

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Arthropods form the greater part of species diversity within the forest canopy and are considered to influence ecosystem function profoundly. However, this is in contrast with our limited knowledge of the (i) relationship between species and their canopy environment and (ii) maintenance of species diversity and its link to ecosystem function in both tropical and temperate habitats. However, in contrast with temperate systems, tropical lowland rain forests belong to the oldest and most diverse terrestrial ecosystems. Understanding such complex questions on the basis of ecological principles derived from temperate ecosystems, usually low in terms of diversity and highly perturbed, proved difficult. A promising approach is to use arboreal arthropod communities as a model system. They may be sampled discretely and apparently quantitatively by insecticidal knockdown ('fogging'). Since anthropogenic disturbance is ubiquitous, I included both primary and perturbed forests in the analysis. In the tropical forest, communities differed dramatically in diversity, structure and dynamics. Comparison of secondary forests of different ages demonstrated how communities reorganized during forest regeneration and how they approximated the conditions of the primary forest provided that recolonisation from a species-rich primary forest is guaranteed. Otherwise regeneration failed to appear, at least within the 50-year time scale investigated.

Based on these results, I am investigating primary and managed forests in Central Europe. In contrast with those in the tropics, primary forests were destroyed hundreds of years ago and, consequently, many studies are not calibrated on natural conditions. What were the consequences for community ecology? Based on these considerations, I am analysing more than 600 fogging samples from both tropical and temperate biomes. Various taxa were identified to species/morphospecies level, including Coleoptera, Formicidae, Ichneumonidae, Araneidae, Heteroptera and Orthoptera. Many patterns of diversity, community organisation, and the functional role of individual taxa may only be understood on a sufficiently large sample size, emphasising the necessity of such a 'top-down' approach in order to ask meaningful questions concerning basic research and nature protection.

## The ants of Central European tree canopies (Hymenoptera: Formicidae) – an underestimated population

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Data on biodiversity and abundance of arboreal ants were obtained by collecting from the ground, climbing on trees, investigation of fallen trees, telescope observation and a canopy crane survey during the years 1979-2004. 68 ant species were observed to forage regularly or occasionally in tree canopies of which 17 species are arboricolous and only 13 true canopy dwellers. These figures mean 40 %, 10 % and 8 % of the total Central European fauna. The distribution of arboreal ants is mainly directed by the factors nesting space required, ability to excavate wood material, foraging range, thermophily, cold-hardiness, position in the dominance hierarchies of ant communities, resistance against desiccation, tree age, tree species and food spectrum. The probability of nesting in canopies is positively correlated with thermophily, cold-hardiness and resistance against desiccation while it is negatively correlated with the nesting space required, ability to excavate wood material, foraging range and position in the dominance hierarchies of ant communities. Estimated nest densities for *Temnothorax affinis* in the canopies of *Pinus sylvestris* and *Quercus robur* & *petraea* ranged between 8-14 nests /100 m<sup>3</sup> canopy volume which corresponds to 560-980 workers or 230-400 mg fresh weight /100 m<sup>3</sup>. The density of *Temnothorax corticalis* in the canopy of a 26 meters high and 240 years old *Quercus robur* was > 11 nests/100 m<sup>3</sup> canopy volume or > 220 nests /100 m<sup>2</sup> ground area. This oak was estimated to carry more than 250 *T. corticalis* nests. The sparse nest findings of the other true canopy species *Camponotus fallax*, *Camponotus truncatus* and *Dolichoderus quadripunctatus* did not allow direct estimations of nest densities but, from observation of worker movements, individual numbers of these species usually should be only 5-10 % of those reported for *Temnothorax*. Densities of ants nests in surmounting oaks with warm canopy mantles in Upper Lusatia and of oaks in xerothermous forests in the warm region near Meissen are significantly higher than in oaks of the moister and cooler floodplain forest NW of Leipzig which has an almost closed canopy.

## Single oaks in beech forests – important stepping stones or lost islands?

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**W**e investigated communities of saproxylic beetles in 30 crowns of individual oak trees (*Q. robur*) in acid beech forests using window traps from April to October 2004. Oak trees represented at maximum 30 % of all trees in the surrounding. Compared to oak forests, individual oak trees were not rare in typical oak and endangered beetle species. I show that the share of saproxylic oak specialists depend not on the share of oaks in the surrounding stands. Decaying beech trees can not replace oaks as habitats. For the protection of endangered species the value of single oaks is a high one!

## Canopy and soil arthropod beta diversity in different scales in subtropical evergreen forests of the Azorean islands

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**I**n this contribution we explore the influence of scale and habitat type in patterns of arthropod species distribution. Within each scale we compare soil with canopy arthropod fauna. We examined how additive beta-diversity can be used for partitioning species turnover between scales. The variation of the slope of the species-area relationship (SAR) between scales is also investigated. The study was performed in the Azorean islands in three scales: small (several transects within reserves); medium (several reserves within islands); large (several islands).

The main results show that for both endemic and all species in the soil and canopy, beta diversity is higher between islands (“the island effect”). In most islands, the  $\beta$  diversity is similar in the small and medium scale, but in some islands there is also an important turnover of species between reserves indicating fragmentation in species distribution within islands due to reserve isolation. Interestingly, slopes of the SAR are similar for communities of arboreal and soil fauna in medium and large scales (reserve and island), which means that in spite of differences in dispersal, both assemblages are ruled by the same geographic factors. Consequently, patterns of fragmentation on the Azorean islands had similar impacts in soil and arboreal fauna, which was not expected from the beginning. The slope of the SAR is not always steeper in the archipelago scale than in the reserve scale which means that within island, fragmentation has a large impact on species distributions. There is no positive relationship between alpha and gamma diversities, which means that the positive slopes in the SAR are due to large scale beta diversity. We also show that each endemic tree plant species behaves as an island with a species-plant cover (area) near 0.40.

Our results suggest that the most effective way to preserve endemic arthropods in the Azores is to manage and protect reserves in all islands, and in some of the islands most of the reserves are needed.

## Diversity and guild structure of different xylobiontic beetle groups in a neotropical rainforest (San Lorenzo, Panama) and a temperate deciduous forest (Germany, Central Europe)

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**X**yllobiontic beetles play an important role in remineralisation of deadwood. Deadwood shows a huge variety of conditions and ecological situations respectively, in dependence on tree species, temperature, moisture, fungi infestation, degree of decay etc.. For analyzing communities of xylobiontic beetles occurring on different kinds of deadwood, it is therefore necessary to classify different ecological guilds related to the dead wood, the “substratum”.

In the present study I compare an evergreen tropical and a humid deciduous temperate forest using the substratum related guild system published by Schmidl & Bussler (2004) which distinguishes five different guilds (guild abbreviation in brackets): Indwellers of: 1. fresh deadwood (f), 2. old and to diverse extent rotten deadwood (a), 3. fungi on deadwood or fungi-infested deadwood (p), 4. rotholes (m), 5. species with other way of living in deadwood (s). This approach allows direct comparison of different forests and settings in relation to deadwood resources, forest structures and decay succession. Furthermore, the method enables working on an ecological, supraspecific level by lumping together species on the basis of common genus or family biology features (for example: all Cisidae as fungi-feeders), an important precondition to work on tropical coleoptera.

Based on fogging samples (with natural Pyrethrum) conducted in the IBISCA project in 2003/04 in Panama and in the floodplain forests of the Danube in Central Europe in 2004, the study evaluates differences and similarities in community and guild composition of selected xylobiontic beetle groups of temperate and tropical forest canopies.

## Comparison of the weevil biodiversity between tropical and temperate primeval forests

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This study aims at comparing the diversity of Curculionidae in tropical and temperate primeval forests. Weevils are one of the most species-rich beetle families in the tropics as well as in Central Europe. As herbivorous insects they show diverse adaptations to their host plants. While there is only little knowledge about tropical weevil biology/autecology, much more is known for Central European species. On the basis of this knowledge we try to compare patterns of speciation of some species groups. Parameter for this comparison are tree species numbers, life histories, and distribution of weevils.

The comparison is based on fogging samples from Dipterocarp primary lowland rain forest in the Kinabalu region (Borneo, Sabah, East Malaysia) and the Bialowieza Primeval Forest (NE-Poland). Taxonomic knowledge of South-East Asian weevils is very poor and we were surprised that between 80 % to 100 % of the hitherto analysed Apionidae, Nanophyidae, Ceutorhynchinae and Rhamphini species (and even some genera) are new to science. Presorting of many of the remaining weevils indicates that identification to species level is nearly impossible in most species-rich groups (e.g. Rhynchitidae, Zygopinae, Cryptorhynchinae). In the species-rich subtribe Ochyromerina (tribe Tychiini) 5 species, which were described from Sabah just recently, could be identified. Total species number from all fogging samples is more than 1000 but this is a preliminary result according to sorting to morphospecies.

## Distribution and biodiversity of Orthoptera in a neotropical rainforest (San Lorenzo, Panama) and a temperate deciduous forest (Germany, Central Europe)

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Climate, fall of leaves, nutrient cycles etc. are factors causing ecological differences between a neotropical and a temperate forest, resulting in different diversities, stratification and life histories of arthropods. Based on fogging samples (with natural Pyrethrum) conducted in the IBISCA project in 2003/04 in Panama and in the floodplain forests of the Danube in Central Europe in 2004, the presented study shows the coherency between the natural conditions and the diversity and life history of canopy orthopterans (s.l.). A comparison between evergreen tropical and deciduous temperate forest as well as a comparison of floodplain forests with and without floodings evaluates the impact of different ecological factors on the distribution and diversity of forest canopy orthopterans. The autecological adaptations of the temperate forest canopy settling orthopteran species are discussed in this context.

## **Ichneumonidae (Hymenoptera) from the canopies of tropical forests in Malaysia and of temperate forests in Poland**

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**I**chneumonidae (Hymenoptera) were collected by canopy fogging from primary forest and secondary forests in Malaysia (Sabah, Borneo) and from primary and secondary oak forests in Poland (Bialowieza Forest). Whereas the numbers of specimens of Ichneumonidae collected from standardised parts of trees were much lower in the tropics, values for alpha-diversity and probably also the numbers of species were higher in the tropical than in the temperate forests. The ichneumonid communities from secondary (managed) forests did not differ much from those from primary forests growing nearby.

## What proportion of tropical forest beetles are found in the canopy?

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Just how many species are there on Earth and where are these to be found? These questions have been central to the problem of conserving the worlds biodiversity. Some 25 years ago it was suggested that there may be many more species of insects on Earth than scientists had previously imagined and that most of these are found in the canopy of tropical forests. Although these suggestions have not been backed up by rigorous scientific data, the notion that there might be 30 or 100 million species of insects on Earth has become part of scientific folklore. This paper brings together one of the first attempts to determine how many species there might be in a single tropical forest area and what proportion of these species are only found in the canopy or the ground and what proportion is shared between these two layers. This work is the result of a four year sampling program at the Australian Canopy Crane in North Queensland and the subsequent sorting of almost 20000 beetles of approximately 1500 species of all families. The difference between this and other previous attempts to answer these questions is that equal sampling effort was applied to the canopy and the ground using combined Malaise and Flight Interception traps and this sampling was replicated at five locations.

## **IBISCA-Panama: a large-scale study of arthropod mega-diversity in a rainforest. General protocol, preliminary results and perspectives**

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**T**he IBISCA (Investigating the Biodiversity of Soil and Canopy Arthropods) project is described; some preliminary results, which will be broadly presented and discussed in this symposium, are introduced and perspectives concerning ongoing IBISCA-like projects will also be discussed.

The IBISCA project aims to study the relationships between beta-diversity and the vertical stratification of arthropods in a neotropical rainforest. To this end, the entomofauna of nine sites (400 m<sup>2</sup>), all less than 2 km apart, was studied from the ground to the upper canopy in the San Lorenzo Protected Area, Panama. In order to conduct investigations in the canopy, IBISCA participants used “fogging”, single-rope techniques and a variety of devices including the Fort Sherman Canopy Crane, the Canopy Raft, the Canopy Bubble and IKOS. These techniques and devices complement each other well and IBISCA represents the first attempt to combine them in a large-scale investigation. They provided spatial replication during a six-week field study that took place in September-October 2003 (rainy season). Seasonal replications were conducted three times at the three different crane sites: one complete replication (all the sampling protocols were used) in May 2004 (beginning of the rainy season) and two partial replications (only a few sampling protocols involved) in February 2004 (dry season) and October/ November 2004 (rainy season). To collect arthropods, 14 different protocols were used involving sampling techniques such as fogging, branch beating, various kinds of traps including pitfalls, small and large flight intercepting traps, sticky traps, light traps, bait traps, Berlese-Tullgren (for microarthropods in suspended soils and on the ground), Winkler sifter (litter) and hand-collecting (ants and termites).

The sampling protocols used by IBISCA at the different canopy/ground sites permitted, for the first time, a large-scale study of the interactions between horizontal and vertical faunal turnover to be undertaken. The analysis of a careful selection of focal taxa from different phylogenies and ecological niches (more than 50 focal taxa studied in all) will provide valuable information on faunal distributions.

The interpretation of the results (in terms of vertical stratification and beta-diversity of the different focal taxa), which is only beginning, will benefit from the information provided by several sub-studies aimed at characterising the sites surveyed (e.g., type of vegetation, canopy thickness, incidence of light, apparent leaf damage, etc.). Informations about the arthropods collected during IBISCA have been entered into a shared database which is accessible (Internet) to all participants, including the taxonomists involved in the identification (at least to the morphospecies level) of the different taxa.

IBISCA, which is an initiative of the Canopy Raft Consortium (CRC-France) and the Smithsonian Tropical Research Institute (STRI-Panama, USA), and whose patron is Pr. E.O. Wilson, may be considered as a model for ongoing large-scale investigation programs. Some IBISCA participants are already involved in the preparation of similar large-scale studies of arthropods megadiversity that may take place in 2006 in Australia (BATH project) and in Espiritu Santo, Vanuatu (ABSINTH project).

## Project IBISCA - one example: stratification and beta diversity of Auchenorrhyncha in a Panamanian rainforest

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This contribution examines patterns of spatial distribution and vertical distribution for ca. 400 species of homopterans (Auchenorrhyncha and Psylloidea, Hemiptera) in the San Lorenzo forest, Panama. The material was collected with protocols used in the IBISCA project (Investigating the Biodiversity of Soil and Canopy Arthropods), which included 9 spatial replicates (20 x 20m plots) and 4 seasonal replicates (September-October 2003, February-March 2004, May 2004 and October 2004). As far as possible, the material was identified with comparisons to large collections of Neotropical homopterans (STRI, NMNH and NHM collections in Panama, Washington and London, respectively), available literature and help from various specialists. Although identifications may be refined in the future and vary widely from one group to the other, preliminary results indicate that 74 % and 30 % of morphospecies could be identified at the generic and specific levels, respectively. Among speciose groups, taxonomic knowledge was best for Cicadellinae, Membracidae, Flatidae, Scarinae and worst for Typhlocybinae, Delphacidae and Idiocerinae. Out of 16 collecting methods applied in IBISCA protocols, 7 were most suitable for collecting homopterans. Several thousands of specimens were collected mainly by light, Malaise, sticky and flight-interception traps, as well as canopy fogging. This dataset is used to discuss beta-diversity of rainforest homopterans at a (very) local scale (maximum distance between plots = 2km) and their vertical stratification as observed in estimating faunal overlaps between the understorey, mid-canopy and upper canopy. Further, we discuss (a) overall patterns of arthropods (45086 specimens) and homopterans (5075 specimens) abundance as observed with sticky traps and (b) relationships between homopteran data and remote sensing data, canopy openness and vegetation characteristics in an attempt to stimulate a collaborative meta-data analysis of all focal taxa studied in the IBISCA project.

## Distribution of ants in a Panamanian rainforest

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**A**nts are abundant in most terrestrial ecosystems where they generally play an important ecological role. In tropical forests and plantations, tree crowns are often dominated by a few territorial species. In contrast, the leaf-litter and soil are inhabited by species with overlapping foraging areas. In general the diversity of the arboreal-nesting ant community is moderate compared to the ground-dwelling ant community. Within the framework of the IBISCA project, we conducted a systematic sampling campaign on eight sites in the San Lorenzo Protected Area (Panama). The aims were to evaluate the differences in community composition among sites and to estimate the local and total species richness of the forest. Arboreal ants were sampled through pyrethroid fogging and the manual collection of ants on branches cut and retrieved by climbers. Ground-dwelling ants were collected by extracting the fauna from 1m<sup>2</sup> quadrats (n = 8 x 51) using a Winkler apparatus. Preliminary results from the IBISCA project will be compared to those from other neotropical ant communities from the Chaco and the Atlantic region.

## Vertical stratification of adult Diptera in a Panamanian rain-forest

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The degree of microhabitat specialisation of adult Diptera in forest canopies has been the subject of some debate. On the one hand, a persistent view from early canopy-fogging studies in tropical forests is that the majority of adult Diptera are ephemeral tourists in the canopy and do not play a significant role in canopy community dynamics. Yet at the same time, some of the best available examples of three-dimensional partitioning of forest microhabitats come from studies of adult drosophilid flies in temperate forests. In the seasonal Atlantic rainforests of Panama, a new large-scale initiative to Investigate the Biodiversity of Soil and Canopy Arthropods (Project IBISCA), allowed us to conduct a comprehensive assessment of the degree of vertical stratification in adult Diptera using all major sampling methods, at six height intervals, across nine sites. From preliminary analyses of more than 100000 Diptera specimens sampled, there is clear-cut and striking three-dimensional partitioning in forest microhabitat use. Even at the family level, community composition differs markedly with height above ground. A number of families (e.g. Phoridae, Sphaeroceridae) are significantly over-represented at ground level, whereas other families are significantly over-represented in the canopy (e.g. Milichiidae, Scatopsidae, Chloropidae and Dolichopodidae). Across the Neotropics, Milichiidae are rarely collected in ground habitats, and only a handful of specimens of Scatopsidae are known from Central America, yet they are comparatively common in the forest canopy. At the family level, the degree of vertical stratification in adult Diptera is as great or greater than that of most other insect orders, and we expect that a full species-level analyses will show that Diptera have at least as high a degree of canopy specialisation as other taxa. We suggest that adult Diptera are no more or less 'tourists' in the canopy than any other insects.

## Termites in the canopy of a Panamanian rainforest

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**T**ermites are inhabitants of warm temperate or tropical ecosystems. Numerous studies focusing on fallen logs, leaf litter or humus have established their importance as decomposers at ground level, but almost no attention has been paid to their presence in the upper strata of tropical forests. Within the frame of the IBISCA project, we conducted the first systematic sampling campaign to evaluate the diversity and richness of a canopy termite fauna, in the San Lorenzo Protected Area (Panama). Dead wood or termite covered runways were examined on a total of 113 trees along two transects, one in October 2003 and one in May 2004. Ground transects were also sampled in the same sites for comparative purposes. Canopy collections (here defined as higher than 10m above ground) yielded 63 occurrences (colony samples) representing 10 species of termites. Small-colony drywood termites (Kalotermitidae) represented 22 occurrences (4 species). Other records included the wood-dwelling *Prorhinotermes molinoi* (Rhinotermitidae, 1 occurrence), *Termites hispaniolae* (Termitidae, 6 occurrences), and arboreal nest builders of the genera *Microcerotermes* (*M. arboreus*, 11 occurrences) and *Nasutitermes* (3 species, 23 occurrences). Species accumulation curves revealed that the inventory of canopy species was near completion. In ground samples, 243 occurrences represented 29 species. The higher diversity of the ground fauna was due to a large proportion of humus and soil feeders (19 species), logically absent from the canopy. Wood feeders (10 species, 113 occurrences) were equally diversified among the ground fauna as in the canopy. However, the species composition was different: *Heterotermes*, *Cylindrotermes* and *Amitermes* were dominant wood feeders at ground level, whereas small-colony termites (Kalotermitidae) were almost absent (1 occurrence). *Microcerotermes arboreus* and *Nasutitermes* species were well represented in the ground fauna, but the latter were vertically partitioned, *N. guayanae* being more frequent at ground level while *N. nigriceps* dominated the canopy fauna. We conclude that the termite assemblage living in the canopy is approximately as diverse as the wood-feeding assemblage found at ground level, but shows a substantial level of specificity marked by the abundance of Kalotermitidae and the presence of canopy-specialized Termitidae. The canopy fauna significantly contributes to the total termite diversity of the ecosystem.

## The bees of the canopy and the ground: new insights from wet forest

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**S**tudies of one to 8 years in Panamanian dry and moist forest canopies have shown large variability in species and abundance of bees, which change unpredictably over time and space. Earlier studies enumerated 45-50 species of each perennial group in Panamanian lowland forests. As part of the IBISCA (Investigating the Biodiversity of Soil and Canopy Arthropods) project comparing canopy and ground-level arthropods, we conducted replicated surveys of stingless bees (Meliponini), which come to honeywater baits, and euglossine orchid bees (Euglossini), which come to volatile fragrance baits at the San Lorenzo Protected Area, Panama. We made use of the Smithsonian Tropical Research Institute (STRI) Sherman canopy crane as well as single rope techniques to reach the canopy. Bees were caught in October, the late wet season when flowering is minimal but when stingless bees avidly seek supplemental food, and in May, the early wet season, when many plants flower, hence a time when many resources used by both bee groups are available. Earlier related studies have suggested that orchid bees, in particular *Euglossa*, are gap or canopy-shy, and predicted that this phenomenon may relate to forest structure or moisture.

Our results show that orchid bees were consistently more abundant and richer in the understory while stingless bees were more abundant in the canopy. For euglossines 22 (May '04) and 18 (October '03) species were collected near the ground as compared to 8 (May'04) and 15 (October '03) species in the canopy; statistical comparison of the 900 euglossines gave a Morisita-Horn similarity index, from the ground and canopy, of 0.80 during early wet season and 0.08 in late wet season. No species occurred exclusively in the canopy. Stingless bees (7-10 species) used canopy honeywater baits, while five species used ground level baits. Six were found only in the canopy and one only at ground level: *Melipona panamica*, *M. micheneri*, *Trigona muzuensis*, *T. fuscipennis*, *Scaura latitarsis*, and *Trigonisca* sp., and *Scaura* cf. *longula*, respectively. Orchid pollinaria were found only on orchid bees at ground level. We suggest that the combination of the presence of epiphytic orchids, which normally grow only on stems of understory plants, and certain understory nectar sources (flowers of Marantaceae, Costaceae, Gesneriaceae, Rubiaceae) may explain the greater number of fragrance-seeking male orchid bees near the ground. In contrast, the broad spectrum of resources used by stingless bee foragers increases the chances of their response to foraging opportunities in the canopy and can explain their comparatively greater presence there.

**Patterns in moth assemblages along vertical forest transects  
in the San Lorenzo forest, Panama: taxonomic sufficiency,  
larval and adult preferences and/or seasonality?**

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**K**ey families of moths have been shown to be sensitive indicators of forest quality. In particular those families the larvae of which feed predominantly on woody plants, climbers and epiphytes make a powerful 'predictor set' of forest quality and ecosystem health. As part of the IBISCA project we have surveyed Geometroidea, Pyraloidea and Arctiidae at up to nine different locations centred on the San Lorenzo canopy crane in the lowland Caribbean rainforest in Panama. The major survey in late 2003 was repeated at subsets of these sites throughout the subsequent calendar year. At each site sets of Pennsylvania-type light traps were operated at ground level and in the canopy above. All moths within the target families were identified, at least to morpho-species, and counts made. These have been analysed using standard methods of ordination and analysis of variance. Contrasts between the ground assemblage and the canopy assemblage have been identified at both the family and species-level. The reasons for these contrasts may variously reflect larval feeding preferences, adult vagility and the environmental conditions in the forest at different seasons.

## Gall-former insect species and density distribution across canopy habitats in a wet tropical forest

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**G**all forming insects species distribution and many aspects of the insect-plant interaction were widely studied in Mediterranean type of vegetation, where this feeding herbivore guild is extremely conspicuous. The greatest diversity of gall species in the world was considered to occur in sclerophyllous tropical vegetation, such as the Brazilian savanna, and was also related to synchronous sprouting. Nevertheless, water and nutrient stress could be high on the active meristems of large canopy tree crowns, thus creating sclerophyllous habitats in the upper canopy, suitable to gall forming insect species, according to current theory. The present work consist of sampling galls in all leaves found within a volumetric space of 1 m diameter from the upper canopy down to the understorey leaves, up to three meters above ground, in a method hereafter called canopy pin-transect. The project was developed within the frame of IBISCA project. Seven independent sites were sampled, and 15 canopy pin-transects were defined and samples repeatedly in October 2003 and May 2004, in the San Lorenzo National Park, Panama. In each site three canopy pin-transects were sorted and in each one the following measures were taken: Height of branches or continuous groups of leaves, comprising a strata; in each strata; Number of leaves; Number of leaves with more than 10 % of leaf area lost by chewing insect herbivory; Number of active meristems; Presence/absence of fruits/flowers. Moreover, in each site an understorey transect of 30 m length was sampled. Leaves with galls were colleted, labeled according to strata and transect, and frost for future analyses. Namely, number of galls, size, presence of lived larvae, parasitoids, or fungi ought to be analyzed. In the canopy, 30 gall populations or subpopulations were sampled out of a total of 64 strata, thus 47 % of leaf strata had some galls species. In the understorey, 80 individual plants were sampled, and nine had some gall populations (11 %). Leaf sclerophylly increased significantly with leaf height in the canopy, and gall populations responded positively to this pattern. Data have been produced about the interrelationship between host tree family or genera biogeographical distribution and gall incidence, in order to test the hypothesis that host tree species radiated from Neotropical savannas could bring galls into the rainforests of Central America, probably during dry Pleistocene periods.

## Session 8

# Forest Canopy Herbivores and Herbivory Across the Globe

*Chair:*

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## The many ways we measure herbivory

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Consumption of plant tissues by herbivores potentially affects canopy structure and processes, including plant architecture, plant chemistry, forest energy budgets, and nutrient cycling. How we measure herbivory, therefore, will influence the significance we attribute to herbivory both spatially and temporally within and between forest ecosystems. Although herbivores commonly eat roots, flowers, apical buds, and phloem (and occasionally the inner bark of trees) in addition to leaves, folivory (leaf consumption) is the primary measure of herbivory used by most investigators and is the focus for this paper. Over the past several decades, canopy researchers have measured herbivory in numerous ways, including static (point-in-time) vs. dynamic (long-term rates) and direct (amount or percent of tissue consumed) vs. indirect (e.g., quantity of frass produced by insects; arthropod biomass/plant biomass) methods. Even direct measurements can be done in a variety of ways, from visual estimates, to enumeration of herbivore damage using gridded acetate transparencies, to computer analysis of digital images. Another variable is how plants or units of plants are selected for sampling. For example, vertebrate herbivores in canopies often eat entire leaves; without tagged leaves or direct observation, this form of folivory is difficult to quantify. We have reviewed these techniques from the literature and assessed their appropriateness for specific goals. We recognize that different methods are useful for different hypotheses, but argue that stronger guidelines for standardized measurements will greatly enhance the degree of accuracy for assessing herbivory at different spatial and temporal scales, and thus our ability to make stronger conclusions about the role of herbivory in forest canopies. In particular, the ability to compare herbivory among forest canopies can be enhanced by adoption of more standardized sampling protocols. We present a case study of a standardized protocol we adopted in recent field studies in temperate and tropical forests.

## The dynamics of insect defoliators and canopies in northern forests of Canada

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Canada is home to more than 400 million ha of forest, much of it in the boreal ecozone. These northern forests are dominated by relatively few tree species which form extensive, often contiguous canopies. Diversity at the landscape level is maintained by disturbances such as fires and insect outbreaks that generate and maintain spatial and temporal heterogeneity in forest composition and structure. Species of spruce budworms and the forest tent caterpillar are among the most common insect defoliators in these northern forests. Periodic outbreaks of these insects are synchronized over large areas and impact directly the forest canopy. The dynamics of these eruptive herbivores and the dynamics of the forest canopies they inhabit are connected via the ecological relationships between the insects life histories and the characteristics of the forest canopy. Outbreaks occur where the forest canopy can support high-density populations but the resulting herbivory, in turn, may change the characteristics of the forest canopy in ways that no longer favor insect survival and so invoke feedbacks to insect dynamics. At the population level, these ecological feedbacks may extend beyond the insect-host plant relationship to influence dynamic interactions between other trophic levels. This presentation examines ecological processes important in the population dynamics of some major North American insect defoliators from the perspective of the distinct forest canopy structures in the respective systems. We advocate a comparative and synthetic approach to the analysis of herbivore population dynamics in forest systems within the context of disturbance ecology.

## Forest herbivory in Puerto Rico and North Carolina: linking the green and brown food webs

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Previous studies suggest that insect herbivory in forest canopies can influence forest floor processes such as decomposition and soil nutrient dynamics, suggesting an ecological link between the green and brown food webs in the system. This paper presents the results and preliminary analysis from parallel studies at the Luquillo Experimental Forest of Puerto Rico and the Coweeta Hydrologic Laboratory in North Carolina. Both established quantifiable links between arthropod activity above- and below-ground via additions (or exclusions) of herbivore-derived inputs. In the Puerto Rican study, we manipulated levels of herbivore-derived inputs (frassfall, greenfall, and throughfall) to test the influence of these litterfall components on litter microarthropod populations, litter decomposition, and soil nutrient availability ( $\text{NO}_3$ ,  $\text{NH}_4$ , and  $\text{PO}_4$ ). We measured mass loss in litterbags at six sample dates through a 36-week treatment period and analyzed the litterbags for their abundance and diversity of springtails, three suborders of mites (oribatids, prostigmatids, and mesostigmatids), pseudoscorpions, and “other” soil mesofauna. Additions of herbivore-derived inputs promoted the abundance and diversity of some soil microarthropods and other mesofauna, particularly among total mesofauna to frass additions. Oscillations in the densities of some mesofauna in the treatment litterbags suggested a predator-prey feedback system. Further, densities of “other” mesofauna increased over time, indicating detrital succession in the litterbag microcosms. No treatment effects were observed for decomposition rates, mass loss at any of the sampling dates, or nutrient concentration in resin bags at any time. Effects of herbivore-derived materials may have been concealed by high variability in the surface terrain, background litterfall inputs, and throughfall volume. In North Carolina we studied the response of litter decomposition to a moisture/productivity gradient with manipulations of herbivore-derived inputs. Litterbags were placed at three elevations along the gradient and sampled monthly for two years. Microarthropods, nematodes, and litter mass loss responses to the productivity gradient were measured. The relative abundance was compared across the gradient for springtails and the three suborders of mites. Mass loss was greater at the middle and high elevation sites in both years and was correlated with increased numbers of oribatid mites per gram of litter. The abundance of all the above microarthropods was also greater on the middle and high elevation sites and greater on two-year-old litter than on one-year-old litter. Experimental additions of frassfall and throughfall showed increased numbers of springtails, and springtails and nematodes, respectively. Similarly, experimental exclusions of litterfall exhibited reduced numbers of oribatid and prostigmatid mites. These results suggest not only significant influences of elevation on litter decomposition, but also direct links between canopy herbivory and responses in population densities of forest floor biota. Herbivore-derived inputs play a significant role in the temporal/spatial dynamics of soil mesofauna in Puerto Rico and North Carolina that then have important consequences for decomposition and, ultimately, for the health of the forest ecosystem.

## Patterns of herbivory in mangrove canopies in relation to nutrient availability

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**M**angrove forests are intertidal wetlands with complex spatial differences in forest structure, diversity, nutrient dynamics, salinity, and tidal inundation. They dominate the world's tropical and subtropical coasts and provide critical ecosystem services for human society. However, nutrient over-enrichment is a major global threat to these and other coastal and estuarine environments. I used long-term fertilization experiments in the Indo West Pacific and Atlantic East Pacific Global Regions of mangrove distribution to compare patterns of nutrient limitation and to determine the effects of nutrient enrichment on growth and herbivory. In Belize, Florida, Panama, Queensland, New South Wales, and New Zealand, experimental plots were established along transects traversing a natural tree height/productivity gradient from the shoreline to the forest interior. Nitrogen (N) and phosphorus (P) were not uniformly distributed within or among these mangrove environments. The availability of N and P affected patterns and levels of herbivory, but it varied depending on location, species, and position within the mangrove landscape. The diversity of herbivores in the mangrove canopy was higher than previously reported. This fauna was characterized by specialized, endophytic species of miners, gallers, and borers. Herbivory by loss of yield was responsible for greater loss than direct leaf mass consumption. However, not all species responded similarly to, or were limited by, the same nutrient. The significance of the grazing pathway in mangrove ecosystems is much greater than previously recognized.

## Herbivory rates and leaf damage distribution in the canopies of Neotropical ecosystems: from savannas, semi-deciduous forests, to wet rainforests

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Comparative studies between forests in the Neotropical region have been stimulated since Gentry (1990). However, herbivory variation is poorly described or understood. In this mini-review, I compare patterns of herbivory in the canopies of wet evergreen, semi-deciduous, and savanna-type arboreal vegetation from Central to South America. To investigate the hypothesis that biogeographic variation in sclerophylly and water stress could be more influential in defining herbivory than canopy structure, shrub montane vegetation data were included. Data were obtained from various studies, including the IBISCA project. Data are based on leaf area lost estimates, explored by meta-analysis techniques. Herbivory on seven species from semideciduous forest (19.7 % 14.1 %), cerrado (13.8 % 4.1 %), and shrub-type of montane vegetation (27.7 % 7.4 %) did not vary significantly between ecosystems, and was greater between species within each habitat. Herbivory was high compared with global patterns. For those cases when seedlings or saplings vs adult trees were measured, no significant differences were found in leaf herbivory between age, independent of habitat. My estimate suggests that herbivory in the canopy of a rainforest of Panama would be substantially lower than found in seasonal vegetations. In another scale, within this rainforest, herbivory decreased significantly with canopy height, likely due to a significant increase in leaf sclerophylly (= specific leaf mass) from understorey to upper canopy. The inverse was observed for gall-forming insects. Gall species responded positively to sclerophylly along the canopy height, as expected from studies in the Brazilian cerrado. The present findings are still exploratory, but there exist evidences that herbivory levels are strongly influenced by variation in sclerophylly between biomes, and that canopy structure is important at a local scale. However, sclerophyllous ecosystems may accumulate greater herbivory due to specialists, while sclerophylly itself seems to be negative for chewers (likely generalists) and positive for gall-forming (known specialists) in Central American rainforests. Unexplored forest types in the region are pointed out, along with a criticism to the consistency of the term Dry forest.

## High above the kangaroos: herbivory Down Under

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**I**n this presentation, we statistically assess herbivory from large data sets recorded over a twenty year period of research in different forest types of Australia. Our overarching hypotheses are: 1. that complex forests will have lower levels of herbivory as compared to low diversity forests, and 2. that high levels of herbivory can correlate with stand dieback or entire forest mortality. We surveyed over a hundred thousand leaves using ropes, walkways, towers, and cherry pickers in Australian cool temperate, warm temperate, subtropical, tropical, and dry sclerophyllous forest types. Two field methods were employed: long-term whereby leaves were surveyed monthly for increments of damage; and short-term (“discrete”) measurements of annual leaf area losses whereby leaf hole areas were calculated at one time period as a quicker method of assessment. The long-term method obviously was the most accurate technique (albeit time-consuming), and canopy herbivory ranged from 4 % to 300 % in different tree species and throughout different forest types. We statistically analyzed different cohorts of canopy leaves to address our hypotheses, and arrived at a multiplier for extrapolating short term herbivory measurements into more accurate long term levels. On a global scale, some Australian forest types appear to suffer significantly higher levels of herbivory than other continents.

## **Insect herbivores on a large tropical island: the ordinary and the extraordinary from New Guinea**

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**N**ew Guinea is the largest tropical island in the world and one of the remaining three tropical wilderness areas still covered with large expanses of tropical forests. It is also geologically very young and dynamic area, with complex geological history. New Guinea thus provides an excellent opportunity for ecological studies contrasting its young island ecosystems with relatively old continental ones, including the intensely studied sites from the Neotropics. We have taken up this opportunity and studied the host specificity, species richness and beta diversity of herbivorous insects in lowland and montane rainforests of Papua New Guinea for the past ten years. The present contribution provides a synthesis of biodiversity and host specificity patterns found in New Guinea and discusses how, and why, these patterns differ from those found in other tropical forests.

## Between diversity, resource, and pollution: herbivores in Central European managed forests

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**H**erbivores are of interest in managed forests. To know which ones are there, how they behave, how they use their environment – sometimes in a sharp contrast to the interests of human users –, and how they react to pollutants is crucial. In this talk results of three comprehensive studies on diversity of herbivores in tree crowns, their resource use regarding forest tree species, and their reaction to ozone pollution are presented. The focus was on man-made and managed forests. In the first project, herbivores in different important forest trees were studied within a gradient of naturalness. Forest stands without management and of free succession were compared with natural-near deciduous stands, nature-apart mono-dominant Norway spruce (*Picea abies*) stands, and with mixed stands of 70 % spruce and 30 % beech (*Fagus sylvatica*), which represent the final goal when converting spruce forests into more stable stands. Results indicate 1. strong differences in the structure of herbivore communities between conifers and broad-leafed trees, 2. a wide range of differently structured communities within the gradient of naturalness, 3. only small differences in communities on spruce despite naturalness of the stands. Results will be referenced to nature conservation and forest protection. Conifers are the most important trees economically in Central European forestry, in particular Norway spruce, and of minor importance, Douglas fir (*Pseudotsuga mentziesii*), Scotch pines (*Pinus sylvestris*), and European larch (*Larix decidua*). On these, mainly polyphagous caterpillars like larvae of the nun (*Lymantria dispar*) cause economic damage. Comprehensive risk assessment has three factors: 1. How large is the amount of frass on the different tree species? 2. How much of this amount is converted into body mass of the caterpillar? 3. How large is the developmental success (in this case pupal weight)? In a laboratory experiment caterpillars of nun were fed on the four mentioned tree species, uptake of food, body-weight, faeces, and pupae weights were measured. Furthermore, content of nutrients and repellents were analysed. Whereas in nutrients (proteins, solvable carbohydrates) a decreasing amount from larch to pine to spruce was observed, more phenols could be found in larch and less in spruce and pine. However, pupal weight was highest in larch, lower to spruce to Douglas fir to pine. Results indicate that polyphagous herbivores are affected by the ingredients of their host plants. Differences in food quality result in differences in developmental success, which influences size of population, which results in different economic impact. Within a mixed forest of beech and spruce a free-air ozone fumigation system applied double ambient ozone concentrations to ten trees during four years to impose chronic ozone stress. The trees showed varying patterns to ozone on the cellular to the whole plant level. In beech, ozone had a greater physiological impact within the shade crown and a greater phenological impact in the sun crown, whereas spruce showed little difference between sun and shade crown. Herbivores (*Fagocyba cruenta*, *Rhynchaenus fagi* and *Pristiphora abietina*) showed differing feeding preferences to the ozone regime and leaf physiology.

## Spatial patterns of folivory at *Acer pseudoplatanus* in a Central-European mixed deciduous forest

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**H**erbivory is a key process in almost all ecosystems but its controlling factors are poorly understood. Therefore we conducted a study on the herbivory in a Central-European mixed deciduous forest using a crane system to access the canopy. We selected the tree species *Acer pseudoplatanus* L. because it is the most abundant tree in the study area and we decided to study folivory, i.e. leaf damages by herbivorous insects, since this can easily be done in a quantitative way. The research question were: (i) What is the overall degree of folivory at *A. pseudoplatanus*? (ii) Are there differences in the degree of folivory between the individuals of *A. pseudoplatanus*? (iii) Are there differences in the degree of folivory at different heights in the canopy?

We randomly selected ten trees of *A. pseudoplatanus* in the study area. At these trees ca. 100 leaves were collected at three heights each in the canopy (0-3 m, 12-16 m, 25-30 m) summing up for a total of 2913 leaves. The leaves were collected in October 2003. The light conditions at each collection site were estimated subjectively using a five-score ordinal scale ranging from very shady to very sunny. The collected leaves were scanned in black/white mode and processed by a graphic software to determine the total leaf area as well as the area removed by herbivores.

The results are: (i) The overall degree of folivory at leaves of *Acer pseudoplatanus* is on average 1.71 % (SD 2.84 %). The Median is 0.59 %. (ii) The distribution of folivory to size classes is always extremely right-skewed, i.e. most leaves do not show notable folivory. (iii) The degree of folivory was significantly different between most of the individual trees as well as between different canopy heights.

The low overall degree in folivory and the striking differences between individual trees and at different canopy heights will be discussed.

## Session 9

# Arthropods in Temperate and Tropical Forest Canopies - 2<sup>nd</sup> Symposium

*Chair:*

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## The distribution and abundance of canopy arthropods and their relationship to canopy structure and microclimate in a Bornean rainforest

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This study applies a novel, vertically stratified fogging protocol to document arthropod abundance, density, and biomass across a vertical gradient in a primary, lowland Dipterocarp forest canopy of Borneo. We fogged arthropods at 5 m vertical intervals along 6 full canopy transects spaced 20-25 m apart and measured microclimate and leaf surface areas along the same transects. Arthropod abundance and biomass were compared to canopy structure and composition, vapour pressure deficit (VPD), transmittance of photosynthetically active radiation, and height per se. The results indicate arthropod biomass in the above-ground regions at 23.6 kg ha<sup>-1</sup>, abundance at 23.9 million individuals ha<sup>-1</sup>, and density at 280 individuals m<sup>2</sup> leaf area. All three numbers are 5 - 10 times higher than estimated by previous mass collections. Using stepwise regression we found that 12 of 14 arthropod groups had significant positive relationships with one-sided leaf area, 8 had significant relationships with VPD, 2 had significant relationships with height, but none showed positive relationships with light. This study suggests there may be many more tropical canopy arthropods than previously estimated, and by extension, more species. It also documents a strong quantitative relationship between arthropod abundance and canopy structure.

## Diversity of Spiders (Arachnida, Araneae) in the Floodplain-Forest Leipzig

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Among arthropods of the forest canopy, spiders constitute one of the most important predatory groups. They show a high species richness and a variety in life strategies making them a good indicator group for biodiversity assessments. In 2002 and 2003 in the research plot of the Leipzig Canopy Crane Project an extensive study of the arthropod fauna was carried out, including the spider fauna. Arboricolous spiders were trapped by upwards directed trunk traps, arranged at three autochthonous and abundant tree species: *Fraxinus excelsior*, *Quercus robur* and *Tilia cordata*. Branch traps were used to sample spiders that dwell in the canopy. Two branch traps each were arranged at lower and two others at upper canopy zones per investigated tree. Flight-interception traps at two different heights were used to investigate the ballooning activity of spiders. Additionally, in 2003 spiders were collected using insectical knockdown fogging. Through the combination of different trap types and fogging a comprehensive diversity analysis was realized. Thus, on the one hand, comparisons of the spider fauna of different tree species became possible. On the other hand, investigations within different elevations in the canopy enabled us to compare two strata of the canopy. The presented preliminary results refer to samples of stem electors, branch traps as well as flight-interception traps taken during 2002. 4199 individual spiders of 68 species (15 families) were identified. In detail, 27 species (111 adults) occurred in trunk traps, 42 species (1436 adults) were trapped by branch traps, and also 42 species (418 adults) were caught in flight-interception traps. More than 80 % of species were characteristic of dry or moist deciduous forests and approximately 50 % form an exclusive arboricolous spider fauna. The Clubionidae were dominant in both strata (stem zone and canopy). Amaurobiidae and Linyphiidae, both dominant at the stems, were replaced by Anyphaenidea and Philodromidae in the canopy. Stems were colonised by 52 % web-builders and 48 % free living hunters, whereas more hunters than web-builders occurred in the canopy. Salticidae preferred the upper canopy. The Clubionidae were also a dominant family in the upper canopy. Linyphiidae and juvenile spiders were more abundant in the lower canopy. Further data from 2003 will strengthen these preliminary results.

## Vertical stratification of the rare beetle, *Rhynchaenus testaceus*, other leaf miners and their parasitoids on alder

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Little is known in general of the diversity, spatial distribution and parasitism of leaf miners in the canopy of U.K. trees, due to the inevitable access problems. For rare leaf miners, such as the alder jumping weevil, *Rhynchaenus testaceus*, known from only three U.K. sites, this makes conservation planning difficult.

Using a double rope climbing technique at Holme Fen National Nature Reserve near Peterborough, England, this study aimed to: (1) Compare the vertical stratification of alder leaf mining insects. (2) Record the distribution, frequency and survivorship of *Rhynchaenus testaceus* at different heights within trees. (3) Compare rates of parasitism of leaf mining species at different heights. (4) Create height-specific quantitative parasitoid food webs.

Six alder leaf mining species were recorded, two moths, two sawflies, *R. testaceus* and a fly. Only *Phyllonorycter stettinensis* and *Heterarthrus vagans* showed significant differences in their mine density with height. A total of 105 *R. testaceus* mines were found, a high proportion of which were parasitized or predated. Two parasitoids were recorded (*Chrysocharis nautia* and a gregarious *Tetrastichus* sp.).

Amongst the leaf miners as a whole, both locally monophagous and polyphagous species were present, with no indication of variation in rates of attack with mine height.

## Disturbance and the fate of a mesocosm fauna

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**B**ird's nest ferns (*Asplenium* spp.) support large numbers of invertebrate animals. These animal communities are rich in species, and contribute a significant amount of animal biomass to the rainforest canopies of Southeast Asia. As well as being important reservoirs of animal species and biomass, the ferns can be used in much-needed manipulative experiments. A high proportion of such experiments are certain to involve disturbances of a biotic or abiotic nature. Here we describe the effects of a severe disturbance (total removal of all animals) on the structure of the animal communities of birds nest ferns in a lowland dipterocarp forest in Borneo. Invertebrate communities became re-established within four weeks, at which time there were no significant differences in the numbers of species in the ferns compared with the numbers of species in the ferns pre-disturbance. Furthermore, when the ferns were re-sampled after a period of eight months, there were no significant differences in the numbers of species in the ferns compared with either the four-week samples or the pre-disturbance samples. In this talk we will compare the identities of the original species with those that returned and shed some light on the assembly rules that govern the reformation of the communities. We will compare the structure of the communities with null models to determine whether the species abundance distributions can be classified as stochastic or deterministic, and consider whether disturbance caused short or longer-term changes to the trophic structure, to the animal size distributions, or to the distributions of animal biomass within and between those species that re-colonised the ferns.

## Invertebrate colonisation of artificial canopy habitats in response to disturbance

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The decomposer fauna of epiphytic habitats are crucial to the functioning of forest ecosystems through their active involvement in nutrient cycling but also as pioneer colonisers of new habitats, which often lays the foundation for the establishment of more complex arboreal invertebrate communities. In April 2004 a study was undertaken to investigate the rate of colonisation of newly available habitats by invertebrates in response to climate change. Twelve artificial habitat islands, consisting of wire baskets (21-30 cm) and sterilised potting mix, were established in the canopy of five northern rata (*Metrosideros robusta*) at two sites each on the West Coast of New Zealand's South Island. The baskets were strapped to bare outer parts of the branches at a height between 12 to 25 m above the ground and at a distance of 10-20 cm from the climate treatments or controls. The climate treatments, a combination of increased temperatures and rainfall, consisted of specially designed irrigated tunnel tents covering epiphyte mats. Parts of each epiphyte mat were removed prior to the establishment of the experiments to determine the composition of the resident decomposer community. The artificial habitats are removed in January and April 2005 and the composition of the decomposer fauna is determined and compared with that of the epiphyte samples. Both data sets will then be analysed to measure the response of the decomposer communities and to determine the rate of colonisation at which decomposers move into newly available habitats in response to the climate treatments.

## The importance of ecological data on the assessment of canopy-arthropod communities

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Arthropod communities of 23 canopy lianas of three plant families were sampled by hand over a period of 10 months within the Surumoni crane plot, Venezuela. Ecological information about trophic association with the lianas was documented in the field and examined with food choice experiments under laboratory conditions. Of altogether 621 arthropod species found on the lianas, 20.4 % exhibited tropical association with them. Calculations of diversity measures made for both the total arthropod fauna (621 species) as well as the tropical associated fauna (127 species) showed significant differences. While diversity measures of the total arthropod fauna indicate a moderate to high  $\alpha$ diversity, a low similarity between the faunas of individuals of the same liana species, and more species to be expected, diversity measures of the tropical associated fauna drew another picture. The tropical associated fauna showed a low  $\alpha$ diversity, tropical associated faunas of individuals of the same liana species exhibited a high similarity, and diversity measures indicate a widely complete sampling.

## Crowns of white fir as diversity hot-spot for true bugs?!

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**T**True bugs in tree crowns of White fir and spruce were sampled at 6 different mature forest sites in Bavaria using flight-interception traps. Mountainous as well as lowland sites were studied. The National Park “Bayerischer Wald” was included as an unexploited reserve. To ensure comparability with previous studies on communities of Heteroptera in tree crowns of different tree species, true bugs were sampled on oak at one lowland forest site. The highest number of specimens and species were collected on white fir as compared with spruce and oak. Moreover, distinct communities were found on different tree species. Densities of aphids as a food resource seem to be an important factor for heteropteran diversity on white fir. Results were discussed concerning biodiversity aspects of different tree species in managed forests of Germany.

## How to tap a rich but nasty resource: on the ecology and evolution of leafhoppers in deciduous forests

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**P**lant sucking is probably one of the most primitive feeding modes in herbivorous insects. Nevertheless, extant suckers show a number of highly specific feeding adaptations since plant sap, notably phloem and xylem fluid, is among the most dilute and unbalanced resources of all living animals.

Since the Tertiary angiosperm forests cover most of the world's land surface. Angiosperm leaves offer a predictable and rich food source and were the evolutionary platform for a dramatic radiation of herbivorous insects, implying an increase in taxonomical, structural and functional diversity. Hemiptera have since been in the shadow of the more derived and more diversified holometabolous insects. Yet they have evolved a number of crucial adaptations to occupy all vegetational strata, ranging from the soil to the canopy. However, purely arboricolous life habits are relatively rare and confined to only few arthropod taxa, whereas most remaining groups are bound to water, the soil or herbaceous vegetation at least during certain developmental stages. This is particularly true for temperate climates as well as for seasonally dry tropical forests, where leaf biomass is lacking for a considerable period of the year. Thus, shortage of food, water supply and shelter during the cold season poses major constraints for a permanent life on trees.

Among true canopy leafhoppers in temperate latitudes it is mainly the subfamilies of Macropsinae, Idiocerinae and Typhlocybinae which play a major role as consumers. The two former feed on phloem sap, whereas the latter have tapped a new food source and suck from leaf tissue, notably palisade and spongy parenchyma. This type of food contains large amounts of tannins, but is much more concentrated than phloem and xylem sap and thus makes filtering organs and most endosymbionts which are otherwise widespread among Hemiptera unnecessary. From these general ideas and from extensive field studies of the leafhopper fauna of all major central European trees the following questions can be addressed: (i) Are there patterns of host utilisation in phytophagous insects in deciduous forest? (ii) Why do some tree species support more insect species than others? (iii) What determines host specificity? (iv) Are there top-down effects on plants?

In general, leafhopper species numbers and also proportions of monophages are high on many dominating forest trees, e.g. *Quercus robur*, *Betula pendula*, *Alnus glutinosa*, *Ulmus minor* and *Pinus sylvestris*. However, *Fagus sylvatica* and *Fraxinus excelsior* are exceptional in holding only few feeding species without any specialist. Highest proportions of specialists are found on members of the Salicaceae and Pinaceae, which may be explained by toxic secondary compounds such as phenolic heterosides and resins. Interestingly, these guilds are dominated by phloem feeders, whereas mesophyll feeding prevails on most other trees. It is evident that bottom-up forces such as plant defense, temporal and spatial plant appearance and nutrient availability are crucial in shaping the guild structure of herbivorous insects. However, the role of other factors such as interspecific competition and predation is difficult to assess. Further, reciprocal effects of leafhoppers on their hosts have not yet been quantified.

## Are sawflies adapted to host individuals?

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Quality of leaf tissue may show considerable variability within and between individuals of a plant species. In particular if the life time of phytophages is much shorter than the lifetime of the host plants, populations of the phytophages may respond to this resource heterogeneity by forming ecologically and genetically distinct groups (adaptive deme formation hypothesis, Edmunds & Alstad 1978: *Science* 199, pp. 941-945). To test for local adaptation we performed reciprocal transfer experiments with the mobile sawfly species *Macrophya punctumalbum* and *Tomostethus nirutus* (Hymenoptera: Tenthredinidae) on ash (*Fraxinus excelsior*). We transferred larvae to other ash individuals and we compared relative growth rate of larvae (after 24h) between transferred individuals and controls. For the two sawfly species, relative growth rate of larvae differed between ash individuals (up to a factor of 1.5). However, for the two sawfly species the transfer of larvae from one ash individual to another had no effect on relative growth rates. Therefore our experiment provides no evidence for an adaptation of the sawflies to particular host individuals. This result is inconsistent with the adaptive deme formation hypothesis of Edmunds & Alstad (1978).

## Arthropod community on 10 canopy tree species in temperate deciduous forest

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The abundance and diversity of arthropod on 10 canopy tree species were surveyed in a temperate broad-leaved deciduous forest in northern Japan using canopy crane system (TOEF canopy project). The leaf quality (nitrogen and tannin contents, toughness, SLA etc.) changed seasonally with the patterns being varied among tree species. There has been noticed the variation in the pattern of leaf flush among tree species; some tree species flush their leaves once a simultaneously in spring (flush type; Kikuzawa 1983, 1984), but others shows successional pattern of leaf flush (succeeding type), and the intermediate pattern between them (intermediate type). These variations caused among-species differences in structure of arthropods community through time. On the flush type tree species, herbivore community showed a conspicuous peak in a number at spring just after the budbreak. On the other hand, the higher abundance of herbivores was kept until late July on the succeeding and intermediate type tree species. These results show a strong effect of the variation in plant phenology among tree species on the arthropod community structure. The effect on the diversity and the other features of arthropods will be presented in the presentation. Further more, we will discuss the relationships between arthropod abundance and diversity (richness and evenness) in relation to the leaf quality, which may give a general explanation for the effect of resource dynamics on the consumer diversities in an ecological communities.

## Estimating faunal diversity: abundance, species richness and faunal similarity of oribatid mite communities (Acari, Oribatida) in the canopy of a temperate mixed forest

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To investigate diversity patterns of oribatid mites in the canopy of a temperate Central European forest, four tree species were sampled in heights above 20 m: *Quercus robur*, *Fagus sylvatica*, *Larix decidua*, *Picea abies*. Sampling took place in late summer at the Swiss Canopy Crane in Hofstetten, Switzerland. For each tree species, three different microhabitats were sampled: outermost branch tips (1 cm  $\varnothing$ ), thin branches (3 cm  $\varnothing$ ), thick branches (10 cm  $\varnothing$ ). Sampling was accomplished by high pressure rinsing as outlined in Weigmann et al. 2004.

In total, 18 species of oribatid mites were found in 300 samples (see Weigmann et al. 2004). Sampling allows inspecting a certain section of an entire faunal community at a given time and place. The true number of species might easily exceed the numbers observed (Colwell 1997). To estimate sampling success, the observed number of species was plotted combined with re-sampled data using 1st order jackknifing. The accumulation curves of all tree species, as well as the plot of the whole stand and the microhabitat “thick branches”, are almost saturated. The estimated number of species approaches the quantities observed. The outermost tips and thinner branches let expect a few more species than actually found. Differences in individual abundance might lead to misinterpretations concerning species richness (Gotelli & Entsminger 2001). To ensure that observed differences in species abundance reflect species richness, the rarefaction method (Hurlbert 1971) was used to refer the observed number of species to the smallest given individual abundance. *Quercus robur* shows highest species richness, for microhabitats thick branches were found to be significantly richer in species than the outermost tips. To determine faunal similarity between different tree species or microhabitats, species identity (Jacquard-Index) was calculated. Especially coenoses on conifers show similarities, as well as all microhabitats in general. Deciduous trees lack faunal conformity.

1<sup>st</sup> order jackknifing indicates sufficient sampling. The few species still to expect in outermost tree sections might recruit from species already found on thick branches, supported by the overall good characterization of this microhabitat and the stand in general. The species-rich *Quercus robur* is a preferred choice for several oribatid mites, three species were found uniquely on this tree (Weigman et al. 2004). In contrast to the conifers in the stand, oaks formed a dense canopy with adjacent deciduous trees, thus not as exposed to radiation, desiccation and other climatic factors. The exceedingly high number of species found on *Quercus* clearly leads to the effect that this tree species appears separated when it comes to species identity. The faunal similarity of different branch types prohibits the determination of distinctive microhabitat-faunas using the Jacquard-Index. The crown as a whole might serve as a habitat for one single oribatid mite community, with euryoecious species (e. g. *Micreremus brevipes*) predominantly dwelling in outermost sections, as in-

dividual abundance and dominance analysis reflects.

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## Session 10

# Informatics Workshop

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## Session 11

# Biodiversity in Forest Canopies

*Chair:*

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## Floristic background of Yunnan Province – with perspectives of forest canopy studies

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Yunnan Province is located in the southwest of China, bordering with Vietnam, Laos and Myanmar. Yunnan shows a floristic mixture of plants from Southeast Asian Continent in the south, Tibetan Plateau in the northwest and central China in the east. At the level of genus, the flora of Yunnan is composed of 15 distribution patterns of seed plants, including a complex floristic background and extensive relationship to other continents of the world. Over 60 % of the genera are distributed in the tropics. This is partially attributed to an important geological event – the collision of the Indian Landmass and the Asian Landmass, which resulted in the uplift of the Himalayas and Tibetan Plateau in the northwest of Yunnan Province. On the other hand, this province maintains also different ecosystem types, ranging from subalpine, subtropics and tropics on an altitudinal gradient of more than 6600 m. A few of pilot facilities for accessing forest canopies were established in tropical forests, either for scientific research or tourism. Further cooperation with GCP and other international institutions will promote the development of ecological study on forest canopies in this province.

## Interspatial phenological differences of a mammal pollinated canopy tree species and associated movement patterns of arboreal mammals in south India: consequences to fruit production

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Our past research has demonstrated that flowers of canopy tree *Cullenia exarillata* acts as a keystone resource for arboreal mammals and in turn are pollinated by some of them in the Western Ghats, India. Western Ghats has less than 4 % of its forest area under protection and these comprises of selectively felled area which generally have lower populations of many tree species. These secondary forests often have lower protection status and are neglected as they are assumed to be less utilized by animals. It is of utmost importance to evaluate the usefulness of these areas with lower populations of *Cullenia exarillata* for arboreal mammals. This study explores in detail if arboreal mammals move across the landscape between areas of high and low occupancy of *Cullenia* and identify the ecological drivers of such spatial dynamics. Here we hypothesize that the inter-annual differences in phenology of *Cullenia* between pristine and disturbed habitats could drive arboreal mammal movements between habitats that could have consequence on the survival of the tree species.

We recorded use of *Cullenia* flowers in the canopy by Camera traps and fruit production was determined using marked flowering branches. For this 10-15 individuals were marked and rigged for accessing through single rope technique in both the forest. Primary forests exhibited a steady state flowering, in contrast to the secondary forest that showed fluctuations. Whenever disturbed forests contrasted the primary forest by having higher flowering intensity within and between year the primate *Macaca silenus* was found to readily cross to sub-optimal habitat while other mammal species did not show such differences. Though fruit production was not directly related to mammal abundance, fruit removal rates were affected by the presence of these mammals. This could have important consequence on the regeneration of the species. Similarly mosaic of disturbed forests around primary forests might act as a buffer for *M. silenus* during certain times, although independently these habitats may not be able to support wildlife.

## Species diversity and spatial distribution of epiphytes in a montane moist evergreen broad-leaved forest at Xujiaba region, Ailao Mts., SW China

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**B**ased on investigation data from 80 host trees, the composition and distribution of epiphyte species were studied in a montane moist evergreen broad-leaved forest at Xujiaba region, Ailao Mts., South-West China. There were abundant epiphytes in canopy of the montane moist forest. The total number of epiphytes was 67 species in 47 genera and 33 families. Of which, 46.4 % and 53.6 % were respectively vascular epiphyte species and bryophyte epiphyte species. The values of Shannon-Wiener index and Simpson index was 2.93 and 0.91 for vascular epiphyte species, 3.31 and 0.95 for bryophyte epiphyte species. The epiphytic fern species comprised of *Lepisorus scolopendrium*, *Vittaria flexuosoides*, and *Polypodiodes amoena* var. *pilosa* was abundant in the forest. *Aeschynanthus buxifolius*, *Briggsia longifolia* and *Agapetes mannii* were the dominant epiphytic seeds species. Most trees were covered with rich bryophyte epiphyte species. The common species were *Bazzania praerupta*, *Bazzania ovistipulam*, *Chandonanthus hirtellus*, *Homali dendron flabellatum*, *Symphyodon perrottetii*, *Dicranodontium denudatum*, *Meteorielletum solutae* and *Oxyrrhynchium praelongum*. The bryophyte epiphyte species distribute mainly on the trunks, while the vascular epiphyte species were in the tree crowns. A significant positive relationship was found between trunk size and epiphyte association. Major epiphytes, especially larger epiphytes species, occurred on middle and large stems. There was no significant positive relationship between epiphyte species and hosts, although a small number of epiphyte species only occurred on individual trees.

## National Biogenetic Information System (NBGIS) for sustainable management of bioresources (biodiversity)

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**T**his paper stresses the need for developing a National Biogenetic Information System (NBGIS) for sustainable management of bio resources. The information generated on biogenetic diversity could be used for a variety of purposes. It includes, obtaining an overview of biodiversity situation, to formulate policy decision, to take strategic decisions in forestry ecosystem management and to the benefit of researchers. Both short term and long term strategies are outlined to develop the NBGIS.

## Development of epiphytic communities and structural Complexity in riparian forests along the Queets River in Olympic National Park, Washington, USA

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The temperate rain forests along the west coast of North America represent the most extensive on the planet. Nowhere is this forest type better developed than the Queets River Valley on the Olympic Peninsula of Washington. Throughout 2003-04 plots were established in the floodplain of the Queets River designed to help explore forest-river interactions. Riparian forests in this region typically go through an *Alnus rubra* *Populus trichocarpa* phase before eventually becoming a *Picea sitchensis* *Tsuga heterophylla* forest. Twenty-one plots spanning an age range of over 300 years and totaling nearly five hectares were mapped and measured for an intensive stand-, tree-, and branch-level analysis of structure and bryophyte distribution within this rain forest environment. 64 trees representing six species were sampled intensively by complete, three-dimensional mapping of all branches, including the distribution and biomass of all foliage, and the mapping and biomass estimations of all epiphytic bryophytes by species. A total of 396 destructive samples were collected to represent the full age and size range of the various species present. These samples were first separated into bryophytes, canopy roots, canopy soil, and fern rhizomes and then oven-dried and weighed. During the first century very little exists in the way of structure or surfaces with which to support epiphytes. During the second century, however, the development of large *Populus trichocarpa* and *Acer macrophyllum* allows thick bryophyte mats to accumulate. In addition, *Picea* become very large and also support massive bryophyte loads. With individual *Picea* trees supporting up to 40 m<sup>2</sup> of horizontal bark surface, their tree-level epiphytic biomass eventually becomes much higher than their angiosperm neighbors up to 916 kg dry weight of bryophytes and canopy soil in a single tree. Large, old branches of *Picea*, *Acer*, and *Populus* develop deep soils under the bryophyte mats, which become further stabilized by root systems of *Polypodium* and *Selaginella*, and in many cases with adventitious roots of the trees themselves.

## How tree structure promotes biodiversity in a redwood rain forest canopy

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We established a 1.0 hectare permanent reference stand in a 100 m tall *Sequoia sempervirens* (redwood) rain forest to represent the most massive and structurally complex canopy remaining on Earth. Rope techniques were used to access the crowns of all trees in the stand containing reiterated trunks or vascular epiphytes, and structural mapping over 8 years enabled us to construct a 3-dimensional map of the entire canopy. We used this map to examine the spatial distributions of trunks, limbs, epiphytes, and canopy soil. Solar-powered sensor arrays have continuously monitored canopy microclimates, including the water storage dynamics of canopy soil and rotting wood, since 2002. The 94 redwood trees in the plot accounted for 95.4 % of the total aboveground dry mass (4283 t ha<sup>-1</sup>), 79.0 % of the leaf dry mass (22 t ha<sup>-1</sup>), and 66.0 % of the leaf area (12.7 LAI) in the forest. The 14 largest redwoods contained two-thirds of the crown volume, four-fifths of the aboveground mass, and nearly all of the canopy soil (2366 kg) and vascular epiphytes (494 kg) in the forest. The most abundant epiphyte was the evergreen fern, *Polypodium scolieri*, which was responsible for the bulk of soil formation in the canopy. The most complex trees had up to 18 % of their total mass in reiterations and supported up to 805 kg dry mass of epiphytes and soil on large limbs and crotches at the bases of reiterated trunks. Water stored in canopy soil and rotting wood reached 48,000 liters ha<sup>-1</sup> during the wet season and dropped to 22,000 liters ha<sup>-1</sup> during the dry season, with dead wood representing 42 % and 54 % of the total canopy water storage during the wet and dry seasons, respectively. Epiphyte biomass peaked at 65 m in the canopy, but water storage and biomass of epiphytic trees both peaked at 55 m. A lungless salamander, *Aneides vagrans*, was regularly encountered amidst soil and rotting wood in several large redwood crowns. The best predictor of its tree-level abundance was whole-tree water storage ( $r^2 = 0.92$ ).

## Construction and management of a canopy walkway in a tropical lowland rainforest remnant the Singapore Experience

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The number of canopy walkways in Southeast Asia has increased in the past decade and quite a few of them have been making good progress in facilitating canopy research in the tropics, in addition to other methods of canopy access. This paper primarily reports the construction of the Hongkong Shanghai Banking Corporation (HSBC) TreeTop Walk, a 250 m suspension bridge supported by two towers in a disturbed remnant of tropical lowland rainforest in Singapore. The walkway took almost 2 years to complete due to the constraints imposed by the forest environment. To date, a total of 87 bird species, 10 mammals and 12 reptiles have been recorded from the walkway. The two most abundant tree species seen along the walkway are *Campospermum auriculatum* and *Litsea elliptica*. The walkway offers a good opportunity as a site for future canopy research due to its unique location and vegetation, and it adds to the growing number of walkways worldwide in contributing to our understanding of the forest canopy. In addition, the walkway also plays an important role in public outreach and education.

## II

# Poster Presentations



# Vascular Epiphytes in Forest Canopies

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## Epiphyte succession in young secondary Amazonian forests

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**I**s there succession in epiphyte communities? Does aroid colonization start from the ground or from the air? How do structure, age or geographic distance between secondary forests contribute to their epiphyte composition? These questions have been addressed in a new project in Colombian Amazonia. In patches of upland fallows of different age, square plots (0.04 ha) were established and epiphyte communities sampled. We took into account vascular epiphyte abundance, biomass, life form, height on ground and location on host trees, as explained by fallow age and structure, as well as geographic distance between plots. Preliminary field results point at strong effects of geographic distance on epiphyte composition, and initial colonization by aroid hemi-epiphytes starting from the ground.

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# Does the bird's nest fern enhance species richness and community diversity of oribatid mites (Acari: Oribatida) in a subtropical forest in Japan?

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The bird's nest fern (*Asplenium nidus* complex) has a basket-shaped rosette of long fronds that catches large amounts of litter fall and can grow very large to reach a fresh mass of more than 200 kg. As a consequence, the organic matter in the ferns can contain abundant and diverse invertebrates (Ellwood et al. 2002). However, no previous work has examined the influence of invertebrate communities in the birds nest fern on the biodiversity of the whole forest. We examined the effect of the presence of the bird's nest fern on the species richness and community diversity of oribatid mites in a subtropical forest in southwest Japan. A total of 47995 oribatid mites (45002 adults) in 211 morphospecies were collected from leaves, branches, and bark of *Castanopsis sieboldii*, the litter and soil at the forest floor, and the litter and root of the birds nest ferns inserted into trees of several species in this region. A PCO analysis classified the oribatid communities from the various habitats into four groups according to the similarity of species composition, and indicates that the species compositions of oribatid communities in the litter accumulated in the ferns are similar to those in the litter and soil at the forest floor. On the other hand, the species compositions of oribatid communities in the root part of the ferns differ from those in other habitats of this forest. A species-accumulation model for a hypothetical forest consisting of a single tree species (*C. sieboldii*) showed no significant difference in the number of oribatid species between the presence and absence of the birds nest fern. The model result suggests that the presence of the bird's nest fern does not significantly increase the number of oribatid species at the whole-forest scale. However, the root part of the ferns creates a unique habitat for two endemic oribatid species (*Machuella* sp. and *Quadroppiidae* sp.). The similarity in the species compositions of oribatid communities between litter in the ferns and litter and soil at the forest floor suggests that it is the presence of the root part of the fern that contributes to enhancing the community diversity of oribatid mites in this subtropical forest.

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## Epiphyte distribution in the Amazonian landscapes

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**F**loristic similarity between vascular epiphyte assemblages in tropical forests depends on geographic distance or niche pre-emptioning. We inventoried epiphytes in 40 plots distributed in four landscapes in Colombian Amazonia (well drained floodplain, well drained upland, swamp, and white sand forests). Using Mantel analyses, we tested how distance or landscape shaped the distribution of epiphytes. Including all landscapes in the analysis, epiphyte composition depended more on landscape than on geographic distance. In upland forests, however, geographic distance was more relevant and the epiphyte distribution more aggregated. We also examined the effect of geographic distance in two groups, dispersed by different agents (aroids by animals and ferns by wind). Including all landscapes, fern similarity was less correlated with geographic distance than that of aroids. In well drained uplands, patterns of aroid and fern similarity were almost equal.

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## Diversity of vascular epiphytes in four forests of Southeastern region of the Serrana de Chiribiquete, Colombian Guayana

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The composition and diversity of vascular epiphytes was studied in four types of forests at the Puerto Abeja river basin, in the southeast region of the Chiribiquete National Natural Park, Colombian Guayana. The forests are named as: riparian or periodically flooded forest (R), upland forest (TF), transitional forest (T), and “Varillar” (V). In 500 m<sup>2</sup> of each forest type, vascular epiphytes were screened in all phorophytes with a DBH > 2.5 cm. We registered 1110 trees and 406 of them harbored epiphytes, with the greater phorophyte proportion found in TF and R. A total of 2015 individual vascular epiphytes were recorded (879 in R, 514 in TF, 405 in T and 217 in V), that included 183 species, 71 genera and 27 families (157 species and 20 families of angiosperms and 25 species and seven families of pteridophytes). R and TF were the most speciose forests (with 100 and 94 species respectively), while V was the poorest (with just 30 species). T and V exhibited 1-2 species with outstanding relative density values, while in R and TF none of the species had a distinct abundance. Orchidaceae and Dryopteridaceae were always part of the most important families (FIV) in all the forests, while families like Araceae, Bromeliaceae, Clusiaceae, Grammitidaceae, Hymenophyllaceae, and Polypodiaceae, had an important significance in some of them. In R and TF the most speciose families were Araceae and Orchidaceae, with the latter also being the most speciose in T and V. According to similarity coefficients based on presence/absence and abundance of species, R and TF presented the highest similarity, while V was differentiated from them, and T could not be distinguished significantly from the others. Of all the epiphyte species, 68 (36.8 %) were found in two or more forests, and 117 (63.2 %) in only one of them.

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## Ecophysiology of the epiphytic fern *Polypodium scolieri* in a redwood rain forest canopy

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**S***equoia sempervirens* is the world's tallest and second-most massive tree species, and less than 4 % of the original old-growth redwood forest has escaped logging. *Sequoia* is extremely long-lived due to its resistance to rot and fire, and individual trees develop structurally complex crowns over centuries and millennia. This complexity provides substrate for soil-building and colonization by organisms ranging from epiphytic trees to arboreal amphibians. Of the 15 vascular plant species that inhabit the forest canopy of old-growth *Sequoia* rain forests, the most abundant is *Polypodium scolieri*. This evergreen fern forms large mats in the mid to upper canopy, with individual *Sequoia* supporting up to 700 kg dry mass of fern mats, including soil. These mats are ecologically vital in buffering within-canopy microclimates. Like giant sponges, they fill with water during rainstorms. After a rain, much of this water is lost via drainage, surface evaporation, and frond transpiration, but some remains stored in the soil beneath living ferns. At the peak of the rainy season, up to 8000 liters of water are stored in the soils within individual *Sequoia*. One of the largest known *P. scolieri* mats occurs at 80 m in a 99 m tall *Sequoia* of California's Prairie Creek Redwoods State Park. This mat covers over 18 m<sup>2</sup> of tree surface and has a dry mass of 335 kg. We used a LiCor portable photosynthesis system to quantify gas exchange of fern fronds in this mat during the refilling cycle from October 2004 to March 2005. These data will be combined with the mats rain, soil moisture, and microclimate record, which has been continuously quantified with a solar-powered sensor array since 2002, to model seasonal trends in net photosynthesis and light response as the mat fills and drains. We will also examine the vertical distribution of *P. scolieri* in the context of its photosynthetic light response along the vertical gradient in *Sequoia* rain forests.

# Canopy Access

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# Networked Infomechanical Systems (NIMS) – new dimensions for environmental sensing in forest canopies

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Canopy access is an obstacle to research if trees are of tall stature or forests are located in mountainous terrain. The Wind River Canopy Crane Research Facility (WRCCRF) and the Networked Infomechanical Systems (NIMS) programs are working to solve this issue using a system of tethered, autonomous, self-correcting measurement nodes, or BBC news called a “tree bot”. Each node of the system is on either a horizontal or a vertical cable transect and capable of taking continuous measurements of micrometeorological variables (e.g., PAR, wind speed, air temperature) and visible imaging and transfer of data via wireless connections to a field microserver. This technology is relatively inexpensive allowing for multiple deployments in forests at different stages of structural development. The first generation NIMS node was successfully deployed temporarily at the Wind River Canopy Crane Research Facility in September, 2003. The second generation has been deployed since the end of March 2004 at the University of California James Reserves. Additions to the JR model are visible imagery suitable for plant phenological measurements and multiple tether pathways.

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## The Canopy-Glider: an innovative flying tool for canopy studies

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The “Canopy-Glider” is an inflatable craft capable of flight that can be used as an observation and sampling tool for scientific and conservation purposes. Its conception is the result of years of experience acquired using the “Canopy-sledge” developed by the Canopy-Raft Consortium. The Canopy-Glider, designed to carry two scientists, uses a “Rozière” structure (the combination of a hot air dirigible and a helium balloon) and is propelled by powerful and totally innovative small gas jet engines. The Canopy-Glider has been designed to be highly efficient for brief flights with short intervening stops. It is particularly appropriate for the collection of botanical and zoological samples, in places that are otherwise difficult to reach, such as the upper canopy.

Continuous flights of the Canopy-Glider can be used for aerial photography for canopy tree identification, detailed mapping, etc. and census of trees, or of other canopy organisms such as large vertebrates (e.g., primates).

Step-by-step flights with short stops in the canopy can be used for the systematic inventorying and sampling of the flowers and fruits of trees and lianas, lianas themselves, epiphytes, lichens, mistletoes, etc.; systematic sampling of invertebrates by means of branch beating, branch clipping etc. and periodic sampling and census of canopy dwelling or flying small organisms (arthropods) using traps (e.g., pitfalls, light traps, flight interception traps), pre-established stations and other sampling devices (such as artificial “phytotelmata”).

Longer-term stops in the canopy can be used for: setting up data-recording stations for biophysical and biochemical parameters, the placement of traps for pollen, air-borne organisms, insects, vertebrates.

The Canopy-Glider is part of the ACCET (Arthropod Communities and Canopy Ecology in the Tropics) Programme which aims to examine factors that shape the distribution, diversity, abundance and composition of arthropod assemblages in the upper canopy throughout different rainforests. Moreover, as has been the case for the “Canopy-Sledge” and other devices used during the “Canopy-Raft” expeditions, the Canopy-Glider provides valuable publicity for the scientific and conservation programmes for which it is used. It is an excellent tool to promote and assist education and public awareness programmes in the field of conservation.

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## Opening the canopy to all – GCP canopy access and science methods training courses

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The GCP has created a virtual ‘Canopy Training School’ which offers training courses in new, safe methods of accessing the canopy using ropes and instruction in the latest scientific methods of studying the forest canopy. GCP and Canopy Access Ltd, a UK based specialist climbing company, have developed the Basic Canopy Access Proficiency (BCAP) course which certifies participants as having reached a standard of canopy access which meets British and European Health and Safety standards for working at height, which are the most rigorous in the world. These methods will satisfy most Health and Safety standards of Universities and are aimed to open up the canopy to students and professionals in the safest way possible. The BCAP system treats the planning and execution of any roped access study in a holistic way, ensuring rescue provision for climbers from any situation and incorporating safety redundancy at all times. The GCP Canopy Training School courses are now available in Brazil, Sabah, Malaysia and in the UK with new courses planned in China, Panama and a number of other locations.

# Forest Structure and Canopy Climate

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# Attempts to infer leaf inclination from hemispherical photographs in stands of high density taking into account different segmentation routines

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**O**ur objective was to test for general applicability of indirect method of inferring leaf inclination angles from hemispherical photographs taking into account different tree species and segmentation routines. For this we applied ellipsoidal leaf inclination model (Norman & Campbell, 1989) and Markov-Poisson model (Chen et al., 1991) to data from broadleaves as well as pine stands and compared predictions with true leaf inclination measurements from within canopies.

Given real LAI values for each stand from autumn leaf fall measurements predictions of clumping index and mean inclination angle proved to be independent from each other. Predictions were all over satisfying and robust for birch, pine and oak and satisfying but sensitive to outliers in beech, hornbeam and basswood. Predictions were better in general by using zenith angle dependent segmentation and subpixel information (Wagner, 2001) than by so called binary method.

Leaf inclination measurements in pure stands of broadleaves can be performed by indirect method with satisfying accuracy as far as independent and reliable LAI measurements are given. However, in very dense canopies, e.g. beech and hornbeam, careful investigation should be carried out to eliminate outliers in advance to regression computations. Further, mean inclination angle predictions from traditional binary segmentation method are biased towards erectophile frequency distributions while zenith angle adapted thresholding proved to be free of bias and thus superior.

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# Fog drip and its relation to groundwater in the tropical seasonal rain forest of Xishuangbanna, Southwest China: a preliminary study

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**I**n this study we collected fog drip, rain, shallow soil water, and groundwater for two years (2002 - 2003) for stable isotopic analysis (hydrogen and oxygen isotopic composition) at a tropical seasonal rain forest of Xishuangbanna (21°09' - 22°33' N, 99°58' - 101°34' E), Southwest China, designed to quantify effects of fog-drip water on groundwater. The fog drip water ranged from - 30 to + 27 ‰ in  $\delta D$  and - 6.2 to + 1.9 ‰ in  $\delta^{18}O$ , conforms to the equation  $\delta D = 7.64 \delta^{18}O + 14.32$ , and was thought to contain water that has been evapotranspired and recycled terrestrial meteoric water. The rain was isotopically more depleted, and ranged from - 94 to - 45 ‰ in  $\delta D$ , and - 13.2 to - 6.8 ‰ in  $\delta^{18}O$ . The shallow soil water had composition usually between those of the rain and fog drip, and was assumed to be a mixture of the two waters. However, the soil water collected in dry season appeared to contain more fog drip water than that collected in rainy season. The groundwater in both seasons had an isotopic composition similar to rainwater, suggesting that fog drip water does not play a significant role as a source of recharge for the groundwater. This groundwater was thought to be recharged solely by rainwater.

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# Fine-scale measurement of three dimensional forest canopy structure in dry season using the canopy crane and laser plane range-finding method.

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**F**orest canopy structure affects both the radiation regime and turbulent transfer characteristics of gas exchange in the canopy. However, obtaining accurate information on forest canopy structure is problematic. To date there are no high resolution methods to measure 3 dimensional (3d) structure of a forest canopy. In this paper, we measured 3d structure of forest canopy around one hectare at a fine spatial resolution. The targeted canopy is a tropical rain forest in Australia. Our purpose is capturing its structure in dry season as digital data. We selected the canopy crane and the laser plane range-finding method considering their merits for complicated porous structures, such a rain forest canopies. As a result, spatial fluctuations of top position of the canopy were obtained and were found to have reasonable correspondence to validation measurements. The results were compiled as a digital elevation map of canopy. Frequency, patterns and size of canopy surface were also examined considering their difference between heights.

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## 20:20 Vision Whole Forest Observatory Network

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**I**n response to a call from the UN Convention on Biological Diversity the Global Canopy Programme proposes a strategic international network of 20 observatories, operating over 20 years to investigate the whole forest from above the canopy to the soil. Their purpose will be to monitor biodiversity and the impact of climate change. Recent advances in forest canopy access methods, based on large construction cranes and balloons, now make it possible to launch such a global effort for the first time. These sites will become centres of excellence managed by universities and research centres, delivering vitally needed information to policy makers, Governments and the corporate sector. The initiative will combine research, conservation, education and community projects stretching from the UK across Europe and worldwide. It will create centres of innovation in environmental science and technology and launch the first major international programme to be focussed on the forest canopy, the richest, least known and most threatened terrestrial environment on earth.

In order to understand how the forest ecosystem will function in response to climate change, it is vitally important to take into account the biodiversity and ecophysiology of the whole forest from canopy to soil. This approach has been neglected in both research and conservation efforts until the recent IBISCA project run in Panama over the last 2 years, by the Smithsonian Tropical Research Institute and the French Canopy Raft Consortium. This pioneering work will be expanded through the use of Whole Forest Observatories. During the first phase the existing canopy crane network will be expanded into the tropics in Brazil, Ghana, Madagascar, India and Malaysia.

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# The microclimate above, within and below emergent tree crowns in a Peruvian cloud forest

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The distribution of canopy microclimate was investigated from above, within and below two emergent *Ficus crassiuscula* tree crowns in a lower montane cloud forest at 2400 m asl in the Central Peruvian Yungas. The steeply sloped site has a heterogenous canopy because of frequent treefalls and landslides. Temperature, relative humidity, rainfall and PAR were recorded from a canopy tower between and above the two emergent trees. A rope and pulley system placed temperature loggers at 10 m intervals within and below the tree crowns at 32 m, 22 m and 12 m above the forest floor during a five month period in both dry (October and November) and wet (December to February) season conditions. PAR was calculated along the vertical transects with hemispherical photography. Transect temperature sensors were alternated between the tree crowns at weekly intervals for four months, while during the last month (February) the transect remained at one tree crown and an additional 2 m site was installed to measure temperature and relative humidity. At both transects the 12 m site below the tree crown had greater diurnal fluctuations in temperature than the tree crown sites (32 m and 22 m). The 2 m site was also more variable than the upper sites. The warmest nocturnal temperatures and the coolest daytime temperatures were in the tree crown among the highest density of branches with heavy loads of vascular and non-vascular epiphytes, despite their close proximity to the outer canopy. The epiphytes may be responsible for amelioration of atmospheric fluxes through evaporation and heat retention. Nocturnal temperatures at the 2 m site (February) were cooler than those above the canopy, which may have been a result of the downflow of the product of radiative cooling through the broken canopy surface, forming pools of relatively calm, cool air on the forest floor. The variation in light penetration and temperature within the heterogeneous canopy maybe one reason why lower montane tropical forests often defy the general pattern of declining species richness with altitude.

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## Leaf senescence of temperate tree plantations in a future CO<sub>2</sub>-enriched atmosphere

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**E**cosystems, and forests in particular, are affected by a changing climate, but at the same time, influence the course of climate change. To better understand possible feedback mechanisms through forest productivity and net carbon storage, one of the questions to be answered is whether rising atmospheric carbon dioxide concentrations (CO<sub>2</sub>) will delay or accelerate leaf senescence. Except for answering this question at the canopy level, we aimed to explain the canopy-level observations through examining processes going on at the leaf level. The Free-Air CO<sub>2</sub> enrichment (FACE) technique offers the possibility to investigate elevated (CO<sub>2</sub>) responses at canopy level without chamber constraints. In the EUROFACE experiment, situated in Central Italy, three *Populus* species (*P. alba*, *P. nigra*, and *P. euramericana*) have been exposed to 550 μmol/mol for six years. FACE and control plots (replicated three times), with an area of 314 m<sup>2</sup> were established within a 9-ha plantation. After harvesting the aboveground biomass in the third year, the plantation was characterised by a number of resprouts developing from each stump. During this second rotation, one half of each experimental plot was fertilized in order to study the interacting effects of nutrient availability and elevated CO<sub>2</sub>. During autumn of 2004 (sixth experimental year), frequent measurements at the canopy and leaf level (sun and shade crown) were made for *P. nigra* and *P. euramericana*. The following measurements were made: hemispherical photography, chlorophyll content (CCM 200, ADC, UK), chlorophyll a fluorescence (Plant Efficiency Analyser, Hansatech, UK and PAM-2000, Heinz-Walz, Germany), imaging of chlorophyll a fluorescence (prototype developed at the Limburgs Universitair Centrum). Hemispherical photographs provided evidence that elevated atmospheric CO<sub>2</sub> may delay leaf senescence of temperate tree plantations and forests. At the leaf level, measurements of chlorophyll a fluorescence showed that the maximum yield of primary photochemistry (F<sub>v</sub>/F<sub>m</sub>) was indeed higher in elevated than in ambient CO<sub>2</sub>. However, results differed between species and nitrogen treatments. These findings will be integrated with additional information obtained from fluorescence images and quenching analysis to explain senescence in a tree plantation exposed to elevated CO<sub>2</sub>.

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## Acquisition of structural patterns at the LAK investigation plot

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The Leipzig Canopy Crane (LAK) enables repetitive and non-destructive investigation of 1.6 ha of a temperate mixed deciduous forest in the close vicinity of the city of Leipzig since 2001. The facilitated access to the canopy allows the scientists to analyse the forest structure in several complementary aspects, thus supplying the basis to a better understanding of interactions among organisms and the occurrence of available resources and niches for insects, fungi, birds and other organisms.

Structure analyses began with the mapping of every single tree in the plot (exact position, dbh >5 cm, total height) providing the most basic data for subsequent studies. The second step consisted of measuring the canopy height based on a regular 2 by 2m grid (n > 4500 perpendicular measurements). These data were spatially extrapolated and visualised to get an impression of the outer canopy relief. They also allowed for a detailed structural analysis and further calculations such as the average volume of the tree crowns. A third source of information is an aerial photo which allows to identify single tree crowns and their contact zones with neighbouring trees. Additionally the canopy structure was analysed from the forest floor applying hemispherical photography. One series before the sprouting of leaves and one series in summer enables us to calculate essential ecological parameters such as separated plant and leaf area indices. Apart from these studies, which describe the plot as a whole, small scale conditions were also under investigation and are ongoing such as PAR measures on vertical transects, microclimatic measurements on a vertical scale, on a horizontal scale contrasting temperature and relative humidity at inner and outer canopy and on a even smaller scale, at upper and under side of branches.

The results of the mentioned studies draw a detailed and precise picture of abiotic conditions in the canopy and are to be combined with mycological, entomological, phenological studies at the same plot to attain a holistic perception of the functioning of this complex and widely unexplored habitat.

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# Quantifying three-dimensional characteristics of forest ecosystems in central florida using a portable field LIDAR system

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**R**emote sensing tools have proven to be effective for quantifying and monitoring important properties of forest ecosystems from local to global scales. Although several remote sensing techniques help distinguish between differences in the distribution of forest cover types, most do not provide information related to the three-dimensional structure of forest canopies and how this structure differs across different ecosystems or as a result of past disturbances and management decisions. Forest canopy structural measurements can aid in assessing many characteristics from above-ground biomass to diversity. Recent studies have demonstrated that LIght Detection And Ranging (LIDAR) technology can reliably provide canopy structural data, even in dense forests. In this study we evaluate the utility of a portable field LIDAR system for mapping the three-dimensional structure of canopies in forest ecosystems of Central Florida, which are highly diverse and are subjected to continual disturbances such as those resulting from fire and hurricanes. We demonstrate that distinct patterns of canopy height and structure can be identified throughout these forest ecosystems. This study demonstrates the value of field-collected LIDAR data in quantifying the three-dimensional structure of forest canopies. These techniques could be used to manage and restore forest ecosystems and for ground-truthing airborne and spaceborne remote sensed data sets.

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# Annual changes of volumetric canopy textures along a forest chronosequence

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The spatial organization of canopy components (i.e., leaves, twigs, branches, etc.) directly influences the microclimate, habitat, atmospheric exchange, tree growth, and physiology of a forest. A canopy is structurally analogous to a fractal sponge volume of spaces and phytomass between two (as found with a planar object) and three (as found with a solid object) dimensions. Quantifying canopy architecture requires a multi-scale approach such as those developed to measure spatial patterns of porosity or heterogeneity by material and soil scientists. To measure annual canopy structural dynamics, data were collected during the growing season over a four-year period using a portable, field LIDAR instrument in four (30 x 30 m) plots from a forest chronosequence. The high-speed laser sensor records distance measures that can be used to estimate heights and areas of zenith-projected surfaces. The plots are in stands representing different successional stages (young, intermediate, mature, and old-growth) of the "tulip poplar" association, a mixed-species broadleaf forest found in the coastal plain eastern Maryland, USA. The vertical structure of this chronosequence begins with a compressed monomodal canopy that expands into a broadened monomodal canopy, then develops a bimodal leaf distribution, and eventually results in an uneven leaf area distribution. Its climax stage typically possesses an overstory dominated by *Liriodendron tulipifera* (tulip poplar). To assess the volumetric textural properties of the chronosequence, we measured the lacunarity of the structure using a gliding box algorithm. Lacunarity is related to fractal geometry. It is a measure of the 'gappiness' of a binary structure estimated by the ratio of the variance of the number of occupied sites to the square of the mean number of occupied sites. Though very different from random, as the forest matured across the chronosequence, lacunarity became more random (for scales ranging from 1 to 40 m<sup>3</sup>) signifying less clumping. This approach was used to detect and quantify annual structural changes in each seral stage.

# Floral Ecology, Reproductive Systems, Pollination and Seed Dispersal

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# Canopy-fruit availability patterns in a terra firme rain forest site in Colombian Amazonia

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**W**ithin a larger study on the role of animals in the spatial distribution of particular tree species in a terra firme rain forest site of Colombian Amazonia, monthly changes in canopy-fruit availability were assessed from December 1999 to September 2002 in eight 50 m x 50 m plots. Total and monthly fruiting was measured as the number of individuals and species bearing fruits, the number of fruits and the amount of fruit mass. Also, to evaluate the contribution of climbers and epiphytes to the canopy-fruit productivity, we discriminated fruiting patterns between growth forms. We found a total of 387 individuals in 166 species bearing animal-dispersed fruits at the canopy level. All metrics showed that fruit production increased with rainfall, a peak is reached, and then decreases until the end of the rainy season. Peaks and troughs were more pronounced in terms of the number of fruits and fruit mass. Ripe fruit availability exhibited similar patterns in terms of the number of individuals, species, and fruit mass; whereas, the number of ripe fruits available was constantly low throughout the time. Although trees and palms were the most important growth form fruiting in this forest site, particularly in terms of fruit mass, climbers and epiphytes provided most of the fruits during fruiting troughs of arboreal growth forms (late wet and early-mid dry season). The most important family regarding the number of fruiting individuals and species was Clusiaceae, which was dominated mainly by climbers. The liana family Marcgraviaceae and the tree family Lecythidaceae produced the greatest number of fruits and fruit mass, respectively. At the species level, the lianas *Satyria panurensis* and *Souroubea guianensis* presented the highest number of fruiting individuals and fruits, respectively, while the tree species *Scleronema micranthum* exhibited the highest fruit mass. In contrast to other tropical forests fruit production in this forest is very rich in species, but very poor in the monthly and total number of fruiting individuals, fruits and the amount of kilograms of fruit produced per ha. The low fruit production largely explained the low frugivore abundance/densities observed in this Colombian Amazonian terra firme rain forest.

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# Nitrogen content and resorption of green and senescent leaves in relation to reproduction in a masting species, *Fagus crenata*

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**T**e investigated the effects of leaf nitrogen contents and resorption for reproduction of a masting tree species, *Fagus crenata*, in a temperate forest at Mt. Chokai, Japan (39°05'N, 140°04'E). Nitrogen contents of green and senescent leaves on reproductive and non-reproductive twigs among the different crown positions were analyzed in a masting and non-masting year. Many reports have stated that resorptive nitrogen from senescing is made available for reproduction (e.g. May and Killingbeck 1992; Eckstein and Karlsson 2001). In this study, we hypothesized that masting trees, which reproduce prolifically at one time within a period of several years, may allocate larger nitrogen for leaves on reproductive twigs and also be increased nitrogen resorption from senescent leaves in masting year, because they need large amounts of nitrogen resources for seed production in a masting year. In 2002, which had a mast seed crop for *F. crenata* in our study area, we selected the three types of individuals of *F. crenata*, such as flowering and fruiting at the whole crown, only upper parts of the crown, or no flowering individuals. Leaf nitrogen contents of green and senescent leaves in all selected individuals were measured at upper and lower parts of the crowns. We used the SPAD-502 (Konica Minolta, Tokyo, Japan) to measure the nitrogen contents of green leaves non-destructively. At the end of August, when the leaf color had begun to turn from green to brown, the measured twigs were covered by a fishing net. Nitrogen contents of senescing leaves were measured using a C/N analyzer (SUMIGRAPH NC-900, Shimadzu, Kyoto, Japan). For green leaves, nitrogen contents of the flowering individuals were higher than those of non-flowering individuals. Also, flowering twigs had higher leaf nitrogen contents than non-flowering twigs. For the crown position, leaves of lower crowns usually had higher nitrogen contents than those of upper positions of the crowns. However, trees, which were flowered only upper parts of the crown, had higher leaf nitrogen contents in the upper crown than lower crown. On the other hand, nitrogen resorption from senescing leaves of reproductive twigs was significantly higher than those of non-reproductive twigs. Moreover, twigs reproduced on 2002 showed significantly lower leaf nitrogen contents in 2003, which was non-masting year, than twigs no-reproduced on 2002. Therefore, our results suggested that translocation of nitrogen from leaves of reproductive twigs may be important source for seed development in a masting year of *F. crenata*. Resource recovery process until next masting will be also discussed.

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# Ornithophilous flowers accessibility along species vertical distribution: corolla length versus hummingbird's bill length in the rainforest of Southeastern Brazil

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**B**irds are a very important component for plant reproduction in tropical ecosystems, being hummingbirds the most important vertebrate pollinators in the neotropics. During a two-year study on floral resource availability for birds, especially hummingbirds, in a tropical rainforest in Southeastern Brazil, were recorded 56 plant species visited by hummingbirds, being 60 % hummingbird-pollinated. Most species are epiphytes and a few are shrubs, lianas or trees. One purpose of this study was to know how ornithophilous flowers and hummingbirds are distributed vertically in relation to corolla length versus hummingbirds bill length. Records about the distribution were made monthly along a path of 1500 m and accessing canopy with climbing equipment. The effective corolla length from 31 plant species was measured with a vernier caliper and the bill length from 10 hummingbird species was taken from literature. Among plants, fifteen species have flowers with long corollas (33-47 mm), from these 86 % were more frequent in the understory, whereas sixteen species have flowers with short corollas (13-30 mm) and occurred mainly (63 %) in the canopy. Among hummingbird species, four are long-billed (24-35 mm) Phaethornithinae which occurred mostly in the understory, and the other six Trochilinae species have smaller bills (12.5-26 mm) and were recorded mainly in the canopy and in secondary areas – exceptions are two resident species, a long-billed and a small-billed, which visited flowers all over the vertical stratification. Most of the flowers were visited by long-billed hummingbirds, while the short-billed visited every short-corolla flowers but only three species with long-corollas, indicating that accessibility to species with long-corollas is limited. These results indicate that there is a clear size relation between corolla length and bill length along the vertical distribution of the species, being the relation long corollas/long-billed hummingbirds more frequent in the understory than short corollas/short-billed hummingbirds in the canopy. CAPES, CNPq, Biot/FAPESP, Funcamp/Unicamp, TNC.

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# Ornithophilous flowers accessibility along species vertical distribution: corolla length versus hummingbird's bill length in the rainforest of Southeastern Brazil

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**T**his study was conducted to understand the distribution of naturally regenerated Korean pine (*Pinus koraiensis* Sieb. & Zucc.) seedlings at the natural mature deciduous broadleaved forest of the 1 ha (100 m x 100 m) permanent plot in Gwangneung, Korea. We measured the height and root-collar diameter and position of all *P. koraiensis* seedlings. To understand the relationship between distribution of *P. koraiensis* seedlings and environment factors, we measured soil moisture content by TDR and LAI in hundred subplots of 0.01 ha (10 m x 10 m). The density of *P. koraiensis* seedlings was 345 trees/ha and 56 % of total *P. koraiensis* seedlings were clumped more than two seedlings in one position. The average height and root collar diameter were 34 cm (from 6 to 211 cm) and 7 mm (from 2 to 40 mm), respectively. The maximum age of *P. koraiensis* was 34 years and 207 seedlings (60 % of total *P. koraiensis* seedlings) were below 5 years. According to the relationship between number of *P. koraiensis* seedlings and soil moisture and LAI, the safe site for the natural regeneration of *P. koraiensis* was from 16 to 20 % in soil moisture content and from 3.1 to 3.5 in LAI. To understand the dynamics and seed dispersal pattern of *P. koraiensis*, additional studies not only long-term monitoring of growth and mortality but also stable isotope analysis and molecular genetic techniques need to be conducted.

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# Flowering phenology in the canopy of an Amazonian rain forest: the importance of solar radiation for the timing of flowering peaks

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**T**he study was carried out in a sporadically flooded, nutrient poor lowland rain forest close to the Surumoni River, a blackwater tributary of the Upper Orinoco, Venezuela. In the canopy of this forest we investigated the flowering phenology of 104 tree individuals comprising 54 species using a construction crane. The number of flowers and flower buds of all this individuals was recorded monthly between June 1996 and November 1999. The observed flowering pattern of the community was analysed in relation to the seasonality of abiotic factors.

In every month of the study period were observed flowering trees. The qualitative flowering pattern (considering only the presence/absence of flowers) of the investigated community showed two annual peaks (qualitative flowering peaks). The first occurred at the end of the dry season/beginning of the rainy season, the second in the transition period between rainy and dry season. The bud formation coincided with high insolation intensities and the flowering peaks occurred immediately after the solar radiation peaks. A Spearman-Rank correlation analysis demonstrates a significantly positive correlation between the number of monthly flowering trees and the radiation intensity of the same and the two previous months. This result corresponds with the hypotheses that, in absence of water limitation, the solar radiation intensity is a important ultimate factor for the timing of flowering peaks on community level.

The number of flowers presented every month was clearly different between the two annual flowering peaks. A high quantity of massive flowering individuals (quantitative flowering peak) could be observed only once a year in the transition period between rainy and dry season. The dry season, following this quantitative flowering peak, is characterized by higher insolation than the rainy season, which occurs after the first yearly qualitative flowering peak. The rainy season is the poorest period in radiation. The Spearman-Rank correlation analysis demonstrates a significant positive correlation between the number of massive flowering trees per month and the radiation intensity of the following months. Therefore the insolation intensity during the phase of fruit development can be considered to be an important ultimate factor for the timing of quantitative flowering peaks on community level. This results indicate that the abiotic conditions during fruit development should be considered in the interpretation of flowering patterns.

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## Fruit development and seed predation of *Oenocarpus bacaba* Mart.

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**D**evelopment and fate of palm fruit have been studied due to a wide range of interests (population recruitment, frugivory, economic use etc.). Most of this studies used observations with binoculars for censusing seed removal, fruit counts by climbing palms or ground sampling of seeds. In many cases primary dispersal of mature palm fruits is by gravity followed by consumption, dispersal and/or predation by a big variety of animals. In this study we accessed the pre-dispersal predation and damage of ripening fruits in situ at the infructescence of the palm *Oenocarpus baccaba* Mart. The study was carried out from August to October 1998 at the Surumoni crane plot (3°10'N/ 65°40'W; 102-105 m asl.) in Venezuela. The crane plot is placed in an evergreen tropical lowland rainforest with parts sporadically flooded by the black waters of the Surumoni river.

*Oenocarpus bacaba* Mart. (locally known as “seje pequeño”) occurs widespread throughout noninudated evergreen lowland and upland rainforests at 50-1000 m asl., mainly along river margins from Amazonian Colombia to North-West Brazil and up to northern Bolivia. It is usually a mid-canopy tree and grows up to 20m tall. At the Surumoni crane plot *Oenocarpus bacaba* is the second most important tree species (IVI=22.72), following *Goupia glabra* (Celastraceae, IVI=48.78). With the help of the canopy crane we were able to mount fruit trapping nets from above directly below the infructescences of four individuals of *Oenocarpus baccaba* (height 13-16 m, DBH 16-19 cm) for sampling of aborted fruit. Within the three months 26 % (SD 13.5) of the unripe fruit were aborted. Out of all aborted unripe fruit 60.5 % (SD 21.7) were damaged. The average fresh weight of the damaged unripe fruit was only half the weight ( $0.73\text{g} \pm 0.16\text{g}$ ) of the fresh weight of undamaged fruit ( $1.43\text{g} \pm 0.34\text{g}$ ). The average abortion rate of unripe fruit is  $0.7\% \text{d}^{-1}$  (SD 0.88), ranging from  $3.6\% \text{d}^{-1}$  to  $0.0\% \text{d}^{-1}$ .

Fungus infections and insects (e.g. cf. Ichneumonidae and Curculionidae) caused the majority of unripe fruit damage. Following two observations, the main on-site predation of ripe fruit is likely to be caused by the very abundant night monkey *Aotus trivirgatus trivirgatus*. Squirrels (*Sciurus* spp.), climbing rats (*Rhipidomys* spp.) and arboreal rats (*Echimys* spp.) are suspected for on-site predation by interpretation of tooth scars at the palm fruits. A certain number of ripe fruit must have been removed entirely by birds (Toucans, *Ramphastos* spp.) and fruit bats.

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# Arthropods in Temperate and Tropical Forest Canopies

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# Chemical strategy of a tropical myrmecophilous cockroach to associate *Crematogaster* ants inhabiting canopy of dipterocarp trees in Sarawak, Malaysia

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The aggressive ant *Crematogaster deformis*, inhabiting under the bark of emergent trees and inside epiphytic ferns, predominates among arboreal ants in a lowland mixed dipterocarp forest, Sarawak, Malaysia. Polymorphic workers of *C. deformis* are active day and night. When *C. deformis* exist, species diversity of arboreal ants was reduced presumably because *C. deformis* workers are aggressive enough to exclude other ant species. The epiphytic stag's horn fern *Platyserium coronarium*, was found to be inhabited by both ant *C. deformis* and myrmecophilous cockroach belonging to a new genus. The new genus of cockroach was described as *Pseudoanaplectinia yumotoi* Roth. Workers of *C. deformis* did not attack *P. yumotoi* as well as conspecific workers, however, they immediately showed aggressive behavior when workers of another species of arboreal ants were artificially offered. Because profiles of cuticular hydrocarbons (CHCs) are specific to ant colony and utilized by ants for nestmate recognition, chemical congruency is essential for myrmecophilous insects to penetrate host ant colony. In fact, many myrmecophilous insects mimic chemical profile of CHCs of the host ants. *P. yumotoi* also shared many CHCs in common with *C. deformis* when they lived together. These hydrocarbons were kept on cuticulae of *P. yumotoi* in a similar profile as in association even when artificially isolated from the host ants. On the other hand, from the cuticulae of the host ants, most of the hydrocarbons except for normal paraffin were reduced after one week rearing without cockroaches. The CHCs profile of *C. deformis* workers collected from emergent trees without the epiphytic ferns or cockroaches were chiefly constituted by normal paraffin, which is seen as not being utilized by ants for nestmate recognition because it is common on plant surface. These results suggest that *P. yumotoi* has a new chemical strategy to penetrate the host ant colony.

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# Dominance structure and species composition of an oribatid mite community (Acari, Oribatida) in the canopy of a Central European mixed forest

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To investigate diversity patterns and spatial distribution of oribatid mites in the canopy of a temperate Central European forest, four tree species were sampled in heights above 20 m: *Quercus robur*, *Fagus sylvatica*, *Larix decidua*, *Picea abies*. Sampling took place in late summer at the Swiss Canopy Crane in Hofstetten, Switzerland. For each tree species, three different microhabitats were sampled: outermost branch tips and thin branches (1 cm  $\varnothing$  and 3 cm  $\varnothing$ , both with side branches and foliage), thick branches (10 cm  $\varnothing$ , no side branches, no foliage except for *Picea*). Sampling was accomplished by high pressure rinsing as outlined in Weigmann et al. 2004.

90 % of all individuals extracted from samples were identified as Acarina, most of them oribatid mites. In total, 18 species of oribatid mites were distributed differently among tree species and microhabitats (see list in Weigmann et al. 2004). To estimate total dominance, Berger-Parker-Indices were calculated. The highest Berger-Parker-Index was determined for the coenosis on *Quercus robur*, the lowest for *Fagus sylvatica*. In microhabitats, communities on thick branches reveal the highest indices. Rank-abundance-diagrams show similar patterns of dominance. All oribatid mite species were classified by their relative abundance (Engelmann 1978). *Micreremus brevipes* was found to be the eu- or super-dominant species on branch tips and thin branches. Only on *Larix decidua*, *M. brevipes* is outnumbered by *Carabodes labyrinthicus*. On thick branches, dominance structure was distributed more evenly among oribatid mite species, sometimes lacking eudominant species. Some species, e. g. *Liebstadia longior*, only show reasonable individual abundance in this microhabitat.

Differences exist in dominance structure of oribatid mite communities in the canopy. As indicated by the high Berger-Parker-Index and by rank-abundance-plotting, *Quercus robur* shows the most balanced dominance structure, while the coenosis on *Fagus sylvatica* tends to be significantly less balanced. Smooth bark surface like in *Fagus sylvatica* seems to be unfavorable for most species, as well as foliage. Only a few euryoecious species like *Micreremus brevipes* dwell on the outermost tips of individual trees and thus become eu- or superdominant in this microhabitat. Thick branches with extended bark surface and sometimes epiphytic lichen growth allow the coexistence of several other oribatid mite species. Interspecific competition usually prevents *M. brevipes* to become superdominant in this microhabitat. In contrast, species associated with lichens (e.g. *Carabodes labyrinthicus*, *Dometorina plantivaga*) (André 1985) tend to become dominant here.

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# Vertical distribution patterns of arboreal collembolan species in the litter of a *Cryptomeria japonica* plantation

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Collembolans are common detritivorous and fungivorous microarthropods found throughout the upper (canopy) to lower parts (soil) of the vertical structure of forests. They play an important role in the functioning of detritus food webs. To clarify the structure and dynamics of collembolan forest communities, it is important to examine their spatiotemporal distributions in relation to the forest structure. Consequently, we examined the vertical distribution and seasonality of arboreal collembolan species in the vertical structure of an evergreen conifer plantation of Japanese cedar (*Cryptomeria japonica* D. Don). The canopy retains a large amount of litter, because dead foliage and branches stay attached to the trunk or are caught in the lower parts of the canopy.

We sampled dead leaves from each layer at intervals of 1 m above the ground and the soil litter at the forest floor (down to 3-cm deep) from May 2003 to May 2004. We extracted collembolans from both the canopy and soil litter using Tullgren funnels. The density of collembolans per unit litter mass increased gradually from spring to summer and decreased from autumn to winter in both habitats, ranging from 0.98 to 17.25 g<sup>-1</sup> dry weight in the canopy litter and from 1.42 to 30.86 g<sup>-1</sup> dry weight in the soil litter. We identified a total of six species of arboreal collembolans during the study period. *Xenylla brevispina* was the dominant species in both the canopy and the soil litter. The species composition of collembolan assemblages differs greatly between habitats; the collembolan assemblage in the canopy litter was much less diverse than in the soil litter.

Each arboreal collembolan species had different patterns of spatial and temporal distribution. The arboreal collembolan community included both species derived from those living in the soil and truly arboreal species, and their vertical distributions changed seasonally. These results suggest that immigration of collembolans from the soil to the canopy is an important process in constructing arboreal communities, and might provide food resources for predators in the canopy.

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# The abundance and biomass of canopy arthropods in coniferous plantations in Japan

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Many studies on forest canopies, especially in tropical regions, have shown a wide spectrum of ecological interactions at various nutrient levels (e.g. Lowman & Rinker 2004). However, technical difficulties in measuring the relative proportions and seasonal characteristics of phyto-resources, herbivores, and other trophic guilds in canopies, have hindered quantification of arboreal arthropod communities, which can be closely associated with the structure of trees.

I analyzed data collected from trees in four coniferous plantations in central Japan (35°11'N, 137°33'E) with different ages, tree species, census method and year (Hijii 1986, 1989; Hijii et al. 2001) as follows: 1) 15-year-old Japanese cedar (*Cryptomeria japonica* D. Don) enclosed by cloth bag using chemical knockdown; 2) 26-year-old *C. japonica* under open conditions by chemical knockdown; and 3) 37-year-old *C. japonica* and 33-year-old Japanese larch (*Larix kaempferi* Carrere) by branch clipping. Foliage mass was related to tree diameter by allometry. For comparison, previous estimates made in the same *L. kaempferi* plantation (16 year old, as of 1980) were also incorporated.

## Principal Results and Conclusion

1.) Dependence of abundance and biomass of canopy arthropods on tree size: A total of 8200 to 14,000 arthropods with a biomass of 340 to 1700 mg dry weight were collected from the five different sizes of 15-year-old *C. japonica* trees. Both measures were approximately proportional to the host tree size (square of diameter at height of lowest live branch – a parameter that is highly correlated with tree total foliar mass). The guilds of scavengers (mainly comprising oribatid mites and collembolans) and tourists showed the most significant correlations of both numbers and biomass with tree size, while the dependence of the phytophagous and epiphyte-grazer guilds (the latter including fungivorous animals) on tree size was less strong.

2. From individual trees to forest: In the *C. japonica* plantation, based on unit ground area, the arthropod biomass in June approximated 203 mg dry weight m<sup>-2</sup> in 37-year-old trees, and the value was comparable to the estimates of 161 mg and 175 mg dry weight m<sup>-2</sup> in 26-year-old trees, even though estimates of foliage biomass at the same site increased 3.3 times over 11 years. In *L. kaempferi*, although maximum foliage biomass increased by only a factor of two (from 0.4 kg in 1980 to 0.8 kg dry wt m<sup>-2</sup> in 1997), arthropod biomass increased 10-fold (from 74 mg to 800 mg dry wt m<sup>-2</sup>) over the intervening 17 years. This study presents some approaches for estimating density and biomass of canopy arthropods in coniferous forests at a given time of year both on individual-tree and per-unit-area bases, directly or indirectly via quantification of and with the phytomass in the canopies of individual trees by using allometric regressions.

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# The distribution of soil arthropods in different strata of oaks in a tropical rainforest (Kinabalu Park, Malaysia)

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**L**eam litter accumulates within the crowns of tropical forest trees harboring a diverse invertebrate community. We investigated the micro- and meso-arthropod community in three different strata (forest floor, low- and top-canopy layer) of six emergent oak trees (genus *Quercus*) in a submontane tropical rainforest in Kinabalu Park (610N, 11635E), Borneo, Malaysia. Altogether we found 16 orders of arthropods in the soil samples. Four of them showed significant differences in abundance between the three layers. In Coleoptera, Hymenoptera (Formicidae) and Diptera, there was a decrease in abundance with increasing height, whereas in mites (Acarina) the abundance of individuals was highest in the top canopy layer. The relative abundance of all other taxa did not differ significantly between the three strata, although there was a trend towards a decrease in total abundance with increasing height. One reason for this pattern, among others, may be differing microclimatic conditions between the ground and the canopy layers.

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# Ground beetles (Coleoptera: Carabidae) in the forest canopy: species composition and seasonality

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**W**e present a two-years examination of ground beetles (Carabidae) in the canopy of a Central European flood plain forest using window traps and branch-electors. The carabid fauna was analysed in 25 trees of *Quercus robur*, *Tilia cordata*, *Fraxinus excelsior*, and some neophytic trees. All traps were fixed at two levels: window traps in heights of 26 m and 22 m average, branch electors in 27 m and 20 m average respectively. A total number of 27 species with 242 specimens were recorded in window traps and four species with 19 specimens in branch-electors. Thus the number of carabid species in the canopy is higher than that on the ground, where 21 species were sampled with pitfall traps. The most common species in both canopy trap types was *Dromius quadrimaculatus*, an arboricolous species. The maximum activity of *Dromius quadrimaculatus* was recorded end of July/beginning of August which probably corresponds with appearance of adults of the new generation. The species set of the canopy can be linked to five ecological groups: (1) arboricolous species; (2) species with ground-canopy-interaction; (3) migrating ground dwelling forest species; (4) migrating ground dwelling urban species; (5) aerial plankton. Beside *D. quadrimaculatus* two further arboricolous species (*Dromius agilis* and *Calodromius spilotus*) were recorded only in scattered specimens in the canopy. Migrating urban species were recorded five times more often than migrating forest species in the canopy.

# Forest Canopy Herbivores

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# Defence strategies of woody plants in a tropical rain forest understorey

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In a tropical rain forest understorey the pressure on plants due to herbivory challenges plant growth and survival. To prevent or minimise the amount of leaf area lost (which results in less photosynthetic capacity and thus less acquisition of carbon) to herbivores, plants have evolved a wide range of nitrogen- and carbon-based chemical defences (e.g. cyanogenic glycosides, alkaloids, monoterpenes, phenolics). In this study, defence strategies in woody plants of an Australian tropical rain forest understorey were characterised and the relationship between chemical defence and other leaf traits (e.g. specific leaf area, leaf nitrogen content, photosynthesis, biomechanical defence) was investigated. Species were chosen due to presence or absence of cyanogenesis a constitutive and resource-demanding nitrogen-based chemical defence known to be effective against generalist herbivores. In order to achieve this, foliage was collected at field sites with contrasting soil nitrogen status. The amount of nitrogen- and carbon-based chemical defence compounds (i.e. cyanogenic glycosides, total phenolics, condensed tannins) and other leaf traits (i.e. leaf nitrogen content, leaf phosphorus content, specific leaf area, total chlorophyll, leaf toughness) was quantified. We found significant variation in defence strategies both between and within species. For example, within sites *Beilschmiedia collina* B. Hyland showed higher amounts of both nitrogen- (cyanogenic glycosides) and carbon-based defences (total phenolics, condensed tannins) than *Cardwellia sublimis* F. Muell.. Furthermore, we found that the amounts of carbon-based defence increased on the lower nitrogen soils. Leaf nitrogen differed significantly between and within species. For example, within *Beilschmiedia collina* cyanogenesis was found to be significantly different, even with similar soil nitrogen status. However, regression analyses did not support the hypothesis that chemical defence (i.e. cyanogenesis, phenolics) is strongly dependent on leaf nitrogen content suggesting that variation in these chemical defences within species may be more dependent on other environmental variables and / or genetic background.

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## Between-year variation in the response of a gall wasp community to a genetic cline in a deciduous oak, *Quercus crispula*

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Hybrid plants often show higher or lower susceptibility to insect herbivores than parental plants. Consequently, the structure of a herbivore community may change along the genetic cline of a host plant, which is caused by hybridization with other species. On the other hand, some studies of plant genetic-herbivore relationships have shown significant effects of interaction between plant genetics and ambient environments. These facts imply that herbivores respond to the genetic cline of host plant differently under variable environmental conditions. Oaks are known to hybridize within a geographical region, and are used as hosts by diverse species of gall wasps. Thus, the oak-gall wasp system offers a suitable system for exploring the responses of multiple species of herbivores to genetic variation in the host plant.

*Quercus crispula* dominates a deciduous broad-leaved forests in Hokkaido, northern Japan. I tested a hypothesis that the structure of a gall wasp community changes along the genetic cline of *Q. crispula* differently between two years, using 12 half-sib families of *Q. crispula*. I examined patterns in the species composition, species richness and abundance of gall wasps along a genetic cline of the host plant.

The genetic relationships among the half-sib families of *Q. crispula* were quantified on the basis of leaf morphology, which represented a morphological cline from leaves typical of *Q. crispula* to leaves resembling another oak species, *Q. dentata*. The morphological cline could be regarded as a genetic cline caused by a history of hybridization with *Q. dentata*. The species composition of gall wasps varied among the half-sib families, and the variation to some extent also reflected the genetic cline of *Q. crispula*. The species composition in each half-sib families also differed between years, and the difference was parallel rather than diffuse between years. The mean species richness differed among the half-sib families and between years, but the effect of interaction between half-sib family and year was not significant. Responses to the genetic cline of *Q. crispula* differed among dominant gall wasps: the abundance of some species increased along, decreased along, or was independent of the genetic cline. However, also on these abundance patterns, the effect of interactions between half-sib family and year was not significant for all the species. Some gall wasps dominated the community only in the latter of the two years. These results suggest that the difference in the community structure between years was mainly due to the entry of new dominant species, not to the shifts of component species along the genetic cline.

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# The estimation of the amount of hare feed by canopy structure

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**W**e developed a method to estimate the hare feeds in 21 km<sup>2</sup> by using the data of vegetation canopy profile and the relationship between canopy height and feed amount. The canopy height profile was made into the digital elevation model measuring the canopy height by aerial photographs taken in 1968, 1983, and 1999. The amount of hare feeds and vegetation canopy height were calibrated by the field data. The plant species and parts that a hare can eat was clipped and weighed. The hare feeds amount was high in young vegetations and small in developed forests, in particular man-made conifer forests. The human land-use pattern greatly affected the spatial distribution of the hare feeds. There were large areas of young man-made forests in 1968, causing large amount of hare feeds, though the feed amount decreased according to the growth of man-made forests. Also, the newly planted man-made forests distributed in the lower elevation in 1968 and changed to higher areas, and caused the great shift of the distribution of hare feeds. It seems the important reason of the decreasing in hare population generally occurred in Honshu Island, Japan.

# Biodiversity and Free Topics

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# Building capacity in canopy research: the Brazilian experience

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The development of ecology projects in the canopy may require a great effort in training, in special due to the risks related to climbing. Here we present the protocol of the post-graduate field course “Research in Canopy Ecology”, held in the Serra do Teimoso Natural Reserve (Bahia State, Brazil) in March of 2002. No other field course had been priorly developed with the objective of exploring the tree tops. Twenty students were chosen based on their experience in forest canopy research. In the field, all of the places used for practical study were inspected by professional climbers to identify the falling risks, phytosanity and climbability. The first week of the course was used to pass on information about the equipment, climbing techniques and safety protocols, for climbing simulations in controlled conditions and knotting, ascending, descending and movement within the tree tops techniques. The students were also exposed to the difficulties of reaching a fishing line across tree branches and of climbing trees. Short duration projects occurred during the second week. The students were organized into groups of six; they contained at least one graduate student, were advised by a lecturer and had the supervision of a climbing professional. Each lecturer advised a different group every day and the projects were presented to the group on the night before they were executed, to allow discussions and adjust methodologies. In the project execution day, data were collected in the morning, statistical analysis was performed in the afternoon and project summation was presented at night. Long duration projects that aimed to respond processes and interactions occurred during the third week. Two days of the last week were reserved for the formulation of hypotheses and methodology adjustments. The data collection occurred during 5 or 6 days. Twelve projects were developed during the second week explored microclimatic variation within the canopy, canopy openings, spatial distribution of hemiepiphytes, epiphytes, lichens, epiphylls, galls and ants, reproductive allocation and vegetative morphology. The six longer projects explored resource utilization by birds, the distribution of epiphytic species among trees, vertical organism distribution differences, plant physiology, and colour preferences by birds. The formation of groups of undergraduate and graduate students forced the graduate students to be well versed in their subject and also improved the learning experience of the undergraduates. The logistics of running a canopy course requires a strict safety protocols in all activities and the presence of climbing experts as well as scientists. Small groups of 3-4 students are necessary because the practice of climbing involves safety, new terms, clear explanation of equipment utilization and demands a correct climbing practice. A unique feature of this course was that the climbing professionals and organizers were responsible for the safety of all the students and scientists engaged in a potentially dangerous practice - rope and tree-climbing demanding a tight security protocol. The course contributed to environmental education and the local environmental education project through the participation of park managers who frequently host local school groups or tourists.

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# Automated Analysis of Canopy Gap Dynamics

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An analysis of canopy surface enables the acquisition of valuable information on processes such as growth and competition or forest stand parameters in general. One way to investigate the upper crown surface is through precise mapping of canopy gaps. These gaps play an essential role in continuous cover forests, as they have a strong effect on regeneration dynamics and species composition. However, canopy gaps and canopy surface, especially, have been widely neglected in current monitoring and forest management practices. This might be due to the fact that terrestrial and analogue photogrammetric measurements are particularly problematic in dense broadleaved stands. In this study an approach to automated canopy gap delineation using digital height models was developed.

Remote sensing can provide the required digital height models enabling surveys of canopy gaps over large areas. Data of sufficient resolution can be derived from laser scanning (LiDAR) or digital photogrammetry using digitized CIR imagery and digital terrain models. These techniques provide very accurate height models for large areas with a minimum of human interaction. A filter based on local median and distribution, which depends solely on canopy height information, was found to provide better results for automated canopy gap delineation than conventional height thresholds. This method was evaluated within a Geographic Information System using a gap delineation done by an interpreter on an analytic stereoplotter.

Based on digital height models not only the true stand height and the number, size, and distribution of gaps were determined, but also other ecological parameters describing the morphology of the canopy surface. Data taken during the last three decades enable studies of the dynamics of canopy morphology, which has previously not been possible on a large.

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## Plant diversity in the forests of Siahkal (North of Iran)

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Siahkal is located at north of Iran. It is 40 Km long, occurring between 37°10'N 49°30'8" E. This region has mild and moderate climate. Our collections began at the end of 2000 and continued monthly until the end of 2003. The high altitudinal differences in this area provide a good tool to study the diversity of species along altitude. In order to find the number of species in various altitudes, the specimens are classified into altitudinal ranges, 300-500, 300-800 etc. Evidently a large number (137 species) are found in altitudes from 300-1200 m. Certainly many factors are responsible for such an altitudinal diversity pattern in this region, such as anthropogenic factors, orographic structures, the interaction of macro- and microclimates, vegetation structure, faunal structure, etc. Some examples of the characteristic species in each altitude range to their distribution map are mentioned.

- 300-550 m: The number of species restricted to this range is not very high, More peculiar is the unique humid and warm climate in those parts. Examples of species restricted to these altitude ranges are: *Acer platanoides*, *Alnus glutinosa*, *Buxus sempervirens*, *Cyclamen coum*, *Diospyros lotus*, *Oplismenus undulatifolius*, *Populus caspica*, *Quercus macrenthera*, *Ruscus hyrcanus* and *Datisca cannabina*.
- 300-750 m: Includes those species with distributions overlapping with the first group but extending further to 800 m. The number of this group is rather high. Examples of species restricted to these altitude range are: *Alnus subcordata*, *Atropa belladonna*, *Carex pendula*, *Cephalanthera caucasica*, *Epimedium pinnatum*, *Euphorbia amygdaloides*, *Fagus orientalis*, *Lamium galeobdolon*, *Luzula foresteri*, *Parietaria officinalis* and *Parrotia persica*.
- 300-1000 m: Most of the species in this group are forest or forest adopted elements with high altitudinal ranges. Such forest elements are common in submountain and mountain forests, dominated by *Quercus castenifolia* and *Carpinus betulus*. Examples of plants in these ranges are: *Cardamine bulbifera*, *Corydalis marschalianus*, *Geranium montanum*, *Polygonatum polyanthemum*, *Petasites officinalis*, *Salvia glutinosa*, *Tilia platyphyllos* and *Vaccinium arctostaphylos*.
- 550-1200 m: The species classified into this category have the highest altitudinal amplitude in the area. Two outstanding woody examples are *Fagus orientalis* and *Mespilus germanica*. Herbal species like *Alliaria petiolata*, *Geum urbanum*, *Lapsana communis*, and *Poa bulbosa* are undergrowth forest elements. *Alchemilla hyracana*, *Anemone blanda*, *Ficaria kochii*, *Galanthus transcasicus*, *Stellaria holostea* and *Veronica gentianoides* are species with high altitudinal amplitude of this region.

We concluded that the diversity of species is positively correlated with the increase of the altitude amplitude. Based on the available data the highest absolute plant diversity in studied area is on an altitude between 550-1200 m.

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## Monthly fluctuations of zoosporic and terrestrial fungi inhabiting sewage at assiut (Upper Egypt)

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One hundred and seven species in addition to three varieties belonging to 43 fungal genera were recovered from sewage samples collected monthly during the period from December 2001 to November 2002. Of these 14 species related to 13 genera of zoosporic fungi, 81 species related to 25 genera of glucophilic fungi, 9 species related to 8 genera of thermophilic or thermotolerant fungi and 10 species related to one genus of keratinophilic fungi. The highest species diversity of zoosporic fungi was recorded during December followed by February. zoosporic fungi disappeared completely during May. *Pythium aphanidermatum*, *Aqualindrella fermentans* and *Allomyces arbuscula* were the most frequent of zoosporic species. The highest species diversity (47 species) of glucophilic fungi was recorded during February whilst the lowest (16 species) was recorded during August. *Aspergillus* (21 species and one variety) *Penicillium* (21 species) and *Fusarium* ( 9 species and one variety) were the most frequent genera. Using yeast starch agar at 45 oC, *A. fumigatus*, *Rhizomucor pusillus*, *Talaromyces thermophilus* and *Torula thermophila* were the most prevalent species. Ten species of keratinophilic fungi belonging to *Chrysosporium* were identified. The physico-chemical characteristics of collected sewage samples varied depending upon the stage of treatment and the sampling month.

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## Genetic and phenotypic variance among and within ashes

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**T**he genetic variation of the semi-natural population of *Fraxinus excelsior* of the Leipzig-Auwald-Kran project (LAK) is analysed, the main questions being whether phenotypic variation is reflected by a genotypic variation, and how large the genetic variability of the population is. One hundred ashes of the canopy, studied in the LAK plot, differed in size, gender, flower and fruit phenology, reproduction and leaf characters. In some cases, within-tree variability in flowering time and fruit set were recognized. Genetic methods (microsatellites and AFLPs) enabled a further and independent quantification of the genetic variability among the trees and within the trees, and a comparison with the phenotypic variability. A genetical grouping of 15 trees in preliminary samples separated male from hermaphrodite trees and clearly differentiated the ash population of the LAK from a control population in Hamburg. A full analysis of all canopy trees, as well as the analysis of somatic mutations and genetic variability within individual trees is underway.

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# Interspecific and intraspecific comparisons of hydraulic properties in tropical forest trees in Sarawak

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**D**ipterocarps are the main timber producing trees in Malaysia. There have been many studies on their systematics, ecology, and productivity. However, studies with ecophysiological approaches are limited. Here, some characteristics of Dipterocarps that are related to leaf water condition were examined to assess their drought resistance and adaptability to water stress. Ecophysiological processes such as stomatal conductance and leaf water potential were also measured. We used 16 lowland tropical tree species (10 species in Dipterocarpaceae *Shorea* and 6 species in other families). The study site, the Canopy Biology Plot (8ha), is located in lowland mixed dipterocarp forest in the Lambir Hills National Park, Sarawak, Malaysia (4°2'N, 113°50'E, 150 m asl). Tree water potential at predawn ( $\Psi_{pd}$ : MPa), hydraulic conductivity (K) of upper branches and tree size (H, DBH) were measured in August and November 2004. Using canopy trees with different sizes, we tested the hypotheses that hydraulic limitation increases with tree size (HL hypothesis).

There was significant negative correlation between DBH and  $\Psi_{pd}$  ( $r = -0.44$ ,  $P < 0.01$ ) between species in Dipterocarpaceae. Negative correlation between H and  $\Psi_{pd}$  ( $r = -0.95$ ,  $P < 0.05$ ) was also found in other families. These results suggest that  $\Psi_{pd}$  tends to be lower in a larger tree species. However, tree height alone does not explain the variance in  $\Psi_{pd}$ . For example, there were significant difference in  $\Psi_{pd}$  of two species with the similar height (35m), *Allanthospermum borneense* and *Scaphium macropodum*. While  $\Psi_{pd}$  of *S. macropodum* was -0.37MPa;  $\Psi_{pd}$  of *A. borneense* was only -0.15 MPa, which is much lower than the value expected from gravitational gradient ( $0.01 \text{ MPa m}^{-1}$ ). Furthermore, in intraspecific comparisons, there was no significant correlation between tree height (DBH, H) and  $\Psi_{pd}$ . Our results only partly support the HL hypothesis. We suspect that what masks the inter- or intraspecific correlation between height and  $\Psi_{pd}$  is the difference in osmotic regulation and/or homeostasis in water status. Investigation of more detailed ecophysiological traits such as diurnal change of leaf water potential and transpiration remains a future study.

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