TROPICAL RAINFOREST ECOLOGY FROM A CANOPY PERSPECTIVE

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Many processes that are fundamental to tropical rainforest maintenance and regeneration take place in the forest canopy. Recently developed access techniques afford biologists non-destructive means to document and quantify canopy biota and their accompanying activities and interactions. Results from studies involving within-canopy observations and measurements of nutrient cycling, epiphyte distribution, species diversity, nutrient cycling, and animal activities in primary and secondary forest are reviewed to identify specific areas of investigation and scientific questions that can be addressed from a canopy perspective. The ongoing progress of current canopy ecology projects in tropical rainforests is described. New data on interactions between neotropical canopy birds and plants and the effects of forest conversion to pasture on these organisms in a neotropical cloud forest suggest that trees left standing in pastures can serve as "island refuges" for a wide variety of bird species using canopy resources such as epiphyte flowers and fruits and accumulated dead organic matter on branches and trunks. This study points out the need for more basic ecological research on canopy ecology in both primary and converted forests.

For those concerned with the ecology and conservation of the diverse genetic and ecological resources of tropical rainforests, studies in the upper tree canopy of rainforests are of fundamental importance. In the treetop region of tropical forests, abundant energy and distinctive microclimatic regimes foster up to 40% of the earth's inventory of species (Perry 1984). Until recently, the canopy has been a largely inaccessible and unexplored area of tropical forests. Indeed, those who did venture into the canopy have been regarded by the scientific community as "Tarzan types" who have had little to contribute outside of providing rarely collected specimens and interesting

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natural history stories. Recent applications of safe and reliable mountain-climbing techniques for routine and extended access into tropical rainforest tree crowns, however, have expanded the range of questions ecologists can pose that bear upon basic and applied aspects of tropical forest ecology. The upper tree canopy is being recognized as an appropriate arena to investigate such ecological questions as the evolution of symbiotic interactions, mechanisms of nutrient conservation, and comparative studies of life histories of canopy-dwelling plants and their associated animal pollinators and dispersers.

A growing body of ecological research indicates that processes occurring in this region of the forest relate directly to the overall composition, function and dynamics of rainforests as a whole. This study addresses the following areas of canopy ecology pertinent to tropical rainforest research:

(1) overall attributes of canopy microclimate;

(2) methods that have been developed for access to the canopy;

(3) some of the questions that can be addressed from the canopy perspective and specific examples of studies addressing such questions; and

(4) new data on the interactions of canopy-dwelling plant and bird communities in a neotropical cloud forest and some of the effects of forest conversion to various types of pasture on these interactions.

THE CANOPY AND ITS MICROCLIMATE

The term "canopy" is generally used to denote "any high overarching covering." More specifically, it defines the upper portion of a single tree crown and/or the entire upper portion of forest ecosystems. In earlier accounts, tropical rainforests were perceived as being strongly stratified into discrete, multiple layers (Aubréville 1965, Richards 1952), with the canopy encompassing the crowns of the emergent trees ("A" horizon) and the contiguous "B" horizon (Richards 1952, Whitmore 1975). This level of the forest may be contiguous or "broken" in horizontal space (Hallé et al. 1978, Richards 1983).

The complex three-dimensional structure of tropical rainforests has stimulated the documentation of physiognomy and vertical stratification of abiotic and biotic attributes of the forest as a whole (Hallé et al. 1978). Stratification of microclimatic regimes and the composition and distribution of the biota are striking, especially in humid lowland forests (Longman and Jeník 1974). Canopy microclimatology has been measured most frequently with instruments mounted on towers at various heights above the forest floor (e.g. Bunning 1948, Carter 1934). Since above-canopy conditions closely resemble those recorded in openings in forest gaps, some studies have directly compared ground measurements of the forest interior with measurements collected at clearings in the forest (Allee 1926, Schulz 1960). More recently,

the use of battery-powered data-loggers has provided continuous monitoring of environmental conditions, with sensors installed at a range of canopy heights (e.g. Chazdon and Fetcher 1984).

In general, canopy abiotic conditions are typified by more intense sunlight, greater extremes of relative humidity, higher water stress, and a smaller, more pulse-supplied pool of nutrients than forest floor conditions (Kira et al. 1969, Lee 1978, Yoda 1974, Benzing 1981a). Sunlight attenuation, for example, can be as great as 98% between the tops of emergent trees and the levels reaching the forest floor (Cachan 1963). Rates of evaporation in the canopy have been recorded that are comparable to those occurring in open savannas. Relative humidity can range from nearly 100% at night to less than 30% during the midday in the dry season (Jeník and Hall 1966). Differences in canopy vs. forest floor wind speeds are most extreme in montane cloud forests. In a Costa Rican ridge cloud forest, Lawton (1980) clocked wind speeds within the canopy (8 m) at 11.3 m/s, while forest floor (2 m) speeds were only 4.0 m/s.

CANOPY ACCESS TECHNIQUES

The biota of the upper tree canopy has attracted attention ever since the first European explorers traveled to tropical latitudes. However, the techniques required for the study of canopy communities have become available only recently. Pioneering work in old-growth forests of the Pacific Northwest, United States by Denison et al. (1972) led to the application of mountain-climbing techniques for safe and reliable access to the canopies of tall trees. These techniques were modified for use in the tropics by Perry (1978, 1984) and others (Nadkarni 1983, Whitacre 1981).

Mitchell (1982) provides an excellent summary of methods of canopy access. He organized the existing techniques into six categories:

(1) construction of permanent towers (e.g. Grison 1978, Haddow 1961);

(2) ascension of the trunk with bolts, spikes, or ladders (Hingston 1932; Denison et al. 1972, Denison 1973);

(3) construction of platforms within tree crowns (McClure 1966, Sutton 1983), and installation of rope webs (Perry 1984);

(4) construction of aerial walkways (Dieterlien 1979, Mitchell 1982);

(5) "miscellaneous methods" such as the use of hot air balloons, helicopters, and hang-gliders (Hladik and Hladik 1980); and

(6) climbing free of the trunk, using single-rope techniques (SRT) (Perry 1978, Whitacre 1981).

SRT techniques are appropriate to collect many types of ecological data in the canopy. They are non-destructive to the tree, relatively inexpensive, rapidly installed, and easily learned. SRT techniques also minimize contact

with tropical tree trunks, their potentially irritating spines, and animals. This method provides maximum flexibility, as it requires a minimum of one strong branch within shooting range of a powerful slingshot, crossbow, or linegun.

This climbing process proceeds in the stages outlined in Figure 1. First, a climbing rope is placed over a suitable branch or branches by shooting a mono-filament nylon line over it with a crossbow or "master-caster." The latter consists of a powerful slingshot mounted on the side of a short aluminum rod (50 cm), with a spinning reel mounted beneath it (Nadkarni 1983). A nylon "parachute" cord is then attached and pulled over the branch with the reel. This is followed by pulling up a standard (9 or 11 mm) climbing rope, which is tied off to the trunk. The climber then ascends the rope with a seat harness, leg loops, and "Jumar" type self-locking ascenders. The climber can rest or take samples and abiotic measurements on the journey up the rope. By shooting lines from one limb to another, one can "leap-frog" to other trees across the canopy. The return to the ground is accomplished by reversing the ascension process or by rappelling down with brake bars.

Equipment for these techniques (approximately US $300) is readily available at outdoor equipment stores. It can be carried in a single backpack. Trees can be rigged in 30 minutes and climbed to 30 m in 5 to 10 minutes. The intermediate nylon line can be left in a tree for rapid re-rigging.

AREAS OF CANOPY ECOLOGICAL RESEARCH

A number of biological questions can be addressed from the canopy perspective, ranging from basic taxonomic studies of canopy-dwelling organisms to applied studies of nutrient cycling and productivity. Canopy studies have enhanced our general understanding of tropical forest ecology in these areas:

(1) tropical forest nutrient cycling, especially with regard to identification of mechanisms of nutrient conservation;

(2) documentation of the overall species diversity of tropical systems;

(3) biotic and abiotic factors controlling plant distribution and abundance;

(4) attributes and evolution of such plant-animal interactions as herbivory, pollination, and fruit dispersal; and

(5) effects of disturbance on natural communities.

Nutrient Cycling

Nutrient cycling within the canopy has recently attracted a good deal of attention. It has been extensively reviewed elsewhere (Benzing 1983, Nadkarni 1984, 1985, 1986). In the last decade, ecosystem-level studies have identified the forest canopy as having important storage and regulatory roles
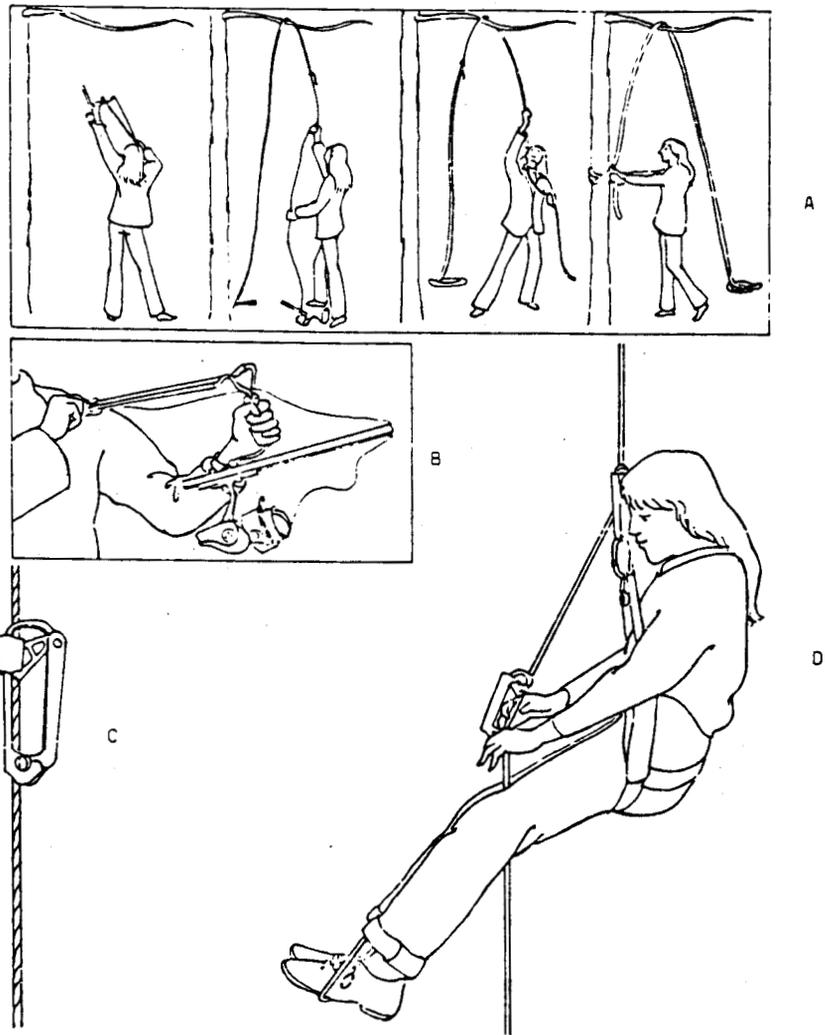
Fig. 1. Sequence of tree-climbing protocol using single-rope technique described in text. A. Tree-rigging sequence. B. "Master-caster" device for placement of initial line. C. "Jumar" ascender clamp attached to seat harness and leg loops. D. Climbing harness and leg loops.

in overall mineral cycling. In contrast to the traditional paradigm of temperate forest nutrient cycling, in which the bulk of the nutrient pool is stored in the forest floor and soil, there is growing recognition that forest fertility in some sites is largely a function of mechanisms within the biotic components of the ecosystem (Jones et al. 1974, Kellman et al. 1982, Golley 1983, Vitousek 1984). Intact forests possessing these mechanisms are characterized by large nutrient fluxes within the biota relative to ecosystem loss. Mechanisms of nutrient conservation are ultimately explained by the living organisms that make up the forest community, especially at the soil-litter-root interface. As one of the constituents of the biotic component of wet forests, canopy-held organic matter may play an important regulatory role in nutrient storage and flux.

Evidence that the canopy subsystem is important in overall nutrient cycling comes from five lines of evidence:

(1) large nutrient pools are contained in live and dead decomposing organic matter within the canopy (Pócs 1980, Nadkarni 1983);

(2) tree canopy structure increases the interception of airborne nutrients in rain, mist, rime, and dust (Weaver 1972, Azevedo and Morgan 1974, Cronan and Reiners 1983);

(3) activities of free-living and symbiotic organisms can biologically fix significant amounts of atmospheric nitrogen (Denison 1973, Roskowski 1980, Sengupta et al. 1981, Yatazawa et al. 1983, Bentley and Carpenter 1984);

(4) active absorptive organs exist within tree crowns, including tree stems (Ticknor 1953), foliar surfaces (Thorne 1955), and host tree canopy root systems (Nadkarni 1981);

(5) many canopy-dwelling plants are morphologically and physiologically efficient at impounding pulse-supplied nutrients and tying them into the biotic portion of the system, which can reduce loss to the system as a whole (Benzing 1983).

In only a few studies, however, has nutrient flux within the canopy been directly measured (e.g. Edminsten 1970, Pike 1971, Nadkarni 1983). No one has attempted to quantify or compare the nutrient dynamics within the canopy with that of the forest overall nutrient cycles. Yet this direct comparison is crucial if we are to determine the importance of different parts of an ecosystem in its overall functioning and to predict the effects of canopy disturbance.

Laboratory studies using newly developed techniques of gamma spectrometry have been carried out to determine the rates and fates of nutrients delivered to canopy vs. below-ground absorptive surfaces (Nadkarni and Primack, in prep.). Above-ground canopy roots of willow saplings, for instance,

are capable of nutrient uptake and circulation of radioactive tracers at rates comparable to those in soil roots, indicating that nutrient cycling within the crowns of epiphyte-laden trees may be significant in the field.

In addition to their probable importance in overall nutrient cycles of natural forests, canopy components have high potential for increasing our understanding of mechanisms regulating nutrient storage and transfer. The epiphyte-organic matter-host tree systems create "natural microcosms" and are excellent arenas for investigating processes of mineral circulation. Unlike laboratory microcosms using columns of sand or water culture, these systems contain all the components that "real" ecosystems have (humus, vascular and non-vascular plants, a substrate) and have occurred in nature over an evolutionary time scale. They can be subjected to controlled and replicated manipulations; nutrient inputs and outputs can be monitored accurately. Undoubtedly this could develop into a fruitful area of nutrient cycling research.

Species Diversity of Canopy Biota

Among the most striking and unique attributes of tropical rainforest canopies are the diversity and abundance of the plant communities that are physically independent of the forest floor for all or part of their life cycle. The species diversity of epiphytes, plants which derive support but not nutrients from their hosts (Abercrombie et al. 1970), has been recently reviewed by Madison (1977) and Gentry and Dodson (1987). They belong to a wide range of vascular and non-vascular plant taxa. Sixty-eight vascular plant families contain epiphytic members; 28,624 species are epiphytic, which comprise about 13% of the total vascular flora. A large number of non-vascular plants, many as yet unnamed, are also abundant in tropical forests, and in fact dominate (by biomass) the epiphyte communities of some neotropical cloud forests and temperate moist forests (Nadkarni 1984, 1985).

Various ecological and taxonomic aspects of other types of canopy plants have been documented. These include parasites (Davidar 1983, Calder and Bernhardt 1983), lianas (Putz 1982), and epiphylls (Bien 1982, Bentley and Carpenter 1984). However, the full scope of their contribution to overall tropical forest species diversity remains unknown.

A body of research concerns the diversity of canopy-dwelling animals (e.g. McClure 1966, Sutton 1983, Sutton et al. in press, Sutton and Hudson 1980). Most of the research has concerned insects and other arthropods. Landmark studies by Erwin (1982), which focused on the diversity of specific groups of beetles, pointed out that overall estimates of species diversity in the tropics are gross underestimates if the diversity of canopy organisms is not included. Use of remote-controlled insecticidal foggers following Gagné (1979) and Gagné and Martin (1979) resulted in an estimate of the total

number of individuals and the degree of host-specificity for a number of insect groups. Erwin (1983) reported 1000 species of beetles (excluding weevils) on a single tree, and 12,448 per ha of forest canopy in Manaus, Brazil. Relating his assessment of the numbers of host-specific species to other arthropods, the estimate of arthropod diversity was 41,389 spp/ha, and overall, 30 million species of tropical arthropods. These studies are an important first step in accurately assessing tropical rainforest diversity.

Biotic Influences on Epiphyte Distribution and Abundance

The biotic factors regulating where and how many plants grow in a given area are a central question for plant ecologists (Grieg-Smith 1983). The variations of within- and between-tree epiphyte distributions present an appropriate arena to test theories on the regulatory factors that control plant distributions. Questions concerning host tree specificity, within-canopy stratification, and mechanisms whereby host trees may affect epiphyte establishment have intrigued botanists for many years (e.g. Went 1940, Barkman 1958). The mechanisms for host tree specificity remain poorly understood, although many have speculated that bark texture and pH, bark and branch shedding rates, and chemical exudates may facilitate or inhibit epiphyte colonization and growth. The few experimental studies have been carried out mainly in the subtropics and temperate regions (e.g. Frei and Dodson 1972, Benzing 1978, 1981b, Schlesinger and Marks 1977).

Descriptive and qualitative studies of epiphyte distributions have been used primarily to make inferences about regulation of epiphyte growth by the host tree. The most exhaustive studies of epiphyte distributions within tropical forests have been based on visual inventories. Various authors concluded that for many species, there is some degree of host tree specificity (Went 1940, Johansson 1974, Sugden and Robins 1979). A more focused study carried out in the lowland forests of Malaysia by Johnson and Awan (1972) compared differences in abundance, biomass, and accumulated organic matter between epiphytes growing on *Fagraea fragrans* and *Swietenia macrophylla*. Their results showed that several of the epiphytes were host-specific (e.g. *Pyrrosia angustata*, *Platycerium coronarium* only on *F. fragrans*, *Phymatodes scolopendria* and *Drynaria sparsisora* only on *S. macrophylla*), while others (*Asplenium nidus*) did not show such host tree preferences. No experimental evidence for causes of these patterns was presented.

Plant/Animal Interactions in the Canopy

A wide range of plant-animal interactions that are fundamental to the reproductive apparatus of the forest occur within the upper tree canopy.

These interactions have been documented mainly from plant collection notes and anecdotal observations, and include canopy herbivory, ant/epiphyte relationships (Huxley 1980, Longino 1986, Madison 1979), and fruit and seed dispersal of canopy trees (Wheelwright et al. 1984). Special attention has been given to reproductive biology of bromeliads (Benzing 1980) and orchids (Dressler 1981). Studies on the highly specific relationships between hummingbirds and epiphytic ericaceous shrubs indicate that morphological and behavioral specialization may function to allow coexistence of diverse species complexes (Feinsinger et al. 1986).

Most of the work on bird frugivory in tropical forest canopies (Snow 1981) has focused on the consumption of fruits of canopy trees with respect to tree dispersal and/or avian nutrient budgets (e.g. Wheelwright et al. 1984). In many tropical forests, the epiphyte community provides energy, nutrients, water, and nesting materials from their foliage, flowers, fruits, accumulated dead organic matter, and rosette pools to canopy-dwelling animals. A recent study (Nadkarni and Matelson, in prep.) was conducted to provide a framework to understand the degree of dependency of particular animals upon various resources held within the canopy, with a focus on bird use of epiphytes.

Epiphyte distribution and bird visitation were monitored in an area of lower montane cloud forest and adjacent pastures in Monteverde, Costa Rica (Fig. 2) from June 29–September 6, 1985. Using SRT techniques previously described, we established canopy perches (hanging collapsible cots) in dominant canopy trees located in primary leeward cloud forest. Bird activities could be accurately seen in tree crowns within a radius of 120 m from the perches (8 to 14 individuals in each of three sites) (Fig. 3). Observation sessions (four 90-minute sessions per day) were timed to occur throughout the day (0600 to 1800) in order to control for diurnal variations in bird visitation. During the 775 hours of observations, we recorded the number of individual bird visits, species, length of visit, behavior (perching, foraging, feeding, nesting, mating, vocalizing), and canopy resource used (epiphyte, host tree, flower, fruit, water, invertebrate, nesting material).

We found that epiphytes provide many birds with habitat and supplies of energy and nutrients. In this preliminary analysis, the most commonly used resource plants were clustered in major family or generic groupings, which provide specific resources presented in Table 1. Resource availability presented here represents conditions that occur during the middle of the wet season (June to September), and vary to an unknown extent, depending on the phenology of the epiphytes and host trees, seasonal changes in weather, and successional changes and disturbances within the epiphyte community.

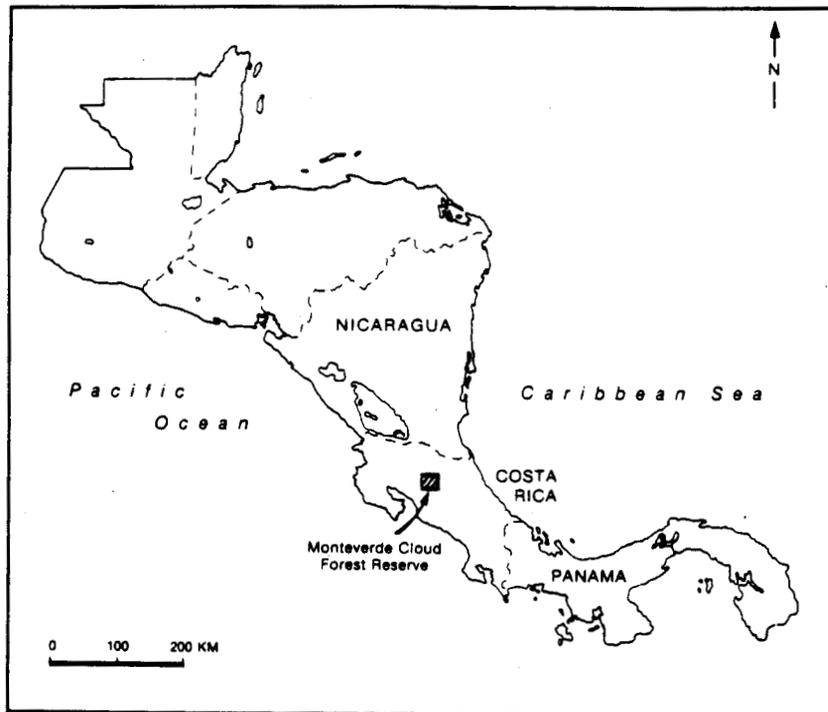Epiphyte resources were used by 46 of the total 86 bird species that used

Fig. 2. Location of Monteverde cloud forest.

TABLE 1. EPIPHYTE TYPE AND RESOURCES
AVAILABLE FOR CANOPY BIRD USE

Epiphyte Resource	Epiphyte Type†				
	A	B	E	M	L
Inflorescence	*	*	*		
Fruit	*	*	*		
Invertebrates		*	*	*	
Water		*			
Nesting Material				*	*

† A = Aroids; B = Bromeliads; E = Ericaceous shrubs; M = Mosses and liverworts; L = Lichens.

Fig. 3. Detailed map of study sites for bird use of tree crowns in forest and pasture areas, Monteverde, Costa Rica. Numbered plots are those used for canopy observations in primary forest. Relict pastures are those where original rainforest trees have been left standing. Scrub pastures are those colonized by a limited number of "invader" tree species. Map drawn from an aerial photograph by Instituto Meteorológico, San José, Costa Rica, 1979.
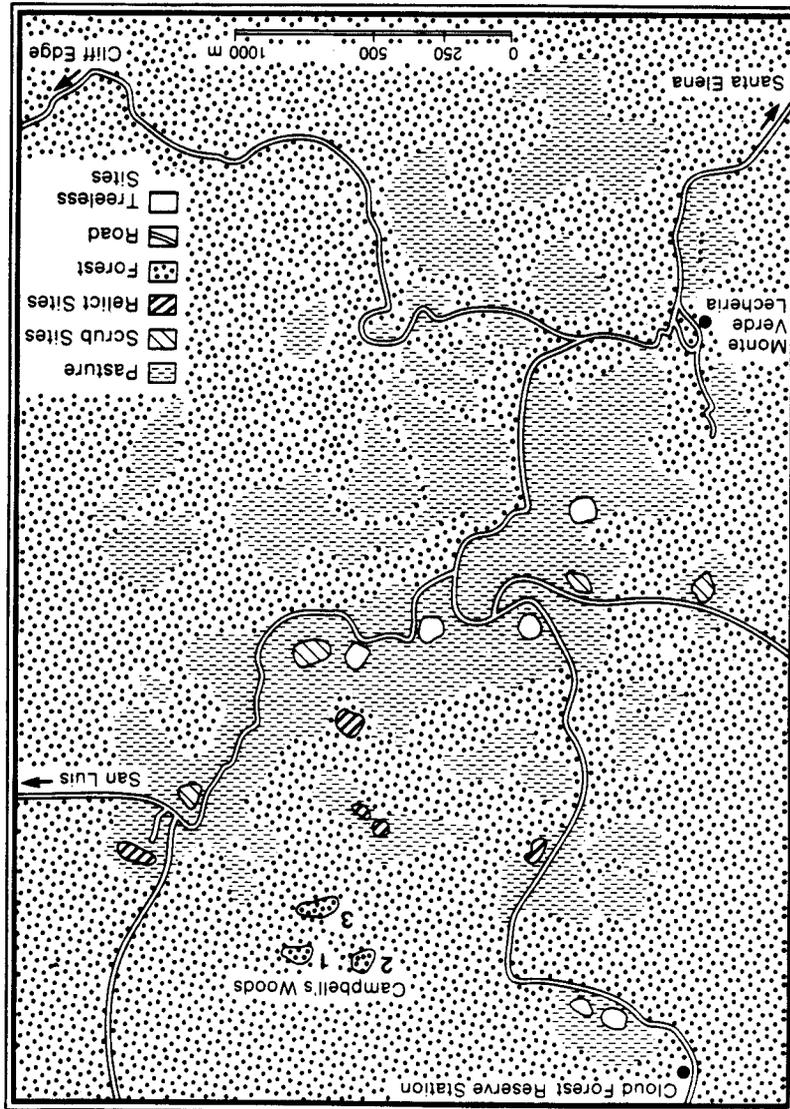
our sites. Mosses and associated dead organic matter were used by the greatest number of bird species, followed by ericaceous shrubs and bromeliads (Table 2). Forty-eight percent of the bird species used only one epiphyte type, but three (Common Bush Tanager, Southern House Wren, and Scarlet-thighed Dacnis) were generalists on all epiphyte types. This indicates that epiphytes in primary forest tree canopies provide potentially important food, water, and habitat resources for the avian community, but further work is needed to determine the degree of bird dependence on canopy-dwelling plants.

THE EFFECTS OF FOREST CONVERSION ON CANOPY BIOTA

In addition to basic ecological questions on canopy biota in primary forests, there is much to be learned about canopy communities of secondary forests and in trees growing in land that has been converted to pasture. Little work has been done in this area. However, the increasing extension and intensity of deforestation has been well documented elsewhere (e.g. Lovejoy and Oren 1981) and is attracting worldwide attention. What is urgently needed is scientific information on the effects of forest conversion on different parts of primary and modified ecosystems in order to understand and potentially mitigate negative effects.

One of these questions is to understand the patterns and processes that occur in the crowns of trees that grow in pastures following conversion of forests. Pasture trees can differ greatly in species composition, architecture, and in the biotic characteristics that potentially determine canopy micro-climate and plant and animal communities. Although this has never been directly quantified, epiphyte loads differ considerably in both composition and abundance between primary and secondary forests. As with other island communities (Wilcox and Murphy 1985), the isolation of "island" trees in a sea of pasture may result in changes that affect canopy-dwelling biota in a variety of ways; canopy organisms may be positively, negatively, or not at all affected by these differences.

Conversion of forest can result in several pasture tree types. In some cases, farmers leave standing a small number of "relict" trees, i.e. trees of the original forest, creating so-called "relict pastures." Epiphyte loads within the upper tree crown appear to remain relatively intact for a number of years, though trunk epiphytes found on their forest interior conspecifics are often absent (N. Nadkarni, pers. obs.). In other cases, all of the original trees are removed, and only "scrub trees" capable of invading and maintaining themselves in pastures occur ("scrub pastures"). These weedy trees are typically short in stature, fast-growing, with open crowns. Their epiphyte loads are usually of smaller biomass and lower species diversity than similarly sized trees in primary forest or in relict pasture trees (Nadkarni, pers. obs.).

TABLE 2. CANOPY BIRD USE OF EPIPHYTE RESOURCES
IN MONTEVERDE, COSTA RICA

BIRD Common Name	Scientific Name	EPIPHYTE RESOURCE*			
Fork-tailed Woodnymph	*Thalurania furcata*			E	
Stripe-tailed Hummingbird	*Eupherusa eximia*			E	
Coppery-headed Hummingbird	*Elvira cupreiceps*			E	
Purple-throated Mountaingem	*Lampornis calolaema*			E	M
Green-crowned Brilliant	*Heliodoxa jacula*			E	M
Prong-billed Barbet	*Semnornis frantzii*	A			M
Rufous-collared Sparrow	*Zonotrichia capensis*			E	
Spotted Barbtail	*Premnoplex brunnescens*				M
Sulphur-bellied Flycatcher	*Myiodynastes luteiventris*			E	
Golden-bellied Flycatcher	*M. hemichrysus*		B		
Boat-billed Flycatcher	*Megarhynchus pitangua*		B		M
Dusky-capped Flycatcher	*Myiarchus tuberculifer*		B		
Yellow-bellied Elaenia	*Elaenia flavogaster*			E	
Mountain Elaenia	*E. frantzii*				M
Paltry Tyrannulet	*Tyranniscus vilissimus*				M
Olive-striped Flycatcher	*Mionectes olivaceus*				M
Brown Jay	*Psilhorinus morio*		B		
Southern House Wren	*Troglodytes musculus*		B	E	M L
Ochraceous Wren	*T. ochraceus*		B		M
Clay-colored Robin	*Turdus grayi*		B		M
Mountain Robin	*T. plebejus*		B		M
Black-faced Solitaire	*Myadestes melanops*	A			M
Brown-capped Vireo	*Vireo leucophrys*				M
Scarlet-thighed Dacnis	*Dacnis venusta*		B	E	M
Bananaquit	*Coereba flaveola*			E	
Black and White Warbler	*Mniotilta varia*				M
Slate-throated Redstart	*Myioborus miniatus*				M
Three-stripe Warbler	*Basileuterus tristriatus*				M
Blue-crowned Chlorophonia	*Chlorophonia occipitalis*			E	M
Yellow-throated Euphonia	*Euphonia hirundinacea*			E	M
Blue-gray Tanager	*Thraupis episcopus*			E	M
Hepatic Tanager	*Piranga flava*		B		M
Common Bush Tanager	*Chlorospingus ophthalmicus*		B	E	M L
Yellow-throated Brush-Finch	*Atlapetes gutturalis*			E	M
Red-faced Spinetail	*Cranioleuca erythrops*		B		M

* A = Aroids; B = Bromeliads; E = Ericaceous shrubs; M = Mosses and liverworts; L = Lichens. Bird names follow Slud (1964) and Ridgely (1976).

One effect of the conversion of primary forest pastures on canopy communities could be reflected in differences in bird use of epiphytes between crowns of trees located in primary forest, relict pasture, and scrub pasture. The study on epiphyte/bird interactions described above also encompassed the question of these interactions in different habitat types (Nadkarni, in prep.). Thirteen study sites (150 x 150 m) were located in primary forest, relict pastures, and scrub pastures within the mosaic of habitat and land use history, determined by information from local farmers of Monteverde (Fig. 3). Bird use of epiphytes was monitored during the same study period and on the same schedule as described above. Observations of bird visitation and bird use of epiphytes were taken simultaneously by three observers at three different sites to allow for direct comparison of these activities.

The number of bird species using various epiphyte resources in each habitat during the study period is presented in Figure 4. The groups were lumped as follows: bromeliads; ericaceous shrubs; *Norantea* sp. (a fruiting epiphytic shrub, Marcgraviaceae); *Lycianthes* sp. (a fruiting epiphytic shrub, Solanaceae), and dead organic matter that accumulates beneath mats of mosses and liverworts. These data indicate that epiphytes on trees growing in pastures are visited by a high diversity of bird species. A surprisingly large
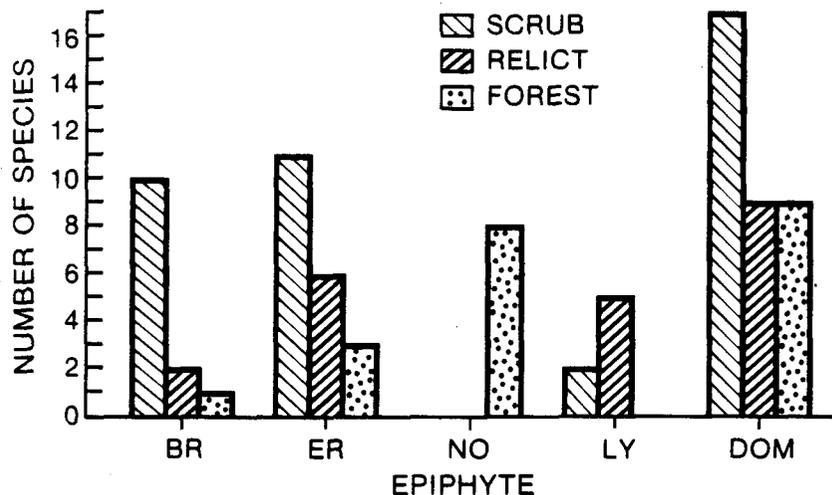

Fig. 4. Total number of bird species using epiphytes in forest, relict pasture, and scrub pasture study sites, June 29 – September 5, 1985. BR = bromeliads; ER = ericaceous shrubs; NO = *Norantea* sp.; LY = *Lycianthes* sp.; DOM = Dead Organic Matter.

number of bird species utilized epiphytes on scrub trees; in the case of bromeliads, ericads, and dead organic matter, scrub pasture trees provided a greater diversity of birds with resources. This preliminary information suggests that trees left standing in pastures and those invading following forest conversion provide canopy-held resources that are accessible to a large number of tropical bird species.

This study is a first step in comparing canopy communities in primary forest trees and in trees located in habitats that have been altered following timber or forage production. Future research should focus on: (a) seasonal dynamics of bird canopy use, (b) migrant vs. resident bird use of canopy resources, and (c) the relationship between epiphyte vs. host tree resource abundance and availability in a wide variety of land use and habitat types.

ACKNOWLEDGMENTS

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