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TROPICAL RAIN FOREST CYCLING AND TRANSPORT PROGRAM

PHASE 1 REPORT

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CENTER FOR ENERGY AND ENVIRONMENT RESEARCH

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Seasonal changes in population densities from tran=

sect counts at £1 Verde vests

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1.0. SYNOPSIS

This program was designed to fulfill the clear neva for a comprehensive understanding of cycling and transport processes in tropical rain forest ecosystems so that the ecological consequences of energy development can be adequately evaluated. The original program plan (June 1980) has been modified, but the basic approach has not been altered. A primary objective of Phase ' was to identify major reservoirs of nutrients and energy within the forest and determine the major pathways of movements atong them. Tasks were organized according to the simplest meaningful ecosystem subdivisions (Figure 1). Other relevant aspects of ecosystem organization (e.g. areal homogeneity, seasonality, etc.) were also investigated.

The study area is situated in tabonuco forest within an eleva tional range of 250-300 m. Average annual reinfall is approxinately

3.3 m, Four randomly selected plots (1 ha each) were surveyed and marked within the study area during July 1980. A transect 200 m Jong was placed diagonally through each plot, and a single 300 x 300 m grid (staked at 30 m intervals) was established during the 1961 wet season.

Calorimetric measurements have been made on plant and animal taxa identified as important components of the ecosystem. Chemical analyses were performed on the same groups in order to determine elemental composition (e.g. calcium, carbon, megnesium, sodium, etc.) and standing crop biomass for each major ecosystem compartment (Figure 1). Preliminary results indicate a general similarity in the Proportions of elements and in the caloric content between taxa sampled within the forest and relat ed taxa from other biotic regions.

Litterfall sampting provided information on primary productivity. Leaf fall was used to estimate net primary productivity and was used as the basis for comparing primary productivity during Phase 1 with four years of similar investigations (1970-73) in the same area. No ?annual differences were detected among the four sample plots in Phase 1, nor were any of the five years significantly different ($p > 0.05$). Highly significant differences were detected among months, however, indicating @ marked seasonality in litterfall. The highest leaf litter

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fall rates occurred at the end of the éry season end beginniny of the wet season (March-June).

A value of 1.389/8° day was obtained from the combined five Years af data. These results are sinilar to the estimate of 1.439/n2 Gay obtained by Wiegert (1970) in his 1965-66 research conducted in ?the ?same area as part of the irradiated rain forest program. This Consistency in rate of litterfall suggests that the tabonuco rain forest at E1 Verde is in a functionally mature state, The uniformity in rates among the four 1 ha sample plots indicates that at that scale of mea Surement the forest is homogenous with respect to prinary produce tion.

Identification of major reservoirs and principal pathways of movenent of energy and nutrients through the rain forest food web ?resulted from Phase I fielé studies and review of the literature, Aithough numerous investigators have conducted studies on animale within the forest, most authors concentrated on selected groups and sslected aspects of trophic interrelationships. Our field efforts, therefore, focused on supplementing published information and determi ring the interrelationships among the major aninal groups.

Many characteristics of food web organization reflect the insular nature of the £1 Verde forest. In contrast with comparable mainland ?ain forests, there are no large herbivores, or carnivores (e.9. monkeys» tapirs, jaguars, etc.). The largest common native species are the red-tailed hawk and red-necked pigeon. The Puerto Rican boa is larger (2-3 kg), but ts rare within the study arca, and Probably uncommon throughout the forest (Reagan and Zucca 1962), Introduced spectes which have become successfully established in the forest (Indian mongoose and roof rat) are also relatively small.

Although smaller in individual size, Tizards (Anolis spp.) and arboreal frogs (Eleutherodactylus spp.) are the dominant secondary and tertiary consumers in the forest because of their high population Gensities, Total lizard densities are greater than 20,000 indivi. duals/ha (see section 5.4.2), and arboreal frog densities within the area exceed 40,000/ha. Despite the relatively slow feeding rates characteristic of cold-blooded animals, the sheer numbers of Tisarde and frogs makes them more important in the food web at El Verde than

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ip comparable mainland sites where these groi ys are less common.

It analyses elucidated the

pathways of movement between compartments within the food web and

Feeding observations and gut con

reveled the presence of ver

ical stratification of foraging among

maior taxa, feeadack loops with large invertebrates, (e.g. tailess whip Scoprions, tarantulas, centipedes) eating small vertebrates, and the existence of parallel day and night food weds; the former dom- ated by lizards and the latter by arboreal frogs. The food web is depauperate compared to similar mainland forests and lacks the Parallel hosterestricted infrastructure that characterize mainland Neotropical forests (Gilbert 1980).

Preliminary studies of the vertical stratification of insects showed that much of the prinary consumption within the forest canopy is by Blanthoppers and leathoppers, groups which feed with sunctorial mouth parts. This indicates that previous st udies of herbivory rates based on leaf area indices may substantially underestimate actual rates of herbivory in the forest. The principal invertebrate groups in- volved in litter decomposition were also identified (mites, mmMipedes, sow bugs, fly larvae), but the importance of these groups relative to other decomposition processes (e.g. micrabial and fungal descomposi. tion, abiotic processes) has yet to be determined

Phase I studies of leaf decomposition were designed to determine Gifferences in decomposition rates due to season, microenvironment, and species composition of the litter. Decomposition bags placed in the field at different seasons and in different plots showed no diffe- ences in rates of decomposition. The species composition of Witter samples placed in the bags also had no effect on decomposition. dif- ferences in the rates of decomposition of leaves of different species are well documented, but these differences are not apparent in hetero Seneous leaf Witter. The processes which control the decompositon of leaves seem to function at a uniform rate independent of local abiotic and biotic variability. The uniformity is another indication of the homogeneity of forest processes, at least at the scale of our study.

Information obtained during the first phase has provided a basis for determing the focus of Phase II research. A prinary objective of Phase I studies in the El Verde study site will be to quantify the

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rates of movement of key nutrients and energy anung major ecosystem in major food chains will be measured to determine transfer rates at higher trophic levels. All studies will consiver seascnality, day and might food webs, and vertical stratification in thelr sampling design, Export studies are planned which examine nutrient loss due to runoff, Research within the stucy site will slso concentrate on the soil fauna because of their probable important contribution to overall animal biomass and litter decomposition. Eyperimental manipulation within the El Verde study site will be limited in scope, whiie those conduc- ted at nearby locations in the Luquillo Experimental Forest will either be conducted in areas with a known nistory cf disturbance (e.g. plan= tations, Tandslide areas) or perforsee in conjunction with planned U.S. Forest Service manipulations.

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2.0 INTRODUCTION

The accelerated development of traditional and unconventional energy resources 1s producing adverse effects on ecosystems. throughout ?the world. The nature and extent of these impacts is related not only to the type of energy development (e.g. fossil fuel, nuclear, biomass, Solar, etc.), but also to the prevailing environmental conditions (e.g. annual temperature fluctuations, rainfall, elevation), There fore, information on temperate ecosystens has limited application in tropical regions. Potential impacts on temperate zone ecosystems are relatively well known but tropical ecosystems, particularly rain forests, are understood in far less detail. Their role in the world carbon cycle and their regional significance have been documented for some systems, but the structural complexity and functional interrela- Honship of species (e.g. food weds, biogeochemical cycles) are poorly known and are likely to differ in major aspects fron their temperate counterparts.

We are therefore investigating cycling and transport processes within a relatively simple tropical rain forest. Initial studies were Conducted in the rain forest near the El Verde Field Station. In- depth studies involving experimental manipulations will be undertaken 8 @ comprehensive overview is obtained through integration of the results of Phase I field studies with published information,

The original program plan (June 1980) wes formated prior to funding changes for fiscal year 1981. Basic objectives and overs!) design have not been altered, but some task elements have been elimi- nated, and sone sampling reduced to a single season where it was felt that sufficient supporting information could be obtained from existing literature. Other subtasks were added on the basis of observations and analyses of preliminary data obtained during the first seasonal sampling period.

This document presents the modified program design and results of Phase I studies from June 1980 through October 1981. Detailed methods are included so that this report can also serve as 2 reference guide for future studies. Substantial and in some cases unexpected results have been obtained and important aspects of ecosystem structure have been identified which have confirmed the value of this phased

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approach. Section 6.0 integrates materia

summarizes important findings.

from separate tasks

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3.0 PROGRAM OVERVIEW

It 4s necessary to understand the major features of ecosysten Structure and function and their response to exogenous env tronnental variables in order to predict the effects of expanding ensrgy tech- nology on tropical ecosystems. Current knowledge of the source-sink role of tropical rain forest biota and the factors which regulate this role is insufficient to foretell the ingact of eneray development on {the mobilization and release of critical elements or the ecosysten's capacity to assimilate elemental inputs.

Cycling and transport processes are being investigated in the tropical (tabonuco) rain forest at £1 Verde by conducting @ two-phased Program so that a firm data base can be established before experi- mental manipulations are undertaken. The long history of environ= mental research in the Luquillo Mountains and the existence of the £1 Nerde Field Station in this forest provide a unique opportunity for this type of research,

Phase I studies focused on obtaining additional information on ?the forest ecosystem and integrating these data with published mate- rial to construct @ model of elemental and energy storage and nove- ment. Faunal components are enphasized in this phase because of the Tack of comprehensive food web data for tropical forests, and because of the relative wealth of vegetation data that exists for the study area. The objectives of Phase I studies are:

1. to sdontify the major reservoirs ana pathways of elements and energy in the forest ecosysten,

2 to sdentify additional aspects of ecosysten organization which are relevant to the assessment of impacts,

3. to develop hypotheses concerning the potential effects of disturbances related to energy development. (e.g. Inputs oF sulfur, carbon, etc.; harvesting of biomass) on cycling and ?transport processes,

The following tasks addressed the above-stated objectives:

1. delineation of trophic structure,

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identification of doninant species iv each food web or foud

web segment,

3+ quantitication of ?vertical, horizontal and temporal pattern

Of the Sistribution of identifiable functionel unite. (Species

trophic groups, food wed segments, cte-) oF the arse eres

systen,

?+ quantification of the distribution of key elenents among

major functional units of the system taking into account, shee

tal and temporal cons iderat ions,

5. development of a refined forest ecosystem model which will

Permit simulation of cycling and transport processes, ara

& generation of hypotheses concerning the potential impacts of

eteray development which are both relevent to tropical forece

ecosystems and testable in Phase {1

The elemental and caloric inventory provide information on key

mtrients and energy value of each major class cf itens (fruit,

leaves, feces, individual species, etc.). Faural studies identity

major reservoirs end pathways and provide preliminary data on the rate of movement for selected segments of the food web. In addition to Studies characterizing study plots, the vegetation work provides a basis to compare the magnitude of elemental flow through conpertnents with direct movenent of prinary production to the deconposer conpart- ment via leaf and fruit ali and litter decomposition.

?An Important result of the study is 2 comprehensive food web in which major aspects of the distribution and transfer of energy and Iutrients are known, Testing of hypotheses generated in Phase 1 is Mkely to produce useful insights on the relationship of food web comlexity to species diversity, ecosystem stobility, potential regu: ator species, and the influence of rainfall, soil type, nutrient Pools, dominant consumers, and food wed structure on tne overall structure of ecosystems. This information will provide an inportant Conceptual basis for inferring tne key points at which perturbations ue to energy development are nost 1ikely to disrupt natural systens.

Phase II will primarily involve the testing of hypotheses, al- though some Phase I studies (e.g. feeding and population turnover

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ates) will be continued. Hypothesis tesiing will teks several fom:

1) direct manipulation of the forest (e.g. narvestirg activities in Conjunction with the U.S. Forest Service), i) conparstive studies of existing plantations and managed forest ercas (see belen), and 3) natural experiments conducted within the forest (e.g. comarison of trophic structure in areas with and without third-order carnivores).

We pose several general hypotheses which involve comparisons between native tropical hardwood (tabonuco) forest and plantations (ecluding those which are managed for energy production). Specitie ally, one can hypothesize that in the native nardwood forest:

1. productivity is higher,

2, consumer biomass is greater,

3. insect pests are less abundant,

4, food wed structure is more complex,

5. nutrient cycling is more rapid, and

6. the system is more resilient to exogenous disturbances

?than in plantations on the sane soil types and under the sane reinfali regimes. The hypotheses selected for testing in Phase II will be based on information acquired in Phase 1, on a realistic evaluation of Potential energy related inpacts, and on available funding.

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4.0 PRASE 1 METHODS

A compartnentalized ecosystem model (Figure 1) was used as a framework for coordinating the various task studies. Mork focusce on those ecosysten compartments above privary producer in the food chain for the following reasons: (1) the importance of higher trophic levels in elemental transport has already been suggested for some forvsts (Weir 1969), but the role of fauna in moving energy and nutriente anong compartnents of terrestrial ecosystens has been largely ne- glected (Sturges gt a1. 1974, Burton and Likens 1975), (2) primary Production and elemental cycles have already been studiea in this moist tropical forest (Odum and Pigeon 1970), and (3) the role of con. Sumer in regulating the ecosystem (Glasser 1979) is potentially sige nificant. For these reasons only a partial weasurenent of elemental fransport in and out of the forest ecosystens mas begun in Phase 1, and values needed for the current study will be taken from the Titera. ?ture and/or from the work of visiting and collaborating scientists.

4.1 Sampling Design

?The study area (Figure 2) was selected because of its long history Of continuous research, beginning with the rain forest garma radiation studies (Odum and Pigeon 1970), and its proximity to the established facilities at the EI Verde Station. Other factors which were evaluated in the study area delineation process were the relationship to U.S. Forest Service research areas and the anount of existing disturbance from previous studies.

The overall design was stratified random. Four sampling loca~ tons (points) were randonly selected within the study area co that subsequent statistically valid analyses could be performed (Green 1878). Sampling points were selected using a grid technique (Phii1ipe 1989). The following criteria were used in the selection of random plots:

* potential | confounding factors (e.g. roads, perennial streans,

previous destructive sampling) were rot present within 40 ¢ of 2 sampling point,

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RESPIRATION

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Figure 1

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Figure 2. Cycling and Transport Program study area

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Sample points were no closer than 200 m to eac: otter so that sampling overlap coula be avoided, ond

Feasonable access was possible.

The size of the area sampled at each randomly chosen point variee according to discipline (e.g. invertebrate surveys were confined to plot 3). AL ha plot with boundaries marked at 10m intervals was

established at each sampling point. Plot and plotless methods, tran-
Sects, and detailed inventory procedures were used in Phase I inves
Tigations, Studies focused on sampling points, but included other
Portions of the defined study area.

Most sampling was conducted during a minimum of two seasons. Most surveys occurred during the wet and dry seasons, but additional sampling was required for sone tasks (e.g. breeding bird surveys). The timing of field surveys was coordinated to avoid sanpling inter. ference yet maintain a close temporal correspondence anong field studies,

4.2 Task Methods

Each task and subtask is described as a separate entity within ?the overall Phase I sanpling design because of the variation in per- tinent information already available for different disciplines. The tasks were of varying durations. Most field studies were completed by October 1981. Some studies are being continued with modifications into Phase II (e.g. growth and population turnover of key species). Although the data acquired should be of immediate value, they arc Intended to provide basis for long-term in-depth studies continued under Phase II of the cycling and transport program,

4.2.1 Physical Phenomena

Basic information on physical aspects of the environment 4

necessary in order to interpret biological observations and to provide

baseline data for Phase 11 studies. Specific objectives were:

a13-

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f0,collect pertinent weather data to be cused in evaluating

information collected fron other tasks

to document seasonal and other temporal changes within the

study area

Materials

rain gages (at 1 Verde Station and toner)

* thermoneters and hygrothermographs (at £1 Verde Station and

four levels at the toner)

4.2.2 Elemental Inventory and Energy Studies

Objective: To construct an inventory of biologically significant ele-

ments present in tissues of the most abundant plant and

animal species and to determine the energy content oF

these tissues

AIT specimens collected were chopped with scissors and dried in an oven at 70°C until constant in weight. The residue was made homogenous by grinding in a Wiley mi11 using a #40 mesh screen. Frogs and Tizards (within species) were divided according to sex and pooled.

Bats and birds were sufficiently large and were analyzed individual ly,

ANT chemical analyses were run in duplicate to ensure reproducibility.

The Tife ions Ca?, wg*, Na", and x* were measured using @ Model 404 Perkin Elmer atomic absorption spectrophotometer. Samples were placed in porcelain crucibles and ashed overnight in a Thermolyne muffle furnace incrementing temperature slowly up to 600°C. After cooling in a desiccator and weighing to determine the amount of none volatile matter, the crucibles were placed in a hot water bath and the residues allowed to dissolve in 50% HCL for one hr. Each sample was then filtered through Whatman #42 paper under suction and taken up to

@ known volume with double glass-distilled water.

All the water used in this study was double distilled in a Tandem

3 gal Corning water sti11 using water pre-filtered through activated

charcoal.

Phosphorus was measured with an adaptation of the nethod of

Chapman and Pratt (1978). Orthophosphates present in the acid soluble

fraction of the ash residue react to form a-yellow color when exposed

a4.

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to the salts amonium vanadate and anner

Gitions. Color intensity becomes stable within one half hour and is

ium Felybdate under acid con=

Measured at 470 nm. Light absorbance determinetions were performed in

@ Zeiss PH-2 U-VIS single beam spectrophotometer equipped with ¢ self

cleaning cel,

Nitrogen was determined by the micro-Kjeldahl procedure using a

modification of the titrimetric protocol presented by the EPA Methods

Handbook (1979). AN biochemical forms of this element are converted

to anronium sulfate by digesting a semple suspended in conc. W804

in the presence of a mixture of sulfates. The amonium icn is chet

transformed into anmonia gas by the addition of strong alkali and di.

filled into boric acid. The resulting besicity is titrated with standardized 504.

Calorimetry was performed according to Parr (1978) using a nodel 1341 plain oxygen calorimeter fitted with 2 Model 1108 oxygen bomb.

Sulfur was measured using an aliquot of the boub washings following the turbidimetric procedure of the EPA Methods Handbook (1979). In this method sulfates produced as a result of corbustion in an oxygen atmosphere are removed from solution in the form of their barium salt, the resulting turbidity being proportional to their concentration.

4.2.3 Vegetation Studies

Analysis of the vegetation was designed to determine the variability within the tabonuco forest type by measuring important. stor~ ages and flows. These baseline data are to be used in the planning of Phase II experimental research.

4.2.3.1 Plot Characterization

Certain types of information were needed in order to provide a basis for interpreting floral and faunal data and for designing the future investigations. Techniques were as follows

Subtask 1. Minimal Area

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eases Te iemar a SEE gle, ge fn wheh specter con

?A wininal representative area is defined 95 that area in which a 10 percent increase in size will yield a 10 percent or less increase 4m the muster of new species. Two areas of the tabonuco forest in El Verde were selected at randon and the nested plot technique for deter- ining mininal area was used (Mueller-Oonbcis and ETlenberg 1974), The initial plot size mas 5x5 m. Fach additional plot was double the size of the previous plot (Figure 3)

ANI trees 5 cn dth were identified and included in the study. The mininal area as defined above wes determined,

Subtask 2. Structural Analysis

Objective: Te,ggtermine standing crop for each specles and for a1)

Plot 3 (Figure 2) was selected as the best representative of the four forest plots and thus the most thoroughly studied. PYC tubing was used to establish 8 10x10 m grid in a 1 ha area (plot 3). All vegetation 2 10 om dbh was identified, mapped, cbh measured, and tagged. A sub-sample of this plot was selected to be analyzed as above within a5 m radius of each twenty randonly located litter baskets. Comparisons were then made between the total plot analysis (10,000 x2) and ?the subsample (1570 n°). Plots 1, 2, and 4 were structurally analyzed as in plot 3 using the sub-sample technique. Basal areas (n2/ha), densities (ind/ha) and species composition were determined and com. pared.

4.2.3.2. Phonology

Objectives: To look for temporal differences in the flowering and fruiting patterns of species among plots

To determine importance of the contribution of each Species to flower and fruit fall

?Arong plot comparisons of flowering and fruiting patterns were measured using materials collected in the litterfall baskets (see section 4.2.3.3 for litter sampling infornation).

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Collections were made bimonthly, The mid-onth collection was

Separated into general categories of flowers and fruits. Collections

at the end of each month were separated by species into the sane two categories. Each component at each collection was counted, dried at 70°C for 72 hours, and weighed. Wet season-dry season satiples were stored by species and by plot for future caloric and element content

4.2.3.3 Litter Fall

Ghjectives: To determine seasonal pattern of litter fall os 2 whole and for individual species,

To detect differences between sites for totel and species Vitter fall

To compare values of litter fall from the current study with data from other years and sampling locations at ET Verde

Twenty 1m? galvanized herdware cloth baskets Vined with 1am mesh fiberglass screen were placed in each of the four plots. Loca-tions of the four litter fall transects were randomly selected at each site with 10 m intervals between potential transect lines. Five baskets were randomly placed along each transect (Figure 4). fach basket was placed at least 10 cm from the forest floor (30 cm where Possible) and leveled.

Mid-month collection of litter fall was separated by basket into eaves, flowers, fruits, wood and miscellaneous ites. Each component at each collection was counted, dried at 70°C for 72 hrs and weighed, Wet season-dry season samples are awaiting analysis for caloric and mineral content.

4.2.3.4 Loose Litter (Litter Standing Crop)

Objectives: To compare seasonal differences in the ground litter storage

To determine variability anong plots in the ground Vitter component

Loose Vitter samples (0.25 a?) were collected at random in each

?18.

---Page Break---

Figure 4. Vegetation sampling locations within study plots.

?19.

---Page Break---

Plot each season. Forty samples (tw at cach Hitter becket) were collected in each plot (160 total samples} during the ary season. Twenty samples (one at each litter basket) were collected in each plot (80 total samples) during the wet season. The wet season decrease in sample number was due to a smaller than expected sample variebility in ?the dry season as well as to personnel and processing constraints.

Collected material was separated into wood and miscellaneous com Ponents, dried at 70°C for 72 hrs, and weighed. Due to the rapid de Composition of ground litter, the miscellaneous component contained all plant parts except wood and could not be successfully separated further, Wet and dry season samples from each plot were reserves for future caloric and mineral analysis.

4.2.3.5 Decomposition

Objectives: To measure seasonal differences in decomposition rates "of freshly fallen leaves

To compare between-plot variability in leat decouposi-tion rates

To determine site and species heterogeneity effects on rates of decomposition

On a single day during the dry season (25 March, 1981), al) leaves that had fallen in the preceding 24 hrs (identified by the Hight color of the petiole abscission areas Zucca, pers. obs.) were collected from the 1 ha area in plot 3. The leaves were separated by spectes and allowed to air dry overnight to renove surface moisture. After drying, the freshly fallen leaves of a species were weighed and the percent of total weight of leaves collected was determined for each.

The 13 most common species were placed in decomposition bags in Proportion to their occurrence in the sample. The remaining species (25) were put in a miscellaneous category and randomly selected tor placing in a decomposition bag.

Bag size was 20x25 cm and bags were constructed of 1 mi mesh Fiberglass screen, Sides were sewn closed with large enoush gaps to

---Page Break---

allow entrance by macrodeconposers but care was taken in handling to assure no loss of leaf material.

One hundred seventy bags were filled with 10 9 of representative leaf material. Five bags were placed on the ground near each of 26 randomly located Vitter baskets (80 bags total). In addition, @0 bags were placed in @ topographically homogeneous area (plot x). Ten bags were reserved for zero tine wet weight-dry weight measurenents.

?The species leaf composite epproach to decomposition was designed ?0 measure total plot decomposition at a specific tine, Placenent of bags at the litter baskets and in a homogeneous area was to establish 2 control for differences in topography (and presunably microenviron=

ment).

Ten randomly selected bags were collected from both plot 3 and havogeneous plot X at intervals of 7, 14, 28, 60, 120, 240, 480 cays. Bags were dried at 70°C, weighed and percent of original dry weight remaining was determined. The decomposed leaves were reserved for future caloric and mineral analysis.

The same procedure was conducted in May, 1980, with leaves from Plot 3 placed as above in plots 3 and X (identified in Table 1 as 32 and 3ax). Leaves from plot 4 were placed in plots 4 and X (identified in Table 1 as 4 and 4x). The only difference from the initial procedure was a change in the number of bags. Due to the small weight variability of the initial study, 40 bags were placed in each plot and five bags collected at each interval. The May study was designed to detect variance in decomposition rates resulting from differences in Species composition, season or microenvironnent.

Finally, during the wet season in October, 1981, a decomposition study in plot 3 (identified in Table 1 as 3b and 3bx) was conducted as before to detect seasonal decomposition differences.

4.2.4 Faunal Studies

?The roles of animals in ecosystem structure and function can be effectively evaluated by conbining eneray flow and nutrient cycling

Studies. Recent work in temperate forest ecosystems has provided

-a-

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Table 1. Decomposition values per cent original dry weight; standard

error in parenthesis).

SANPLES*

2 ia oa a

7122) 72) 1001) 14/3) ta(2)_ N14) D402) 103)

14 2e(2) 15(1) 1702) 15(2) 1912) 20(1) 194) 12/2)

28 26(1) 18(2) 18(3) 182) 1903) 211)

60 37(1) 29(2) 322) 2a(1) 36(5) 3401)

90 393) 36(3)

120 43(3) 42(1) 443) 422) 45(3) 4603) 51(5) a7(3)

240 73(3)70(3) ma) 770)

300 68(2) 66(2) 65(5) 67(4) 70(2) 72(6)

a

?Key to the sample designations

Leaves collected and decomposition bags placed in field

March 1981

3. Je2ves from plot 3; placed randomly in plot 3

x Teaves from plot 3; placed in topographically homogeneous plot x

May 1981

3ey_jeaves from plot 3; placed randomly in plot 3

3axcleaves from plot 3; placed in plot »

4 = leaves from plot 4; placed randomly in plot 4

?x= leaves from plot 43 placed in plot x

October 1981

30> leaves from plot 3; placed randomly in plot 3

Sbxeleaves from plot 4; placed in plot x

---Page Break---

valuable information on the roles uf aniuel oojvlationt © utr vent ?sinks? and as agents of nutrient transport (heir 146%, Stuoues et al. 1974, Burton and Likens 1975),

Because of their high turnover rates at relatively hisn anbient temperatures, underestimating the inportarce of organisms with short Tife spans and low standing crops in cycling and trenspur: processes is even more likely in tropical systems than in touperate systens. The role of consumers as ecosystem regulators is potentis!iy import-ant. The Phase I faunal studies were designed to invest icate these Possibilities in the tropical forest ecosystem et £1 verde.

The major faunal sampling effort was eined at obtaining informa tion on the food habits and general abundance of animals. From these data emphasizing top carnivores and herbivores 3 comprehensive food web has been constructed. Initial food web analyses have defined major pathways rather than focus on parallel food subwebs (Paine 1966, Gilbert 1980) which may or may not be important structural units in this insular tropical rain forest.

Studies focused on those intermediate consumers serving es princi-pal diet items for higher order carnivores. Attempts will be nade to estimate population turnover rates for key (i.e. abundant, frequently eaten or large) consumers in Phase II. Because of the large number of different intermediate consumers, their roles and rates will have to be estimated in a pooled fashion from differences between rates of Primary productivity litter fall and decomposition and consumption rates of top carnivores.

The faunal studies ranged from nighly diversified qualitative collection (e.g. species inventory) to more selective sampling aimed at relative abundance to highly spectalizea quantitative sampling aimed at key species (e.g. population estinates of birds and !izards). Relative abundance and absolute abundance data were conbined to refine Portions of the food web. Turnover estinates*plus metabolic data, as available, will be used to quantify Flows. Because of expected sea-sonality some types of sampling were continued throughout the entire Period of study. However, with each successive sampling period, more

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effort was placed on relative ana absolute «bundance estimation for key species and species groups rather than upon the icentification of new species,

4.2.4.1 Invertebrates

The invertebrates (austly insects and mites) are an inportant art of the LuquiTlo Forest ecosysten. Chief among problens has been the proper identification of the multitudes of species inhabiting the forest. Most are small, fragile, inconspfcuous forms that inhabit virtually 11 areas of the ecosystem. The nunber of identified spe-cles found in the vicinity of El Verde Field Station is at least 1200 (Orewry 1970) but the true nunber 1s probably greater than 3000. Many authors (e.g. Janzen and Schoener 1966; Allen et al. 1973; Janzen 19732, 19735 Janzen et al. 1976; Denlinger 1980) in reporting their ecological studies have identified forms to ?norpho-species", or recognizably different kinds. Since one of the goals of this study has been to determine the important invertebrate components of the food web, we have tried to identity most taxa to the species level. Our success has been directly proportional to the ancunt of taxonomic Viterature available for Puerto Rican arthropods. Sone groups, such as the Auchenorrhynchus Homoptera are fairly well known because. they are common and conspicuous. Other groups, e.g. the mites and som Diptera, are poorly known and due to tine (1 yr) and budget limita. Hons, we have been forced to deal with these invertebrates at higher categorical levels such as families and orders.

A reasonably complete conspectus of the inportant groups of ine vertebrates inhabiting the LuquiTlo Rain Forest is currently not available and Tess can be said about their seasonel abundance and Population turnover rates. However, ongoing studles on the vertical distribution of flying insects in the rainforest, nacroinvertebrates assoctated with leaf litter decomposition, and gut analysis of four species of Anolis lizards have yielded important information on the role played by many macroarthropods in the food web. These findings 4a1so corroborate various samplings of the invertebrate fauna we have conducted at various times throughout the year.

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In acaition to the curated research collection at une El Verde Field Station, the following taxcuomic references were helpful in identifying invertebrates: invertebrates in general - Brues et al. 1954, Hickman 1973; spiders - Kaston 1978, Petrunkevitch 1929, 19302, 19300, Velez 1971; sowbugs - Velez 1966a3 milVipedes-velez 19660. centipedes - Sentiago and Velez 1974; insects in general - orror et al, 1976, Borror and White 1970, Waterhouse et 21. 1970; springtails ~ Mari Mutt 1976, Wray 1953; Hemiptera - Barber 1939, Capriles 1969; Homoptera - Caldwell and Martorell 19502, 1950D, Ramos 1957; Coleop-tera = Arnett 1968, Boving and Craighead 1930; ants - Lavigne 1970, Smith 19363 insect larvae - Peterson 1948, 1951. AN1 specimens were ?examined under a Wild M-5 binocular stereoscopic microscope.

Phase I work was divided into the following subtasks:

Subtask 1: Vertical Transect Sampling

Objectives: Determine dominant (by relative abundance) groups of flying insects during a two week sampling period in the rainy season

Determine significant differences, if any, between mean mean numbers of insects anong vertical strate end bets ween day and night,

Nineteen 5 oz plastic cups, each a meter apart, were covered with ?Tanglefoot? sticky trap adhesive and suspended on @ string parallel to the El Verde Tower. Samples were changed at 0900 and 1800 hrs over @ two week period (10 days, 8 nights) excluding weekends from 9-22 June 1961. After identification of invertebrates was completed, results were tabulated and mean numbers were compared using one-ney analysis of variance (ANOVA) and sum of squares simultaneous testing Procedures (SS-STP) (Sokal and Rohlf 1970).

Subtask 2: Macroinvertebrates Associated with Leaf Litter Decomposi-

Objectives: Piternne suspected eacrodecomposers of leaf 1itter for

Determine possible changes in species make-up through

Hime, .?.. if species succession occurred in leaf it~

ter

Ninety seven 10 g fresh weight leat litter bags were constructed

and placed in plots 3 and 4 representing vegetation types typical of

---Page Break---

those areas. Bag nunbers 3a and 2x containcd ieaf litter represen

tative of plot 3 and 4 and 4x representative of plot 4. bays 3a ana 4

were returned to their respective plots, but bags Jax ana 4x were

Placed in homogeneous vegetation areas descrived in section 4.2.3.5.

Five bags from each sample (total 20) were collected after 7, 14, 28,

0, and 120 days and the contents were placed in Berlese Funnels. AIT

arthropods extracted were preserved in 70% £TUH and identified to

lowest taxonomic category. Since leaf decomposition occurs most

rapidly during the first month (section 5.2.3.5) intensive sampling

WS restricted to that tine frame. Each sample consisted of five bags

except for 60-

tively.

iy 4 and 4 which contained four and three bays respec

Subtask 3: Anolis Food Habits

Objectives: Determine if different species (Anolis cuvieri, A,

undlachi, A. evermanni, A. stratulus) show preferences

Forcattteren stvertebrate probes

Determine diet overlap, if any, among Anolis species

Determine if Anolis are obligate carnivores as has been

stated in the Tfterature

Determine if quantitative differences of prey length and

volume occur between wet and dry seasons Of Satie species

of Anolis

A series of specimens for each species (Table 2) was collected

during wet and dry seasons and stomachs were removed and preserved in

70% ETOH. Because A. cuviert is a relatively rare species, their

Stomachs were pumped (see Sexton and Bauman 1972 for details) and the

lizards were weighed, measured and released, No A. cuvieri were found during the dry season (Table 2). Male A. stratulus were difficult to obtain during the wet season and this explains their low sample size. Anolis evermanni also occurs along the margins of rivers, therefore 20 A, evermanni (10 male, 10 female) were collected from the Rio Sonadora OF surrounding area so that they could be compared with forest specimens. The entire contents of each stomach was examined and identities to the lowest taxonomic category (to species, it possible) and length

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Table 2. Sample sizes of Anolis 1izeres used in evaluating foot data

ary season

cuvieri 7 :

2 - rs

A. gundtacht 0? 0 10

8 10 10

?Ay evermanni 6 10 13

@ 8 20

A. stratulus @ 8 4

2 10 9

?data conbines

?includes 10 specimens fron edge of Rio Sonadora, a ron-forest

habitat.

---Page Break---

(rm) and volume (length times wisth tines heights mm?) for each

Specimen was calculated or estimated. ata for A. cuvieri were pro-

Dably underestimates because al] of the stomach contents may not have

been removed by punping,

4

4.2 Amphibians and Reptiles

These poikilothermic vertebrates are conspicuous components of ?the animal community in Puerto Rican rain forests. Considerable data are available for some groups, but additional information 1s needed In order to evaluate their role in cycling and transport pro-Cesses. The basic data required are: i) elenental and energy con-tent, 2) status in food web (food habits and predators), 3) biomass, and 4) population and feeding turnover rates. Phase I studies focused on acquiring information for the first three areas and icentifying ?Species and groups for continued investigation in Phase II, Phase 1 work was divided into the following subtasks:

Subtask 1: Species Inventory

Objective: To determine the presence and general abundance of al? amphibian and reptile species inhabiting the study area

Intensive searches were conducted at randomly selected locations and in particular mfcrohabitats (e.g. boulder areas) periodically throughout Phase I field studies. Random observations were also noted. Surface debris and litter were overturned in order to locate Secretive and fossorial species. The species, location, date, and activity was recorded for each individual observed.

Subtask 2: Presence and Relative Abundance of Amphibians

Gdiective: To determine the species composition and frelative ebun-

dance of amphibian (anuran) species within the study area

in order to identity important species and to in correlate

information collected at study plots with the more cee

tatled information being collected by Or. M. Stewart ond

hher colleagues in adjacent areas of the forest

Surveys were conducted along transects (50x2 m) through the tour

Fandonly selected plots within the study area (Figure 2). Each tran-

Sect was surveyed on three separate evenings during the wet season.

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The sex (where possible) and size class was recorded for eatt species,

Species heard calling outside the transects but within plot: were also

noted. Relative abundances were then calculated,

Subtask 3: Anolis Food Habits

Objective: To determine the types of food taken, frequency of occurs rence, and percentages of food for each species

Detailed methods for food habit analyses are provided in section 4.2.4.1, Subtask 3.

Subtask 4: Anolis Population Densities

Gejectives: To obtain aininum and relative population density esti- imates dfor common species of Anolis at? four? randomly Selected locations within the study aree

Roafgtinate the absolute density of the canopy species, Anolis stratulus at the tower within the study oreo

Minimum and relative population densities - A permanent transect 180 m long was estabished in each plot, extending from the center dia- gonally through the plot along existing bird transects (Figure 2). Each transect was surveyed by slowly walking the marked line on three occasions: morning (0700-1000), midday (1000-1430), and afternoon (2430-1800) during wet and dry seasons. The species, sex (or size class), and distance to the centerline were recorded for each lizard cbserved. Relative abundances were computed and minisun population Gensities were calculated according to Frye's strip census technique (Overton 1971):

1 a Br average perpendicular distance

Hh Between Observed? aninat aed

transect center! ine

correction factor for units of

measurenent

Li transect length

A: area of study site

Ts estimated population density

tr number of animals observed on

transect

-29.

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Population density estimates for Anolis stratulus - data were

obtained from multiple mark and resight data collected during the éry season (February - March) of 1981. Vertical transect surveys were Conducted from the tower during midday (1000 - 1430) for four days within a two week period. Transects were not conducted during periods of rain. Each individual was warked with paint (2 different color for each dey) and hot branded with an individual mark, Lizards were cap- ?tured and marked on each of the first three days, but only cbserved on day four.

Mark and resight data were analyzed using the Jolly-Seber, Nenly-Parr, and Lincoln-Peterson techniques (Kanly and Parr 1968, Jolly 1965, Overton 1971). Because transects were conducted verti. cally, results are expressed as a point sample with the area surveyed calculated from the maximum observation radius fron the toner, and Population estimates projected to ground level.

Subtask 5: Vertical Distribution of Anoline Lizards

Objective: To determine the vertical distribution of common lizard Species in the rain forest

Casual observations from the 22 m tower in the study area (Figure 2) suggested that the three common Anolis lizards differ in their ver- tical distributions. To test this hypothesis, vertical transect sur- veys were conducted at the tower during Phase I studies. The fol- lowing procedures were used.

Fifteen transects were conducted at each of three times of day: ?morning (0700-1000), midday (1000-1430), and afternoon (1830-1800) for ® total of 45 transects during wet season 1960 (Septenber ~ Novenber) and again during dry season 1981 (January - March). Each transect was

Surveyed by slowly walking up the tower and recording the species, sex (where possible), height above ground level (marked on the tover), distance from transect centerline and date/time of day for each lizard observed, Mean sighting distances were calculated for each species and used to compute the relative number of lizards at each meter ine terval for the 22 m transect for each species. Data were analyzed by Species, season, and time of day in order to determine what, if ary,

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Gifferences existed wnich might be relevant te the truphic structure and organization within the forest.

Subtask 6, Anolis Population Growth and Turnover Rates

Objective: To obtain reliable estimates of population turnover and Growth rates for Anolis stratulus

Pertinent data for this important species are presently unavail~ able. Individual Tizerds captured during the mark and resight studies were weighed and measured at tine of capture. Periodic visits are being conducted at the tower to record the proportion of marked to unmarked Vizards present, Individual marked lizards are periodically recaptured and are reweighed and remeasured. These surveys will con-Finue into Phase Il. Information on population turnover rates, longe-Vitys and growth rate will be calculated fron these data.

4.2.4.3. Biras

Five subtasks were carried out in the avifaunal studies by methods described in the original work plan and modified in the Phase 1 Progress Report (January 1981). A complete description of the methods for each subtask is given below.

Subtask 1: Population Density

Objective: To obtain reliable population estimates for each species in all sites studied ?and to detect changes in population density throughout the year

Single avian census techniques are often insufficient to estimate Population densities of the wide variety of species found in tropical habitats (Waide et al. 1980, Waide and Hernéndez 1962). To accommo-date the diversity of behavioral types and vertical partitioning found in tropical birds, multiple census techniques are often needed (Terborgh and Weske 1969). In the mineral cycling and transport Study, three different census techniques were used to obtain absolute and seasonal estimates of population density.

Transect counts - A diagonal 300 m transect line was established ineach of the 1 ha study plots and marked et 10 m intervals with

a3

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Stakes and plastic flagging (Figure 2). Each month, transect counts were conducted for two days in each site. Counts began at 0730 and consisted of an outgoing traverse of the transect line, a five-minute wait, and a returning traverse. A single observer conducted the July-September counts in 1981 and two observers divided the rest of counts. After the termination of one year of monthly cunts, subse-Quen sampling was conducted at two month intervals (August and Ucto~ ber 1961). Afternoon counts beginning at 1800 were run in July, October and January.

Data recorded during each count included date, location, tine, observer, and weather conditions. Each bird detected was identified to species and the perpendicular distance to the transect line was estimated within the following distance classes: 3, 6, 9, 12, 15, 30, 60, 120 m. Detections were not recorded if they were nore than 120 © from the transect line or more than 30 m ahead or behind the observer.

Further data included position along the transect line, side of the transect Tine, and height of the bird if it was seen, Detecticns by Sight, song and call were recorded separately. A sample data sheet is shown in Appendix 1.

Population densities were calculated separately for each detec+ tion class following Enlen (1971). Results are reported separately and as the sum of detections by sight, song and call. Observations were summed over the entire sampling period to determine effective Getection distance which was then used to calculate densities in each month for each plot. Currently, further analysis is underway using a Computer program (TRANSECT) developed by Burnham et al. (1960).

Mist nets - Sampling with nylon mist nets is often effective in determining abundance for shy or unobtrusive species that are under- estimated by observational techniques. A net line was established in each plot bisecting the transect line. Mixtures of 30 and 36 am Standard 12 m black mist nets were strung end-to-end on poles mede of conduit tubing. Nets sampled the space from 15 cm to 2 m above the Found. During Septenber-October 1980, nets were opened fron dawn to dusk on consecutive days, weather permitting. All birds captured were

---Page Break---

marked with colored plastic eg bands or ly cripping + cerbinedion of

Uatl feathers. Data collected are shown in tm sanile ds*e sheet in Appendix 1.

Sampling continued unti? the day's catch of new biras was less

than half the mean catch of previous days. Reletive pepula-ion estimates for comonly caught species were calculated by regressing capture rate on cumlative number of birds caught (Terborgh and Fasborg 1973, MacArthur and MacArthur 1974).

Spot maps - A grid with Vines at iv m intervals was establ ished i 2 9 ha area which inciuded plot 3 (Figure Z). Geginning in Februa- "¥» 1981, sampling with mist nets was conducted along alternete oric Hines. ANI birds captured were marked 25 indicated above. Two prov ductive nets near @ bathing area were used more intensively. concluded in Apri}.

Sampling

In June anc July, the entire grid was traversea by @ single ab- Server on 10 aifferent days. The location of each singing bird was ecorded on maps of the gridced area, At the end of the sampling Period, data for each species were transferred to master maps of the Study area. Territories were delineated on the waps around clusters of observations with special weight given to territorial disputes and marked birds. The minimum requirenent for the definition of @ territory was three observations of a singing bird on different days (Int. Bird Census Comm. 1970). Nunber of whole and fractional territories were totaled for each species and doubled to account for females. Absolute density in individuals/na was calculated by aivide ?ing by the area in ha of the study site.

Subtask 2: Feeding Behavior

ae Ts eetteanes bse uetneters of, foam. te set

viduals

Approximately equivalent anounts of tine were spent collecting foraging data in each study plot. in addition, incidental ebsers vations were made during transect censuses and between study plots, A Lined observation was made of each bird found foraging. Location, ate, tine, weather and observer were routinely recorded for eoch

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individual. Time of observation, tree syecis:, hebitat cinpartnent, activity, canopy, tree, and bird height, type of invenent, direction and distance of movement, substrate attacked, prey taker and perch Gianeter were the foraging parameters. Each indivicual was followed through at least one feeding attempt or until lost fror. sight. A sample data sheet is shown in Appendix 1,

Foraging data collected in the Luguillo National Forest by Cane= Fon and Angela Kepler is available for comparison with the current Study. Data will be compiled and analyzed on an Apple 11 computer using techniques described by Waide (1981). Statistical treatment will? be designed to test for 1) seasonal differences within species, 2) differences between sites for each species, 3) aifferences between species, and 4) differences between individuels of the same species.

Subtask 3: Diet and Weight

Gojective: To determine differences in diet and weight between spe-Gies, sites, seasons and individuals; to describe the avian section of the food wed

All birds captured in connection with Subtask 1 were weighed and 30 stomachs were sampled with antimony potassium tartarete enetic (Prys-Jones et a1, 1974, Tomback 1975). In addition stomachs of 45 individuals of nine species collected for elemental analysis were exo-mined for their contents. AI1 birds were weighed on an Ohaus Triple~

beam balance to the nearest 0.1 g.

Birds collected for elemental analysis were frozen within two
ours of death, During processing for chemical analysis, entire
Stonachs were removed and opened and their contents were placed in 202
ETOH. Birds captured during marking studies had 0. ml of 1
antimony potassium tartarate solution introduced into their stonachs
Via a syringe and tygon tubing. Each bird was placed in a closed con-
tainer for 15 min and the regurgitated stomach contents were collected
with forceps and placed in 70% ETOH. The contents of stomachs were
Separated into animal and vegetable renains and proportions of each
were estimated on a relative volume and per ites basis. Aninal
remains are being {dentified to the lowest taxonemic level possible by

ote

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R. Garrison, Seeds were identified using » ri rercne+ collection este-
blished for that purpose by A. Estrada.

Construction of the avian section ct che toc4 web wil! use date
from foraging observations, storach analyses, published literature and

unpublished field observations of other workers. A compartnental ized model will be developed into which individual species will be placed according to the proportion of their diet derived from each conpart= ment. In addition, a trophic diagram will) be aeveloped showing the amount of biomass assignable to different trophic levels.

Subtask 4: Materials Discharge

Gbjective: To obtain reliable estimates of the ancunt of fecel and regurgitated material produced/individual of each species

Per unit time

Although completion of this subtask has been postponed until Phase 11, the methods to be used are presented here. Mistenetted

birds will be placed in holding cages for 1) 1 hr during the day and 2) overnight. Fecal and regurgitated material will collected, dried and weighed. Samples of fecal materiel will be combined and analyzed to determine mineral content. Using observed rates of defecation in the wild and in birds caged overnight, the anount of material returned to the environment/individual/unit tine will be caleulatea.

Subtask 5: Elemental Content

Gdjective: To obtain reliable estinates of the elements! content per ynit weight of 1) whole stonach contents and individesy food itens, 2) body tissue, 3) Teathers and?) feces and

regurgitated material

Key food items will be identified in Subtask 3 for important

Species in the food wed. Chemical analysis of specific fruits and

Seeds and general analyses of invertebrates are under way ond results

are reported in Section 5.2.

Forty-five individuals of nine species have been analyzed for

energy and mineral content of feathers and body tissue. Specific

methods are given in Sectfon 5.2, Results of these enalyses used in

conjunction with data on molt and population turnover will allow the

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development of models of mineral ec enesgy 110m st indivewuely popu

ation and comunity levels.

4.2.4.4 Manmals

Objective: To determine the presenice and general atundance of

ynanimal species within the rain forest study area

The role of manmals in the rain forest ecosystem is of interest

Primarily because the larger species (c.g. Inctan mongoose and root rat) have been introduces by man and al) native inhabitants are bats. Field studies focused on determining the species present, their gen eral abundance, and identifying their place in the overall trophic structure,

Bats - Night surveys were conducted using nist nets (30 nm end 36 mm mesh). Vertical nets were erected in the cpering at the station during Novenber and Decenber, 1980, and July, 1961. Horizontal nets were rigged in plots 1 and 2, at two forest locations near the field Station facilities, and on the Rio Sonadora foot bridge east of the field station. Nets were openec at sunset and closed at dawn to avoid capturing birds. Nets placed in renote locations (plots 1 and 2) were closed at 2300, For each bat captured, the species, sex, weight, tarsus and forearm measurenent were recorded. Some specimens were retained for calorimetry and nutrient analyses and the remaining in dividuals were released. Food habit information was taken from the Viterature, although some data was obtained from gut snalysis of a

Single Stenoderma rufum captured at a low net in July 1961,

Saal) manmals - Two traplines of 10 Sherman live trops (3X3X9 in) each were placed parallel to each other between plots 3 and 4. All traps and traplines were spaced at 15 m intervals. Lines were Surveyed for three consecutive days and nights from 18 to 21 Novenber 1980. Traps were checked daily and rebaited as necessary.

Large terrestrial mammals - Twenty-five Tomahawk double-ended Vive traps (61624 in) were deployed at 30 « intervals in a 5X5 grid at plot 3. Traps were baited, opened, and checked daily for three Consecutive days and nights from 22 to 24 Novenber 1980 and again tror

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© to 9 January 1981. The species and sex of each trapped individual Was recorded, and each was marked with 2 different paint warking so that recaptures and individual movenents could be detected.

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5.0 RESULTS AND DISCUSSION

Initial surveys have produced substential and in som cases unex Pected results. Gecause these data are preliminary, intesrstive ana- lyses are not possible at this tine for all tasks. Kesuits are herein reported and discussed by task.

5.1 Physical Phenomena

Datly rainfall and continuous records of relative humidity and temperature fluctuations have been collected at the E! verde Field Station since the radiation studies in the rain forest during the mid-1960's. The toner station was established in July, 1960 ana wilT be maintained throughout the program field studies. Prior to the ?implementation of Phase II studies a rain full event recorcer will be installed at the tower and a wind (velocity and direction) gage and a stream flow gage may be added to the program,

5.2 Elemental Inventory and Energy

We wanted to establish normal steedy-state values for chemical parameters of ecological importance to be used as "control" guidelines for studying mineral cycling dynamics and the environnental inpacts of new forms of energy. The group of elements selected had to be of biological as well as geological significance and present in suf- ficiently large amounts to be measured with oreinary laboratory equip~ ment. The following elements were chosen: nitrogen, phosphorus, calcium, sodium, potassium, magnesiun and sulphur. Gross heat of conbustion and percent ash were also measured.

5.2.1 Elenental Inventory

Tables 3-6 show elemental and caloric data for ail groups anal=
yeed. The ash content for the various species varied between 13 and
19%, except feathers, whose values were considerably lower, at approx-
imately 2% of their dry weight.

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Inorganic on composition of amphibians, reptiles, and bats.

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Calcium was the most abundant inorganic ion in the ash, being an average of 3.5 times the amount contributes by Mot, Na?, and K* conbined. At approximately 40 mg/g this was true cf al1 groups except birds whose average content was auch lower, near 30 mg/g dry weight. This 15 consistent with their need for a light skeleton in order to achieve flight. Bats on the other hand, averaged 43 mg/g. Calcium was present in feathers below the detection level of cur assay, but in special tests conducted, the content was estimated to be around 1 mg/g dry weight.

Potassium, sodium and magnesium averaged 7.8, 6.0, and 1.9 mg/g respectively, but agein these values were lower for bird samples. It was not unusual that feathers, being mostly keratin, contained 0.38, 0.27, and 0.12 as much Mo", Na", and Xk", respectively, as their body counterparts,

The average amount of mitrogen for all species studied was between 19 end 23%. The protein nature of the feathers justitied their sonewhat higher value of approximately 262. Sturges et 1 (2974) reported much lower values for nitrogen from whole birds col. lected at Hubbaré Brook. Their values were roughly one order of magnitude smaller than those presented here. However, on the other hand, our values for ripe fruit from the genus Ficus are in agreement with those of Milton and Ditznis (1981). This confirms, at least in part, the precision of our assay and is evidence for the accuracy of our data.

Phosphorus averaged 4.5% for all species. in feathers this element was nearly 30 tines less, around 0.163 of their dry weight.

Sulphur values varied between 0.6 and 15, but the average of al Species combined was approximately 0.75 percent. (Frogs were an exception as they averaged only 0.262). The reason for this is not known. Feathers hed slightly over twice as much sulphur as tissue. This 1s consistent with the presence of disulphide links for the structural integrity of keratin fibrile.

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2 Calorimetry

The caloric valve of all materfuls analyzed remained around 5,000 S2l/G- Bird data except for nitrogen are still incomplete. Trends Seen to indicate that average Figures will not differ significantly from the few velues collected thus far.

Using population data from Table 7 (Woolbright and Reagan, unpub, Geta), the amounts of the various elements were calculated on a per hectare basis. Results are shown in Table @ for Vizards and frogs. Not evident from these data is that population density is more import. ant in determining the standing crop value than average elenental content of a species. This was true for each of the parameters deter+ wwined.

5.3 Vegetation Studies

Considerable information has been gathered on the vegetation of the Luguilo mountains in Puerto Rico. Britton and Wilson (1923-1930), Wadsworth (1951), white (1963), Little and Wadsworth (1964), Odum aré Pigeon (1970), Little and Woosbury (1976), Crow and Keaver: (1977), Grow (1960), and Brown et al. (1981) are sone of the most inportant contriputors. Of the many studies, sumaries and surveys, no one had previously conducted a within forest type (tabonuco) varisbi-. lity study of the vegetation,

Variation in structure and function in a forest is mainly related {0 the physical environment (water and energy regimes) and its effects on soils and topography (Brunig and KIinge 1975). However, variabili- {y must be analyzed at different levels of organization. At the spe- cies Tevel, water, light, soil and topographical diversity may deter- wine vartations in composition and rates of productivity. At the scosystem level, the same forest and abiotic inputs function together asa unit.

A measurenent of the tebonuco forest variability was essential in order to detect organizational levels as well as yield baseline data for future comparistons anong other natural forests and plantations. The present studies were designed, therefore, to measure and conpare

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variability of each and all species storages and flows among and, in Some cases, within four 1 ha randomly selected plots.

5.3.1 Plot Characteristics

Minimal Area

?The mininal area curves constructed for El Verde on the design of uelTer-Donbois and Ellenberg (1974) indicated that a plot size of 2180 a would yield =10 percent increase Jin the nunber of new plant ?species (Figure 5). A plot area of 3400 n° would yield a = 5 per-cent increase in the number of new species (Figure 6).

An area of 1 ha (10,000 né) was selected as the size of each of the four plots. This larger size was considered to be more than ade-(uate in earlier studies at £1 Verde (Smith 2970). One ha would also assure valfd results with multiple plot usage.

The tabonuco forest basal area of live trees = 10cm dbh (a mean of the four study sites) was 30.75 mya. This value is within the range (17-50 9@/ha) reported by Sortano-Ressy et al. (1970) and Odum (1970) ang close to the 35.7 n@/na value Crow (1980) reported for stu 4 en dh in this area. A nearby ?0 year old multi-species natural succession stand had @ basal area of 27.9 m@/ha; 2 40 year old Plantation of Calophylium calaba, 30.2 m@/ha; and a 17 year old plan tation of Pinus caribaea, 33.9 a¢/ha (Jordan and Farnworth unpubl ished dato). However, a similar tebonuco forest site on the island of Doai- nica, British West Indies, had basal areas of 90.5 - 130.9 wha (Soriano-Ressy et 21. 1970), The basal areas of the Dominica sites are probably representative of the structural potential of a complete |y undisturbed tabonuco forest.

Individual plot live tree basal area date are given in Table 9, Values less than 30 m¢/ha in ?the Odum (1970) studies were generally from cutover or sisturbed sites. Judged ty species composition and canopy cover, plot 4 1s disturbed. The basal area of plot 4 (24.8

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'a) supports this premise. Plots 1 and 3 with basal areas of 39.0 and 34.3 n/na respectively, fall within the range represented in Puerto Rico as a mature forest.

Mean density of the study site trees was 729 ind/ha. Wadsworth (1981) reported 655 ind/na in his measurenent of a virgin tabonuce forest near E1 Verde, The densities of plots 1-4 (Table 9), were 247, 73% 816, and 515 ind/ha, respectively. White (1963) indicated an increase of density with elevation. However, the 150 m elevation dif. ?erences among plots cannot account for the differences in density. in plot 4, the disturbed site, the lower density is probably represen. ative of selective cutting known to have occurred there (Crow 1980).

Twenty-three families of tree spectes were represented in the four V ha plots (Table 10), Of these families, 14 were represented by {the dominants of the plots. The greatest number of species (5) were from the Euphorbiaceae; the greatest basal area (4.3 m@/ha) in the Leguminosae; and the greatest density (197 ind/ha) in the Palnae.

There are 547 native tree species found in Puerto Rico (Little and Wadsworth 1964), Two hundred twenty-five species are found in the Caribbean National Forest (Little and Woodbury 1976). Sixty-five Species were found by Wadsworth (1951) in 25 ha of the same tabonuco forest type. In this 4 ha study, 44 species were found,

Varsation in forest structure anong the four plots is shown in

Teble 9. The dominant species in each plot (determined by largest basal area) are Visted by basal area, density and importance value (relative dominance + relative density + relative Frequency = impor Fance velues Cottam and Curtis 1956). Two species, Dacryodes excels: (tabonuco) and Prestoea montana (sierra palm) were dominant in all four plots: five (Bc, Wor, Ifa, Ok and Sb; see Table II for species symbol Key) in three plots; two (Cp and Cep) in two plots; and thirteen (ap. Ce, Da, Dm, Gt, MD, Mg, Mys, NS, Ol, SI, Thy and Zm) in one plot. The dominant species at each site represented 80-90 percent of the basal area, 72-83 percent of the density, and 69-86 percent of ?the Species importance. The remaining 22 species comprised the rest of the forest.

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Table 10. List of species in each family incluging average basa? areal (BAné/ha) and density (Ind/na) for each family,

. Fagily Family

Family Species Ban? na Ind/na

Leguninosae Ai, Ifa, Iv, Ok 43 54

Palmae Prm 3.8 197

Euphorbiaceae Aly APs Cb, Dg, SI 3.7 7

Burseraceae De, To 3.5 6

Flacourtiaceae Ca, cbi, cs, Hor 3.2 75

Elaeocerpaceae ey 2.2 45

Conbretaceae Bc 18 10

Meliaceae be 1s B

Sapotaceae Mo, Mg, Mic 13 7

Lauraceae Bp, Ns, 01, Om 1.2 a

Mortaceae cep 12 10

Aral iaceae Da, Dn 1.0 18

Bignoniaceae Th 0.6 10

Melastromataceae sg, mt 0.4 16

Myrtaceae Es, yd, Mys 0.4 16

Rutaceae In 0.3 3

Arnonaceae Oka, oT on 8

Boraginaceae csi on 6

Oleaceae ld ot 3

Sapindaceae Ma ot 2

Nyctaginaceae Pia 0.08 2

Polygonaceae Cos 0.02 2

Rubiaceae a 0.02 2

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Table 11. Species symbols and corresponding scientific names for trees,

Species symbot Scientific name

a Andira inermis

a Alchornea latifolia

Ap Alchorneopsis. portoricensis

Be Buchenavia capitata

ca Casearia

coi Casearia bico

cep Cecropia peltata

os Coccoloba swartzit

cp Croton poset tanthus

cr Gyritla raceniflore

os Casearia sylvestris

cst Cordia sulcata

oso Calycogonium squamuTosum

o Dendropanax arboreus

oe Dacryodes excelsa

05 Orypetes glauca

on Ofdymopanax morototont

fs Eugenta stantiy

i Guettaros

se Guares trichi iotdes

for Hora ius racenosun

Ifa nga fagitolie

w Anga vera,

ls Linociera doningensis

% Manitkara bidentata

ma Mataybe domingensis

Mo Microphol's garciniaefotia

Mic Wicropholis.chrysophyoides

nye Myreia deftexa

Ys Yureia splendens

ts Nectandra sintenistt

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Continued table 11.

Species synbot

Ok

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Scientific name

Srmosia kruat

Gxandra laurifotia

Oxandra_ Janceolata

Ocotea levcoxyton

Ocotea moschata

Pisonia albida

Prestoea montana

Rourea glabra,

Sloanes berteriana

Sapium laurocerasus

Tetragastris balsamifera

Tabebuia heterophylia

Zanthoxylun nartinicense

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With regard to similarities and aifferences, plots 1 and 3 are most similar in basal areas and densities; plot 4, the most different, AIT plots are dominated by the tabonuco and the sierra pala, even though species composition is different. The proportion of basal area, density and importance of the dominants in each plot 1s similar although the dominant species are different. These differences are Probably the result of microclimatic and microtopographical plot variability.

5.3.2 Phenology

Phenology of the trees in the tabonuco forest in £1 Verde was extensively studied by Estrada (1970) from 1963 to 1967. Since flowers and/or fruits were expected to be an inportant energy source ?in the current faunal food web studies, anong plot and species phenol- eatcel patterns occurring during the study were sampled using mate- vials collected in the litter fal1 baskets.

Fruits contributed twice as mich to litter fall as flowers with values of 29.9 to 14.6 g/n®.yr, respective (Table 12). The greatest fruitfall was in January (5.6 g/m); flower fall in duly (2.8 g/m). Fruits consisted of 3.9 percent of the total yearly litterfall; Flowers, 2.0 percent. The individual spectes input to the flower and fruit fall has yet to be enalyzed,

5.3.3 Litter Fall

The return of litter to the soit (1itter fa11) is an important ?utrient cycling mechanism (Exel 1976). Jordan (1970) states from a Study conducted in ET Verde that litter fall is a relatively unimport- ant nutrient transfer mechanism a5 conpared to throughfall and sten- flow. Jordan corrected his calculation in Brown et al. (1981) and now concurs with Ewel. Oue to its importance, Iitter fall was measured on 2 dimonthly basis to detect between site and species variability, Similarities at an ecosystem level and differences at a species Tevel are most apparent in the leaf fall component of litter fall. A five year monthly mean §s shown in Figure 7. The month-to-month

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Table 12, Hean monthly Titker fall values (g/t?) by categories

for 1981,

Months Leaves Flowers Fruits Wood Miscellaneous Tot,

a 35 0.7 5.6 ao 9.0 46.6

F 304 kg nz 40.6

" 7.5 07 ake 3.8 15.4 28.7

A M0 08 at tae 16.0 72.9

s a8 03° 11 tao 22.8 123.4

a wt 0 sone 19.1 65.7

3 7 28 21 ag 0 76.3

A 6 1.9 a3 120 19.2 ne

s 99 1.0 639.3 27.0 16.7

° 28 16 30 50 a6 60.7

" 35 kg 5.8 19.6

> N92 2 9.0 9.0 43.2

Men 31.41 29,9 156.1 a0. 870.2

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Figure 7. Five year mean leaf fa11 plus or minus one standard error.

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variations during the § yrs. are shown in Table 13 (1970-73 from Estrada, unpublished data plus this year). An analysis of variance (Table 14) indicated no significant difference (p»05) among years. However, differences were highly significant (p<.001) among months but there were no significant differences among plots.

The 1.39 g/m day value obtained fron the § yr leaf fell mean was

Similar to the 1965-1966 mean leaf f2l1 input of 1.43 g/m? day in a Study conducted by Weigert (1970) in E1 Verde. Thus, in spite of a Span of 18 years and site and species composition differences, the tabonuco forest type consistently cycles the same amount (g/m) of leaves annually fron trees to forest floor; the tabonuco forest is functioning as a mature ecosystem with respect to leaf fall.

Similar biotic and climatic regimes should exhibit similar leaf fall inputs, Table 15 illustrates the effects of general climatic conditions on the rate of leaf fall, demonstrating the trend that leaf fall decreases with increasing latitude (Jordan 1971). The £1 Verde value of 5.1 mt/ha/yr corresponds to other sub-tropical forest leaf fall studies.

Bray end Gorham (1964) show variable yearly Vitterfall input in temperate, less diverse forests, Since in our study six years of leat fall measurements yielded no significant differences, variation of leaf fall yearly inputs may be buffered by high species diversity in the tropical forests. However, a six-year sub-tropical mangrove lit~ ter fall study (Lugo et a1. 1980) with two species varied less than 11 Percent among annual means. A favorable climate may be more important for consistent litter production than species diversity.

The four plot monthly mean litter fall components are in Table 12. These inputs are represented as a percent of total in Table 16 and graphically in Figure 8. Bray and Gorham (1964) report a mean value in which 33 percent of non-leaf litter wes found in litter fal1

from a tropical forest. In addition, 16 percent of total litter fall

consisted of wood and 20.8 percent miscellaneous (unidentifiable)

material. The greatest amount of wood and miscellaneous material in«

put occurred during September as the result of high winds from a

tropical storm.

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Table 13. Mean monthly leaf-fa11 of four plots in g/m? for 5 years ine

Sluding the S year mean. Yearly totals and rates in? g/m? day

are also given.

year

Month 1970 19 "sre 1973__198)__5 yr. ean

a 21.1 26.7 30.3 20.5 26.5

F 9 22.7 29.8 28.8 an 28.3

" M1 43.7 2.9 36.2 57.5 48.9

A 47 74 99.3 86.5 a0 es

? 9 675 4895.7 he 4.2

a 5 57.6 $9.6 55.2 ar 58.0

a 45.0 45.1 46.7 3158.7 we

A 5 407 5.8 we 66 ae

s 4.6 542 32.8 64.1 a7.9 42.5

° 8.7 4.1 30.6 301 ae 30.4

4 5.8 185 27.525 24.8

o 0 283 6 sans 24.7

Neat se 309 a0 eto. ane 505.9

g/t ay 1.46 1.45, 1.27 1.40 1.35 1.39

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Table 14. One way analysis of variance anong Titter fat) and Teat fal) in

1981. F values demonstrate significance anong plots. mecays

and years,

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mos. 19.3) 14.8)

?Among 5 ns

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four plots).

Conponents of litter fall (means of

Figure 8.

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Rainfall dete are sn Table 17, & Tones regression comparing litter fal) to rainfall showed little correla? 2, 1.16). Leaf fall cannot be associated with wing speed, day length, or moisture alone but more likely to a combination of environmental factors (Hopkins 1966).

Differences in leaf fali are nost noteble at the species level (Table 18-19). Values are given by piot for the 15 species that contributed the greatest amount to the leaf fall component. Plot A refers to collections fran 19/3 (Estrada, unpublished data). Although leaf fall input does not significantly eiffer anong plots, the anount that each species contributes varies signiticently. Apparently the

?input oF Tack of it by one species is compensated by another species ina diverse system,

Plot 4 yielded the greatest leaf fall input. If leaf fall is a measure of net prinary productivity (Murphy 1977), plot 4 is the mst Productive, Yet plot 4 exhibited the lowest basal area end density of all plots and is considered to be the earliest successional stage of the four plots. In Ewet's (1976) study of tropical forests in Guatee mala, litter fall from a successional 14 yr old stand did not sige nificantly differ from a mature forest. In some cases, Vitter fall in successtone} areas is greater than mature forests. Apparently the energy obtaining couponent ?leeves) receives greatest priority in & ?successional system. The rapid growth of vines, shrubs, and short-lived trees compensates for the original plent production while the forest slowly rebuilds,

on (x4

5.3.4 Loose Litter

Litter standing crop constitutes the ground storage of plant

Parts during the decomposition process when plant organic matter is

Converted to soil organic matter or mineralized. Loose litter builds

uP during the successional process until Vitter fall is balanced by

decomposition (Ewel 1976). In a mature forest, loose litter is at

equilibrium,

Litter standing crop generally varies inversely to litter fall at

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Table 17. Rainfall in am from £1 Verde, P.R.. during the Titterfai? study

pertod.

Year Mean Mean

Months 1970 ten) ge s?3 tg) ayy

3 646.5 308,3 256.3 216.6 208.4 249.5

Fo 109.2 277.1 tee 233.1 200.2 193.8

H 78.7 102.0 10.2 zea 158.7 169.9

A 80.8 19.46 156.5 538.0 203.3 as.

Mo 925.6 te.6 5.6 BO gst.e seo are

3507.5 90.2 140.7 ose eae ane

J 5.0 72.7 V8.8 4.5.0 2.0

A 3.8 203 aire 02.8 29.8 338.7

S 208.0 197.0 148.5 198.6 197.0 307.7

0 545.1 328.6 202.4 238.4 320.6 369.0

N 36.2 208.8 158.2 We9.8 225.8 32.9

> s.0 405.9 222.0 37.0 369.0 360.0

Yearly

total (om)3923.4 2612.9 2188.5 3672.1 3148.0 3602.5

Tots" (in) 154.5 102.0 ae 152 123.9 137.9

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ane

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Table 18. Mean Veaf fa11 input (a/n?. year) by species iNustrating bet-

ween plot variability and mean contribution to total? forsee

lot A refers to the 1973 collection while plots 1-4 Sonsecirate

?input. during 1981-

Mean

2 tof

Species Plot Plot Plot Plot. ?Pot g/m? year fovhy

A 1 2 3 4

De 69.9 107.9 78.0 Naa 22 7916

Be 35.3 350 63.100 46.70 753.3

ca 00 6136 00 ag 99 102.4 26.9 5

Ifa 10.0 83 64.1 10.3 20.3 22.6 5

Ok 25.8 23.0 38.4 4.8 41 9.2 4

cy 0 0-226 00 a0.6 10.6 18g 4

ot 0.0 04 6.0 66.3 W778. 4

cep 0.7 1.9 28.7 20.2 3.3 16.6 3

Hor 5.2 14.2 29.2 30,7 oo 18.9 3

sb 64 36.8 9.8 ahs Ww 188 3

Rg a4 35°39 0 48.7 930 148 3

Pr 00 21.9 (6 0.0 20.5 148 3

cr 68.3 00 0.0 0.0 0.00 13.7 3

Ma 55.6 5.5 2.0 M7 00 © 13.0 3

cp 13.2 45.0 0.0 48 00 126 3

81 other

species 1.0 a9

Total $02.5 451.4 491.9 509.3 512.8 493.6

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increasing latitudes, Jenny et al. (1989) states thet in @ Colombian forest loose litter (1076 g/m?) was one tenth loose litter in» Californian forest (11609 g/n?) while Vitter fall in the Colonbian site (1023 g/nt) was five times the value from Californian (200 e/a), Table 15 gives comparative latitudinal litter storage values,

Slemy et al. (1949) calculated from litter Fa11 rates and storage values that it would take @ Colombian rain forest 1-3 years to reach equilibrium; Californie, 26-332 years depending on forest type (oak or pine) and altitude.

Ground litter storages in the four study plots in £1 Verde are shown in Figure 9 and Table 20 by category, site and season. The aie. Gellaneous category consisted of alt plant parts in all stages of de. Composition except wood. The yearly mean ground Vitter storage wes 392.2 g/af. This value is considerably lover than Ketgert's {lav0) eh verde mean of 598 g/n. Me believe the four plot, two season mean of the current study (240 samples) is more reliable than Weigert's 1970 mesn (100 samples). The present. study's sampling design included Greater representation of the tabonuco forest micro-topographical heterogeneity. Analysis of variance (Tables 21 and 22) demonstrated no significant variation in the miscellaneous category (leaf, flower and fruit component) anong plots or between seasons. Greatest vari ability wes in the wood component in two plots during the wet season, The lack of variability in the leaf fe17 and miscellaneous category of the ground litter indicates steady state.

Assuming equilibrium, annual input (leaf F211) can be divided by annual storage (loose Nitter) and the resulting turnover rate (TOR) of Nitter determined (Table 23). The four plot mean TOR was slightly faster during the wet season (1.90) than the dry season (1.68). A latitudinal comparison of TOR 1s given in Table 15.

TOR measures the rate of internal cycling within a forest and can ?epresent decomposition. The mean TOR of 1.78 for 1 Verde would ?indicate complete decomposition of leaves within 0.56 years.

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Loose litter components by plot. and season

Figure 9.

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(e°S2) vere (6°21) 6°96 ee) bese (abe) 6-92 (0°91) 2-921 AL 014

OE) Site (B92) 67652 (BBL) 9UEL (ze) e-S~ (9°42) 9°e62 (K-02) S181 THT Q014

(61) 91s2 ? (e-BL) E02 (9°8) Z¥y (592) LIV (S°6R) 2962 (6-EL) S°SOL 11 G0Le

(O°K8) Occ (OE) E842 (O°LL) 6-86 (0'RE) B'¥9 (9°52) L562 (¥'02) 0°61 1 201g

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Table 21. F values fron one way analyses of variance of loose litter

?among plots at each season.

ee

Hood Miscellaneous Tota of.

Head ____Miscellaneous __ Total.

Dry Season 2,41" 1.59" 2.00 3,156

Wet Season 7, 7944 2.478 6.2 3,76

ns = p> .05

se = 9 < 001

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Table 22

Wood

Plot 1 5.01

Plot 11 g.g7e+

Plot 111 0.208

Plot v1.43"

Combined

plot com

Parison 9. 7406

F values from one sey analyses of variance for lose

Vitter between wet and dry seasons.

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Miscellaneous Total of

oui" 26 58

2.5608 7.50 1,58

o.03"* 0.02" 158.

3.876 3.998 1,58

3.35" 8.6 1,238

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Table 23. Leaf 211 and miscellaneous loose litter (kg/ha) and turn

Quer rates (TOR = leaf fall/misc. loose Vitter) by plet and

season,

Dry Season

Leaf fat 4514 491950935128 aang

tiscelaneous 295625602038 Geen,

Loose fitter

TOR W830 92 72s?

et Season

Leaf #217 gsl¢ 4195093129 aog,

Wiscetlaenous 2784 20723000 Sase,?SM

Loose 1itter

TOR Nez 2.3770 2051.90

Yearly Mean

Leaf fant ase 4195093 S28 aoa

{yscellaneous 287023162563,

Loose litter

oR M87 2n2 eee

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5.3.5 Decomposition

Since weathering releases elements at too slow a rate to meet

Plant nutrient requirements, decomposition regulates the rate elements are returned to the system. decomposition either mineralizes litter storages (converts organic compounds to an inorganic useable form) or forms soil organic matter from the residue or both, The rate of decomposition regulates the net primary productivity of a system and the aoiotic environment regulates decomposition (Swift et al. 1979(,

Decomposition rates are much slower in temperate clinates than in the tropics (Table 15) and account for the increased litter standing crop and decreased TOR in tenperate areas. Decomposition varies with species (Madge 1965, Ewel 1976, Swift et al. 1979, Edwards 1977) and site (Neigert and Murphy 1970, UNESCO 1978).

Species level differences were well docunented. However, no one fhad looked at the decomposition rates of fresh leaf composites. Table 24 shows the species composition and the percentage of a species represented in each bag. Every bag was representative of the composition of the freshly fallen leaves in each plot at that tine,

There were no significant differences in decomposition resulting from species composition or site nor were there significant differenes in tine of Field placement up to 120 days. There appears to be a aifference tn decomposition due to the tine of field placement after 120 days. This study 4s sti11 in progress and seasonal-rainfall differences are yet to be verified. We conclude that neither species. nor site influenced decomposition when the total group of species repre Sentative of an area was placed in a decomposition bag. This study

Senonstrates ecosystem level functioning in the decomposition process a5 well as leaf fall,

Turnover time (TOT) defined as the time necessary for Yeaf fall to replace leaf storage was 0.56 years. If only decomposition were involved, leaves should decompose 100 percent in 0.56 years, but this study indicates that decomposition was 75 percent in 1 yr. Thus, fac= tors other than decomposition must account for the rapid TOT; sone organic matter may be incorporated into soil organic matter or lost to

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Table 24 . Species composition and g fresh weight/species in decom position bags.

pecies Species Species

st as se 18 on 27

ons % ww 31 10

07 oe 1 ce 0.7

ceo. Yor 0.7 mn 0.7

m 0.6 9 07 a 0.8

3 06 om 0.6 om 05

fa 0.6 Cos os He 0.5

Yor 0.3 si 0.8 us 0.5

"50. cep 03 8s 0.3

Ww 03 Me 0.2 de 0.3

B& og us 01 a 0.3

cos 0.2 me ot sp 0.2

Soe sb 0. he 0.2

oe ac on

Misc. 1.8 Misc. 1.2 Mise 18

Tota 10.0 Total 10.0 Total 19.0

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Table 25. Numbers of invertebrates collected over 10 days, @ nights, 9-22

June 198),

a

Day, Night

ARTHROPODA

Arachnida

Acarina

Oribatidae 1

Araneiaa

unidentifiable to family 1 2

Photcidae

unidentifiable to family 1

Modismus sexoculstus 2

Araneiéae

unidentifiable to species 1 1

Leucage regnys 1 2

Clubjonidae 1 5

Cinyphiidae

Diplocephatus gtoriae 1

Thom sidae

Epicaudus mutehlert 1

satticiaae 3 1

Colembola

Entonobry idae

Lepidocyrtinus sp.? 1

Insecta

Epheneroptera

Leptophiebtidae? 1

Blattodea

Blattidae

Blattellidae

Cariblatta hebardi

Orthoptera

Ory at

Grocheris vaginalis or terebrans

Cyrtoxiphe ?gundtachi

Undetermined Trigonidinge

Isoptera

Kalotermi tidae

Glyptotermes pubescens (winged) 3 2

Termitidae

Nasutitermes sp.)

Psocoptera

Lepidopsocidae v2

Polypsocidae

Epipsocidae

Psocidae

?82

---Page Break---

Continued table 25

Tysanoptera

Phlacothripidae 8 10

Thripidae 5 2

Hemiptera

Dipsocoridae 1

Niridae

undetermined species 1

Polymerus pallidus 1

Lygeetdse 6

Cydnidae 1

Homoptera

Menbracidae

Nessorchinus esbel tus 1

CicadelTidae

unidentified species)

unidentified species (nymph) 1

Sibovea coffeacola

ia insularis

Xestocephalus maculatus

aelphociaae

Ugyops occidentalis

verblaae

unidentified spectes 1

Dawnaria. sordidu 9

ysinia maculata 1

Patara albida? 1

Cixiidae (nymph) 1

Kinnaridae

fasciata

Catonia cinerea

fatonia dorsovit Fata (eyes),

?Anblycratus striatus? (nymphs;

Ghadrana punctstay tonyeh

Undetermined species trymphs)

Tropiduchidae

Ladera stati. 1 8

Issidae

?Thione. borinquensis 3

Tolpoptera nacuT iftons 6

?olpopters Brunneut 3 5

Neocalpspters sorticotens 1

1

sya

Coccoidea

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Continued table 25

Coleoptera

Histeridae

Staphy}inidae

unidentified spp.

Palaminus sp.

Pselaphidae

Ptiliidae

Actinopteryx sp.

Scaphidifdae

Elateridae

Eucnenidae

. Anobiidae

Trogositade (Tribe Tenebroidini)

Cucujidae

Coccinetl idae

Colydtidae

Tenebrionidae

. Nelandryiidae

Mordeltidae

Euglenidae

ChrysomeT idae

Anthribidae

Curculionidae

. Scolytidae

Lepidoptera

Cosnopterygidae?

Gelechi idae?

Gracialaridae?

Diptera

. Tipulidae

Psychodidae

Ceratopogonidae

Chirononidae

Mycetophi idae

Sciaridae

. Scatopsidae

Cecidony! idee

Asiligae

Enpididae

Dol ichopodidae

Phoridae.

. Pipunculidae

Tephritidae

Lauxaniidae

Chanaenyi idae?

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Continued table 25

Lonchaeidae

Hel ionyzidae

Chloropidae

Bgromyzi

Odini dae

Ephydridae

DrosophiTidae

Anthony idae

Tachinidae

Call iphorigae

Sercophagidae

Hymenoptera

Brachonidae

Ichneumonidae

Mymaridae

Trichogramatidae

Eulophidae

Encyrtidae

Eupeimidae

Agzonidae

Torymidae

Preroma idae

Cynipidae

Ceraphronidae

Diapriidae

Sceliontdae

Platygastridae

Bethylidae

Orymtdae

Formicidae

Nononoriun floricola

Tessonprmex meTTeus

jrme echists rasetorum

Serchympracs nese

Untdent Fed harks

Winged males

?Sphecidae (Cabroninae)

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Night

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Table 26. Nunbers of invertebrates collected (by order). for dayentght,

fombined tctals; and percentage composition of overait tor

tal. Day-night totals are from 10 days and 8 night samples.

Order	Day	Night	Total	?t0veral? Tota?
carina	°	1	1	02
Araneidae	so	23	31	
Col lendota	°	1	1	02
Ephemeroptera	1	°	1	02
Blattodea	°	7	7	a6
Orthoptera	°	8	8	18
Isoptera	?	2	6	13
Psocoptera	2	26	58	
Thysanoptera	13,2	25	55	
Hemiptera	4	é	10	2
Homoptera	a2	1	2.02	
Coleoptera	Be	8	1.35	

Lepidoptera ° 3 2 07

Diptera 19632087 4030 89.42

Hymenoptera 152 gk 47

?_,__

Totals 22132294 4507 100%

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Sroqunu ueaw 40 sasuada4s1P 40) 41S-Ss ?OL aunbiy

BR Gow ae Te ol Fl oO eee

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the systen as export. Future studies should be directed toward inves igating the fate of this unaccounted organic matter. It is essentisl fo Getersine input, cycling, and export from 3 natural system in order to monitor effects of future perturbations.

5.4 Faunal Studies

5.4.1 Invertebrates

Subtask 1, Vertical Transect Samp! ing

A otal of 4506 invertebrates representing 15 orders and 105 families (Table 25) vere coltected over the 10 day-8 night sampling Beriod, ?Flies constituted the most abundant insect group (4030 or 89%) followed by Hymenoptera (214 or St), Homoptera (91 or 24) and Coleoptera (61 or 1s) (Table 26). Phorid flies (representing severe Species) mace up 75% of the entire invertebrate fauna and were abviously the dominant invertebrate group during the two week period. The Diptera comprised the sost families (27) followed by Coleopters (20) and Hymenoptera (19).

No significant difference in mean abundance of invertebrates was found between day and night samples, but there were significant diffe. ences among the mean number of invertebrates collected at the 19 hetahts ($F_{r,o13}(18.19) = 6.68$, $p < .001$). An SS-STP test (Figure 10) Showed the firSt 2 m to contain a significantly greater number of in- wertebrotes thon the upper 17 m, The Phoridae likewise showed sige nificant aifferences in meen munbers collected among the 19. a ?F[,o1)128+19) = 6.68, P=.001) and were the major contributing factor fe the differences observed anong total invertebrate groups. An SS-STP of Phorids showed the sane resuits as for all invertebrates, hen all invertebrates minus the Phoridee were conpared, no nean dif. ferences were detected. :

Nesbers of the superfamily Fulgoroidea (Delphacidae to Issidae, ?Inclusive, Table 25) or planthoppers are conspicuous herbivores in the rain forest. Though they are often seen and collected in sweep net and D-vac samples near the ground, more of these insects were found near the canopy than below. When the 19 m strata were divided into three equal samples of 6 m (the first meter sample was deleted because

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it had so few specimens) a significant eifference occurred between the top 6 mand the lower 12 m (Figure 11),

Next to the Phorids the scalypterate families (Tipulidse to Cectdonyiidae, inciusive) were the most common group of insects and their numbers were relatively constant throughout the 19 m.

Discussion

The Diptera, and in particular phortd Flies, were the most abune dant flying insects at the tower. Phorids area large group with varied habits. Adults and larvae probably feed on decaying organic matter and this explains their greater numbers near the ground, Prorids collected st 1m sbove ground during separate 24 hour periods ranged fron 0 to 913, No specimens were taken on 9 dune, one was teken on 10 Jurey two on 11 June, six on 12 June, and 265 on 16 June, the ext 24 hour sampling period. A culmination was reached on 16 june (913) but munbers were reduced to 84 on 17 June, The data indicate 2 sudden mass emergence over a short period of time, It 12 not known if several broods occur throughout the year, or whethes these emergences are restricted to the wet season.

The ?small, inconspicuous nenataceran Oiptera appear to be the most abundant insects on a regular basis, As weak flyers, they were Probably caught passively by the sticky traps. Large invertebrotes such a5 dragonflies and butterflies were generally absent. from aur Samples and they may have avoided the traps or escaped by sheer Strength when caught. The absence of Odonata, large Coleoptera and large Lepidoptera, a11 seen in the forest, support this betiet,

Although no significant ifterences of mean numbers of invertebrates were detected between day and night, sone groups, showed 2 strong nocturnal preference (8lattodea - 7 night, 0 days Orthoptera- & night, 0 days Lepidoptera 3 night, 0 day) white the dipteran sute grders Brachycera and Cyclorrapha (except Phoridae) were strongly divrnat (114 day, 28 night).

Numbers for sone orders were too low to establish meaningful re-

sults fn stratification. Ideally, stratification studies of familieg

Of & single order would be useful for an overall picture of forese

Zones, but the Phoridse was the only family with sufficient numbers to

show @ significant. difference, Significant stratification results

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Figure 11.

SS-STP for differences of meon numbers of

Fulgoroids per 6 meter increments (Ist meter deleted)

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were observed for all invertebrates, but the difference was solely due to the presence of Phorids. The comparison of superfamilies, as with the Fulgoroides, was useful in revealing vertical stratification within an order. The homopterans feed on phloem from leaves and smal twigs which explains their abundance in the canopy, since the high canopy contains most of the leaves and small stems. Pscoptera are a relatively rare group, yet we collected 26 individuals from four families. Though Coleoptera comprise only 1.35% of invertebrates collected, they represented, next to the Diptera, the most families collected. This is probably due to their overwhelming taxonomic diverstty a5 compared to other invertebrates. Most Hymenoptera collected were small to minute paresistic taxa from superfamilies Chalcidoidea and Proctotrupoidea which are primarily insect egg parasites. Among the hymenopterans collected were two male dryinids, rare wasps which are parasitic on homopterans, and two female agaonids, or fig wasps. Agaonids are obligate pollinators of fig trees and indicate the presence of fig trees in the forest.

One commonly accepted theory of the tropical rain forests is that 4 great diversity of forms exists at the expense of abundance of any fone or few species. However, in this study, 75.30% of all invertebrates sampled consisted of menbers of one insect family, the Phoridee. This indicates thet, like some tenporatezone areas, sone invertebrate Groups may become very abundant end can comprise a significant compoent of the invertebrate biomass. The results are in agreement with Penny and Arias (1981), who after a year of light and trap sampling in the Anazon rein forest found 84 to 91% of the invertebrates to be

Diptera, primarily Luzomyia spp. (Psychodidae).

Subtask 2, Macrodecomposers Associated With Leaf Litter Decomposition

A total of 2565 invertebrates were collected from 97 bags (Table 27) over a 120 day period. The seven day samples contained the lowest total sample size (442) and the 14 day samples the highest (602), a difference of 160 animals. Twenty eight day total samples (535) were Similar to 120 day samples (519) and the 60 day total sample size (467) would have been higher had the total sample size have been 20 instead of 17. AS expected, mites (Acarina) were the most abundant animals (1217 or 47.4%) followed by Diptera (503 or 19.6%) of which

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nenatoceran and drachyceran larvae (Tipulidae to Strattonyidae, Table 27) wade up 11.7% of the total. There appear to be no real diffe-

ences among any of the plots: common erthropods (e.g. Menthus sp., staphylinid beetles, Actinopterys sp.) found in one leaf litter sample of five bags were generally found in the other three samples of 15 bags. Uther organisms (e.g. 211 Hemiptera, Homoptera) were rare and sporadically distributed in the bags through time. These results agree with data previously presented (section 5.3.3) which indicate that litterfall rates and other vegetative aspects of the forest are relatively honogeneous.

Though there appeared to be little difference in the invertebrate fauna among samples at eny given collection period, there were changes of certain invertebrate groups through time. Larvae and pupae of idges (Chironomidae) were found in a1} four samples during the seven and 14 day periods but were scarce or absent thereafter. The follow ?ing groups had distribution patterns similar to chrironomids, though because they were not as abundant, it is difficult to see as obvious a trend: Copopoda, Dicranocentropha springtails, blattellid nymphs, and Grosophilid larvae. AI] of these organisns are probably important fmacrodecomposers. Both adults and larvae of feather winged beetles {Actinopteryx adults end larvae) were common only during the 14 day collection. Terrestrial isopods (Phitocta richnondi) and to a lesser extent, cladocerans (Podoccpa) were common only during the 60 and 120 Gay collections. Apparently, these two invertebrate groups prefer Vitter which has alreagy reached an advanced state of decomposition.

Discussion

The results show that mites, the isopod Philocta richmondi, the mill ipede Prostenmiulus sp., entomobryid springtails and chironomid larvae were the most comon invertebrates found in leaf litter bags and these organisns are probably the most important macrodecomposers. Menthid pseudoscorpions and staphylinid beetles were frequent in many Samples but they ere carnivorous arthropods. Their predatory activi- ties (including defecation of prey remains) are probably important in 2iding small microscopic organisms in decomposing leaf litter. Few ants were collected in the samples not because they were rare, but

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probably decause these anbulatary insects escaped capture when litter bags were collected, Thus their importance in aiding the decompo- sition process of leaf litter 1s probably underest inated.

Mites were the most abundant arthropods in the leaf Titter but they are smail so their quantitative contribution to decomposition may not be as great as the larger isopods or chironomid larvae.

No obvious differences in arthropod species or numbers were observed for same day litter collections among plots. The comonly collected arthropods are probably widespread throughout the study

The most dramatic successional differences in arthropod species was between chircnomid larvae and the terrestrial isopod Philoci, Lichwondi. Chironomid larvae were common in all semples of 7 and 14 ays but, except for 4 and x during 28 and 120 days, were absent in aN) Tater samples. Philocia richwondi seers to prefer partially decomposes leaf Vitter. Only one specimen was found in any of the 7 day bagsi low munbers were found in each 14 day sample and their nun-bers increased after 16 days. These two arthropod groups are probably important macrodeconposers @s both are known to be detritus feeders,

Melahan and Suilins (1970) reported Hymenoptera (ants) to be the ost abundant arthropods in their sampling of forest litter for E1 Verde, but their collection method (suction apparatus) was more likely to collect ants. They did not count larval insects in their studies but our results indicate thet holonetabolous insect larvae are proba-bly a siontficant component of the leaf litter ecosystem.

Subtask 3, Anolis Food Habits

One hundred thirty eight stomachs were examined (Table 2) which had a total of 1989 items comprising at least 169 different taxa

(Table 2). No Anolis were found with empty stomachs, but several did have only one item. Sone had eaten their own skin and these were the only contents in some specimens. The greatest quantity in numbers and Species of prey was taken by an A. evermanni female from the Rio Sonadora (hereafter called creek"). It had 77 itens representing 21 species (20 species of invertebrates, one species of seed). Although mites appear to the most abundant arthropods in the forest, ants, primarily Myrmelachista ramulorum, Iridomyrmex melleus and Pheidole

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fmorrens were the most numerous prey ites. A wide variety of

organisms were taken by all four species although some (Acarina,

Collenbola, leaf debris, ichen-moss debris, and rocks) were probably

?ingested accidentally or inadvertently while securing another prey

item. Anolis cuvieri seemed to confine themselves primarily to medium

sized gastropods and large phasmatids. One female A. cuviert a

tempted to seize @ full grown male A. gundlachi but succeeded only in getting a part of the tail.

Average size prey for each Anolis group is shown in Table 29 and Figure 12. Anolis cuviert, as expected, had the largest average prey Size (22.2 m) but the fewest mean nunber of taxa (1.7). Because of sexual dimorphism, Targe male wet and dry season A. gundlachi had larger mean prey sizes (6.6 and 6.4 mm respectively) conpared to fe- mmeles of both seasons (2.6 and 2.7 mn). The longest prey item was an earthworm (about 130 mm) taken by a male wet season A. gundlachi, Mean prey sizes for all other lizards are similar and range from 2.4 to 3.0 mm. Few lizards were totally carnivorous and the mean percent. ?amine! volune for creek A. evermanni males was only 59% (Table 30) and ?indicates that this species (and probably others) will eat consider= able amounts of vegetable matter from time to tine.

Because minute differences in prey dimensions are accentuated when volumes are calculated, greater differences were observed anong Vizards when this parameter is measured (Table 30). Anolis cuviert hhad the greatest mean volume (1223.6 mm?) followed by wet season male A, gundlacht (1093.9 mn?). Except for the wet season females, all A. Gundlacht had greater mean volume estinates than did A. evernanni, If only mean animal volumes are compared, thon all A. gundlachi estimates surpass estinates of A. evermanni. Wet season A. stratulus had alaost double mean volume estimates over dry season species despite similar mmean pray size estimates (Figure 12) and shows that these lizards may bbe food limited during the dry season.

There was little difference between mean volune estimates of wet and ary season A. evermanni but there were large differences between males and females. The results may be due to sampling error or to different predatory habits between sexes between wet and dry seasons. Except for male wet season A. evermanni, creek A. evermanni had sreater mean food volumes than all of the forest A. evermanni. Except

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for wet season A. stratulus, male Anolis had greater mean volumes than

their females of the same season, but females had greater numbers of

taxa compared to males of the same season.

Most animals eaten were mature (Figure 13). Female lizards ate slightly higher percentages of larvae relative to males. No invertebrate larvae were found in stomachs of dry season A. stratulus.

We classified animal prey taxa into predators, herbivores, and Scavengers. The last category included mites, millipedes, sow bugs, all fly larvae, most adult flies, and ants. Although ants were the ?most numerous prey ?tens, their small mean volume size contributed less to the diet makeup than did herbivorous prey (Figure 14). Large Planthoppers and orthopterans are bulky and primarily accounted for the great herbivore biomass consumed by all species. Snails and walkingsticks made up the major part of the herbivore biomass in A. cuvieri. Spiders were the largest contributor to the predatory biomass. Only five spiders were consuned by A. stratulus and accounted for low percentages of predator biomass in that species. Specimens of all Anolis species were found which had eaten their own skin.

Discussion

Identification of invertebrate taxa to lowest taxonomic levels

did aid in the further understanding of prey availably for Anolis.

Greatest differences were observed among ants because they were the most comonly consuned organisms. Three species of ants, [ridonymes Belleus, Pheidole moerens, and Mymelachista ramilorum are very common ?in the forest but they do not necessarily occur in the sane habitats. Other scientists in the LuquiTlo forest have noted that M. ranvlorum is primarily an arboreal species. We have found this species to be associated with birds; they are commonly used in feather maintenance (aide, pers. comm.). The vertical transect studies indicated that M. anvlorum was found above 3 m (others were found at 1m, 1 at 3 m, at 11 m, 2 at 13 m). None were found in the litter samples tee subtask 2). Myrmelachista ranulorum was cosmonly found in several Individuals of A. evermanni and A. stratulus but only two specimens were found in A. gundlachi. On the other hand, Pheidole moerens were

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found almost exclusively in A. gundlachi and in six female A, evermanni at the creek (a ground habitat). Only one P. moerens was found in a female dry season A. stratulus. Iridomyrmex melleus were Commonly found in all three species of lizards. Two reasons can be postulated for the observed predation patterns: 1) the lizard spectes are ant specific, actively choosing one species over another, or 2) the diet "preference" is a result of the habitat selection of the Mzards. We believe the second hypothesis is suitable because Anolis Probably cannot discriminate between various species of ants. They Probably attempt to eat any moving object within a given size range. Thus, Iridomyrmex probably occurs from ground level to the canopy and ?s therefore preyed upon by all Anolis species. Pheidole merens is Primarily a ground ant, and M. ranvlorum a canopy species and each is Primarily preyed upon by Anolis species which inhabit those stratified areas of the forest. Though numbers are few, the data indicate that Strumigenys rogeri and Mycoceperus smithi are primarily ground inh biting spectes because they are consumed by A. gundlach and creek A, evermannt.

Two large, primarily terrestrial inhabiting crickets, Grylus assimilus and Anurogryllus mutfcus, were found only in A. gundlacht and creek A. evermanni (Table 28). Crickets of the genera Anaxipha and Cyrtoxipha are small, slender, arboreal (canopy) crickets and these insects were found only in A. evermanni and A. stratulus. Knowledge of the habitats of these crickets also correlates with the vertical distribution patterns of the three species of Anolis.

Veliids and saldids are water surface and shore inhabiting bugs respectively. They were found in stomachs of creek A. evermanni and are proof that these lizards feed near the stream. Interestingly, Seven saldids and three veliids were also found in specinens of &. undlachi which further implies a terrestrial habitat for this species,

The large. bulky, herbivorous planthoppers (Cixiidee to Fulgorot- dea, Table 28) were most commonly found in arboreal A. evermanni and A, stratutus and parallel findings with the vertical transect sampling experiment (Subtask 1).

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In surmary, the following conclusions were derived from this

study:

* The four species of Anolis are probably not prey specific.

The apparent food specificity observed by various species of

Anolis is due to coincidental vertical and horizontal (forest,

Stream) distribution patterns of lizards and prey.

* Male lizards generally eat greater anounts of food than their

females of the same season, but females ingest greater nunbers

of prey resulting in a greater diversity of taxa.

Anolis stratulus, the most abundant lizard in the forest ap-

pears to be the only species which is food limited during the

?ry Season compared to wet season,

Ants, planthoppers, Tepidoptera larvae, and spiders appear to be the most important prey taxa.

5.4.2 Amphibians and Reptiles

Subtask 1. Species Inventory

AI] spectes known to inhabit the tabonuco forest near E1 Verde, are listed in Table 31. Information was compiled from existing Vite ature (Turner and Gist 1970, Rivero 1978), specinens in the El Verde Field Station collection, and from surveys conducted during Phase 1. No new species were observed fn the study area during Phase I, and all species previously known to occur within the forest were found during the course of field studies with the single exception of Anolis occultus.

The presence and general abundance of comon species appears to be unchanged since the intensive studies performed in the area during ?the 1960s. Differences in abundance estimates discussed in Subtask 4 are the results of different census techniques and probably do not reflect changes in actual abundances.

Subtask 2. Presence and Relative Abundance of Amphibians

Results of amphibian abundance surveys conducted during wet season 1980 are presented in Table 32. Eleutherodactylus coqui was by far the most abundant species observed in all four sampling locations.

E, wightmanae, 2 smaller spectes, was second in abundance and was the

only other species found in all areas. Although E. hedricki was heard

calling within each of the four sample plots, its densities were suf-

ne.

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Table 31. Vertebrates recorded from thy L1 Verde Study Area.

Status

Class: faphibia

Oréer: Salientian

Fanity: Butontdae

Giant Toad? (Bufo marinus)

Fonily: Leptodacty fase

2

Codui (Eleutherodactyus coqui) abundant (40,000/ha)

Yottled Coaut (e, eneidae)

Tree-hote Cogut (£. hedricki)

Forest Coqui (E. portortcensis)

Ground Cogut (E Frchamnde)

wrinkled Coaut (E~ wightmanae)

Wite-1ipped Frog (Leptodacty!us

Class: Repeitia!

Order: Squamota

Suborder: Lacerti Via

Fanny: tektoniage , ;

Upland Gecko (Sphaerodactylus Klaubert

Connon Dwar Geka? (Sauer teptsy

Family: Iguanidae

Lagartjo Verde (Anolis evermann}

Puerto Rican Giant Anole (hcuvieri)

Yellow-bearded Anote (A. gundlachiy~ abundant (2,000/ha)>

Prony" Anote (A. eecultaa) rare

Lagartijo Manchado abundant (25,000/ha)

Family: Anguidae

Culebra de Cuatro Patas (Diploglossus pleet)

Fondly: Aaphisbsen\ dae ?

Culebra Ciega (Anphisbaena caeca)

Suborder: Serpentes

Family: Boidee 4

Puerto Rican Tree Boa (Epicrates inornatus) rare

Family: Colubridae

Ground Snake (Alsophis portoricensis

Class: aves?

Order: Falconi fornes

Fanily: Aceip\trigae

fed tatiea Honk (Butea araicenss)

Broad-winged Hawk (Buteo platyiterus)

Sharp-shinned Hawk (Rccipiter strigtes) rare

Order: Colunbi fornes

Feaity: Columpidae) 4

Red-necked Pigeon (Colunba squanosa: abundant

Tenaida Dove (Zenaids auritay

Ruddy Quail-Dove (Geotryaon montana)

ris)

oir

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Status

Order: Psittact formes

Family: Psittactdae

Puerto Rican Parrot (Arazona vittata)*" rare

Order: Cuculiformes

Fanity: Cuculidae

Puerto Rican Lizard Cuckoo (Saurothera viefMoti)

Order: Serigifornes

Fanity: Strigidae

Puerto Rican Screech Ow? (0

Order: Apodi formes

Fanily: Trochil idee

Puerto Rican Enerald (Chlorostilbon maugaeus)

Grecn Mango (Anthracothorax viridis) rare

Order: Coract formes

Fanily: Todidae

Puerto Ric

orcer: Pietfornes

Family: Pieiéae

Puerto Rican Woodzecker (Melanerpes portoricensis)

Order: Passeriformes

Fanily: Tyrannidae

Stolid Flycatcher (Myiarchus stolidus) rare

Losgernead Kingbird {Tyrannus caudifasciatus)® rare

Fontly: Mimidae

early-eyed Thrasher (Margarops fuscatus)

Family: Turdigae

fed-legged Thrush (Minocichla plunbea)

Fanily: Vireonigae

Puerto Rican Vireo (Vireo latineri) rare

Black-whiskered Vireo (V. ale{Toquus) abundant

Famsty: Parulidae e

Black and White Marbler (niotéltg varia)

Porula Warbler (Paral anerteana)® ?ey

Cape May Warbler (Dendroica tigrina)®

soci throated Blue WaroTer (Q caerulescens)®

Prairie Warbler (D. discolor

Fife Woods uarbler {Oe angelae)* rare

Ovenb iva (Seturus aurocasttTes

Louisiana haverthrush (Seturus noveborgcensis)®

Anerican Redstart (Setophaga rutict

Fanily: Coerebidae

Bananaquit (Coereba fla

iy: Thraupidae

Blue-hooded Euphonsa (Euphonia. musica rare

Stripe-headed Tanager (SpindaTis. zena)

Puerto Rican Tanager (Nesospingus: speculiferus) abundant

Fanily: Icteridae

Black-cowled Oriole (Ieterus dominicensis rare

Family: Fringi Vise

Puerto Rican Bullfinch (Loxigitia portoricensis) nudipes)

Tody (Todus mexicanus) abundant,

a) abundant,

-ne-

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Status,

Class: Marmatia|

Order: Chiroptera

Fonily: PhyNostonatidae

Greater AntiTTean Long-tongued Bat

(tonophy lus, redeon

fruit Oat (Artibeus jar abundant,

Re Fruit Sat (Sten

Brow Flower 831

Order: Rodentia

Fani ly: Muridae

foo? Rat (Rattus, rattus) abundant

Order: Carnivora

Family: Viverridae

Stoll Indian Nongoose (Hernestes auropunctatus)

"common and scientific names from Philibosian and Yntema (1977)

Buocioright anc Stenart (persone? communication 1982)

Shurner and Gist (1970)

4visted as endangered (U.S. and Puerto Rico)

Scomnon and scientific mazes from Bond (1971)

Srecher (1370)

TSurmer resident

Syinter resident

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ficiently sow that it was only recorded along two of the four tran=

sects.

Preliminary population density estimates were obtained by Larry Woolbright (SUNY Albany) who, using multiple mark and recapture surveys in the study erea, calculated an estimate of 2,900 adults/he and ® total population density of coquis (adults, subadults, and juveniles) of 43,500/ha (Larry Wolbright, pers. com.). The high density and generally uniform distribution of this species throughout the forest (at and near ground Tevel) strongly indicate the importance of this species in the nocturnal food wed.

Subtask 3. Anolis food Habits

Detailed analyses of gut contents were conducted on the four forest species (Anolis qundlachi, A. evermanni, A. cuviert, and A. Stratulus). The results of these analyses are presented in section 5.4.1, subtask 3,

Subtask 4. Anolis Population Densities

The initial program design provided for relative abundance Studies based on minimum population density estimates (Overton 1971). Population density studies had not been planned because of the existing information provided by Turner and Gist (1970) on what was ?then thought to be the two most common species, Anolis gundlachi and A. evermanni, The discovery of large numbers of A. stratulus in the forest canopy (see subtesk §) part way into Phase I demanded absolute Population density studies because of the potential importance of this species in terms of biomass and overall trophic structure. Data on relative abundance and density estimates for A. stratulus are presented below.

2, Minimum population densities of the three comon anole species (Anolis gundlachi, A. evermanni, and A. stratulus) were obtained by Frye's strip census technique (Overton 1971). Because of known differences in approachability for different anole species

(Heatwole 1968), separate mean distances were calculated for each

slat

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Species in the overall calculation of relative abundance. Results are presented in Table 33,

?Anolis gundlachi was the most abundant and A. evermanni the Second most abundant species in the study area during wet and dry Seasons, based on ground level transects. Seasonal trends were consistent among plots. A. evermanni and A. stratulus increased in relative abundence during the dry season at the expense of A. Gundlachi. Vertical studies (Subtask 5) suggest that these Gifferences result in part froma shift in the vertical distribution of Vzards from the canopy toward ground level rather than indicating 8 change in absolute population densities.

A. cuvieri was observed twice along transects and was infrequent Ty encountered in the course of other Phase I field studies. Nine of ?the 10 individuals sighted were females and all were seen near ground evel during the wet season suggesting that egg deposition may be the Primary stimulus for coming to ground level. The species normally inhabits the forest canopy (Rand 1964, Williams 1972).

Relotive ebundance data are in general agreement with most. previous studies conducted in or near the study area (Rand 1964, Turner and Gist 1970, Schoener and Schoener 1971, Lister 1981), but differ from those of Mol] (1978) who found A. evermanni to be relatively more abundant than A. gundiacht in sinilar habitat.

Because vertical surveys showed that A. stratulus is primarily a canopy species within the forest, the relative abundance data obteined here are chiefly of value in demonstrating the general homogeneity of ?the study area, providing baseline estimates for future studies, and relating present conditions to previous research.

b. The results of multiple mark and resight surveys of A. Stratulus conducted at the tower are presented in Table 34. Reasonable numbers of recaptures and high recapture success produced relatively accurate population estimates. The three methods used to calculate population densities (Jolly-Seber, Manly-Parr, and Lincoln Index) provided similar estimates of 32.5, 32.0, and 35.0 lizards respectively (Table 35).

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Table 33. Relative abundances of the three common anoline Vizard

?species during wet and dry season surveys* at four ran=

domly selected locations within the study area

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Transect, Anolis Anolis Anolis

No. guadlachi evermanni stratulus

Wet oy Wet ory Met or

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2 eer ont Ver 25 - ?an

3 90x 6a 3B n 6

4 est 136 - vt

Mean 86: 6a we oat a oe

*Wet Season = Septenber 1980, Ory Season = January-March 1981

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Table 34. Mark and resight data for ary season 1981 tower surveys.

DRURY anc

Dates (1981)

ts

Total Sight ings 3 ? 20 2

Total Resighted 7 B 6 18

Percent Resighted - ? eo: te

Table 35. Population censity estimates obtained by three standard me-

thods for Anolis Stratulus at the ?ower during the 198) ary

Season (February - March

Methods of Population

Analysis Population Estimates* Average Estimates* Density

Manly - Parr 28.3 5 5.5 32.0 + 85 2.5ye

35.6 $18

dolly - Seber 29.0 + 6.1 32.5 + 88 2.6/m"

33.9 Fe

Lincotn Index 32.7 $8.6

38.0 $14.9 35.0 13.0 2.6/n°

38.2 415.6

* Including 95% confidence interval

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Because of the vertical orientation of the transect, it was a point sample with respect to areal density. Population densities were estimated on the basis of maxinun (and alternatively the mean) sight and resight distances to lizards observed during surveys as the radius of a circle around the tower and dividing the population estimates by the area in square meters within this circle. Density estimates range from 2.5 to 7.0 Vzards/a® (25,000 to 70,000 lizards/ha). Additional surveys are planned to obtain wet season estinates. In the meantine ?it 4s prudent to use the Tower estinate until supporting data can be obtained. Even at that level (25,000/ha) it fs the highest Tizard Population density known, exceeding the density estimates of 20,000/ha obtained for A. pulcheltus by Gorman and Harwood (1977) at 2 nearby lowland site in eastern Puerto Rico,

The high densities appear to be the consequence of A, stratulus ?inhabiting home range territorial volunes layered within the canopy rather than subdividing the habitat on a strictly areal basis. Supporting evidence for this was obtained by recording the vertical range of movenent of individually marked lizards which were observed a minimum of 10 tines. Males, females, and juveniles el] appear to confine their activities to a vertical range of five to six neters (Figure 15 and 16).

Although these overlapped considerably, none of these spanned the total vertical range of available habitat (10 to 22 m) in the forest canopy. Occasional movements outside the hone range were usually toward ground level, accounting for the limited sightings of this Species by ground-based observers. None of the lizards had hone ranges extending below the 5 m level (Figures 16 and 16).

The high population density of A, stratulus in the forest ?indicates that the species is an important component of the diurnal food web and suggests that a considerable anount of foraging takes place in the forest canopy. Canopy foraging is also «indicated by the gut analysis studies (section 5.4.1, Subtask 3). The high abundance of this insectivore suggests that it my play an important role in controtling herbivorous insect abundance in the canopy, thus playing a potentially significant role as a regulator spectes in the forest ecosystem (Glasser 1979).

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Adull Females

No. of Observations

Figure 15. v

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20.

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Subtask 5, Vertical Distribution of Anoline Lizards

Surveys conducted at the tower demonstrated differences in ver= tical distribution among the three comon forest anoles. Wet season (Septenber - Noverber) 1980 and dry season (January - March) 1961 results are presented in Figures 17 and 18,

Anolis gundlachi was rarely observed more than 5 m above ground level during either season. The few sightings made above this level were males and were made during the late afternoon, suggesting that these individuals may have been moving toward their night resting Jocattons. The species is normally a trunk-ground forager which explains its confinement to the lower levels of the forest.

Anolis evermanni 1s distributed throughout the vertical extent of the forest, but appears to be more conmon at ground level. This may be due in part to the difticulty of detecting green lizards in the dense canopy foliage. Although seasonal differences in verticel distribution were not detected, data obtained from horizontal transect sampling at ground level (Subtask 4, section a) suggests that they nay exist.

Anolis stratulus was found most abundantly in the forest canopy ?turing both seasons. Only 2 small percentage (approximately 10%) of the total observations were below § m, the zone predominantly occupied by A. gundlachi and A. evermanni. Significant differences (p 0.05) were found between wet and dry season distributions using the Kolno-sorof-Smirnoff test. During the wet season activity 1s concentrated within the canopy. During the dry season the vertical distribution is wore dispersed into the high cenopy and toward ground level. Pre-Viminary gut analyses (Section §.4,1, Subtask 3) indicate that less food my be taken at that season, suggesting that the change in dis-tribution could be related to foraging. The majority of lizards observed below § m were females who may have been coming to ground level to deposit eggs. Previous researchers in thé forest. have been confined to ground level. Although some (Rand 1964, Lister 1981) have attempted to census lizards throughout the vertical extent of the forest, most observations have been made below 5m. This is undoubtedly the result of poor light conditions, distance, and the fact that

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many lizards in the canopy perch on the upper sides of branches and

Teaves and cannot be seen from below. These limitations have lead to

?the erroneous conclusion that most anoline lizards inhabit the lower

few meters of the forest (Rand 1964, Lister 1981). Rand (1964) specu-

lated that A. stratulus might occur high in trees but was unable to document this.

The discovery of A. stratulus as a canopy species present at high population densities (Subtask 4) is an important aspect of overall trophic organization. Vertical stratification as a means of habitat partitioning has been demonstrated for other lizard communities at other locations in the neotropics (Andrews 1971, Schoener 1968) in. addition to the basic studies conducted in Puerto Rico (Rand 1964, Schoener and Schoener 1971). The discovery of A. stratulus as an abundant canopy species in the rain forest has important implications with respect to ecosystem trophic structure. The vertical stratification of lizard species indicates the probable significance of vertical structure in the overall food web, and provides additional information relevant to the controversy concerning the interrelation ship between anoline lizards and insectivorous birds in West AntiTTean forests (Moermond 1961 in press, Wright 1981, Waide and Reagan 1962).

Subtask 6, Anolis Population Growth and Turnover Rates

Anolis stratulus branded during multiple mark and resight studies at the tower (Subtask 4, Section b) are providing information on the Growth vate and population turnover of this species in the forest. Marked individuals will be recaptured periodically to obtain weight ?and length measurenents for comparison with data collected at the time of initial capture, Population turnover data will be estimated by noting changes in the relative proportion of marked to unmarked individuals through time. Additional studies may be undertaken, but ?these are presently considered peripheral to the.main thrust of Phase II research.

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5.4.3 Birds

Subtask 1. Population Density

Transect Counts - Figures 19-21 show seasonal changes in Population density for the 13 most common bird spectes at EI Verde. Each graph represents the monthly sum of population densities calculated from sight, song and call detections and indicates a ?minimum density. Data from all plots were combined to estimate densities.

Figures 22-25 show separate population densities in each plot for four species common at £1 Verde. Densities calculated from detect fons by sight, song and call are shown on separate graphs in order to Genonstrate seasonal fluctuations in population estimates that are due to changes in activity.

Mist Nets - Table 36 gives the nunber of individual birds captured in mist net surveys of plots 1-4 during Septenber-October 1980. The Ruddy Quai1-Dove was the species most commonly captured in 21) study sites and far out-nunbered all other species except in plot 4. Samples from plots 2 and 4 had equal numbers of species (7), even ?though sample size was mich greater in the former (31 and 11, respectively). The sample from plot 3 had § species and that of plot 1 had 4

Spot Maps - Table 37 gives the results of spot map and transect censuses from June-July 1981. Plot 3 was contained within the gridded area used for spot mapping (see Figure 2). Densities from transect counts represent the greater of 1) double the nurber of singing males detected or 2) the sum of detections from sight, song and call (Emlen 1971). Thirteen spectes were found in spot mapping and only nine in transects, @ result that is not unexpected considering the greater area (9.0 vs 7.2 ha) and amount of time (10 vs 2 days) spent in spot ?map counts. Population densities of two species (Stripe-headed Tanager and Puerto Rican Tanager) could not be determined in spot map Censuses since these birds were not singing at the time of the counts.

Table 38 compares densities from spot map counts conducted by Recher (1970) in April-May, 1964-66, with transect censuses performed in April 1981 during the present study.

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Figure 19. Seasonal changes in population densities from transect.

counts at ?1 Verde.

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REO-LEGGED THRUSH

ao ?.

BLACK-WHISKERED VIREO

Figure 20. Seasonal changes in population densities from transect counts at E1 Verde,

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RED-NECKED PIGEON

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STRIPE-HEADEO TANAGER

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PR. TANAGER

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PR, BULLFINGH

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Figure 21. Seasonat changes in population densities from transect

counts at &1 verde.

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RED- NECKED PIGEON

Figure 22, Seasonal changes in abundance of Red-necked Pigeons in four

plots at EI Verde. Plot 1 = (O--), plot 2= (@?), plot

= (O?-), plot 4= (

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PUERTO RICAN TOOY

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Figure 23. Seasonal changes in abundance of Puerto Rican Todies in

four plots at 1 Verde.? Plot 1 = (o =

plot 3= (G?+), plot ¢ = (me-n-).

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BLACK -WHISKERED VIREO

Figure 24, Seasonal changes in abundance of Black-whiskered Vireos

in four plots at 1 Verde. Plot 1." (@

(@?), plot 3= (O?), plot 4

)s plot 2

7138

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BANANAGUIT

sign

Figure 25, Seasonal changes in abundance of Bananaquits in four plots

at El Verde. Plot 1 = (O--), plot 2= (@?), plot

(0-9, plot $= (me),

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Table 36. Number of captures and capture rate for various birds

species in Plots 1-4.

_ ee

- Plot 1

Ruddy Quail-Dove 9

Puerto Rican Emerald 2

Puerto Rican Tody °

Pearly-eyed Thrasher 1

Reg-Tegged Thrush °

Black-throated Blue Warbler 0

Ovenbire o

Bananaquit, 3

Stripe headed Tanager o

Plot 2 Plot 3 Plot 4

16

2

1

°

o

1

°

Total

?4

6

1

Puerto Rican Tanager © 6 o 9 6

Total captures 6

Number of nets n

Number of days 3

Captures /net-day 0.45

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Table 38. Conparison of population estimates from territory mapping

(1964-66) and transect counts (1981) during April-Hay at

£1 Verde. Data fron 1964-66 from Recner (1979)

INDIVIDUALS /HA

1964 1966 __1981

Puerto Rican Emerald 0.4 0.4 ne)

Ruddy Qual? Dove 0.6 0.5 04 03

Red-necked Pigeon 0.4 0.3 03 582

Puerto Rican Tody 19 2.0 2200 27

Pearly-eyed Thrasher 12 1.6 06 08

Bananaquit 13.3 12.0 ee 132

Black-whiskered Vireo 3.3 3.0 1816

Puerto Rican Tanager 0.7 1.0 os 47

Stripe-headed Tanager oz 02 02 09

Puerto Rican Bulfinch O86 08 02 0

nae

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Discussion

Absolute population densities are necessary to calculate elemental and energy storage and flow through the food web. Spot or territory maps are the most widely accepted method of determining absolute densities, but they suffer from the disadvantage that they are labor intensive and appropriate only during the breeding season. To monitor seasonal changes in populations or to compare different areas, a more rapid method such as transect surveys is often used to obtain relative densities. The best features of each technique can be exploited by calibrating transect surveys to a spot map count performed in the same location (Holmes and Sturges 1975). This approach has been used in this study.

Density Estimates

Comparison of spot maps and transects from the plot 3 (Table 37) reveals two general differences in density estimation. The transect survey misses several rare species (Hawk, Enerald, Woodpecker, Flycatcher) detected in spot mapping. This is most likely a result of the smaller sampling effort put into transect surveys and the lack of replication as these species were detected in other transects. The most abundant species (Bananaquit, Vireo, Pigeon, Tody) have densities that are higher measured by transect counts than by spot maps. The difference in this case cannot reflect the presence of juvenile birds toward the end of the breeding season since transect values for these four species were determined by doubling counts of singing adult. males. A more likely explanation is that territorial birds sing less and have reduced site fidelity toward the end of the breeding season, resulting in a blurring of territorial boundaries and an underestimate by the spot map method. Spot map and transect counts will be repeated during the peak of breeding in 1982 to see if 2 closer agreement between the two methods 1s possible.

One of the problems of the spot map method is illustrated in Table 37. Not all spectes breed at the same time, and the effort required to perform spot map censuses precludes repeated sampling throughout the breeding season. Puerto Rican and Stripe-headed Tanagers were not breeding when the census was conducted and popula-

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tion estimates could not be made for these two species. Ruddy Quail Doves were singing vigorously at the time of the fcensus (see Figure 19) but all other species were less active than earlier in the breeding season. Spot map censuses must be carefully timed to sample a8 many species as possible,

Teble 38 shows the results of spot map censuses conducted by Recher (1970) from 1964-66 and compares them to transect censuses from 1981. Six of the 10 species studied by Recher (Emerald, Quail Dove, Tody, Thrasher, Bananaquit, Bullfinch) have not changed appreciably in ?abundance, to judge by transects in April 1981 (Table 38) and spot maps and transects in June-July 1981 (Table 37). Three species (Hawk, Woodpecker, Flycatcher) did not appear in Recher's censuses but showed up in the 1981 counts. Four other species (Pigeon, Vireo, to Tanagers) were more abundant in 1981 censuses. Differences in abundance of the Puerto Rican Tanager between Recher's and the present Study are due to the species? habit of travelling in large foraging Flocks which results in extreme local fluctuations in abundance. Increases in calculated densities between 1964-66 and 1981 for the other three species reflect real increases in abundance during this period,

?The general agreement between densities calculated from spot maps and transect censuses suggests that either technique 1s acceptable. Hence, transect densities will be used to calculate nutrient and energy storage. This practice has the advantage of allowing data from ?the peak breeding month for each species to be used to determine density at equivalent times in the breeding cycle. Whenever there is Gisagreement between transect counts and spot map censuses from the Some month, a range of values will be given. For the Ruddy Quail Dove, mist net data suggest a higher density than calculated from other censuses, and this will be taken into account in the nutrient and energy calculations. No other spectes requires such special treatment.

Seasonal Density Changes - The trends shown in Figures 19-21 reflect seasonal changes in activity patterns as well as fluctuations in num ber. In general, birds are more conspicuous when defending territo- ies, feeding fledglings, or foraging in post-reproductive flocks and

---Page Break---

Jess conspicuous during periods of incubation and molt. Despite the fect that seasonal trends are determined by changes in activity and abundance related to each species, a few general patterns are still apparent.

During duly-Septenber 1980, eight of the 13 species shown had their lowest densities of the year. This period follows the peak breeding for the avifauna as a whole (March-June; Recher 1970) and reflects @ diminution of singing ané territorial defense and reduced activity related to molt (Waide, unpublished data). For those species ?that breed only during the spring, the following months should show the greatest population size, although there my be local density fluctuations due to flocking and aggregations around food sources.

Seven of 13 species show their highest densities between December and March. This period reflects increased singing assocfated with territorial defense and the onset of reproductive activities.
Exceptions to this general pattern are usually due to variations in breeding pattern, Ruddy Quail Dove density peaks in June-August (Recher 1970) during the main breeding period for this species.
Benanaquits and Todies show less pronounced peaks extending over mich of the year resulting from non-synchronized breeding in the former and year-round territoriality in the latter (Kepler 1977), The Red-necked Pigeon shows two peaks, the first (Noverber-Decenber) associated with aggregations of foraging birds in the plots and the second (March-June) due to singing males. The density of Pearly-eyed Thrashers shows only a small peak in October as a result of similar activity patterns throughout the year.

Seasonal changes in density for four common species are shown in Figures 22-25. Data from each plot and for sight, song and call detections are shown separately. Each of the four species represents a Gifferent pattern of seasonal density fluctuation based on differences in reproduction and foraging.

?The Red-necked Pigeon shows a single peeked curve for detections by song, with all four plots showing maxima between March and June (Figure 22). Many birds were sighted from Septenber-January in ag-gregations around fruiting trees resulting in the double-peaked curve of Figure 21. These birds are shy and flush noisily at the approach

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of an observer and as 3 result most birds in the census area are de-tected even when they are not vocalizing. Maximum densities of sighted birds in the fall are about the same magnitude as those of singing birds im the spring (1,540 birds/ha) but fall densities Tluctuate greatly as birds move between transient fruit sources. The species can be characterized as having @ sychronous breeding season with habits thet make it conspicuous during the rest of the year.

The Puerto Rican Tody (Figure 23) is an inconspicuous understory bird that is seldom seen without being heerd first. The Tody occupies territories in pairs year-round and both sexes vocalize (Kepler 1977). As 9 result, densities are fairly uniform throughout the year with minor peaks in October, January, and March. Densities decline in the spring a5 the activity of adults is centered around the nest. burrow. Seasonal abundance patterns for all four plots are similar. The species can be characterized as having permanent territories with synchronous breeding (April-July, Kepler 1977).

?The Slack-hiskered Vireo is the only Puerto Rican land bird to migrate from the island after breeding. Singing activity shows a plateau during February-April (Figure 24). It 1s noteworthy that. density values for the different plots maintain a constant relation-ship throughout the breeding season, with plot 4 having the most individuals and plot 1 the fewest in all months. The species has synchronous breeding and is a summer resident.

The Bananaquit's extended breeding season is reflected in the prolonged singing activity seen in Figure 25. A pronounced peak in song occurs in October-November and 1s followed by a peak in calling individuals (fledglings begging?) in January. Biaggi (1955) states thot Bananaquits nest throughout the year, but Figure 25 suggests sone seasonality in breeding activity. Wetmore (1927) also found the species to breed year-round with most occupied nests occurring between February and June. The species can be described as having asynchrous breeding with multiple broods.

Subtask 2, Feeding Behavior

Figure 26 shows the proportion of observations at different

heights for 10 common species at El Verde. The species are arranged

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50 that members of the same trophic level are adjacent for easy compa-

ison, Hence, nectarivores (Emerald and Banenaquit), vertebrate

Predators (Lizard Cuckoo), frugivore/granivores (Pigeon and Quai]~

Dove), insectivores (Tody), omnivores (Vireo and Tanager), and

frugivores (Tanager, Thrasher and Thrush) are all grouped together.

Preliminary foraging data are sumarized in Table 39. Field work

?in this subtask is stil] underway and will be augmented by 2800 unpu-

blished foraging observations by Cameron and Angela Kepler and

information from the literature.

Discussion

Data from Phase I studies can be used to give a preliminary idea Of feeding behavior. Accumation of information under this subtask 4s Stil] underway and will continue in Phase 11.

Only two species, the Puerto Rican Emerald and the Bananaquit, have been observed to take nectar in their diet (Table 39). The Bananaquit forages from ground height to the canopy, but concentrates fon mid-levels. The Emerald specializes on undergrowth flowers (Figure 26). The Puerto Rican Lizard Cuckoo, a predator specializing on reptiles and amphibians (Wetmore 1916), ranges throughout the forest. The Puerto Rican Tody, an insectivore, forages principally under 10 m while the Black-whiskered Vireo takes both insects and fruit above 10 m. The Puerto Rican Tanager also consumes both fruit and insects but ranges more widely in the forest. Two colunbids take both fruit and seeds, but one (Red-necked Pigeon) specializes on the fruits of canopy trees while the otier (Ruddy Quatl-Dove) searches for fallen fruits and seeds on the ground. All of the pairs or trios mentioned show at least some vertical stratification between one another.

?Anong other frugivores the situation {s quite different, The Pearly-eyed Thrasher and Red-legged Thrush consume mostly fruit (Wetmore 1916) and overlap broadly in their vertical distribution,

?The Thrush 1s less common in dense forest and occurs more often on the round where the Thrasher is never found. Insufficient data exist for the rarer frugtvores (Puerto Rican Woodpecker, Stolid Flycatcher, Stripe-headed Tanager, Puerto Rican BulTfinch) to describe their

foraging behavior,

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Table 59. Preliminary data on diet of 14 bird species.

Nunber of Observations

Insect___Nectar__Lizard

Red-necked Pigeon 2 ° ° °

PAR, Lizard Cuckoo ° ° ° 1

PR, Enerala ° 5 2 °

PAR. Tody ° 2 ° °

P.R. Woodnecker ° ? ° °

stolid Flycatcher ° 3 ° °

fed-Tegyed Thrush 3 , ° °

Slack-whiskered Vireo ° 4 o °

Black-and-white Karbler ° 1 ° °

Black-throated Blue Karbler ° 1 ° °

Parule karbler ° 3 ° °

Anerican Reestart ° 2 ° °

fananaguit 1 0 10 °

P.R, Tenager 5 2 ° °

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Subtask 3. Diet and Weight

Table 40 gives the number of birds color-banded during population studies and the number of stomach samples obtained to date from sacrificed birds and emetic chemicals. Analysis of stomach samples is Underway to augment foraging observations in describing diets for each species. The comprehensive study by Wetmore (1916) and monographs on the Benanaquit (Biaggi 1956), Red-legged Thrush (Rolle 1965), and Puerto Rican Tody (Kepler 1977) provide basic material for structuring the food web.

Tables 41-42 give sample sizes, means and their standard errors for weight, wing chord, tarsus length, and bill length, depth and width for birds caught in Phase I studies. Whenever possible, male and fenale-plunaged birds are shown separately.

The weights given in Table 41 will be used to calculate nutrient and energy storage upon completion of the elemental analysis. Each bird collected was plucked and the proportion of body weight in feathers and tissue was determined as were dry and wet weights for each component. This information will be used to calculate storage in the avifauna and nutrient and energy turnover due to molt and population turnover,

Subtask 4, Materials Discharge

Because of difficulties in perfecting methodologies for collecting feces from caged birds without contamination, this subtask has not. been completed. Changes in experimental design witl be implemented in Phase 11 and will lead to completion of this task at an early date.

Subtask 5. Elemental Content

Forty-five individuals of nine bird species were collected and analyzed under this subtask. In addition, sone fruits commonly found in the diets of birds have also been analyzed. Results of these analyses are presented in 5.2.1.

5.4.4 Mammals

No mouse-sized manmals were trapped in 80 trap nights, and none

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have been observed in rain forest habitat in the vicinity of the El

Verde Field Station, The common house mouse (Mus musculus) is found

near dwellings and in drier habitats elsewhere in Puerto Rico, but apparently 1s restricted from wetter areas.

Both the black rat (Rattus rattus) and Indian mongoose (Herpestes auropunctatus) were live-trapped within the study area. Two mongooses and 23 rats were trapped during a total of 175 trap nights and 150 trap days for trap success rates of 1.3 percent and 13.1 percent respectively. These results are consistent with general observations of both species. The Indian mongoose is occasionally seen foraging during the day, but the black rat is comonly observed on vines and in trees at night. The rain forest appears to be marginal habitat for ?the mongoose which reaches much higher densities in grassy and brushy lowland habitats in Puerto Rico and elsewhere in the West Indies (Seaman 1952, Pimentel 1955, Seaman and Randal] 1962).

Three species of bats were captured during field surveys. Artibeus jamaicensis, a large frugivorous species, was the common species netted. Stenoderma rufum, a small frugivore, and Monophylla rednani, a nectarivorous species were less common. Artibeus was captured only in forest openings and usually at a height of several meters while the other two species were captured only in horizontal nets less than two meters above the ground and within the forest. A fourth species, Erophylla bonbifrons, is also reported from the ET Verde rain forest (Tamsitt and Valdivieso 1970) but was not captured during our field studies.

Abundance estimates were not obtained for any mammal species.

The black rat and large fruit bat (Artibeus jamaicensis) are potentially important species in the movenent and storage of energy and nutrients through the animal community because of their relatively large size, high metabolic rate (compared to the more abundant poikiTotherms), and probable high biomass,

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6.0 INTEGRATION

Nutrient cycling and energy flow are basic processes which characterize all ecosystems (Mason 1977). Solar energy is the ultimate force which drives energy flow, and energy is dissipated from the system without being recycled, Nutrients, however, cycle among ecosystem components. Inputs and outputs of many nutrients (elements and simple compounds) can be Targe or small, and their magnitudes in major ecosystem compartments (Figure 1) may directly influence ecosystem structure, Reciprocally, the storages in different compartments influence overall fluxes. It therefore follows that external factors which alter energy flow and elemental input or directly change conpartment sizes may have @ profound impact on overall ecosystem structure and processes.

Ke are attempting to develop a comprehensive description of ecosystem structure and function in terms of compartments and principal pathways of movenent among them in order to understand how tropical vain forests might be affected by exogenous influences. Potential ?impacts resulting from eneray development are being emphasized, This first phase of the Rain Forest Cycling and Transport Program has focused on expanding the information needed to elucidate these patterns and processes for the rain forest ecosystem near £1 Verde, Puerto Rico. The following sections consider the status of our present knowledge of cycling and transport processes, describe aspects of ecosystem organization relevant to these processes, and discuss the need for additional research on specific portions of the ecosystem.

6.1 Ecosystem Organization

A greatly expanded although largely qualitative food web description was developed in Phase I (Table 43). Given existing food web comPlexities only @ few selected pathways could be quantified for eneray flow and nutrient transfer. We have identified many of the major taxonomic groups comprising the several consumer levels and analyzed samples for elemental composition and caloric content. With few exceptions, chemical values do not differ greatly from those esta blished for related taxa from other biotic regions.

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Table 45,

Fey species and species groups in the trophic structure of the

fy Verde vain forest. whi

nvere identified in "hace T.

snails

rats.

Rucdy Quai ove (Geotrye:

montana), Red-necked Pigeon

(olunbs? squanosa), Red- iegoed

Thrush (Mino punbea)

Bananaguit (Coereba fiaveola),~

Puerto Rican emerald (Chlare~

stitbon naugacus)

Purse fly larvae

(Orosophitidae)

Jeat hoppers (Cicacellidse), -

plant hoppers (Fulgoroidea),

walking sticks (Phasmatidae)

crickets (Grylliaae!, noth

Tarvae Moctuidar, Arctiidae,

Nicroiepidoptera)

Honey Bees (Apis mellifera), -

otis (Noctuidae, Frevi dae,

Sphingioae), butterflies

(Dismorphia spio)

Giant Puerto Rican Land Snait ~

(caracolus caracolta)

SECONDARY CONSUMERS

Yertebrates

Birds

Reptiles

Puerto Rican Tody (Todus

jexieans)

lizards (Anolis stratulus, =

Anolis: gundlachi}

fruits and seeds

fruits and seeds

nectar

fruits and seeds

nectar

leaves

insects

insects, snails,

Tizards

---Page Break---

Continued table

?Amphibians.

?Arachnids

Centipedes

Insects

Vertebrates

Birds

Reptiles

Aaphibians.

Invertebrates:

Arachni¢s

43,

arboreal frogs (Eleuthero- = insects, snails

dactylus cogui

pseudoscorpions (Menthus sp.), = insects, small

tailess whip scorpions vertebrates.

(Phrynus? paimatus), spiders

(Theraphosidae, Uloboridae,

Pholcidae, Arafeidae, Ctenidae,

Sparassidae)

sites (Acarina) = animal parasites

Giant Centipede (Scolopendra - insects, smal

alternans) invertebrates

beetles (Staphylinidae) = insects, smal]

invertebrates

biting gnats, (Ceratopo- = invertebrates and

gonidae), mosquitoes (Culici- vertebrate para

dae), bots (Calliphoridae), sites

tachinid flies (Tachinidae),

parasitic wasps (Chalcidoidea,

Scelionidae)

TERTIARY CONSUMERS

Faget Ream ttzerd Cuchgo = Tzarde, rate,

Seurothera vieilloti), Red- centipedes

tailed Hawk [Buteo jandicensis)

Vizerds (Anolis stratulus, = insects, frogs,

A, gundtachi) ~ Vizards

Snakes (Alsophis portori- = Tizards, frogs

censis

arboreal frogs (Eleuthero- = insects, snails,

dactylus, coast frog e995

Tarantulas (Cyrtophilgs portoricae),

giant crab spiders (Olius spp.) - predatory insects

---Page Break---

Continued table 43.

Centipedes

Invertebrates:

Arachnids

Crustaceans

Springtails

Insects

HiT fpedes

tailless whip scorpions = lizards, frogs

(Phrynus? paimatus)

Giant Centipedes (Scolopendra - predatory insects,

alternans) * lizards, frogs

MACRODECOMPOSERS.

mites (Oribatidae and other

families) detritus

sow bugs (Philocta richnondi)

detritus

springtails (Entomobryidae) detritus

termites (Nasutitermis cos- - detritus

talis), crane fly larvae

pulidae), moth fly larvae

(Psychodidae), biting midge

Tarvae (Ceratopogonidae)

midge larvae (Chironomidae),

dark-winged fungus gnats

larvae (Sciaridae), fungus

gnat larvae (Mycetophi1 idae),

a1) midge larvae (Cecidony?idae),

soldier fly larvae (Stratio-

myidae), ants (Formicidae)

nil ipedes ~ detritus

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The primary producer level was evaluated as a compartment by estimating litterfall within the study site, evaluating previously un- published data collected in the same area, and by consulting published information (see section §.3). Similarities among different years and ?among different plots at the same site indicate site homogeneity at the chosen sampling scale (1 ha) and suggest a uniformity in annual Vitterfell rates, Seasonal variation was detected and is an important aspect of energy and nutrient transfer from the producer to the deconposer compartment even in the relatively aseasonal rain forest environtent..

?The primary consumer compartment (herbivores) differs in taxono- mic composition fron that found in comparable mainland forests (Fittkau end KTinge 1973). While insects are stil] prominent herbi- vores, monkeys and native rodents are entirely absent, bats are relatively important, there are no predominantly herbivorous reptiles, 16 the insect order Homoptera (planthoppers and leathoppers) is subs~ tantially more important at £1 Verde than in the Anazon rain forest.

Table 43 lists major species and taxonomic groups in the food web of the ?1 Verde Forest. An introduced species, the roof rat, 1s the only odent in the forest, but its importance as a primary consumer has not been determined. Herbivory by vertebrates is almost exclusively

Vimited to fruits, seeds, and nectar, thus influencing the ecosystem by seed dispersal and pollination rather than by direct grazing.

Reliable estimates of the biomass of herbivorous arthropods have not yet been obtained, but preliminary sampling indicates that closely related taxa tend to be vertically stratified. Planthoppers and leaf-hhoppers (sucking insects) are more abundant in the canopy than near ground level (section 5.4.1) Rates of herbivory have not yet been estimated, but in view of the substantial biomass of insectivorous predators supported by herbivorous arthropods, the rates are probably quite substantial.

Higher order consumers (secondary and above) are conplexly inter-related in the food web. Arboreal frogs (Eleutherodactylus spp.) and anoline lizards (Anolis spp.) are the dominant secondary consumers. Unlike comparable mainland rain forests, large carnivores (e.g. Jaguars) are not present. Several insect groups and other large

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arthropods (e.g. tarantulas, centipedes, tailless whip scorpions, etc.) are prominent predators.

In spite of the lack of quantification for many ecosystem com partients, important species and significant aspects of the food web were identified. Feedback loops exist in which large invertebrates (e.g. crab spiders) feed on snall vertebrates (arboreal frogs) while the larger arboreal frogs eat small crab spiders (Formanowicz et al. 1981). Verticel stratification is also an important characteristic of Foraging patterns within closely related taxa (e.g. anoles). Arboreal frogs and anoles, in spite of their small individual size, constitute a significant portion of total consumer biomass because of their extreme abundances (see section 5.4.2). Parallel day and night food subwebs are both important in terns of nutrient and energy movement. between producer and consumer and between primary consumer and secon= ary consumer compartments. This partitioning of the overall food web is incomplete, but supports the basic concept of food subwebs in tropical ecosystems (Gilbert 1980),

The decomposer level remains the least known, both in terms of taxonomic composition and in terms of biomass. Macroarthroped decom- posers include mites, crustaceans, millipedes, springtails, and a variety of insects. Termites, millipedes, springtails, and ants are abundant, but reliable estimates of biomass, population turnover rates, and numbers have not yet been obtained. Decomposition field Studies focused on the pathway from producers to decomposers because of its quantitative importance. The role of soi] fauna, especially large oligochaetes (earthworms), was not addressed during Phase 1. Fittkau end Kiinge (1973) estimate that as mich as one half of the total animal biomass in their Amazon rain forest study area was soil fauna. If our study site 1s comparable in terms of macrodecomposers , earthworms are probably eso important in the forest at £1 Verde.

6.2 Phase II Research

Information acquired in Phase I has contributed substantially to an understanding of cycling and transport processes, and has 2150 provided a basis for determining the scope and emphasis of Phase IT ine

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vestigations. Major taxonomle groups in each ecosystem compartment (Figure 1) have been identified (Tables 43 and 44), but quantitative data on their biomass, population levels, foraging rates, etc. are stil] needed in order to calculate rates of movement for nutrients and energy. This is particularly true of groups which influence the rate of accumulation of nutrients in the system or higher taxa which may regulate ecosystem structure (Glasser 1979).

The movement of energy and nutrients from producers to consumers was not considered quantitatively during Phase 1. Herbivory studies are planned for Phase II which will take into account aspects of ?trophic organization which were identified in the first phase. Ver~ tical stratification, seasonality, and the existence of day and night food subwebs will be considered in the development of the sampling program. Preliminary studies indicate that a substantial amount of total herbivory is performed by sucking insects (e.g. planthoppers and Jeaf-hoppers}; therefore leaf area indices which estimate grazing will be supplenented with appropriate methods to determine the ?importance of sucking insects.

Soil and litter fauna received little attention during Phase I because of manpower Vimitations and logistic constraints but we believe them to be important in terms of overall decomposition proces- ses and overall animal biomass. Obtaining qualitative and quantita- tive information on these groups will be a primary objective of base- Vine dat colectfon during the second phase of our cycling and trans~ port program.

Additional chemical analyses are planned in conjunction with other sampling studies in order to determine rates and patterns of

?movement for selected elerents. Nutrient export will be investigated by establishing a stream gage and analyzing the chemical content of samples taken during periods of normal low flow and during rain fall events. These studies will provide essential: data for addressing questions concerning critical nutrients in tropical rain forest eco-systems (Jordan and Herrera 1981).

Experimental manipulations will also be undertaken during the second phase of this program. Habitat modification within the study site will be of a limited nature and will be approved in advance by

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Table 44. Comson (smostly likely be seen) invertebrates of the vi-cinity of the El Verde Field Station, Taxa are identified to genus or species except for most holonetabolous insects.

Class: Mollusca

Order: Stylonmatophora

Family: Camaenidae

Caracolus caracola

Class: Arachnida

?Order: Acarina

Family: Oribatidae

other fani lies

Order: Araneida

Family: Theraphos dae

Cyrtophilos portoricae

Family: ?Uloboridae?

raniiye Boteidne e

?Micromerys dalei

Foster SexocuTatus

Family?

?aligectenss ottleyi

Family: Sparassidae

?Olius spp.

Family: SaTticidae

several spp.

ly: Araneidae

Leucage regnyi

Order: Amblypygi

Family: Phrynidae

Phrynus palmatus

Order: pseudescarptontda

Family: Menthidae

Menthus sp

Class: Chilopoda

Order: Scolopendramorpha

Family: Scolopendridae

Scolopendra alternans

Class: Crustacea

?Order: Tsopoda

Family: Onisctdae

Philocia richmond?

Order: Decapoda ?

Family: Potamnidae

foi situatifrons

Class: Collenbota

Order: Collenbola

Famfly: Entonobryidae

?Dicranocentropha spp.

Dicranocentruga spp.

Leptdocyrtus spp.

Fa

?162

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Class: Insecta

Order: Blattodea

Family: Glattel? idee

Cariblatta spp.

Epilanpra wheeleri

Plectoptera spp.

Order: orthoptera

Family: Tett igoniidae

Anauloconera Tat icauda

Hicrocentrum triangulatum

?Turpitia rugosa

Famity, GryMidae

Inphicousta caraibes

Tnaphixa? sp.

Anuroary lus mut ?cus

Cyrtoxipha.gundlacht

ryllus.assinilu

oben pp

Grochar is ?spp.

Order: Phasinodea

Family: Phasmatidae

Lamponius sp.

Order: Isoptera

Family: Termitidae

?Nasutitermes costa?

Order: Psocoptera

serval families

Order: Homoptera

Family: Cicadidae

Borencona aguadilla

Family: CicadelTidae

Siboven cofteacota

Yestocephalus macu

Family: Cixtidae

Bothriocera undata

italia spp.

Family: Delphacidae

Uayops occidentalis

Family: Derbidae

Ladella stali

Fanily: Flatidse

Petrusa. spp.

Family:

Colpoptera spp.

Order: Coleoptera

Fanily: Staphylinidae

Family: Pselaphidae

Fomily: Ptilitdae

Fomily: Lenpyridae

Photinus spp.

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Family: Scolytidae

subfamily Ipinae

Order: Lepidoptera

Family: Pieridae

Dismorphia spio

Fanity? Noctatdse

several spp.

?Wicrolepidoptera®

several spp.

Order: Diptera

Family: Tiput

Psychodidae

Culicidae

Ceratopogonidae

Chironomidae

Mycetophilidae

Sciaridae

Cecidonyt idae

Strationyidae

Dol ichopodidae

Phoridae

Drosophitidae

?Anthony? idae

Tachinidae

Order: Hymenoptera

superfaimily Chalcidoides

Family: Scelionidae

Family: Formicidae

Iridomyrmex neTeus

Hyrmelachista ranulorun

Phetaote necrent

Family: Vespidae

Myschcocyttarus cubensis

Family: Apidae

Apis nel}

ifera

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?the Institute of Tropical Forestry of the U.S. Forest Service which has jurisdiction over the land. Larger scale disturbances will be investigated in conjunction with planned U.S. Forest Service manipula tions at nearby locations within the same forest type, Research will alse be conducted in areas of forest with a known history of distur- bance (e.g. plantations, land slides, successional areas). These should provide relevant information on the nutrient content, biomass, food wed structure, etc., which will enable us to evaluate the impacts of different types of disturbances of natural rain forests, and will allow us to evaluate long term aspects of disturbances without having to wait for several years before sampling.

The overall program for this next phase of research will expand upon Phase I by continuing to gather baseline information on mature natural forest. Phase II studies will be more quantitative and will Focus on key pathways and major food chains. Experimental manipula tions are an important aspect of the Phase II effort and will enphasize the evaluation of impacts which may result fron implementa~ tion of various energy development alternatives on natural tropical rain forests.

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7.0 PERSONNEL AND ORGANIZATION

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9.0 APPENDIX 1

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10.0 KNOW EDGEMENTS

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