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Network Analysis of Trophic Dynamics
in South Florida Ecosystems
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FY 96: The Cypress Wetland Ecosystem

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EXECUTIVE SUMMARY

A 68- component budget of the carbon exchanges occurring during the wet and dry seasons in the cypress wetlands of South Florida has been assembled. These networks of exchange will serve as independent benchmarks against which the performance of the ATLSS multi-model, now under construction, will be assessed. During the construction of these networks, it soon became clear that the received wisdom, that these systems are driven by cypress litterfall, is simply not true. Less than half the carbon reaching the higher trophic levels has spent any time in the form of detritus. Production by the understory of vines, epiphytes and aquatic vegetation play the key roles in sustaining the system, and phytoplankton is especially important during the dry season. The structure of the lower trophic level ATLSS module for the cypress wetlands will need to be revised in the light of these new findings.

The middle trophic level fish and amphibians appear to exhibit the highest trophic efficiencies found in the cypress ecosystem. Taxa at either end of the trophic chain appear less efficient by comparison. The result is a peak in trophic efficiency at trophic level four. The trophic levels of most taxa do not change appreciably between seasons. Most dietary replacements occur at the same trophic levels. In fact, the entire trophic structure does not change much between seasons, although the overall system activity during the dry season falls by some 25%.

One may employ the contributions by the various taxa to the overall measure of system ascendancy to create an index of that compartment's "intrinsic value" to overall system performance. These new criteria nicely spotlight the potential values of rare and endangered species, such as the Florida panther, to system functioning.

Relatively little cycling takes place in the cypress ecosystems, even by comparison with physically more open systems, such as the Chesapeake estuary. What recycle as does occur, however, is exceedingly complex. In particular, the predation on eggs and juveniles of higher trophic elements by lower level species complicates the cycling structure enormously and provides tens of millions of new pathways for recycle. Such "ovi-predation" has been neglected in most trophic budgets, but it could be of enormous significance in forecasting the results of system impacts.

Finally, ecologists are accustomed to thinking that the norm for this ecosystem occurs during the wet season, because water level appears to be the limiting factor for the dominant vegetation, the cypress trees. Network analysis reveals, however, that the system is actually somewhat more organized during the dry season. Viewed with this as background, the high water levels of the wet season appear more in the light of a defining stress to the ecosystem.

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1. RATIONALE

A primary goal of coordinated research on South Florida's environmental resources is to understand those communities as whole ecosystems. Toward that end, the Across Trophic Levels System Simulation (ATLSS) project is an attempt to simulate the interactions of the various elements of wetland biotic communities within the framework of a single, encompassing computational scheme.

The resulting ATLSS model is one of the most complex and sophisticated models ever attempted. It will consist of simulation modules of varying, and often very high complexity that represent the important components of all the wetland ecosystems of South Florida. It follows that the output from ATLSS will be exceedingly complicated, and it may not be a straightforward task to elucidate the causal origins of any particular model behavior. Such uncertainty could become problematical, especially if the initial trials of ATLSS should behave "pathologically" (as is highly probable during the initial runs of such a complex model). Even should outputs not appear unrealistic, the difficulty remains that there exist no precedents for evaluating how well such a "multi-model" performs as an analog of the real system. I.e., there are no set protocols for "calibrating" such complex simulations. ATLSS, therefore, requires a partially independent benchmark against which one may gauge the plausibility of its outputs; and, towards that end, ATLSS investigators have chosen to create a suite of trophic flow networks that estimate material exchanges in the ecosystems being modeled. These will serve as calibration standards. In addition, these networks will be analyzed by a set of quantitative methods called Network Analysis (NA) that will serve as a guide for calibrating and debugging the initial modeling trials.

Trophic flow networks are graphical and mathematical depictions of the answers to the questions, "Who eats whom, and by how much?" Typically, diagrams of flow networks are comprised of boxes that represent the major components of the ecosystem. The boxes are connected by arrows, which indicate the transfers of material or energy between the components. Usually, each arrow is labelled with the magnitude of its transfer as averaged over a prescribed period of time.

Accordingly, the University of Maryland contingent of ATLSS investigators is assembling very detailed networks of carbon exchanges as they normally occur in the ecosystems of the South Florida wetlands. Networks consisting of some 60 - 70 important compartments are being estimated for each of four habitats, using existing data and ongoing field work. Separate networks for wet and dry seasons are being created for the ecosystems of the forested wetlands, the graminoid marshes, the mangrove estuaries, and the shallows of Florida Bay. Each network will be a snapshot of the trophic flows and biomasses as averaged both over the hydroperiod in question and over the spatial domain of that particular biotope.

Analyses are to be performed on the resulting networks at several scales. The key questions that can be answered for any fully-quantified trophic network include: (1) To what extent does each taxon depend upon (or contribute to) all other taxa over all trophic pathways, both direct and indirect? (2) What are the efficiencies with which material is being transferred up the trophic ladder? (3) What are the pathways by which material is being recycled within the system? and (4) What is the current organizational status of the ecosystem? Any or all of these answers can be used to debug an ATLSS model that is not performing realistically.

Below, we present the estimation and analysis of the first of these four habitats -- the cypress wetland ecosystem. In the ensuing two annual reports we will present the corresponding results for the networks of Florida Bay, the estuarine mangroves, and the gramminoid wetlands (or Everglades proper.).

2. STUDY AREA

2.1 Physical Characteristics

The 295,000 hectare wetlands of the Big Cypress Natural Preserve and the adjacent Fakahatchee Strand State Preserve in southwest Florida have been described by the US Forest Service (1996) as a flat, gently sloping limestone plain. During the rainy season (June through September) water flows slowly southward over this plain into the mangrove swamps bordering the Gulf of Mexico. This flow rate, however, is slower than what occurs in the sheet flow that originates from Lake Okechobee and flows southwestward through the (mostly) Cladium-dominated (gramminoid) prairies. During low water periods there may be no discernible flow through the cypress wetlands. In places, the flow of water has cut channels into the limestone, allowing deep organic soils to develop. These channels, or drainage sloughs, are occupied by tall, dense, elongated swamp forests that stand out on the horizon in contrast to the open terrain that borders them. The local term for this type of elongated swamp is "strand."

Another type of deepwater, cypress-dominated swamp, is called a "dome". Cypress domes are generally small in size, usually 1 to 10 hectares and consist of poorly-drained to permanently wet depressions that are dominated by pondcypress. They are called "domes" because, when viewed from the side, the larger trees in the middle and the smaller trees toward the edges present a vaulted profile. This domed appearance has been attributed variously to a deeper deposit of peat in the middle, fire that is more frequent around the edges, or a gradual increase in water level that causes the dome to "grow" from the center outward. But a definite reason for this profile has not been determined yet, nor do all domes display the characteristic shape (Mitsch and Gosselink, 1993).

During periods of low water levels, water is impounded in numerous ponds. Elevation ranges from 3.6-12 m above mean sea level in the northern part of Big Cypress to sea level where it grades into mangrove swamps.

The climate of southern Florida is moist and mild; it is frost-free nearly all year. Mean annual precipitation is around 1,500 mm, 80 percent of which falls from May to October, creating distinct wet and dry seasons. Precipitation received in 1 year has ranged from 760 to 2,540 mm. Occasionally, drought in summer (normally the wet season) can result in complete cypress defoliation, which otherwise would not occur until fall.

2.2 Vegetation

Baldcypress (*Taxodium distichum*) and the almost-indistinguishable pondcypress (*T. ascendens*) dominate the alluvial floodplain forests. Plant associates in cypress swamps vary with depth, duration, and frequency of flooding, soil type, geographic location, and stand density. Cypress domes and strands have few associates in the center; most of those present are shade-tolerant species of epiphytic bromeliads, orchids, ferns, and nettles, or aquatic macrophytes such as tall flag (*Thalia geniculata*) and arrowhead (*Sagittaria* spp.). Associates on the perimeter of cypress domes and strands include buttonbush (*Cephalanthus occidentalis*), redbay (*Persea borbonia*), sweetbay (*Magnolia virginiana*), magnolia (*Magnolia* spp.), cocoplum (*Chrysobalanus icaco*), dahoon (*Ilex cassine*), myrsine (*Myrsine florida*), southern bayberry (*Myrica cerifera*), Coastal Plain willow (*Salix caroliniana*), and Florida poison tree (*Metopium toxiferum*). Red maple (*Acer rubrum*), pond apple (*Annona glabra*), strangler fig (*Ficus aureus*), water ash (*Fraxinus caroliniana*), swamp bay (*Persea palustris*), and paurotis palm (*Paurotis wrightii*) are frequently found in cypress domes and strands.

2.3 Faunal Characteristics

Cypress swamps do not have a distinct fauna, but share many species with adjacent plant communities. Most species and individuals spend only part of their lives in the swamp. Benthic invertebrates form the heterotrophic base of the food chain. A high diversity of invertebrates has been recorded for cypress domes and strands. This is strongly related to water quality. Parameters such as oxygen concentration and pH, play an important role in shaping benthic community (composition and abundance).

During summer, reptiles and amphibians dominate cypress swamp vertebrate communities, while in winter birds become more abundant. Reptiles and amphibians are prevalent in cypress swamps because of their ability to adapt to the fluctuating water regime. In

addition, the relatively high winter temperatures allow them to remain active through the cooler seasons. Among amphibians, the ranid frogs showed the highest numbers: common species also included southern leopard frog (*Rana utricularia*), cricket frogs (*Acris* spp.), oak toad (*Bufo quercicus*), and green treefrog (*Hyla cinerea*). Two of the most interesting reptiles are the well known American alligator (*Alligator mississippiensis*) and the cottonmouth moccasin (*Agkistrodon piscivorus conati*), a poisonous water snake. Other water snakes, such as several species of *Natrix*, are usually more important in terms of number and biomass.

The reason why bird densities are higher in cypress swamps during winter is due largely to the presence of wintering birds. Birds that use cypress swamps include wild turkey (*Meleagris gallopavo*), ibis (*Plegadis* spp.), double-crested cormorant (*Phalacrocorax auritus*), herons (*Ardea herodias*, *Butorides striatus*, *Nycticorax nycticorax*, and *Nyctorax violaceus*), snowy egret (*Egretta thula*), great egret (*Casmerodius albus*), anhinga (*Anhinga anhinga*), and belted kingfisher (*Ceryle alcyon*). The limpkin (*Aramus guarauna*) is a characteristic occupant of cypress swamps due to the availability of snails. Canopy-feeding passerines are common, but there usually are only few mid-story species, such as red-bellied woodpecker (*Melanerpes carolinus*), pileated woodpecker (*Drycopus pileatus*), tufted titmouse (*Parus bicolor*), and great crested flycatcher (*Myiarchus crinitus*). The wood duck (*Aix sponsa*) is common in the larger cypress domes that contain sufficiently large trees. Prothonotary warbler (*Protonotaria citrea*) is also a typical member of the cypress swamp avian community.

Most mammals occurring in cypress swamps occupy ecotones. Mammals include white-tailed deer (*Odocoileus virginiana*), gray fox (*Urocyon cinereoargenteus*), fox squirrel (*Sciurus niger*), raccoon (*Procyon lotor*), and Virginia opossum (*Didelphis marsupialis*). River otter (*Lutra canadensis*) and bobcat (*Lynx rufus*) are common residents of large cypress domes. There are many rodents and shrews including short-tailed shrew (*Blarina brevicauda*), cotton mouse (*Peromyscus gossypinus*) and hispid cotton rat (*Sigmodon hispidus*), which nests in trees to avoid floodwaters. Away from the center of cypress domes one finds small mammals such as the marsh rabbit (*Silvilagus palustris*) in addition to species mentioned previously. Arboreal mammals include the eastern gray squirrel (*Sciurus carolinensis*), and several species of bats. Rare and endangered species, and species whose ranges formerly included cypress swamps, include mangrove fox squirrel (*Sciurus niger avicenna*), black bear (*Ursus americanus*), Florida panther (*Felis concolor*) and mink (*Mustela vison*).

3. PARSING THE NETWORK

As with most analyses, some of the most important assumptions in Network Analysis are made at the very beginning. They concern decisions as to what the elements of the network will be and how these taxa are to be connected. In this project, these decisions are simplified

somewhat by the requirement that the network be comparable to the ATLSS simulation. That is, each state variable of the ATLSS model must have a counterpart in the accompanying network.

Network analysis, however, can treat far more complicated webs of interaction than are possible using simulation modeling. Keeping the simulation dynamics of many coupled processes from becoming pathological is a difficult balancing act. Because NA does not deal explicitly with dynamics, far greater taxonomic resolution becomes possible with this form of analysis. As a result, some taxa in the ATLSS model will be represented by several compartments in the cypress network. In addition, compartments can be added to the network with relative ease. For example, the creation of an individual-based model for one of the less "charismatic" mammals, like opossum, would entail significant effort. As will be described below, it requires nowhere near as much work to include the opossum compartment into the quantified trophic web.

Although the primary purpose for creating the cypress networks is to serve as a calibration benchmark for ATLSS, it should be mentioned that the network and its ensuing analysis can also serve independent purposes. For example, some biologists will be curious to know how their particular species of interest, which might not appear in ATLSS, will fare under the proposed hydrological scenarios. With regard to trophic interactions at least, the results of NA should allow those investigators and managers to make some educated guesses about how the excluded population might change. For example, NA quantifies the direct and indirect trophic interactions of each compartment with all other compartments in the web. In particular, the stocks and activities of each compartment not appearing in ATLSS can be compared with all those that do participate through NA, and such coefficients and ratios as may result can be applied to the predicted outputs from ATLSS to estimate the accompanying trophic status of the non-included species. In other words, after calibration NA can serve to expand the scope of predictions from ATLSS.

From an ecological viewpoint virtually all the important trophic components (i.e., those comprising at least 5% of the standing biomass or activity) have been written into ATLSS. These include: macrophytes, periphyton, terrestrial invertebrates, crayfish, prawns, apple snail, piscivorous fish, planktivorous fish, frogs, lizards, snakes, turtles, salamanders, the American alligator, wading birds, and white-tailed deer.

It happens, however, that data exist to make at least crude estimates of the stocks and activities of a number of other ecosystem members. For example, there exist census figures on most of the mammals that occur in the cypress swamps (Environmental Impact of the Big Cypress Jetport, 1969; Sowde and Woodall, 1985; Smith and Bass, 1994.) Using these figures it becomes possible to estimate the standing stocks of carbon in these populations; and, using techniques described in the next section, to approximate as well the magnitudes of their transfers

with predators, prey and detritus. Hence, it was decided to include these "parallel" species into the NA.

One major lexical question involved how to treat the manifold species that comprise such functional groups as the heterotrophic microorganisms and the benthic meiofauna, for which data at the level of individual species are not available. As a result it was decided to create two general compartments called "living particulate organic matter (POC)" and "living sediment" to include these poorly resolved parts of the ecosystem. The "living POC" include bacteria, microprotozoa and zooplankton; while "living sediment" brings together bacterioplankton, microfauna and meiofauna.

In the end, the network consisted of a total of 68 separate components. Only those species closely associated with the dominant patterns have been retained in this model. Hence, only reptiles, amphibians, birds and mammals commonly found in cypress forest and mixed swamp forest made the final list of species. Some additional species have been included following suggestions by experts. Once completed, the list was aggregated somewhat according to criteria, such as species sharing same diet, available data and the goals of ATLSS. For example, most species to be included in ATLSS as individual-base models have been maintained as separate compartments in the network.

The final list of species, along with a very brief description of what they entail, includes:

1. Living Particulate Organic Carbon (See description above.)
2. Living Sediment (See description above.)

3.1 Primary Producers

3. Phytoplankton - A single compartment has been used as representative of the whole phytoplankton community, because available data relate only to aggregate chlorophyll-a concentration.

A description of the dominant primary producers is reported in the "study area" section of this report. They have been divided as follows:

4. Floating Vegetation - Such as pond lillies and duckweed
5. Periphyton - Most diatomaceous forms of algae
6. Macrophytes - Such as *Utricularia* and *Bacopa*
7. Epiphytes - Bromileads, orchids, ferns, etc.
8. Understory - Mostly forbs, such as redbay, willow and bayberry
9. Vines and associated Leaves - Such as strangler fig
10. Hardwood Leaves - From maples, bays and ashes
11. Cypress Leaves

12. Cypress Wood
13. Hardwood Wood

Taxodium spp. are included as a separate compartment, because they comprise a major percentage of the total biomass and also serve as major source of detritus. Furthermore, the leaves and woody parts of the trees have been relegated to separate compartments to follow better the role of production by cypress and other trees in the domes and strands.

14. Roots - Roots found in the first 5-19 cm soil horizon have been included in this compartment.

3.2 Invertebrates

The macro invertebrates of the cypress systems were divided into five categories. Crayfish, apple snails, and prawns, appear as distinct compartments in order to distinguish their separate contributions to higher trophic levels, which are thought to be substantial.

15. Crayfish (*Procambarus alleni*)
16. Apple Snail (*Pomacea paludosa*)
17. Prawns (*Palaemonetes paludosus*)
18. Aquatic Invertebrates - This compartment includes all the other aquatic invertebrates not listed above; the most representative are:
 - Annelida (*Nais obtusa*)
 - Arachnoida (*Hydrachna* sp)
 - Amphipoda (*Hyaella azteca*)
 - Isopoda (*Ascellus militaris*, *Lirceus louisianae*)
 - Coeloptera (*Agabus* sp, *Bidessus* sp. *Halipus mulcheri*)
 - Diptera (*Brillia alticola*, *Chaoborus albides*, *Chironomus* sp, *Glyptotendipes lobiferous*, *Goeldichironomus* sp *Polypedilum convictus*, *Procladius culiciformis* *Stichtochironomus exquisitus*, *Tanypus punctipennis* T. *stellatus*)
 - Hemiptera (*Neocorixa snowi*)
 - Odonata (*Anomalagrion hastatum*, *Enallagma triviatum*, *Erythrodiplax minscula*, *Ischnura posita*, *Libellula depressa*, *Orethmis ferraginea*, *Pachydiplax longipennis*)
 - Mollusca (*Lioplax subcarinata*)
19. Terrestrial Invertebrates - Studies of terrestrial invertebrates in cypress systems are sorely lacking (especially for BCNP). Hence, no single species have been compartmentalized. The most representative groups are:
 - Coeloptera (beetles)
 - Non-chironomid diptera

Tricoptera (caddisflies)
 Turbellaria
 Lumbriculidae (earthworms)
 Nematoda (roundworms)
 Odonata (dragon and damsel flies)
 Spiders
 Mites
 Collembola (springtails)
 Orthoptera (grasshoppers crickets)
 Psocoptera (bark lice)
 Homoptera (leafhoppers and aphids)
 Lepidoptera (moths butterflies)
 Hymemoptera (ants and bees)
 Centipedes
 Millipedes
 Psuedoscorpions

3.3 Fishes

The fish community has been partitioned into three components, based on feeding behavior and size. The grouping is based on Kushlan's (1976) categorization of fish community structure. The three compartments are :

20. Small Fish, herbivorous and omnivorous. This is the largest of the three categories defined in the fish community. The most representative species are: *Gambusia affinis* (mosquitofish), *Poecilia latipinna* (sailfin molly), *Heterandria formosa* (least killifish), *Cyprinodon variegatus* (sheepshead minnow), *Jordanella floridae* (flagfish), *Adinia xenica* (diamond killifish), *Erymizon succetta* (Eastern chubsucker), *Lucania goodei* (bluefin killifish), and larval fish of the two following compartments while they are herbivores and omnivores.
21. Small Fish, primarily carnivores. The most representative species are: *Fundulus confluentus* (spotfin killifish), *Fundulus chrysotus* (golden topminnow), *Fundulus seminolus* (Seminole killifish), *Notemigoneus crysoleucas* (Golden shiner), *Labidesthes sicculus* (brook silversides), *Notropis petersoni* (coastal shiner), *Notropis maculatus* (tailight shiner), and larval fish that are carnivorous.
22. Large Fish, primarily carnivores. The most representative species are: *Lepisosteus platyrhincus* (florida gar), *Ictaluris* sp. (catfish), *Micropterus salmoides* (large-mouthed bass), *Ennacanthus gloriouus* (blue spotted sunfish), *Lepomis*

gulosus (warmouth), *L. macrochirus* (bluegill), *L. microlophus* (read ear sunfish), *L. punctatus* (spotted sunfish), and *Amia calva* (Bowfin).

3.4 Reptiles

Reptiles have been divided into four different compartments:

23. American alligator - (*Alligator mississippiensis*)

24. Turtles - The most representative species are:

Florida snapping turtle (*Chelydra serpentina osceola*)

Stinkpot or Common musk turtle (*Sternotherus odoratus*)

Striped mud turtle (*Kinosteron baurii*)

Florida red-bellied turtle (*Pseudemys nelsoni*)

Florida chicken turtle (*Deirochelys reticularia chrysea*)

Florida soft shelled turtle (*Apalone ferox*)

25. Lizards - The most representative species are:

Green anole (*Anolis carolinensis*)

Southeastern five-lined skink (*Eumeces inexpectatus*)

26. Snakes - The most representative species are:

Florida green water snake (*Nerodia floridiana*)

Florida banded water snake (*Nerodia fasciata compressicauda*)

South Florida black swamp snake (*Seminatrix pygaea*)

South Florida ribbon snake (*Thamnophis sauritus*)

Eastern mud snake (*Farancia abacura*)

Rough green snake (*Opheodrys aestivus*)

Yellow rat snake (*Elaphe obsoleta quadrivittata*)

Everglades rat snake (*Elaphe obsoleta rossalleli*)

Florida kingsnake (*Lampropeltis getula floridiana*)

Florida cottonmouth (*Agkistrodon piscivorus conati*)

3.5 Amphibians

27. Salamanders - The most representative species are:

Two-toe amphiuma (*Ampiuma means*)

Greater siren (*Siren lacertina*)

Everglades dwarf siren (*Pseudobranchius striatus belli*)

Peninsula newt (*Notophtalmus viridesens pianopicola*)

Frogs were subdivided into three components, based on size:

28. Large frogs

29. Medium frogs

30. Small frogs

The most representative species are:

- Southern toad (*Bufo terrestris*)
- Oak toad (*Bufo quercicus*)
- Green tree frog (*Hyla cinerea*)
- Barking treefrog (*Hyla gratiosa*)
- Squirrel treefrog (*Hyla squirella*)
- Little grass frog (*Pseudacris ocularis*)
- Eastern narrow-mouth toad (*Gastrophryne carolinensis*)
- Southern leopard frog (*Rana utricularia*)
- Pig frog (*Rana grylio*)
- Florida chorus frog (*Pseudacris nigriverrucosa*)

31. Salamander larvae. This compartments include the first stages of salamander life cycle.

32. Tadpoles. This compartments include the first stages of frogs life cycle.

3.6 Birds

33. Pelecaniformes - The most representative species are:

- Double crested cormorant (*Phalacrocorax auritus*) and
- Anhinga (*Anhinga anhinga*).

34. Anseriformes - The most representative species is the wood duck (*Aix sponsa*).

35. Vultures - The most representative species are:

- Turkey vulture (*Cathartes aura*) and
- Black vulture (*Coragyps atratus*).

36. Kites & Hawks - The most representative breeding species are:

- Swallow-tailed kite (*Elanoides forficatus*)
- Red-tailed hawk (*Buteo jamaicensis*)
- Red shouldered hawk (*Buteo lineatus*)
- Short-tailed hawk (*Buteo brachyurus*)

The most representative nonbreeding species are:

- Cooper's hawk (*Accipiter cooperii*)
- Sharp-shinned hawk (*Accipiter striatus*)
- Broad-winged hawk (*Buteo platypterus*)

37. Galliformes - The most representative species is the turkey (*Meleagris gallopavo*).

38. Egrets - The most representative species are:

Great egret (*Casmerodius albus*)

Snowy egret (*Egretta thula*)

39. Great Blue Heron - (*Ardea herodias*)

40. Other Herons

The most representative species are:

Little blue heron (*Florida caerulea*)

Green heron (*Butorides virescens*)

Black-crowned night heron (*Nycticorax nycticorax*)

Yellow-crowned night heron (*Nyctanassa violacea*)

41. Woodstork - (*Mycteria americana*)

42. White Ibis - (*Eudocimus albus*)

43. Gruiformes - The most representative specie is:

Limpkin (*Aramus guarana*)

44. Owls - The most representative species are:

Great horned owl (*Bufo virginianus*)

Barn owl (*Tyto alba*)

Barred owl (*Strix varia*)

45. Caprimulgiformes - The most representative breeding species are:

Chuck-will's-widow (*Caprimulgus carolinensis*)

Common nighthawk (*Chordeiles minor*)

The most representative nonbreeding specie is Whip-poor-will (*Caprimulgus vociferus*)

46. Hummingbirds - The most representative specie is

Ruby-throated hummingbird (*Archilochus colubris*)

47. Woodpeckers - The most representative breeding species are:

Pileated woodpecker (*Dryocopus pileatus*)

Red-bellied woodpecker (*Centurus carolinus*)

Downy woodpecker (*Dendrocopos pubescens*)

The most representative nonbreeding species is:

Yellow-bellied sapsucker (*Sphyrapicus varius*)

48. Passiformes, omnivorous - The most representative breeding species are:

- Tufted titmouse (*Parus bicolor*)
- Mockingbird (*Mimus polyglottos*)
- Brown thrasher (*Toxostoma rufum*)
- Common grackle (*Quiscalus quiscula*)
- Cardinal (*Richmondia cardinalis*)

The most representative nonbreeding species are:

- Tree swallow (*Iridoprocne bicolor*)
- Catbird (*Dumetella carolinensis*)
- Robin (*Turdus migratorius*)
- Cedar waxwing (*Bombycilla cedrorum*)
- Solitary vireo (*Vireo solitarius*)
- Rusty blackbird (*Euphagus carolinus*)
- Swamp sparrow (*Melospiza georgiana*)

49. Passiformes, predatory - The most representative breeding species are:

- Eastern kingbird (*Tyrannus tyrannus*)
- Great-crowned flycatcher (*Myiarchus crinitus*)
- Purple martins (*Progne subis*)
- Carolina wren (*Thryothorus ludovicianus*)
- Blue-gray gnatcatcher (*Poliophtila caerulea*)
- Loggerhead shrike (*Lanius ludovicianus*)
- White-eyed vireo (*Vireo griseus*)
- Prothonotary warbler (*Protonotaria citrea*)
- Parula warbler (*Parula americana*)
- Pine warbler (*Dendroica pinus*)

The most representative nonbreeding species are:

- Eastern phoebe (*Sayornis phoebe*)
- Solitary vireo (*Vireo solitarius*)
- Rusty blackbird (*Euphagus carolinus*)
- and many other migrating warblers.

3.7 Mammals

50. Opossum - (*Didelphis marsupialis*)

51. Shrews - The most representative species is:

- Short-tailed shrew (*Blaarina brevicauda*)

52. Bats - The most ~~representative~~ species is:
Evening bat (*Nycticeius humeralis*)
53. Black Bear - (*Ursus amarus*)
54. Grey Fox - (*Urocyon cinereoargenteus*)
55. Raccoon - (*Procyon lotor*)
56. Mink - (*Mustela vison*)
57. Otter - River otter (*Lutra canadensis*)
58. Florida Panther - (*Felis concolor*)
59. Bobcat - (*Lynx rufus*)
60. Squirrels - The most representative species are:
Eastern gray squirrel (*Sciurus carolinensis*)
Fox squirrel (*Sciurus niger*)
61. Mice & Rats - The most representative species are:
Cotton mouse (*Peromyscus gossypinus*)
Hispid cotton ~~rats~~ (*Sigmodon hispidus*)
no Rice rat (*Oryzomys palustris*)
no Florida ~~water~~ rats (*Neofiber alleni*)
62. Rabbits - The most representative specie is marsh rabbit (*Silvilagus paulstris*)
63. White-Tailed Deer - (*Odocoileus virginianus*)
64. Hog - Feral Hog (*Sus scrofa*)
65. Armadillo - (*Dasypus novemcinctus*)

3.8 Detrital Compartments

66. Refractory Detritus - Refractory detritus represents organic matter that decomposes at a relatively ~~slow~~ rate. For this network we use the information reported in Dierberg and Ewel (1986), where the decomposition rate for refractory detritus is 0.17/yr.
67. Liable Detritus - ~~Liable~~ detritus is organic matter that decomposes at a faster rate. The decomposition ~~constant~~ in this case is 5.7/yr (Dierberg and Ewel, 1986).
68. Vertebrate Detritus - Some of the species listed in this network, primarily vultures, feed on carrion. In the economy of this ecosystem this mode of feeding turns out to be very singular. A third derital compartment consisting of vertebrate bodies just after death ~~was~~ created so as to avoid vultures feeding directly on living species and thus acting as a top predators.

The stocks and activities of all 68 compartments vary during the course of the year. Seasonality at this latitude, however, is marked more by variations in water level than by changing temperature. Thus, seasonality is depicted in the form of two separate networks -- one for the wet season (from June to November) when water levels are high and another for the dry season (December to May), when water levels are relatively low and the canopy is more sparse, due to the deciduous habit of the cypress trees.

4. METHODS

After the "lexical" phase of model building, the next step involves connecting the selected compartments to one another via feeding and detrital pathways. This topology is determined from information about the diets of each taxon. But the purpose here is not merely to formulate a qualitative "foodweb". We wish to quantify the connections as well. Toward this end, it is useful to concentrate first on assessing the densities, or stocks of the participating taxa. Knowing the concentration of biomass is the key to scaling all the activities of a particular population.

4.1 Estimation Techniques

The biomasses of some species are known with reasonable precision. For example, the number of animals per hectare is available for many of the compartments. As the standard units used in NA are grams of carbon per square meter, the available data had to be transformed to maintain dimensional consistency. Towards this end, information on the average weight (grams) of animals was gathered from technical manuals. The percentage of carbon per gram of dry weight was then combined with wet weight/dry weight ratio to calculate the biomasses in gC/m². In the case of primary producers, most sources report data on biomass in grams per hectare. In this case only the wet weight/dry weight ratio and the percentage of carbon per gram of dry weight (Jorgensen et al., 1986) were necessary to convert the biomass into the correct units.

The conversions for phytoplankton were a little more complicated. Data from the area of the Big Cypress National Preserve were given in micrograms of chlorophyll-a per litre. To convert these figures into carbon a C/chl-a ratio of 50/1 was assumed as representative of living phytoplankton (Strickland, 1965). By assuming an average water depth for the wet and dry seasons (Duever et al., 1986), the number of liters of water per square meter could be calculated. Multiplying gC/l by l/m², yielded concentrations in gC/m². For living POC, biomass was reported in gC/l, and the same procedure used for phytoplankton was followed.

Once the biomass had been approximated, information was sought on the consumption rate (or primary production rate) per unit biomass of each species. Multiplying a biomass density by this factor establishes the total input to the compartment in question. At this point, if one has solid data on the dietary proportions of heterotrophs, the total input can be apportioned among

the various prey and the magnitudes of those transfers can be set. Unfortunately, the dietary components of some taxa are available only as a list of species. In such cases we had no other option but to apportion the total input to the several prey in proportion to the standing stocks of these prey.

The two networks were assumed to balance over each season. While this is unlikely to be the actual case, balance is required for the critical input/output phase of NA (described below.) Furthermore, assuming balance facilitates the estimation of many rates. For example, when a component is balanced, its total output can be equated to its total input, as just calculated. It remains to apportion this compartmental "throughput" among the output processes—respiration, excretion, natural mortality and losses to predation. Fortunately, respiration and excretion rates per unit biomass are available from the literature for most species, so that these outputs can be immediately established. Most of the losses to predation are reckoned from the predator (input) side, as described above.

At this point, the balance is almost complete. It remains to estimate the exchanges of carbon with the outside world. Exogenous imports occur in three different ways: (1) Carbon from the atmosphere may be fixed as biomass through the process of primary production. The magnitude of this import is assessed by multiplying the standing stock of the autotroph by its primary productivity per unit carbon, as mentioned above. (2) Biomass may enter or leave the system advected by water flow into and out of the study area. These exchanges can be estimated from the overall water budget for the swamp (Duever et al.; 1986), which includes figures for gross advective water exchange with the surrounding areas. Multiplying these water exchanges by the concentrations of those species suspended in the water column will provide an approximation for these exogenous transfers. (3) Biomass may enter and leave the system as animal populations migrate across the boundaries of the study area.

Migration applies to many animals species in the model, and especially to birds. Wading birds might nest on the trees of a particular dome but may feed elsewhere. Such feeding could be classified as an import to the system. Furthermore, different types of birds have different feeding techniques. For example, some need high water level and others, low. It may also happen that birds nesting outside of a particular dome come to the dome to feed. This activity would constitute an export from the system. Due to a lack of detailed information on these aspects of feeding, it has been assumed that such imports and outputs balance. That is, all the birds in the model are assumed to feed inside the cypress and none come from outside just to feed there.

The techniques for estimating all the flows entering and leaving each compartment now have been described. Of course, uncertainties inherent in these partially independent estimations will keep many of the compartments from balancing exactly. The degree of imbalance can be computed by entering the existing flow estimates into a spreadsheet format. (EXCEL[TM] was

used for this purpose.) One may compare marginal sums of inputs and outputs to identify those compartments that are most out-of-balance. The investigator has several options for treating an imbalanced compartment. If the imbalance is severe, it is probably best to recheck the sources and the arithmetic. Failing the discovery of an error, one might search for other references to cross-check the data being used.

If no amendments to a compartmental budget can be made on the basis of new data, some investigators prefer to bring the system nearly into balance by adjusting the least-well known flows. Others would rather maintain the flow proportions for each compartment as they appear in the literature and to rebalance the whole system under the covering assumption of linear, donor-control, which always maintains positive flows (Ulanowicz 1989.) In this study all compartments could be balanced to within a few percent using literature values, and final balance was achieved using the program DATBAL, which assumes linear, donor control.

The resulting networks are too large and complicated to display easily as illustrations. Even a matrix representation of one such network spans several pages and is cumbersome to use. For these reasons, we have decided to present our detailed results in hypertext format. The user is strongly urged to access the results over the World Wide Web at

[<http://www.cbl.cees.edu/~bonda/ATLSS.html>.](http://www.cbl.cees.edu/~bonda/ATLSS.html)

There one may follow simple instructions to locate the estimated value of any stock or flow in either the wet or dry season. Furthermore, the entire rationale and associated references pertaining to the estimation of any particular value have been documented in hypertext. By pointing and clicking one may examine a trophic flow network in minute detail never before available for a network of such size and complexity.

The authors feel that this format for disseminating the network results should have important benefits for ecosystem science in general and for the visibility of the ATLSS endeavor in particular. We are aware of no other single source where the structural elements of an entire ecosystem can be examined and scrutinized so readily. Even if a user has no idea of the benefits of NA, he/she can begin with the species that interests them most and trace the sources and fates of material in that compartment -- simply by pointing and clicking. The presentation also makes it easier to critique the networks, and online suggestions for improvements and amendments are welcomed.

4.2 Network Analysis

4.2.1 Background

Sometime during the mid-1970's it became apparent that ecological modeling in the form of a set of coupled, deterministic differential equations was a problematical undertaking that required support from other, independent methods for systems analysis. In the search for parallel

methods of describing the behavior of total ecosystems, various computations performed on the underlying network of trophic flows have figured prominently (SCOR, 1981).

The original impetus for diverting attention from dynamics and concentrating analysis on flow structure came from the field of economics, where success in elucidating indirect economic effects had been achieved by manipulations on matrices of economic flows (Leontief, 1951; Hannon, 1973). Thereafter followed a number of other topological treatments of the underlying flow graph (e.g., Finn, 1976; Levine, 1980; Patten et al., 1976; Ulanowicz and Kemp, 1979). Eventually, Ulanowicz collected most of the methods for analysing flow networks into a single executable package, called NETWRK (Ulanowicz and Kay 1991.)

Four types of analyses are performed by NETWRK. First, so-called input-output structure matrices are calculated. These allow the user to look in detail at the effects, both direct and indirect, that any particular flow or transformation might have on any other given species or flow. Next, the graph is mapped into a concatenated trophic chain (after Lindeman 1942). Then all the simple, directed biogeochemical cycles are identified and separated from their supporting dissipative flows. Finally, global variables describing the state of development of the network are presented. NETWRK and its accompanying documentation may be downloaded from the WWW at <http://www.cbl.cees.edu/~ulan/ntwk/network.html>.

In addition to NETWRK, a package called IMPACTS was used to gauge both the positive and negative, direct and indirect impacts that heterotrophic predation may cause. The method was described in Ulanowicz and Puccia (1990). Of particular interest is how negative impacts at one level can ramify to become positive indirect effects.

The data required to run either of these programs have already been discussed. Above it was detailed how, for each compartment, it is necessary to know: (1) all the inputs from outside the system, (2) all the various inputs flowing from other compartments of the system, (3) all the outputs which flow as inputs to other compartments, (4) all exports of useful medium outside the system, and (5) all rates of dissipation of medium. Each of these flows can be represented by a positive scalar element of a matrix or a vector; the absence of a flow can be represented by a zero.

4.2.2 Input/Output Analysis

The initial section of the NETWRK package is founded upon an ecological variation of input-output analysis. So-called "total contribution coefficients" (Szyrmer and Ulanowicz 1987) are calculated that describe exactly what fraction of the total amount leaving compartment *i* (prey or row designation) eventually enters compartment *j* (predator or column designation) over all pathways, both direct and indirect. Alternatively, the "total dependency coefficients" portray the

fraction of the total ingestion by j which passed through compartment i along its way to j . The columns of this matrix are particularly useful in that they portray the "extended diet" of the species in question (or, correspondingly, the trophic "pyramid" that underlies each heterotroph.) As we hope to demonstrate, such indirect ratios can provide valuable information about how a system is functioning.

As an example of indirect diet coefficients, we consider the lizard compartment in the cypress swamps. These reptiles feed almost entirely on terrestrial invertebrates, so that the "total dependency coefficients" of lizards on this the latter compartment is 100%. Because Terrestrial invertebrates feed, among other things, upon compartment 8, the understory, contributions from 8 will pass to the lizards through the invertebrates. This indirect contribution to lizards is about 20.6%. Some of the same material that was present in the understory, eventually became terrestrial invertebrates, and hence the sum of the numbers down a column in the "total dependency matrix" usually exceeds 100%.

Hannon (1973), Finn (1976), Levine (1980) and Patten et al. (1976) give various examples of how one may employ input-output analysis. One highly useful such application is the decomposition of the graph according to each input. That is, the eventual fate of each of the nonzero inputs to the system is traced independently of the other inputs to the system. Not only does this decomposition portray the isolated effects of the various inputs, but these sub-networks can be linearly recombined to recreate what the effects of any other combination of inputs would be, if the flow structure were kept the same.

4.2.3 Trophic Aggregation

The second section of our output from NETWRK interprets the given network according to the trophic concepts of Lindeman (1942). Of course, it is impossible to relegate omnivorous heterotrophs entirely to a single trophic level, but Ulanowicz and Kemp (1979) indicated how input-output techniques could be used to apportion the activities of omnivores among a series of integer trophic levels. This method has been expanded to include the effects of biogeochemical cycles by Ulanowicz (1995a).

In order for trophic aggregation to be meaningful, it is necessary that trophic pathways among living compartments remain finite in length, otherwise one is forced to interpret an infinite regress of trophic levels. Fortunately, Pimm (1982) states that cycles among living taxa are rare in ecosystem networks (although we shall encounter some interesting exceptions in the cypress networks.) The absence of such feeding cycles avoids trophic pathways of infinite length. As a preliminary to trophic aggregation, therefore, all cycles flowing only through active feeding links are first removed from the network. So long as the Finn cycling index for such heterotrophic cycling (see below) remains sufficiently small (say, below two percent or so), no

appreciable distortion of results should ensue. The 2% requirement is more than satisfied by the cypress networks.

When the fractions by which each component feeds at a particular trophic level are weighted by the value of that trophic level and the results are summed, one arrives at the effective trophic level for the given species (Levine 1980.) For example, if a species or compartment is receiving 15 units of medium along a pathway of length 2 and 5 units along a pathway of length 3, then it is acting 75% as a herbivore (trophic level=2) and 25% as a carnivore (level=3). The effective trophic position becomes $(.75 \times 2) + (.25 \times 3) = 1.75$. It is often interesting to compare the average trophic position of species under different circumstances (as is done below for the wet and dry seasons.)

The section on trophic aggregation culminates with the partitioning of activity into a trophic "chain" of transfers along aggregations of heterotrophs. Each such integer aggregation feeds back into detrital return loops. Such a depiction of the underlying trophic dynamics has been termed "canonical" by Ulanowicz (1995), because any ecosystem can be mapped into this equivalent and simple form to allow the relative magnitudes of corresponding flows to be compared directly.

4.2.4 System-Level Indices

The next section of output from NETWRK provides values for global attributes of the network that were defined by several information theorists to gauge the pattern of development in ecosystems (Ulanowicz, 1980,1986; Hirata and Ulanowicz, 1984; Ulanowicz and Norden, 1990). One begins by calculating the "total system throughput", or the gross sum of *all* transfers, to act as a measure of the size of the system. Multiplying the total throughput by the system indeterminacy (according to the Shannon Wiener formula) of the individual flows yields what has been termed the "development capacity" of the system. This quantity serves as an upper bound on the ascendancy, which is a measure of the network's potential for competitive advantage over other real or putative network configurations. Ascendancy is the product of a factor of size (total system throughput) times a factor representing the coherence of the flows (the average mutual information of the flow structure.)

The difference between the realized structure and its upper bound is the overhead (Ulanowicz, 1986.) Overhead has conflicting interpretations. On one hand, it is a catchall for the system's inefficiencies in processing material and energy. What is a disadvantage under benign conditions can turn in the system's favor when it is perturbed in some novel way. Then, the overhead represents a "strength-in-reserve" of degrees of freedom which the system can utilize to adapt to the new threat. Overhead is generated in any of four ways: there is overhead due to indeterminacy of imports, exports, dissipations (respirations), and about which of several parallel

pathways flow will proceed between any two nodes (redundancy.) The fractions of the development capacity encumbered by the ascendancy and by each of the overhead components provide a profile of the structural composition of the system that often is useful for assessing the organizational status of a system.

4.2.5 Cycles

Most networks of ecosystem flows contain cycles of material or energy, and the magnitude and structure of these cycles is fully described by NETWRK. The program enumerates all of the simple cycles in the given matrix of exchanges (an enormous task in the case of the cypress networks.) Furthermore, the simple cycles are grouped into "nexuses" of cycles all of which share the same "weak arc." A weak arc is defined here as the smallest flow in a given directed cycle. The assumption is that the weak arc is the limiting or controlling link in a cycle, and that by grouping according to critical links, one identifies the domain of influence for each weak arc. Presumably, any change in a weak arc will propagate throughout its associated nexus. The nexuses are listed roughly according to ascending order of the magnitude of their defining weak arcs.

The cycles are then subtracted from the network in a fashion described in detail by Ulanowicz (1983). Briefly, the magnitude of flow in the smallest weak arc is distributed over the flows in that particular nexus and the resulting amounts are subtracted from each arc in that nexus. This process zeroes the weak arc, thereby eliminating all the cycles in that nexus, but it does not disturb the balance around any compartment, nor does it change any exogenous input, export or respiration. None of the remaining arcs of the nexus are driven negative. After that nexus has been removed, the next smallest weak arc is located; and nexuses are subtracted iteratively until all cycles have been removed from the network.

As each cycle is removed, the flow associated with that cycle is added to the magnitudes of other cycles of the same trophic length. The end result is a distribution of the magnitude of cycling according to the trophic length of cycles. This profile could be useful in assessing system response to perturbation. For example, cycling via the larger loops is often more sensitive to disturbance. The cycle distribution is then normalized by the total system throughput. Summing this normalized distribution yields the Finn cycling index, which is the fraction of total activity that is devoted to cycling (Finn 1976).

Finally, the separation of cycled from transient flow is reported in the form of separate matrices for each type of flow. The row sums and column sums of the matrix of aggregated cycles will always balance; no further reference to exogenous exchanges is necessary. The visual structure of the aggregated cycles existing in more complicated networks very often reveals separate domains of control in the network (e.g, Baird & Ulanowicz 1989.) Finally, it should be

remarked that the starting network has been neatly decomposed into an acyclic "tree" of dissipative flows and a wholly conservative nexus of cycled flows.

4.2.6 Trophic Impacts

NETWRK treats only positive mass flows and does not consider the propagation of the negative effects that accompany predation. Ulanowicz and Puccia (1990) outlined how to treat the propagation of both positive and negative trophic effects, and their technique has been implemented in the algorithm, IMPACTS. For any particular component (designated as the "focal taxon"), IMPACTS provides a ranked listing of all the positive and negative impacts (both direct and indirect) upon that focal species. Also a ranked listing of all the direct and indirect trophic effects that focal species has upon all the other taxa is likewise presented. Of special interest are those predators that exert a direct negative impact upon a prey, but whose combined indirect positive influences more than compensate the prey for its direct losses. Such "beneficial predators" are more common than might be supposed and often highlight particular ecological roles that otherwise might have gone unnoticed. IMPACTS can be downloaded from <http://www.cbl.cees.edu/~ulan/ntwk/network.html>.

5. RESULTS

5.1 Input/Output Analysis

Perhaps the most useful indices to result from the Input/Output section of NETWRK are the "total dependency coefficients" (Szyrmer and Ulanowicz 1987) or, more appropriately, the "indirect diets" of each taxon. By reading down the column of these dependency coefficients one notes the quantitative trophic history of material reaching that given taxon. For example, it is commonplace to think of forested wetlands as detritus-based ecosystems. The basis for this view is that the dense tree canopy does not allow a significant growth of understory (aquatic vegetation, periphyton, vines and epiphytes) so that litterfall, mainly from cypress, is the major source of energy for secondary producers. The total dependency coefficients calculated for the cypress swamps suggest that this picture is not entirely appropriate here. Dependencies on detritus (compartments 66, 67, 68, 1 and 2) are appreciable, but not as high as expected (Fig. 1).

Of the total amount of carbon reaching many top predator compartments, only a minor fraction transits through detrital pathways. In particular, for Florida panther, gray fox and black bear, the dependence on detritus is less than 40%, and the fraction for bobcat is extremely low. In addition, the total dependency matrix reveals that many species in this ecosystem are almost totally dependent on the *grazing* chain. White-tailed deer and squirrels, for example, receive almost no material from the detritus compartments (Figs. 2 and 3)..

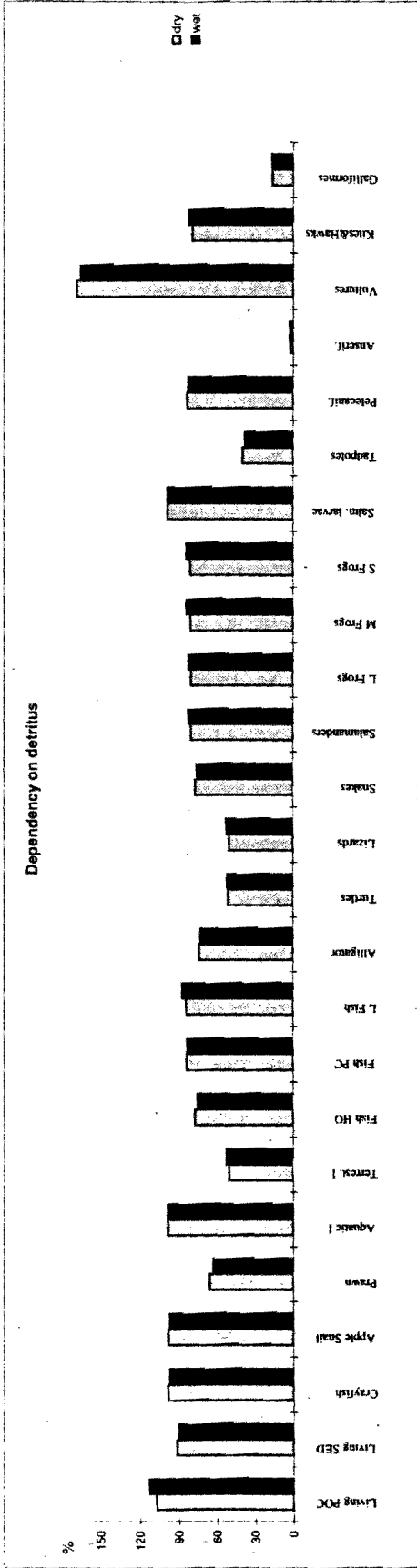
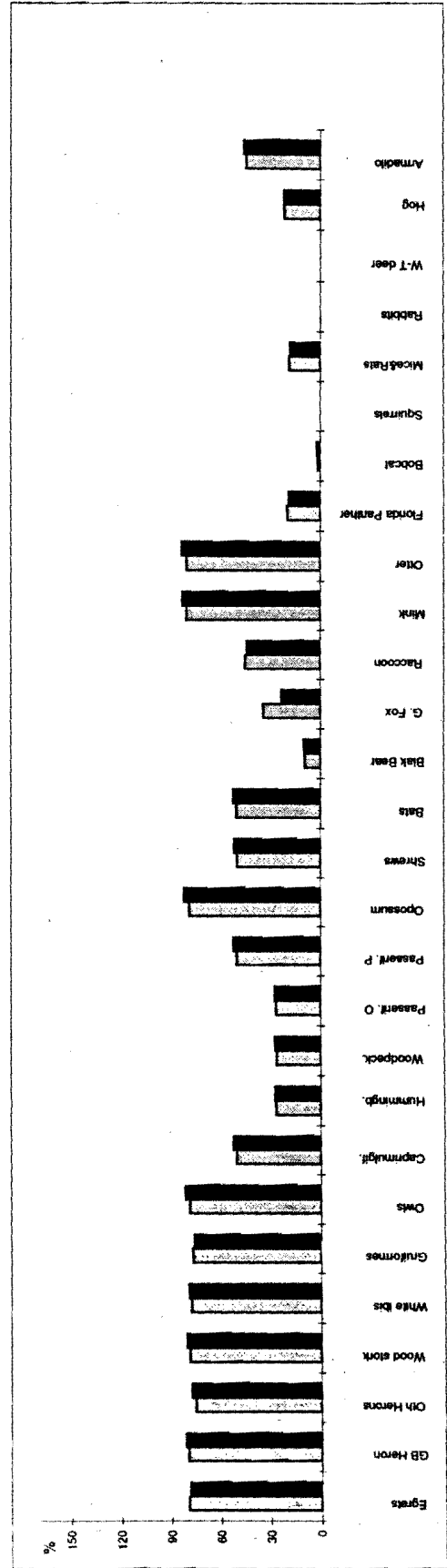
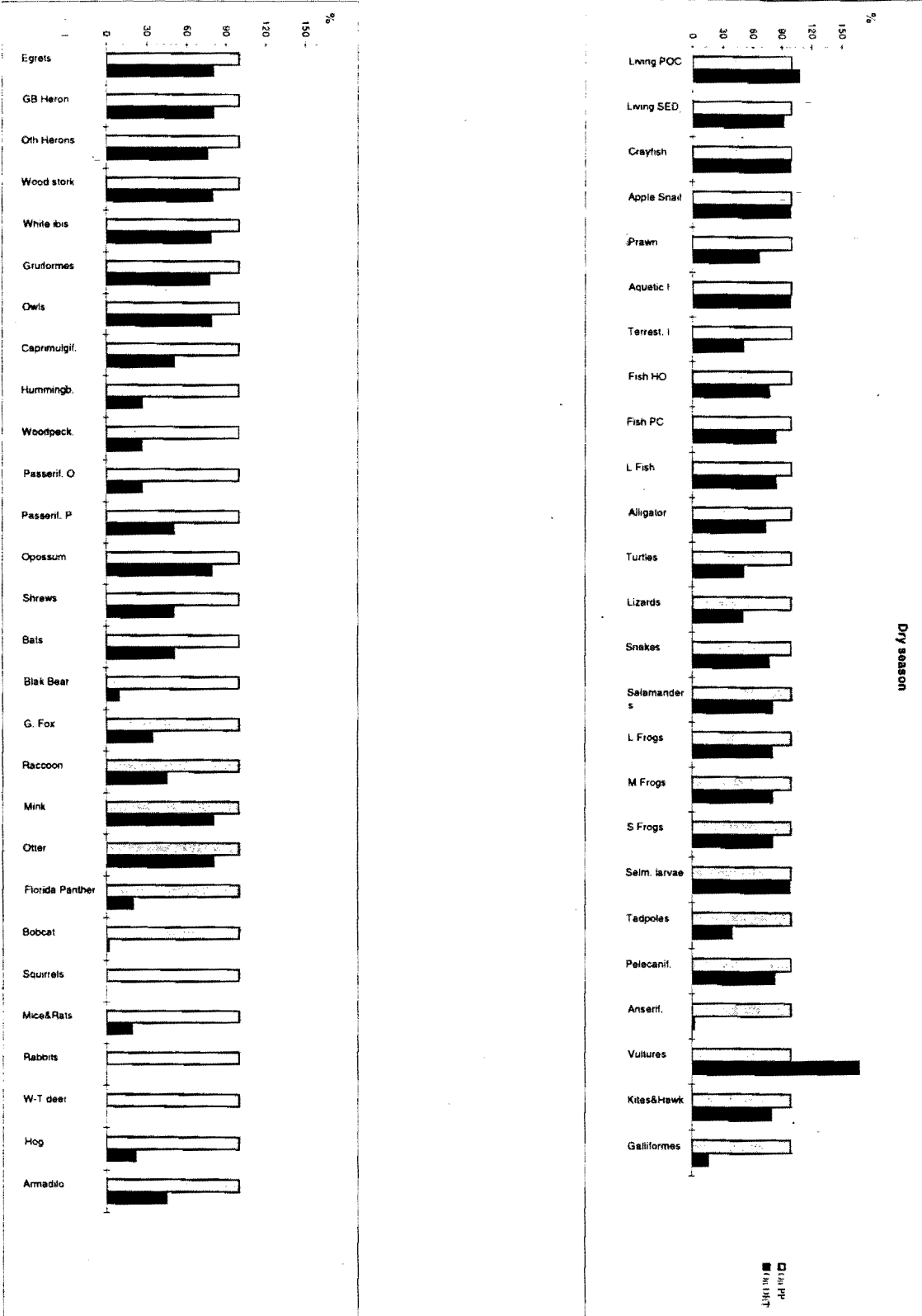


Figure 1

Figure 2

Dependency on primary producers and detritus



Dependency on primary producers and detritus

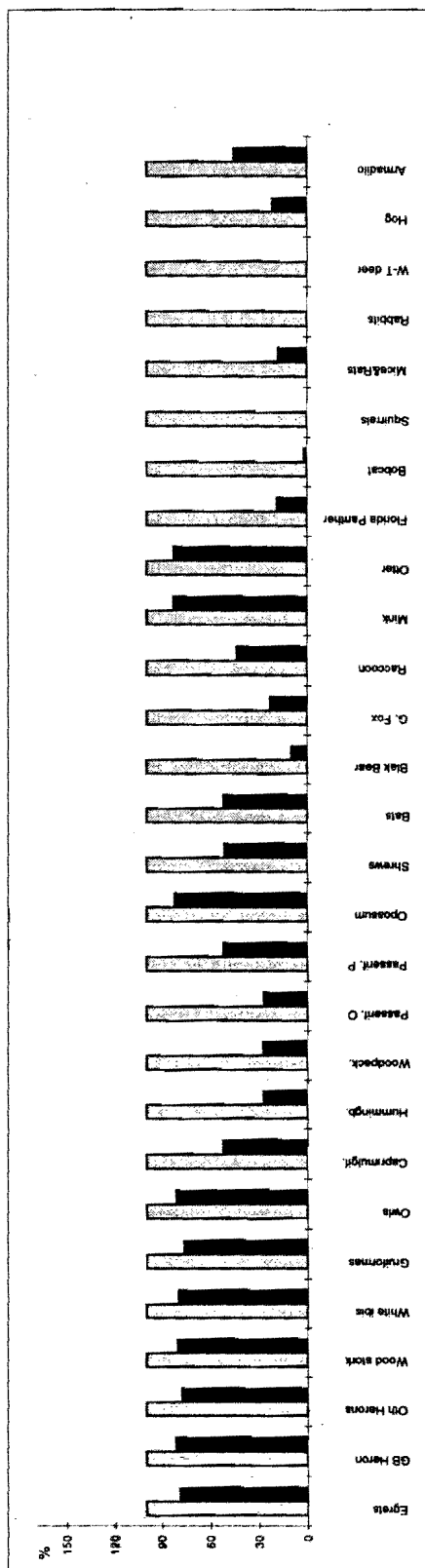
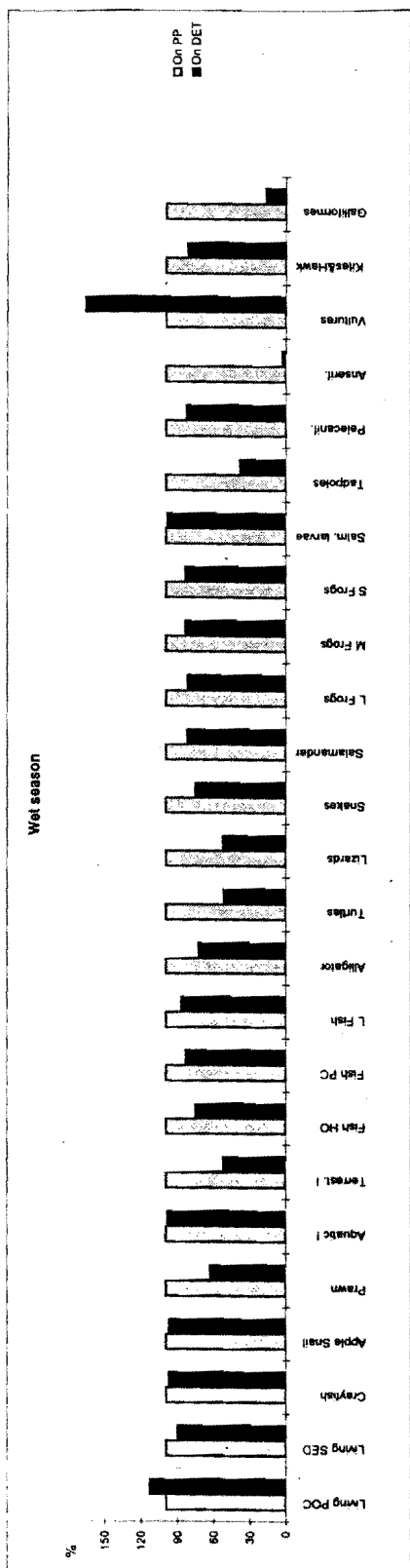


Figure 3

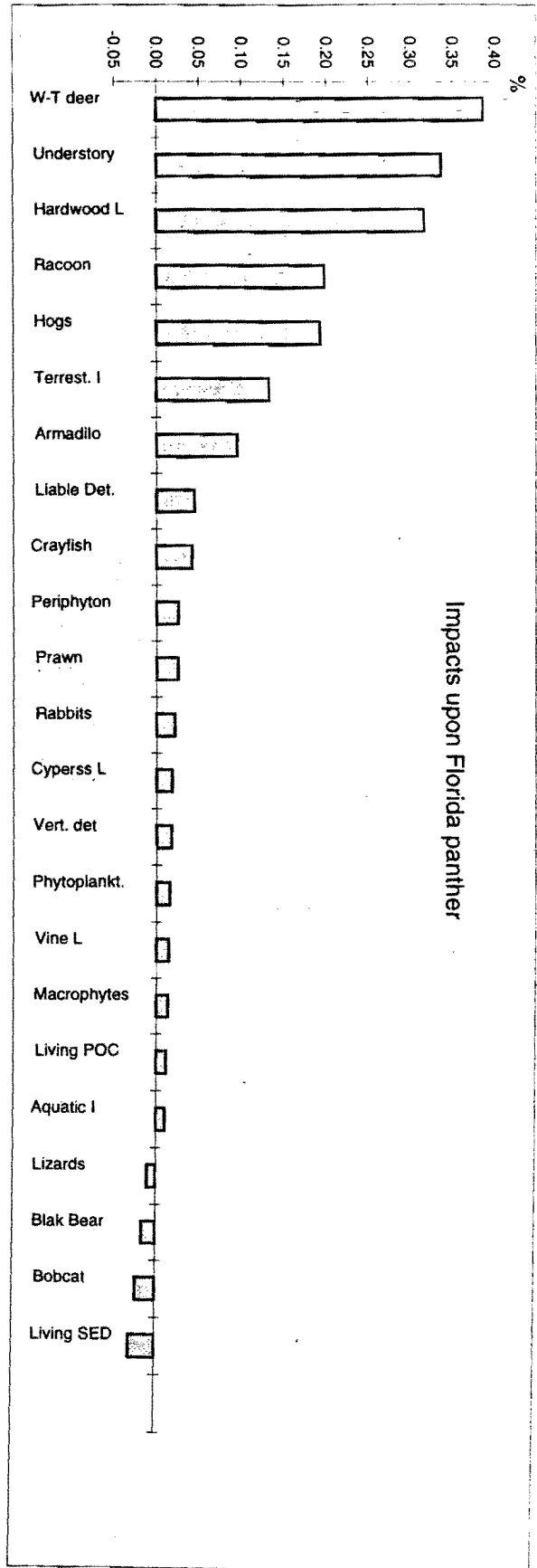
During the dry season, when the canopy is negligible, the importance of primary producers other than cypress, such as periphyton biomass and other subcanopy vegetation, grows considerably. Even during the high water period dependencies on these items are significant. Aquatic vegetation in considerable quantity can be observed in the middle of domes and strands where many big ponds provide holes in the canopy. We considered these open aquatic zones to be part of our forest wetland model. It should be noted that quantitative data on the subcanopy vegetation in the study site were not available, so the model was built by adapting information from the Everglades area. The adaptation of Everglades data to forested wetlands was guided by expert opinion (G. Dalrymple, J. Browder, J. Snyder), and personal observations.

5.2 Trophic Impacts

The results of impact analysis reveal that primary producers have a surprisingly strong influence on top carnivores. The overall positive impact on bobcats by their prey is 94%, while the total positive impacts of primary producers on the same species is almost as great (91%). Similarly, Florida panther benefits directly from prey and indirectly from primary producers by 90% and 74%, respectively. One of the main reasons behind these results is the importance of deer and other herbivores in the diets of these two top carnivores.

It is obvious that indirect effects can play important roles in ecosystem dynamics. Compartment 2, living sediment, for example, exerts a strong negative effect on the Florida panther, (Fig. 4). The same applies to black bear (53) and bobcat (59). The direct negative effects of the latter compartments on panther are due to competition for food, as they share many elements of their diets with the Florida panther. The reason why compartment 2 has a significant negative impact on Florida panthers and Black bears (but not on bobcats) is not as straightforward. Living sediment negatively affects a great number of components (53, 23, 24, 26, to name only a few), that are not directly linked with them. The most intuitive explanation for such impact might be the competition for common resources by these species with the invertebrates and fishes, which are an important source of food for many other compartments. But this would not explain the positive indirect role played by living POC, the other segment of the microbial community. In contrast with "living sediment", POC has positive effects on many compartments (esp. 23, 24, 26). This suggests that living POC is more important as a prey, rather than as competitor, to many compartments, such as invertebrates, which are important energy sources for secondary producers. To explain better why living sediment and POC have opposite impacts would help to clarify trophic dynamics in this system. Direct and indirect effects between alligator (23), turtle (24) and snakes (26) are also significant and important. Snakes are part of the alligator diet, so that one would expect them to exert a positive impact on alligators. However competition between the two for invertebrates, fish, and many other species becomes a crucial factor, and the net effect of this asymmetric competition is negative. Much the same configuration explains the impact coefficient of alligators on snakes and those between turtles

Figure 4



and snakes. The alligator diet includes turtles, making the effect of gators on this prey negative. Turtles impact alligators in a positive way, even though alligator (eggs) are one of their prey. In this case predation by alligator on turtles is stronger than the competition between the two for many common sources of food, and turtle predation on alligators is negligible.

Components with similar diets compete with each other, and the more the diets overlap, the stronger is the competition. In a complex network, such as the forested wetlands, one would expect this effect occur very often; and, in fact, the coefficients in the impacts matrix support this expectation (although there are interesting exceptions.) Mink and Otter, for example, feed on the same compartments, but seem not to compete with one another. The reciprocal negative impacts are less than 1%. Turtles seem to compete with otter and mink, although the intensity of this phenomenon is modest. No significant negative impacts have been observed between other pairs of animal groups that have similar diets, such as great blue herons and woodstork, kites hawks and owls. Significant competition seems to occur, however, between frogs (28, 29, 30) and fishes (20, 21, 22).

The direct impact of a predator on its prey is obviously negative; however, the overall effect can become positive, due to the multiplicity of interaction pathways involved. In such cases we speak of "beneficial predators". In the forested wetlands network a surprisingly large number of beneficial indirect links between predators and their prey exist, and the number of instances is higher during the wet season (78) than in the dry (67). Compartments that exert a positive effect on their prey are numerous: (21) small fish-primarily carnivorous, (36) kites & hawks, (44) owls, (42) white ibis, and, most significantly, (23) American alligator (Table 5.1). The alligator behaves as a beneficial predator to a conspicuous number of prey (Fig. 5): invertebrates (15, 16, 17, 18, 19), frogs (28, 29, 30), galliformes (37), and mice & rats (61). This behavior appears to be related to the combined effect of strong predatory and competitive relationships between the alligator and turtles and snakes, and these latter two are the most important predators of the compartments just listed.

Analysis of the total dependency matrix yields interesting information about differences between the two study periods. Some changes in direct diets could be related to changes in the availability of primary producers. Squirrels (60), for example, feed more on (8) understory, during the dry season, when the latter is more abundant, and less on (10), hardwoods; the opposite occurs during the wet season (Table 5.2). Primary producers also play a very important role on changes in indirect diet coefficients (Table 5.3). Of particular interest is the fact that phytoplankton, although not a direct source of food to many higher trophic taxa, becomes a key element in their indirect diets during the dry season. Of the 55 seasonal changes in indirect diet coefficients that exceed ten percent, thirty involve phytoplankton (although it forms only eight direct connections.)

Table 5.1. Beneficial predators

WET SEASON	
PREDATORS	PREY
Small fish Herb and Omniv.	Living SED
"	Terrestrial inverts
Small fish carnivorous	Living POC
"	Living SED
"	Phytoplankton
"	Periphyton
"	Macrophytes
"	Epiphytes
"	Terrestrial inverts
Large fish	Living POC
"	Living SED
"	Terrestrial inverts
Alligator	Crayfish
"	Apple snail
"	Prawn
"	Aquatic inverts
"	Terrestrial inverts
"	Large frogs
"	Small frogs
"	Sal. larvae
"	Tadpoles
"	Galliformes
"	Mice&Rats
Turtles	Aquatic inverts
"	Terrestrial inverts
"	Small frog
Snakes	Clayfish
"	Apple snail
"	Prawn
"	Aquatic inverts
"	Terrestrial inverts
Salamanders	Aquatic inverts
"	Terrestrial inverts
Large frogs	Aquatic inverts
"	Terrestrial inverts
Medium frogs	Terrestrial inverts
Small frogs	Aquatic inverts
Pelecaniformes	Small fish Herb and Omniv.
"	Small fish carnivorous
"	Large frogs
"	Small frogs
Anseriformes	Terrestrial inverts
Kites&Hawks	Small fish Herb and Omniv.
"	Small fish carnivorous
"	Large fish
"	Large frogs
"	Small frogs
"	Mice&Rats
Egrets	Terrestrial inverts
Great blue heron	Small fish Herb and Omniv.
"	Small fish carnivorous
"	Salamanders
Other herons	Terrestrial inverts
"	Small frogs
Wood stork	Small fish Herb and Omniv.
"	Small fish carnivorous
"	Salamanders
White ibis	Terrestrial inverts
"	Small fish Herb and Omniv.
"	Small fish carnivorous
"	Small frogs
"	Sal. larvae
"	Tadpoles
Gruiformes	Terrestrial inverts
"	Small fish Herb and Omniv.
"	Small fish carnivorous
Owls	Small fish Herb and Omniv.
"	Small fish carnivorous
"	Large fish
"	Large frogs
"	Small frogs
"	Mice&Rats
Gray fox	Understory
"	Hardwood wood
Raccoon	Terrestrial inverts
Otter	Terrestrial inverts
Armadillo	Understory
"	Hardwood wood

DRY SEASON	
PREDATORS	PREY
Small fish Herb and Omniv.	Living SED
"	Terrestrial inverts
Small fish carnivorous	Living POC
"	Living SED
"	Phytoplankton
"	Periphyton
"	Macrophytes
"	Epiphytes
"	Terrestrial inverts
Large fish	Living POC
"	Living SED
"	Aquatic inverts
"	Terrestrial inverts
Alligator	Apple snail
"	Prawn
"	Aquatic inverts
"	Terrestrial inverts
"	Large frogs
"	Small frogs
"	Tadpoles
"	Galliformes
"	Egrets
"	Other herons
"	Mice&Rats
Turtles	Aquatic inverts
"	Terrestrial inverts
Snakes	Clayfish
"	Apple snail
"	Prawn
"	Aquatic inverts
"	Terrestrial inverts
Salamanders	Aquatic inverts
Large frogs	Aquatic inverts
Medium frogs	Aquatic inverts
Small frogs	Aquatic inverts
Pelecaniformes	Small fish Herb and Omniv.
"	Large frog
"	Medium frogs
"	Small frogs
Anseriformes	Terrestrial inverts
Kites&Hawks	Small fish Herb and Omniv.
"	Large fish
"	Large frogs
"	Mice&Rats
"	Rabbits
White ibis	Terrestrial inverts
"	Small fish Herb and Omniv.
"	Small fish carnivorous
"	Medium frogs
"	Small frogs
"	Tadpoles
Gruiformes	Terrestrial inverts
Owls	Small fish Herb and Omniv.
"	Large fish
"	Large frogs
"	Mice&Rats
"	Rabbits
Gray fox	Understory
"	Hardwood wood
"	Terrestrial inverts
Raccoon	Terrestrial inverts
"	Small fish Herb and Omniv.
Mink	Small fish Herb and Omniv.
Otter	Small fish Herb and Omniv.
Armadillo	Understory
"	Hardwood wood

Figure 5. Beneficial predators

American alligator

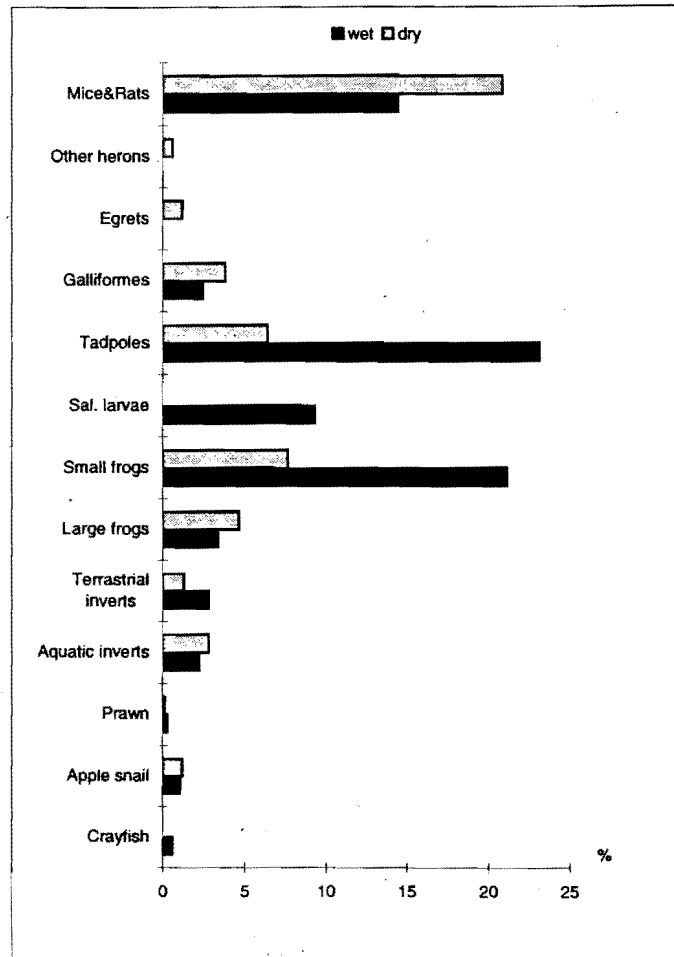


Table 5.2. Direct diet changes

PREDATOR	PREY	WET	DRY	Δ diet
Gray fox	Squirrels	41.46	17.75	23.71
Liable detritus	Phytoplankton	16.73	37.05	-20.32
Refractory detritus	Understory	10.10	29.34	-19.24
Refractory detritus	Cypress leaves	27.30	9.55	17.75
Gray fox	Rabbits	6.03	23.00	-16.97
Tadpoles	Periphyton	44.32	28.20	16.12
Tadpoles	Phytoplankton	29.74	44.90	-15.16
Squirrels	Understory	43.32	57.44	-14.12
Rabbits	Hardwood leaves	48.69	35.93	12.76
White-Tailed deer	Hardwood leaves	48.65	35.89	12.76
Rabbits	Understory	51.31	64.07	-12.76
White-Tailed deer	Understory	51.35	64.11	-12.76
Great blue heron	Alligator	13.95	1.46	12.49
Wood stork	Alligator	13.77	1.45	12.32
Gruiformes	Lizards	22.67	10.47	12.20
Black bear	Understory	39.97	51.30	-11.33
Medium frogs	Terrestrial inverts	7.13	16.39	-9.26
Small frogs	Terrestrial inverts	7.12	16.36	-9.24
Great blue heron	Terrestrial inverts	5.65	14.88	-9.23
Black bear	Hardwood leaves	37.85	28.73	9.12
Large fish	Aquatic inverts	35.42	26.34	9.08
Snakes	Small fish Herb and Omniv.	41.92	32.92	9.00
Wood stork	Terrestrial inverts	5.49	14.46	-8.97
Mice&Rats	Hardwood leaves	41.12	32.17	8.95
Otter	Terrestrial inverts	6.76	15.67	-8.91
Mink	Terrestrial inverts	6.76	15.66	-8.90
Egrets	Terrestrial inverts	6.19	15.00	-8.81
Liable detritus	Periphyton	15.66	6.88	8.78
Galliformes	Hardwood leaves	33.03	24.24	8.79
Gruiformes	Terrestrial inverts	4.72	13.43	-8.71
Galliformes	Understory	34.85	43.23	-8.38
Large fish	Prawn	18.87	27.18	-8.31
Snakes	Medium frog	2.37	10.60	-8.23
Other herons	Terrestrial inverts	6.05	13.96	-7.91
Owls	Terrestrial inverts	6.15	13.99	-7.84
Kite&Hawk	Terrestrial inverts	6.16	13.99	-7.83
Hog	Hardwood leaves	27.99	20.52	7.47
Large fish	Crayfish	12.24	4.87	7.37
Bobcat	Rabbits	1.92	9.27	-7.35
Liable detritus	Cypress leaves	10.23	2.93	7.30
Raccoon	Hardwood leaves	22.74	15.49	7.25
Hog	Understory	29.60	36.63	-7.03

Table 5.3. Indirect diet changes

PREDATOR	PREY	WET	DRY	Δ diet
Liabile detritus	Phytoplankton	21.76	46.06	-24.30
Gray fox	Squirrels	41.48	17.76	23.72
Living POC	Phytoplankton	19.61	41.20	-21.59
Tadpoles	Phytoplankton	33.84	54.33	-20.49
Refractory detritus	Understory	10.46	30.44	-19.98
Living SED	Phytoplankton	15.35	34.89	-19.54
Tadpoles	Periphyton	50.31	31.71	18.60
Refractory detritus	Cypress leaves	28.19	9.95	18.24
Gray fox	Rabbits	6.13	23.18	-17.05
Sal. larvae	Phytoplankton	28.11	44.23	-16.12
Aquatic inverts	Phytoplankton	28.11	44.23	-16.12
Crayfish	Phytoplankton	17.42	32.72	-15.30
Apple snail	Phytoplankton	17.47	32.68	-15.21
Squirrels	Understory	43.32	57.44	-14.12
Bobcat	Understory	49.06	62.27	-13.21
Small fish carnivorous	Phytoplankton	25.80	38.67	-12.87
Large fish	Phytoplankton	23.69	36.46	-12.77
Withe-Tailed deer	Understory	51.35	64.11	-12.76
Rabbits	Hardwood leaves	48.69	35.93	12.76
White-Tailed deer	Hardwood leaves	48.65	35.89	12.76
Rabbits	Understory	51.31	64.07	-12.76
Pelecaniformes	Phytoplankton	19.78	32.29	-12.51
Gruiformes	Phytoplankton	16.76	29.16	-12.40
Great blue heron	Alligator	14.42	2.09	12.33
Liabile detritus	Periphyton	25.27	12.95	12.32
Gruiformes	Lizards	22.71	10.53	12.18
Wood stork	Alligator	14.36	2.23	12.13
Egrets	Phytoplankton	18.26	30.39	-12.13
Small fish Herb and Omniv.	Phytoplankton	23.72	35.81	-12.09
Bobcat	Hardwood leaves	46.42	35.00	11.42
Large frogs	Phytoplankton	20.44	31.84	-11.40
Otter	Phytoplankton	19.35	30.66	-11.31
Mink	Phytoplankton	19.32	30.61	-11.29
Living POC	Periphyton	23.27	12.00	11.27
White ibis	Phytoplankton	18.96	30.24	-11.28
Salamanders	Phytoplankton	20.13	31.39	-11.26
Small frogs	Phytoplankton	19.18	30.40	-11.22
Medium frogs	Phytoplankton	19.18	30.39	-11.21
Living POC	Cypress leaves	16.16	4.98	11.18
Alligator	Phytoplankton	20.46	31.61	-11.15
Owls	Phytoplankton	19.15	30.30	-11.15
Kites&Hawks	Phytoplankton	9.16	30.30	-21.14
Black bear	Understory	45.05	56.12	-11.07
Great blue heron	Phytoplankton	19.49	30.55	-11.06
Wood stork	Phytoplankton	19.31	30.26	-10.95
Snakes	Phytoplankton	21.38	32.28	-10.90
Living SED	Periphyton	32.21	21.40	10.81
Vultures	Phytoplankton	19.52	30.31	-10.79
Vert. detritus	Phytoplankton	19.52	30.31	-10.79
Other herons	Phytoplankton	18.08	28.83	-10.75
Living SED	Cypress leaves	15.12	4.69	10.43
Black bear	Hardwood leaves	42.42	32.16	10.26
Liabile detritus	Cypress leaves	14.48	4.25	10.23
Medium frogs	Terrestrial inverts	7.59	17.68	-10.09
Small frogs	Terrestrial inverts	7.58	17.66	-10.08

5.3 Trophic Levels

The changes in diet composition just discussed concern mainly primary producers and don't seem to induce big changes in the average trophic levels of most heterotrophs (Fig. 6). This relative constancy could be due to the fact that alternative food sources for a given compartment often belong to the same trophic level as the prey they replace. An example already cited is the squirrels' alternating preference for understory and hardwood leaves, both of which belong to trophic level one. The same compensation applies in some cases to indirect diets.

Those compartments that do undergo major dietary changes between seasons, such as living POC and living sediment, feed only on level-one compartments, so that any change in their diet distributions will have no effect on their trophic positions. The only compartments that show any significant diet modification are the Gruiformes, great-blue heron and woodstork. During the dry season they feed more on lower trophic levels, especially compartment 19, terrestrial invertebrates. During the wet season, however, they feed more on alligator eggs and lizards.

Trophic analysis also addresses ecological efficiency. Among the compartments with low production efficiencies were many mammals and birds (Fig. 7). These are mainly top predators, such as vulture, owls, panther, and black bear, whose productions go almost entirely to detritus compartments (Fig. 8). The same applies to alligator. Although some predators feed on alligators eggs and juveniles, this predatory loss represents only a small proportion (0.2%) of alligator assimilation. The remaining reptiles exhibited ranges in efficiency from 10-17%. The significant predation on these taxa is more than balanced by the high amount of biomass they produce. They account for 50% of the total vertebrate biomass, which is due in part to moderate predation and in part to their low metabolic rates. Large biomasses and high secondary production likewise characterize invertebrates as having middle to low efficiencies (2-15%). They represent 88% of the total system animal biomass.

Amphibians and fishes are the most efficient compartments. The trophic efficiencies for fish range from 21 to 61%, and for amphibians, 46 - 87%. They sustain many compartments and their losses to predation are comparable to their productions. The high efficiencies reflect their importance in energy transfer.

The trophic efficiencies for each trophic level, for wet and dry season, are depicted in Fig. 9. The pattern in the efficiencies is quite unusual. In most other studies) efficiency decreased more or less monotonically along the trophic chain (Baird and Ulanowicz, 1989), while here the efficiency fluctuates markedly. For wet seasons, after an initial sharp decrease from 47.3% in level I to 2.64% at level II, trophic efficiencies rise over the next two steps, reaching 8.46 % at level III, and 15.1% at level IV. From this point onward efficiency decreases along the trophic

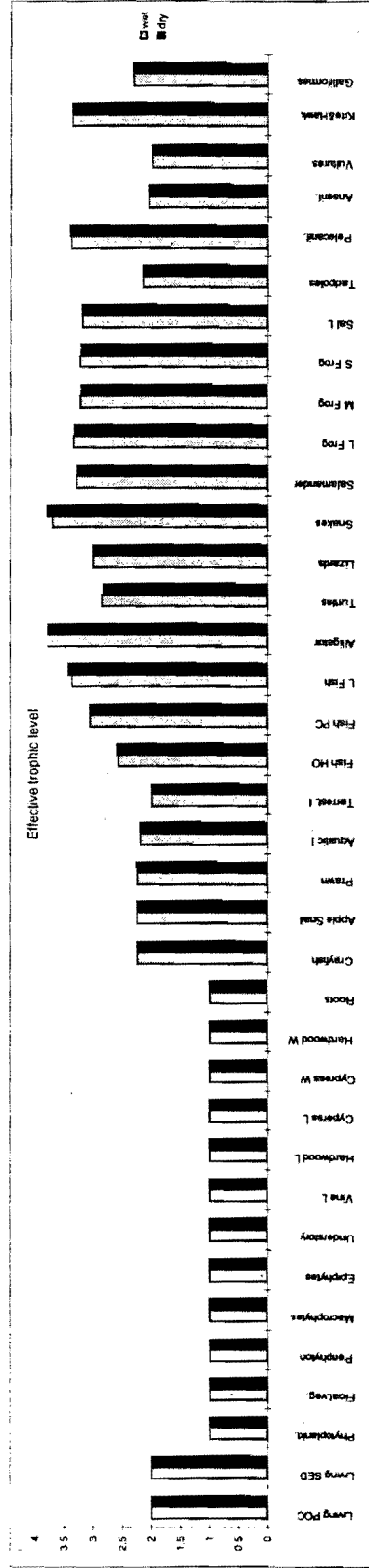
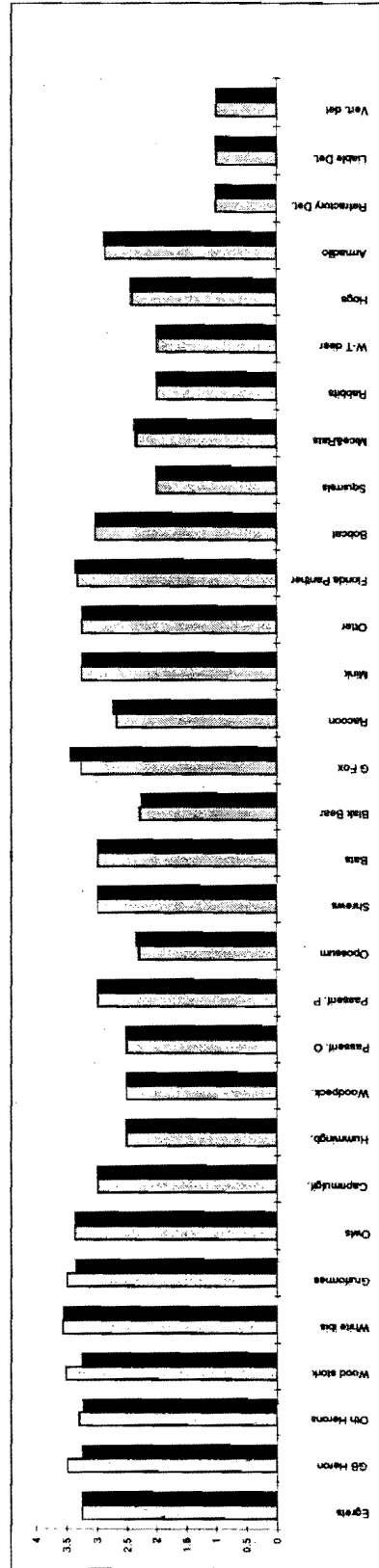
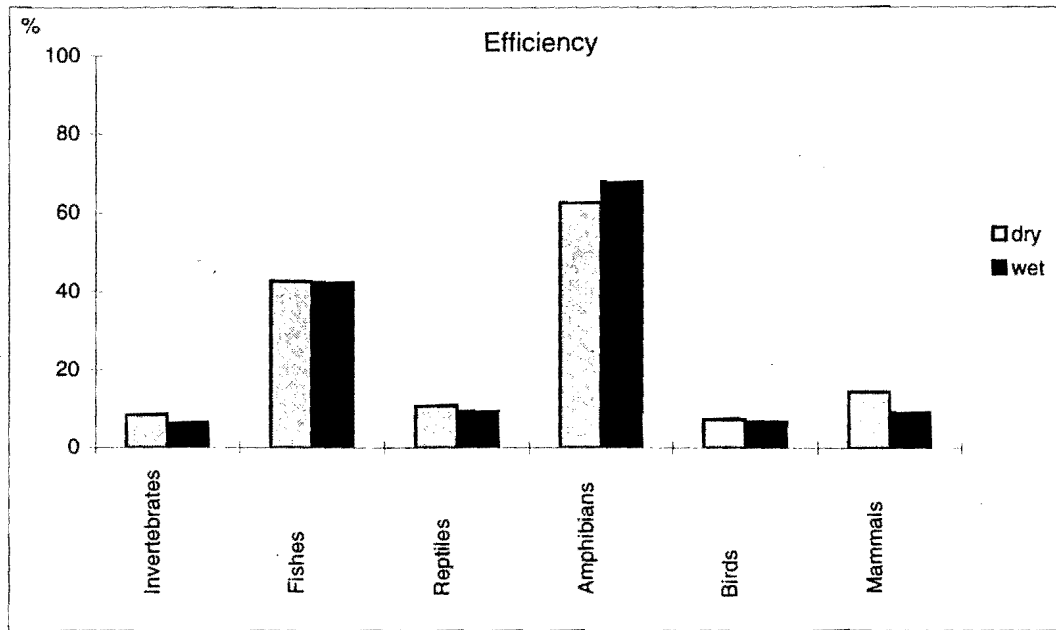


Figure 6

Figure 7



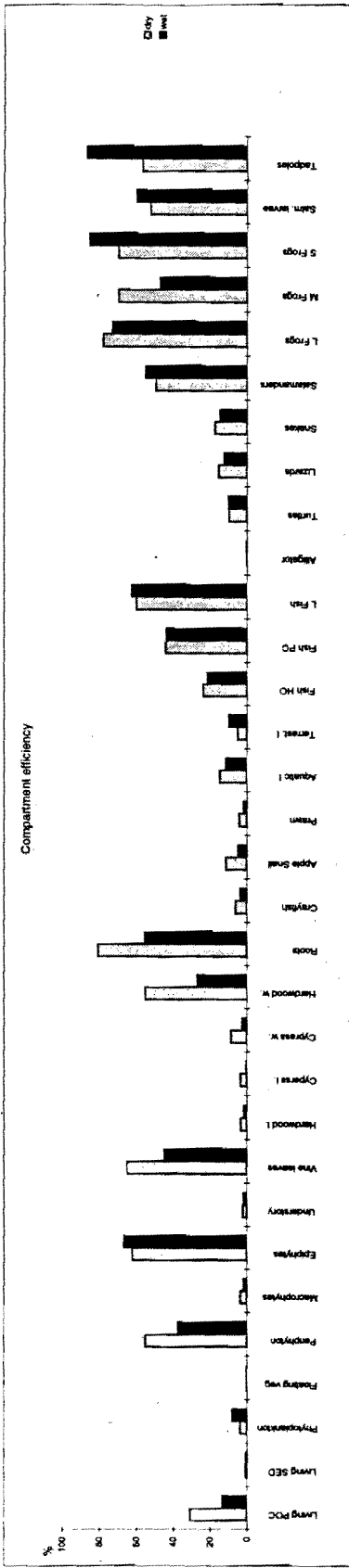
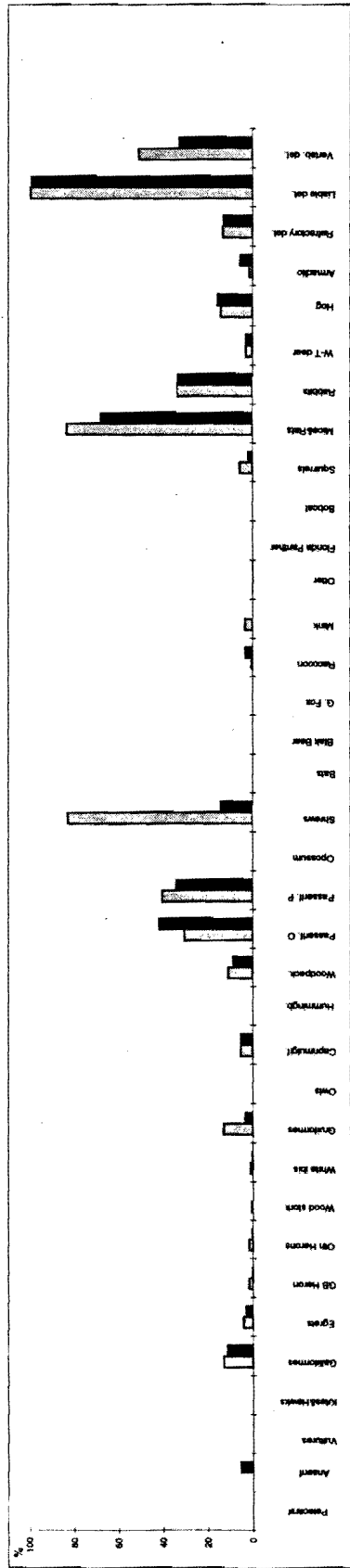
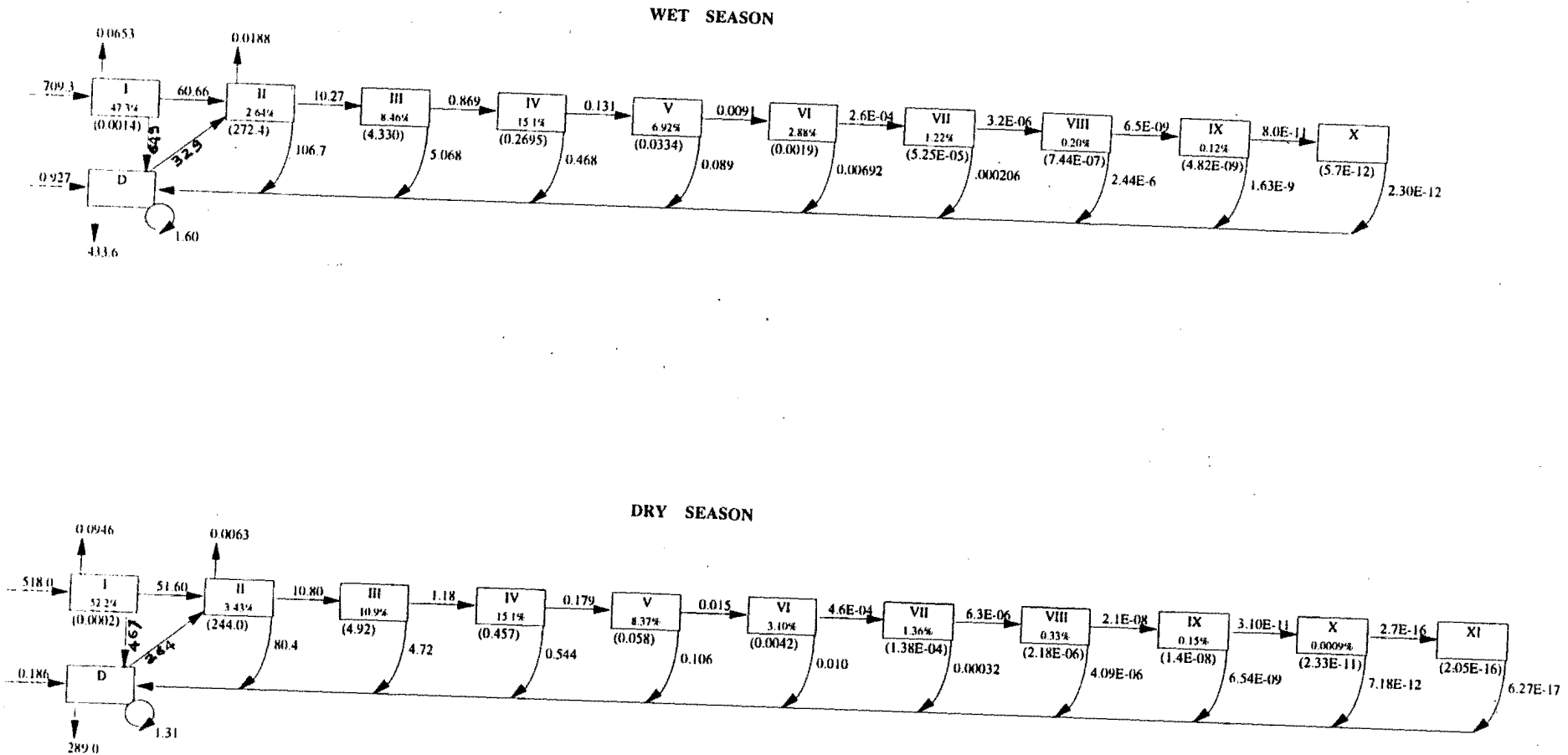


Figure 8

Figure 9



chain. The low value for level II is attributable mainly to "living sediment". Only 0.69% of what goes into this compartment reaches the third level. Of the total amount of material entering the second trophic level, 90% passes through this "living sediment". Part of it is dissipated and part becomes detritus. This very low trophic efficiency also contributes to the strong negative effect that this compartment has on many other taxa, as described in Section 5.2. By way of contrast, the positive effect of compartment 1, living POC, likely results from a higher efficiency coefficient (14%). More than 50% of what comes out of level II and enters level III issues from the living POC. The efficiencies at levels III and IV rise, mostly due to the high efficiencies of the fishes and amphibians. Wet and dry seasons show similar trends in trophic efficiencies, but values are generally higher during the dry season. The same pattern applies to the efficiencies of single compartments: they are higher during the dry season, as shown in Fig. 9.

5.4 System Level Indices

Perusal of the community organizational indices (Table 5.4) reveals a familiar story. Ulanowicz and Baird (1989), for example, examined how the system ascendancy and related variables calculated for the Chesapeake mesohaline ecosystem varied over the four seasons of the year. They concluded that the magnitude of system activity (total system throughput) modulated almost all the seasonal variation in the ascendancy-type variables. The seasonal variation in the informational factors (e.g., ascendancy/ throughput, capacity/ throughput, etc.) was insignificant by comparison. In other words, the magnitudes of trophic processes changed markedly over the course of a year, but the kinetic relationships among them remained essentially the same. (The assumed topology was held invariant over the seasons, but the relative magnitudes of the flows still could have changed the values of the information indices. It did so only to a slight degree.) In evaluating the impacts of thermal additions to a tidal marsh ecosystem Ulanowicz (1984) also observed that the resulting change in activity level was strong, but the underlying trophic structure remained relatively unimpacted.

A comparison of the organizational status of the wet and dry season networks reveals this same pattern. The total system throughput falls by some 25%. This drop is repeated in virtually all the other indices, so that, proportionally, there is very little change in any of the information factors. The proportion of capacity that appears as ascendancy (A/C) actually rises by 0.6% during the dry season. Somewhat noteworthy, the flow diversity (C/T) also rises from 4.64 to 4.71 bits. (If the dry season were the period of greatest system stress, one would expect both these values to fall instead of rise.) The proportion of internal ascendancy (A_i/C_i) shows a bit more of an increase during the dry season (1.4%). (One must bear in mind that the information indices are logarithmic in nature, so that small differences in them reflect somewhat larger changes in the underlying kinetics.)

Table 5.4 -- Information Indices
(gCarbon-bits/m²/y)

	Wet Season	Dry Season
TOTAL SYSTEM THROUGHPUT	= .25853E+4	.19192E+4
DEVELOPMENT CAPACITY	= .12000E+5	.90402E+4
ASCENDENCY	= .51943E+4 (.433)	.39672E+4 (.439)
OVERHEAD ON IMPORTS	= .19613E+4 (.163)	.14518E+4 (.161)
OVERHEAD ON EXPORTS	= .12196E+3 (.010)	.75320E+2 (.008)
DISSIPATIVE OVERHEAD	= .40258E+3 (.034)	.33158E+3 (.037)
REDUNDANCY	= .43202E+4 (.360)	.32142E+4 (.356)
INTERNAL CAPACITY	= .64322E+4	.48885E+4
INTERNAL ASCENDENCY	= .21120E+4 (.328)	.16743E+4 (.342)
REDUNDANCY	= .43202E+4 (.672)	.32142E+4 (.658)
Connectance Indices (Links per node)		
OVERALL CONNECTANCE	= 1.909	1.906
INTERCOMPARTMENTAL CONNECTANCE	= 3.221	3.158
FOODWEB CONNECTANCE	= 2.026	2.277

The connectance indices are the log- averaged number of connections per node (Ulanowicz, in press). The value for the overall connectance (includes all flows, internal as well as external) of ca. 1.9 links per node is somewhat low, indicating the system should possess a strong internal stability, but possibly will exhibit little resilience to externally imposed stress. Surprisingly, the intercompartmental connectance (includes only internal flows) is very high and exceeds the theoretical maximum (ca. 3.01) for a stable system. This high value is probably inflated by the large number of passive returns to the detrital compartments; because, when only feeding flows are included, the connectance drops to a very reasonable value of 2 - 2.3 links per node.

Heretofore, the information indices have been applied only to whole systems. Evidence is accumulating, however, that the various subcomponents of the ascendancy-like variables can serve to gauge the contributions of individual system elements to the performance of the whole system (Ulanowicz 1996.) For example, the ascendancy is comprised of terms that are generated by each transfer in the system. If, for example, one sums up all the terms generated by the inputs to a given taxon (say, the j th one), the result is a measure of the contribution of that compartment to the full system ascendancy (call it A_j). Because ascendancy may be viewed as an indicator of efficient system performance (Ulanowicz 1997), the same partial-sum, A_j , represents the contribution of taxon j to overall system performance. Furthermore, if one then divides A_j by the corresponding throughput for taxon j (call it T_j), the ratio A_j/T_j will represent the contribution per unit of activity of j to the total system ascendancy.

Calculating and ranking these "contribution coefficients" proves to be a most interesting exercise (Table 5.5). When the average trophic levels of the 68 compartments were presented (Fig. 6), it may have surprised some to see the alligators, snakes and wading birds feeding at trophic levels that are higher than some other "charismatic megafauna", such as the Florida panther, Bobcat, or Grey Fox. The relative contributions to ascendancy by the latter, however, outweigh the former, as shown in the table. Perhaps even more surprising is the very high ranking of the Vertebrate Detritus (fifth). The relative values of these coefficients seem to accord well with most people's normative judgments of the specific "value" of the various taxa to the organization of the system as a whole.

5.5 Cycling

In comparison with the gramminoid wetlands to the southeast, which are more rapidly flushed by sheet flow from Lake Okechobee, one expects the cypress wetlands to appear more like a closed system, with materials cycling within for long times. With respect to carbon, however, the numbers do not bear out this conjecture. The Finn cycling index, for example, measures the fraction of the total system throughput that is engaged in recycling. It is only 8.8% during the wet season and 9.2% in the dry. These values are less than half the relative amount of

Table 5.5 -- Ascendency Component Sensitivities (Bits)

Wet Season				Dry Season		
Rank	Comp	Taxon	Sens	Comp	Taxon	Sens
1	67	Liabile Det.	1.395	67	Liabile Det.	1.524
2	66	Refractory D	1.696	18	Aquatic I	1.662
3	18	Aquatic I	1.743	66	Refractory D	1.748
4	3	Phytoplanto	1.863	3	Phytoplanto	1.888
5	4	Float VEG	1.863	4	Float VEG	1.888
6	5	Periphyton	1.863	5	Periphyton	1.888
7	6	Macrophytes	1.863	6	Macrophytes	1.888
8	7	Epiphytes	1.863	7	Epiphytes	1.888
9	8	Understory	1.863	8	Understory	1.888
10	9	Vine L	1.863	9	Vine L	1.888
11	10	Hardwood L	1.863	10	Hardwood L	1.888
12	11	Cypress L	1.863	11	Cypress L	1.888
13	12	Cypress W	1.863	12	Cypress W	1.888
14	13	Hardwood W	1.863	13	Hardwood W	1.888
15	14	Roots	1.863	14	Roots	1.888
16	15	Crayfish	1.981	2	Living SED	2.123
17	2	Living SED	2.042	15	Crayfish	2.200
18	16	Apple Snail	2.276	32	Tadpoles	2.399
19	32	Tadpoles	2.570	19	Terrst. I	2.457
20	1	Living POC	2.583	1	Living POC	2.462
21	17	Prawn	2.725	16	Apple Snail	2.480
22	19	Terrst. I	3.218	34	Anseriformes	2.706
23	20	Fish HO	3.289	17	Prawn	2.910
24	34	Anseriformes	3.398	60	Squirrels	3.096
25	60	Squirrels	3.751	20	Fish HO	3.195
26	24	Turtles	4.266	62	Rabbits	3.352
27	55	Racoon	4.356	63	White-Tailed	3.352
28	62	Rabbits	4.441	53	Blak Bear	3.524
29	63	White-Tailed	4.441	37	Galliformes	3.635
30	53	Blak Bear	4.870	55	Racoon	3.707
31	37	Galliformes	4.964	61	Mice & Rats	3.772
32	61	Mice & Rats	5.059	64	Hogs	3.912
33	21	Fish PC	5.130	24	Turtles	4.009
34	64	Hogs	5.322	47	Woodpeckers	4.278
35	46	Hummingbirds	5.769	46	Hummingbirds	4.296
36	47	Woodpeckers	5.773	48	Passfrm omni	4.296
37	48	Passfrm omni	5.773	21	Fish PC	5.050
38	36	Kites & Hawk	6.163	50	Opossum	5.295
39	44	Owls	6.164	41	Wood stork	5.465
40	56	Mink	6.173	36	Kites & Hawk	5.476
41	57	Otter	6.241	44	Owls	5.477
42	27	Salamanders	6.296	39	GB Heron	5.480
43	29	M Frog	6.316	38	Egrets	5.511
44	30	S Frog	6.316	56	Mink	5.588
45	41	Wood stork	6.401	57	Otter	5.612
46	39	GB Heron	6.422	29	M Frog	5.615
47	28	L Frog	6.430	30	S Frog	5.616
48	22	L Fish	6.432	40	Oth Herons	5.688
49	33	Pelecaniform	6.460	27	Salamanders	5.691

Table 5.5, Continued

50	50 Opossum	6.496	28 L Frog	5.764
51	40 Oth Herons	6.536	43 Gruiformes	5.908
52	38 Egrets	6.559	33 Pelecaniform	5.987
53	42 White ibis	7.102	65 Armadilo	6.031
54	43 Gruiformes	7.389	42 White ibis	6.304
55	65 Armadilo	7.803	22 L Fish	6.381
56	31 Sal L	8.191	25 Lizards	7.020
57	26 Snakes	8.481	45 Caprimulgifo	7.020
58	23 Alligator	8.562	52 Bats	7.020
59	25 Lizards	8.887	49 Passfrm pred	7.021
60	45 Caprimulgifo	8.887	51 Shrews	7.040
61	52 Bats	8.887	23 Alligator	7.676
62	49 Passfrm pred	8.888	26 Snakes	7.975
63	51 Shrews	8.935	31 Sal L	7.996
64	68 Vert det	9.005	68 Vert det	8.294
65	35 Vultures	10.080	35 Vultures	9.487
66	54 G Fox	12.540	54 G Fox	10.590
67	59 Bobcat	14.960	59 Bobcat	13.770
68	58 Florida Pant	16.730	58 Florida Pant	14.370

recycling that one encounters in the ecosystem of Chesapeake Bay (21%), which is flushed at a much higher rate (Baird and Ulanowicz 1989.)

This difference between the swamp and estuary seems to have its origin in the relative availabilities of material that falls to the sediment in each habitat. In Chesapeake Bay, carbon reaching the sediment is more likely to be reused and fed back up the trophic chain. In the cypress networks, by contrast, material reaching the bottom is more likely to stay buried. (These are muck - producing systems.) Also, material not reaching the bottom is likely to be respired sooner, due to the higher ambient temperatures.

Despite these low magnitudes of recycling, the structure of the recycle pathways that do exist is exceedingly complex. The wet season network, for example, possesses exactly 3,975,514 simple cycles of carbon. (A simple cycle is one in which no taxon is visited more than once.) The dry season configuration is even more complicated, possessing 27,084,903 cycles. The analysis of so many pathways for recycle was far beyond the capabilities of the version of NETWRK that was available at the beginning of the project year. The way that version was written, it was necessary to store the individual identities of all they before the cycles could be separated from the network. When only several thousand or fewer cycles were identified, this requirement proved to be no obstacle. There is simply no way, however, using most desktop computers, to store over 27,000,000 cycles (some up to 20, two- digit links long) in RAM, and even attempting a RAM-ROM tradeoff proved to be prohibitive.

It was obvious that the cycle identification routine of NETWRK needed to be rewritten, in order to treat the multitude of cycles in rigorous fashion. Eventually, a way was found to remove a very large number of cycles while staying within RAM during most of the procedure. In effect, speed of execution was sacrificed to avoid a massive need for storage. Thus, instead of storing the identities of all the cycles at any time, only summary information about the nexus (a group of cycles with the same limiting link) with the smallest link is stored during one pass through the identification routine. That nexus is then removed, and the whole procedure is started anew with the residual network. This amended algorithm requires many passes through a combinatorial search routine, all of which entails a prodigious amount of computation. This disadvantage is offset somewhat by the enormous speed of the newer PC's on today's market. Even so, the task remained daunting. It took a Sun- SPARC Ultra (TM), one of the fastest mid-range computers on the current market, over 177 hours to strip the 27M cycles from the dry season network.

The big question is why do there exist so many more cycles in the dry season network than during the wet period? To answer this, it was necessary to examine the list of nexuses that were unique to each season. It turned out that there were roughly the same number of nexuses particular to each season; and, furthermore, most of the nexuses that exist only during the wet

season contained more individual cycles than those unique to the dry season. There were, however, several overwhelming exceptions to this pattern. In particular, those nexuses unique to the dry season that involved as prey the 6 taxa, Woodstork, Other Herons, Egrets, Great Blue Heron, White Ibis, and Alligator, added over 15,500,000 cycles to the dry season count. (Presumably, predation upon these taxa also inflated the numbers of cycles in the nexuses common to both seasons.)

The reader may already have noted that the taxa just named feed near the top of the foodchain, and as adults they rarely become prey for others. This is not true of their eggs or juveniles, however. "Ovi- predation" is quite common during the dry season, when the birds and gators are nesting, and it seems to be this type of feeding that creates an enormous number of new channels for recycle. Predation on large, energy rich eggs is common in terrestrial and freshwater communities, and the eggs of amphibians, reptiles and birds are the predominant prey. Nest predation seems to be consistently lower in the marshes and higher in the adjacent upland habitats. Deep water and dense vegetation plays an important role in restricting predation to only very water-adapted predators, such as mink. Moreover, nests became more vulnerable during the dry season, as they remain exposed to predators, such as raccoons and foxes. Because of the high bird density in this area during the dry season and because of the high energetic value of big wading bird eggs, we think that "ovi-predation" deserves particular attention in the cypress network.

The distribution of cycled flow among loops of different trophic lengths can provide clues to system performance. Presumably, less impacted systems are able to cycle material over longer and slower routes. In comparing cycling during the wet and dry seasons, one observes that 6.9% of system activity consists of recycle over loops of trophic length two. This is slightly higher than the 6.7% that circulates over pathways of the same length in the dry season. (No single- link feedbacks are present in either network.) Because the Finn cycling index of the dry season is higher than that for the wet, one deduces that proportionately more material is cycling during the dry season over longer, slower cycles, and the output from NETWRK confirms that as fact. Once again, the dry season shows comparatively less evidence of impact.

6. SUMMARY

The cypress swamp ecosystem of Southwest Florida provides probably the closest subtropical analog in the continental United States to the much- reputed complexity of the legendary tropical rainforest. It is a highly complex ecosystem, whose workings are not easily captured by simple models. The 68- compartment network of trophic exchanges developed in this ATLSS subproject is the most highly- resolved and complicated trophic budget ever to be assembled.

Previous studies of cypress- dominated ecosystems in Florida have characterized the biotype as being primarily detritus- based (Odum & Ewel 1984), so that the preliminary ATLSS model of the lower trophic level processes in this habitat were written according to this scenario (Ulanowicz 1995b.) In light of this legacy, the most significant and surprising result to issue from the current work is the conclusion that the cypress ecosystem is *not* primarily a detritally- based ecosystem. To be sure, the input of carbon and energy from the cypress litterfall is significant, but available evidence and expert opinion point to the likelihood that most of this particular input ends up buried in the sediments. This is, after all, a peat- producing system.

There is ample evidence to support the contention that over half of the carbon reaching the higher trophic levels arrived there via the grazing chain, without passing through any detrital compartment. The understory vegetation of phytoplankton, periphyton, vines and epiphytes constitute the trophic foundations for most of the higher trophic level production. The production by phytoplankton is especially important to the sustenance of the system during the dry season, when the mostly deciduous canopy is relatively open. It will be necessary to rewrite the lower trophic level ATLSS module for cypress wetlands to accommodate this new scenario for trophic dynamics. In a sense, even before the preliminary ATLSS model has been assembled, network analysis already has begun to fulfill its purpose to serve as a benchmark against which to judge the performance of the ATLSS simulation.

Trophic efficiencies are greatest among the fish and amphibians. Predation on these groups comes close to matching their assimilation and growth. Efficiencies of the reptiles and mammals are low by comparison, with much of their assimilation being respired or going to detritus. The efficiency of the "living sediment" is especially low, causing it to exert a negative trophic impact upon a number of compartments. Trophic levels do not change much between the wet and dry seasons. Although several species showed significant dietary changes between seasons, these mostly involved replacement by alternate prey at the same trophic level. Trophic efficiencies at each level do not decline in monotonic fashion, as is usually the case, but rather fluctuate in magnitude. There is a sharp drop in efficiency from level I to II, followed by a gradual rise in production efficiency in the next two levels, which are dominated by fish and amphibians. The trophic level efficiencies during the dry season differ from those during the wet period only in being slightly higher.

Total system activity drops 25% during the dry season, but the accompanying trophic structure seems to change little between seasons. In fact, structural measures indicate a slightly higher level of system organization during the dry season. Experimentation with the terms of the system ascendancy led to the discovery that the quotient of the contribution of a taxon to overall ascendancy divided by the activity of the same compartment yielded a very useful index of the relative contribution by that taxon to overall system performance. According to this measure, taxa such as panther, bobcat and fox exhibited the highest "intrinsic values" in the

ecosystem, despite their being lower on the trophic scale than reptiles, such as alligators and snakes.

Although the cypress swamps appear to be somewhat isolated as regards physical transport, there is relatively little cycling of carbon in this system. The percentage of activity in cypress ecosystems that comprises cycling is less than half the corresponding fraction found in physically more open systems, such as the Chesapeake estuary. It appears that much of the carbon flow exits the system in the burial of cypress litterfall before it can be included into the trophic dynamics. Despite the low relative magnitude of cycling in cypress systems, the structure of cycling in these communities is exceedingly complex. For example there are over 27 million simple cycles in the dry season network, most of which owe their existence to "ovi-predation", or the consumption of nutrient rich eggs and juveniles of higher trophic species by populations lower on the trophic chain.

Although one is inclined to think of the wet season as being the normal configuration for the cypress ecosystem, this judgement is rendered on the basis of the dominant vegetation, not on the trophic status of the system as a whole. All indications issuing from this analysis suggest that the dry season configuration of trophic processes performs under less stress.

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