Network analysis of the South Florida Everglades graminoid marshes and comparison with nearby cypress ecosystems

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Abstract

Network analysis (NA) is used to compare two ecosystems with different spatial extents to understand the different patterns and dynamics that arise. NA allows one to study the system at different scales: At the level of bilateral interactions, input-output structure matrices are calculated to look at the direct and indirect effects that one flow has on another; at the functional level, the food web is mapped into a concatenated trophic chain, and all simple, directed biogeochemical cycles are identified and separated from the supporting dissipative flows; and at the system's level global variables describe the state of development of the total network. The systems in question are the Everglades graminoid marsh and the adjacent cypress swamp. The graminoid marsh is essentially a two-dimensional system, with reduced diversity of primary producers, and a more focussed dependency of higher trophic levels on one particular primary producer, the periphyton. Although the cypress swamp system contains most of the same flora and fauna as the graminoids, it extends into a third dimension, and contains additional forms of terrestrial vegetation that increase the diversity of primary production, and thereby the resilience of the ecosystem. The importance of detritus to both systems is marked, although recycling within detritus is far more important in the graminoids than in the cypress. The linkages to higher trophic levels are relatively fewer in the graminoids, and the diversity of interactions between the detritus and higher trophic levels is much higher in the cypress. Overall, the presence of a third dimension imparts diversity and resilience to the cypress system, although the faster turnover rates of the graminoids make them more productive. © 2002 Elsevier Science B.V. All rights reserved.

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1. Introduction

The issues of scale as they pertain to complex systems such as the Everglades are described by Ulanowicz (1997) in '*Ecology, the Ascendant Perspective*'. The notion of ascendancy, central to Ulanowicz's theory, is rich in scaling implications (Allen and Roberts, 1998). According to Ulanow-

icz (1997) the universality (i.e. laws applying uniformly over all scales of time and space) that is taken for granted in physical science is viewed by some ecologists with much skepticism. The new picture of the world is more 'granular' and laws are now thought to apply to only a finite range of spatial and temporal scales (Ulanowicz, 1997). Attempts to stretch explanations and applications of certain terms over several scales should be scrutinized carefully. Thus, it is not sufficient to look at one animal, and describe the ecosystem around it. Instead, a conservative systems theory has evolved that uses a triadic approach (Salthe, 1985). That is, one must observe phenomena at scales both above and below the focal level. In network analysis (NA), analytical methods themselves are used to look at the ecosystem at different scales, i.e. one may regard the effect of one species on another, on a group of other species, or on the whole ecosystem. Similarly, one cannot compare systems with different vertical scales without taking into consideration that the different dimensions will impart differences to these systems.

Therefore, the aim of this paper is to use NA (that works at various scales) to discuss the various effects that vertical extent has on two closely related, but spatially different ecosystems: the two dimensional graminoid marshes of the Everglades National Park and the adjacent three dimensional forest swamps of the Big Cypress Preserve and the Fakahatchee Strand State Preserve. The final stage of NA (global-system comparison) aims to explain the difference in the two systems caused by the added vertical dimensionality in the cypress, and the changes in stability and resilience in the systems due to the additional dimension.

In order to compare these systems, the ecosystems have been modeled for both habitats as pairs of trophic flow networks. These models were commissioned to serve as calibration standards for the Across Trophic Levels System Simulation (ATLSS) Program (DeAngelis et al., 1998) where the interactions of the various elements of wetland biotic communities are simulated within the framework of a single, encompassing computational scheme. The networks were analyzed using a set of quantitative methods called NA as discussed below.

2. Materials and methods

Highly detailed networks of carbon exchanges within the two sub-ecosystems of the Everglades (the graminoids and the cypress) have been constructed. Networks consisting of more than 60 of the important components have been estimated for each habitat, using existing data and ongoing fieldwork. Each resulting network is a snapshot of the trophic flows (in gC m^{-2} per year) and biomasses (in gC m^{-2}) as averaged both over the seasons in question and over the spatial domain of that particular biotope. For this comparison only the dry season models of the graminoid and cypress habitats were used, as the dry period is the time when most of the wading birds are present in the systems. The wading birds nest and roost in the cypress trees but feed mostly in the graminoid marshes, a habit that links the dynamics of these two systems and their food web models.

2.1. Study area

The graminoid habitat used in this study consists of the freshwater marshes in the Everglades National Park (Fig. 1), South Florida, and occupies an area of approximately 214 000 ha (Gunderson and Loftus, 1993). Historically, the Everglades system occupied a 9300 km^2 basin that extended from the southern shore of Lake Okeechobee south and southwest to the Gulf of Mexico (Hoffman, et al. 1990). Currently, the basin can be divided into three sections: Everglades Agricultural Area, Water Conservation Areas, and the Southern Everglades, the latter of which includes the marshes south of Tamiami Trail and the Shark River Slough.

There are two distinct communities in the graminoid system that are differentiated according to short and long hydroperiod areas (Lodge, 1994) and occur in areal ratio of approximately 3:1. Short hydroperiod, marl (mixed) prairie occurs on thin, calcitic soil over limestone bedrock, which occasionally is exposed as jagged, foot-tall projections called pinnacle rock, or dissolved below the surface into pockets or solution holes. Short hydroperiod areas flank both sides of the southern Everglades, and are occupied by a low

sawgrass community of plants with a high diversity (100 species) (Lodge, 1994). Typically, vegetation in the short hydroperiod marsh is less than 1 m tall (Herndorn and Taylor, 1986). Long hydroperiod, deeper marsh communities are developed over peat soil (Goodrick, 1984). The long hydroperiod community occurs more commonly in the central Everglades where they typically are straddled between sawgrass marshes and sloughs. These inundated areas are important for fish and aquatic invertebrates, such as prawns. Long hy-

droperiod areas provide an abundant reserve of prey for wading birds towards the end of the dry season (March–April).

The cypress model used in this analysis represents the 295 000 ha wetlands of the Big Cypress Natural Preserve (Fig. 1) and the adjacent Faka-hatchee Strand State Preserve. Both areas cover a flat, gently sloping limestone plain (Bondavalli and Ulanowicz, 1999) with many strands and domes of cypress trees. The cypress swamp does not have a distinct fauna, but shares many species
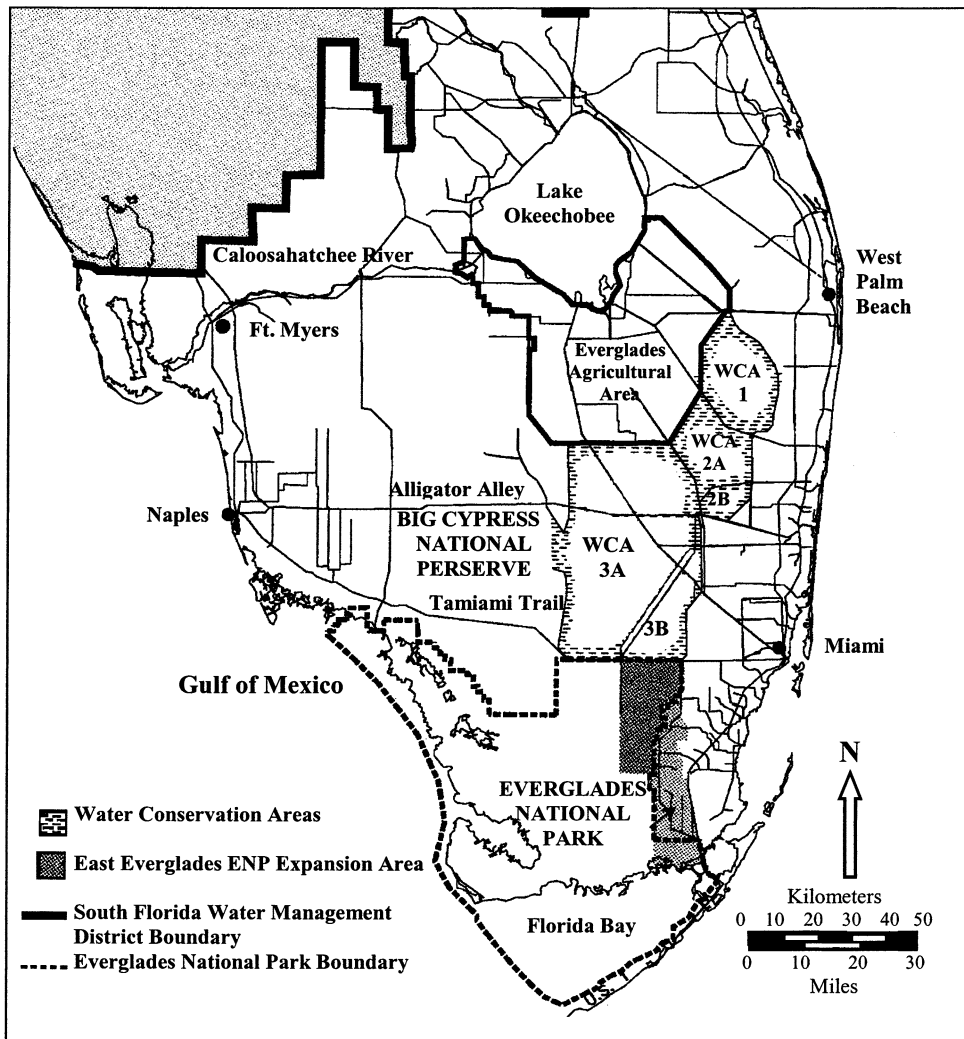

Fig. 1. Southern Florida including the Everglades National Park, Big Cypress Preserve and Water Conservation Areas (adapted from Light and Dineen, 1994).

with the adjacent communities (Bondavalli and Ulanowicz, 1999).

2.1.1. Freshwater graminoid ecosystem compartments

The freshwater marshes of the Everglades are relatively oligotrophic and have been typified as not being very productive-averaging only about 150 g m^{-2} per year in wet prairie areas according to DeAngelis et al. (1998). Graminoid ecosystems provide valuable habitat for a wide range of animals, including species listed by the U.S. Fish and Wildlife Service as endangered, threatened or of concern. Examples of federally protected species include the Florida panther (*Felis concolor coryi*) and the eastern indigo snake (*Drymarchon corais couperi*) (Odum and McIvor, 1990). The Everglades mink (*Mustela vison evergladensis*) (Layne, 1978), snail kites (*Rostrahamus sociabilis*), Cape Sable seaside sparrow (*Ammodramus maritimus mirabilis*), sandhill crane (*Grus canadensis*), and the wood stork (*Mycteria americana*) are also species of concern that are listed as rare or endangered (Kushlan, 1990).

The model of the freshwater graminoid marshes constructed for this study consists of 66 compartments, of which three represent non-living groups and 63 depict living compartments. The construction of the model is described in Ulanowicz et al. (2000). The three non-living compartments include sediment carbon, labile detritus and refractory detritus, all of which are utilized mainly by bacteria and micro-organisms in the sediment (living sediment) and in the water column (living POC-Particulate Organic Carbon).

The primary producers include macrophytes, periphyton, *Utricularia* and other floating vegetation. The macrophyte compartment consists of various species that were combined into short and long hydroperiod macrophytes. For example, the short hydroperiod, sawgrass marsh community consists almost exclusively of *Cladium jamaicense*, while *Eleocharis* spp. was most abundant species in the long hydroperiod community (Daoust and Childers, 1999). Gaiser et al. (1998) found that floating mat communities contained a matrix of *Utricularia purpurea*, cyanobacterial filaments (mostly *Schizothrix hofmanni* and *Scytonema cal-

cicola*), and other associated algae, bacteria, fungi, and invertebrate animals. *Utricularia* is a carnivorous plant that generally occurs in nutrient-poor, sunny and moist (at least in the growing season) habitats, which they usually dominate (Givnish, 1989). They obtain most of their nutrients via normal uptake from the dissolved phase, but they also capture zooplankton (Ulanowicz, 1995a)-here classified as mesoinvertebrates.

Lodge (1994) suggested that: 'the Everglades does not have a great diversity of freshwater invertebrates due to its limited type of habitat and its nearly tropical climate, which many temperate species cannot tolerate'-the source of most fauna in South Florida is from temperate areas further north. Accordingly, the invertebrate component of the graminoid marshes are broken down into eight compartments, consisting of apple snails (*Pomacea paludosa*), freshwater prawns (*Palaemonetes paludosus*), crayfish (*Procambarus alleni*), mesoinvertebrates, other macroinvertebrates, large aquatic insects, terrestrial invertebrates and fishing spiders.

Loftus and Kushlan (1987) described an assemblage of 30 species of fish in the freshwater marshes, of which 16 species are found in the sawgrass marshes. Small species of killifishes (Cyprinodontidae), livebearers (Poeciliidae), and juvenile sunfishes (Centrarchidae) are common, because killifishes and livebearers are short-lived, rapidly growing species (Haake and Dean, 1983) that are able to respond to favorable conditions with quick surges in population. The deeper, open-water alligator holes are used by larger fishes such as Florida gar, yellow bullhead, and adult sunfishes, although smaller species including mosquitofish and sailfin molly are also common (Loftus and Edlund, 1994).

The Everglades assemblage of herpetofauna consists of some 56 species of reptiles and amphibians, which Diffendorfer et al. (1999) classify into nine functional groups: snakes, turtles, salamanders, salamander larvae, large frogs, medium frogs, small frogs, tadpoles and lizards. In addition, the American alligator (*Alligator mississippiensis*) also occurs in the Everglades (Dalrymple, 1988).

Nine compartments of mammals were identified for the graminoid marshes. Raccoons (*Procyon lotor*) and marsh rabbits (*Sylvilagus palustris*) are probably the most common species (Humphrey, 1992; Layne, 1984), although otters (*Lutra canadensis*) are also reasonably common, but usually are seen only in the dry season (Lodge, 1994). Other compartments include mice and rats (Gaines et al. 1998), muskrats (*Neofiber alleni*, Burt and Grossenheider, 1961), white tailed deer (*Odocoileus virginianus*) and bobcats (*Lynx rufus*, MacDonald, 1997). Everglades mink (*M. vison evergladensis*) is a rare mammal (Layne, 1978), while the rarest mammal in the Everglades is the Florida panther (*F. concolor*) (Lodge, 1994). Opossums (*Didelphis virginiana*) are the only marsupials found in the graminoids (and in North America Burt and Grossenheider, 1976).

Approximately 350 species of birds have been recorded within the Everglades National Park, and just slightly less than 300 species are considered to occur on a regular basis (Robertson and Kushlan, 1984). Sixty percent of these birds are either winter residents, migrating into South Florida from the north, or else visit briefly in the spring or fall. The remaining 40% breed in south Florida (Lodge, 1994), but of these only eight groups nest or breed in the graminoids. Four of these are aquatic, including the grebes (*Podilymbus podiceps*), bitterns (*Ixobrychus exilis*), various Anseriformes and Gruiformes (Stevenson and Anderson, 1994). The Anseriformes in this system include the fulvous whistling duck (*Dendrocygna bicolor*), green-winged teal (*Anas crecca*), mottled duck (*A. fulvigula*), mallard (*A. platyrhynchos*), blue winged teal (*A. discors*), northern shoveler (*A. clypeata*), ring necked ducks (*Aythya collaris*) and the ruddy duck (*Oxyura jamaicensis*). The Gruiformes include species such as the American coot (*Fulica americana*), the limpkin (*Aramus guarauna*), king rails (*Rallus elegans*), common moorhens (*Gallinula chloropus*) and Sandhill cranes (*G. canadensis pratensis*) (Stevenson and Anderson, 1994).

Terrestrial birds include the snail kites (*Rostrhamus sociabilis*), the common nighthawk (*Chordeiles minor*) (Werner and Woolfenden, 1983), the endangered Cape Sable seaside sparrows (*A. maritimus mirabilis*) and other passerine birds, such as the red winged blackbirds (*Agelaius phoeniceus*), common yellowthroat (*Geothlypis trichas*), swamp sparrow (*Melospiza georgiana*), eastern meadowlark (*Sturnella magna*), boat-tailed grackle (*Quiscalus major*) and the common grackle (*Q. quiscula*) (Stevenson and Anderson, 1994). The seaside sparrow was not grouped with other passerines due to the endangered status of that species. It was singled out, as a separate compartment in the ATLSS modeling endeavor, and the aim of the parallel NA was to preserve such emphasis.

Various species of wading and terrestrial birds roost or breed in the cypress wetlands and feed in the graminoid marshes, these include the anhingas, egrets, herons, wood storks and ibises. These birds are explicit components of the cypress network. They feed on the aquatic and terrestrial invertebrate members of the graminoid wetlands, however, so that this capture of prey is represented as an export from the graminoid system and an import into the cypress swamp. Whence, it was not necessary to include the waders as explicit components in the graminoid network.

2.1.2. Cypress swamp compartments

The cypress swamp model consists of 68 compartments and similar to the graminoid system, the cypress model has three non-living compartments (refractory detritus, labile detritus and vertebrate detritus) and two microbial compartments (living POC and living sediment). Ulanowicz et al. (1997), Bondavalli and Ulanowicz (1999) give a breakdown of the construction of the model. The primary producers are more diverse than those found in the graminoids and are represented by 12 compartments, seven of which are essentially terrestrial producers: understory, vines, hardwood leaves, cypress leaves, cypress wood, hardwood wood and roots (Bondavalli and Ulanowicz, 1999). These seven compartments ramify the spatial dimension of the ecosystem in the vertical extent-an attribute not shared by the graminoid marshes. Other primary producer compartments include phytoplankton, floating vegetation, periphyton, macrophytes and epiphytes (Bondavalli and Ulanowicz, 1999).

According to Bondavalli and Ulanowicz (1999), cypress swamps do not possess a distinct faunal assemblage, but rather share most species with adjacent plant communities. Most fauna spend only parts of their lives in the swamp. Benthic invertebrates form the heterotrophic base of the food chain. A high diversity of invertebrates has been recorded in cypress domes and strands, but a dearth of data at the species level mandated that we resolve the invertebrates into only five compartments, crayfish, apple snails, prawns, other aquatic invertebrates and terrestrial invertebrates (Bondavalli and Ulanowicz, 1999). Similarly, the fish component of this model could not be resolved into more than three compartments-two containing small fish and a third consisting of large fish (Bondavalli and Ulanowicz, 1999).

The herpetofauna compartments of the cypress model were similar to those of the graminoids. During summer, reptiles and amphibians dominate the vertebrate communities of the cypress swamp, 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 even through the cooler seasons (Bondavalli and Ulanowicz, 1999).

The bird community of the cypress swamps was much more diverse than that in the graminoids. The increased diversity can be traced to the inclusion of wading birds in the cypress model. The wading birds do not roost or nest in the graminoids, although they do feed there; therefore, it was assumed that an export of energy and carbon flowed from the graminoids into the cypress. The 17 bird taxa in the cypress include five types of wading birds, two passerines collections, and various predatory birds, such as owls, nighthawks, kites and hawks, and vultures (Bondavalli and Ulanowicz, 1999).

The mammals of the cypress include all the mammalian compartments of the graminoids, as well as some terrestrial mammals unique to the cypress. Mammalian species that do not occur in the graminoids, but do occur in the cypress are the shrews, bats, feral pigs, squirrel, skunks, bear, armadillos and foxes (Bondavalli and Ulanowicz, 1999). These species are found mostly in the cypress trees and cypress domes, which extend the spatial extent of the ecosystem into the third dimension.

2.2. Network analysis

The NETWRK suite of algorithms is a powerful tool for interpreting ecosystem structure and functioning via the investigation of quantitative food webs. It depends on both the topology of the flows between the system components and their magnitudes. The pattern of these flows contains valuable information about the dynamics of the ecosystem (Field et al., 1989). Four types of analyses are performed by NETWRK (Ulanowicz, 1987). First, at the level of bilateral interactions, 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 (Ulanowicz and Kay, 1991). Next, the graph is mapped according to functional groupings into a concatenated trophic chain, after Lindeman (1942), using the methods of interpretation developed by Ulanowicz (1986, 1995b). At the same level, all simple, directed biogeochemical cycles are identified and separated from the supporting dissipative flows (Ulanowicz and Kay, 1991). Finally, global variables describing the state of development of the network are presented (Kay et al., 1989). These include the Finn cycling index (FCI), total systems throughput, ascendancy, development capacity and overhead. These terms are not part of the general literature, and so are defined in Appendix A.

Information theory is employed to quantify how well 'organized' the trophic web is (expressed in terms of an index called the system's 'ascendancy'), how much functional redundancy it possesses (what is termed the 'overhead'), what its potential for development is, and how much of its autonomy is encumbered by the necessary exchanges with the external world (Ulanowicz and Kay, 1991). Information indices usually are applied only to whole system networks. Evidence is accumulating, however, that the various sub-components of the ascendancy-like variables can serve

to gauge the contributions of individual system elements to the performance of the whole system (Ulanowicz and Baird, 1999). For example, the ascendancy is comprised of a number of terms, each of which is generated by a specific transfer in the system. If one sums all the terms generated by the inputs to a given taxon (say, the jth one), the result is a measure (in gC-bits m^{-2} per year) of the contribution of that compartment to the full system ascendancy (call it A$_j$). Since 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. If one then divides A$_j$ by the corresponding throughput (in gC m^{-2} per year) for taxon j (call it T$_j$), the ratio A$_j$/T$_j$ (in bits) will then represent the contribution that each unit activity of j makes to the total system performance. (The dimensional factor 'bits' arises from the application of logarithmic transformation particular to information theory. In calculating the sensitivities, the units of flow cancel from the quotient.)

The software routine that performs all these analyses is called NETWRK 4.2a, and it may be downloaded along with its attendant documentation from http://www.cbl.umces.edu/ ~ ulan/ntwk/network.html. To run this program it is necessary to know for each compartment all the inputs from outside the system, inputs flowing to any specific compartment from other compartments of the system outputs, which flow as inputs to other compartments, exports of medium outside the system, and rates of dissipation of medium. The magnitude of each of these flows can be represented as a positive scalar element of a matrix or a vector and a zero represents the absence of a flow. In general the authors depended as much as possible on data issuing from the sites, but occasionally one has to resort to data from similar systems when in situ data were not available. A complete and detailed description of all sources of data and the accompanying calculations used to estimate the graminoid and cypress networks can be found on the World Wide Web at http://www.cbl.umces.edu/ ~ atlss/, and the reports (Ulanowicz et al., 1997, 2000) are also available on this site.

3. Results

In this section the results of NA performed on the graminoid marsh ecosystem will be compared with those resulting from the same methods applied to the cypress network. The differences between the fundamentally 2-D graminoid habitat and the 3-D cypress environment are highlighted, and the importance of the difference in spatial extents is reviewed.

3.1. Input/output analysis

Perhaps the most useful indices calculated by the input/output section of NETWRK are the 'total dependency coefficients' (TDC's) (Szyrmer and Ulanowicz 1987) or, 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 particular compartment. Conversely, reading the same matrix horizontally reveals the dependencies of all other taxa on any particular compartment, the aggregate of which indicates the importance of that compartment to the whole system. This pertains especially to primary producers. It should be noted that the dependencies for any given component usually sum to more than 100%. This is because the same material is incorporated into different living forms along its way from primary producers to the population in question.

The TDC's of the heterotrophs in the graminoid ecosystem reveal that a significant fraction of the carbon reaching many of the predators originates in the periphyton compartment, while the detritus and vegetation are comparatively less important to the heterotrophs (Fig. 2). Fig. 2 portrays the average dependency coefficients on periphyton, detritus (labile, refractory and sediment detritus as well as living sediment and living POC) and 'other vegetation' (macrophytes, *Utricularia* and floating vegetation) by all other taxa. The dependencies on apple snails, freshwater prawn, crayfish, mesoinvertebrates, other invertebrates, and large aquatic insects were grouped into 'aquatic invertebrates', while the dependencies on the fishing spiders were grouped with that of other terrestrial invertebrates. Living POC and
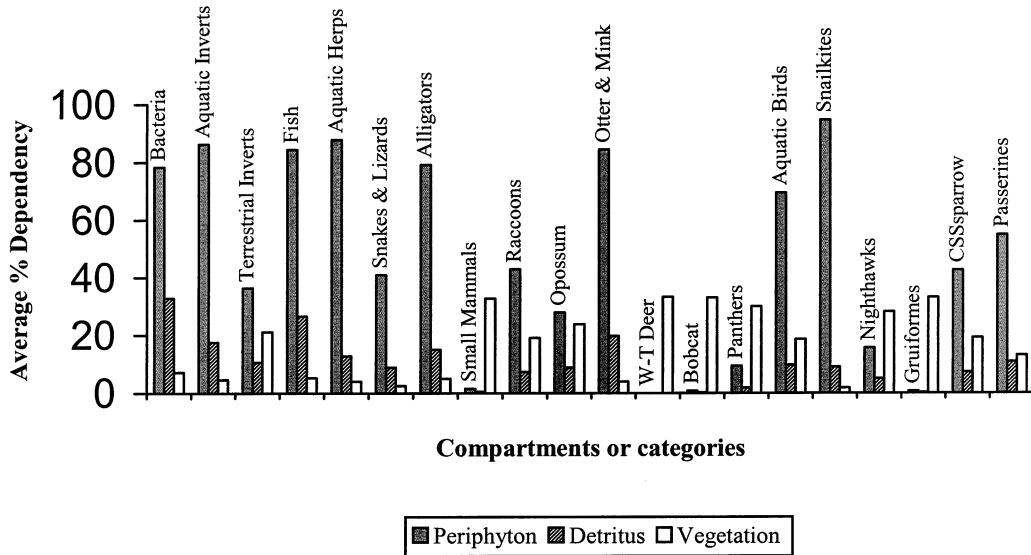
Fig. 2. The dependency on periphyton, detritus and other vegetation by various compartments and categories in the graminoids. These values do not add to 100% as the dependency includes both direct and indirect dependencies, so that bacteria depend on periphyton (80%) that is broken down to detritus (38%).

living sediment were assembled into a compartment called 'bacteria'. All the fish compartments were aggregated; snakes and lizards were combined, and all other herpetofauna except alligators were grouped in the compartment 'aquatic herpetofauna'. Muskrats, mice, rats and rabbits were grouped into a 'small mammals' compartment. Otters and mink were merged, and the ducks, grebes and bitterns were grouped into an 'aquatic birds' compartment.

From Fig. 2 it becomes evident that in the graminoids, bacteria, aquatic invertebrates, fish, aquatic herpetofauna, alligators, otters and mink, and snail kites depend on the periphyton compartment on the average for 80% or more of their sustenance. In particular, the high dependency of snail kites on periphyton derives from their high dietary intake of apple snails, which feed mostly on periphyton. By way of contrast, only very small flows link periphyton with terrestrial invertebrates, snakes and lizards, terrestrial mammals and terrestrial birds, while 'other vegetation' becomes more important in their diet.

For the most part, dependencies on detritus are less important than dependencies on periphyton, even in the case of bacteria (which one would

expect to feed directly on detritus). Detritus is more important than other vegetation as a food source for bacteria, aquatic invertebrates, fish, aquatic herpetofauna, snakes and lizards, alligators, otters and mink and snail kites (Fig. 2). 'Other vegetation' is more important, however, to obligatory terrestrial mammals and birds.

One would expect to see greater dependency on detritus in the cypress system, because forests are generally perceived as detritus-based ecosystems (Moran et al., 1988). This view is predicated upon the dense tree canopy's not allowing any significant growth of understory plants (aquatic vegetation, periphyton, vines and epiphytes), so that litterfall (here mainly from cypress) remains the major source of energy for secondary producers (Bondavalli et al., 2000). The total dependency by fauna on detritus (refractory detritus, labile detritus, vertebrate detritus, living POC and living sediment) in the cypress ecosystem is comparable to what occurs in the graminoids; however, faunal dependencies in the graminoids pale in comparison to the influence of periphyton there (Fig. 3).

In the cypress system the vegetation compartments were combined according to 'terrestrial' vegetation (the understory, vines, hardwood

leaves, cypress leaves, cypress wood, hardwood wood, and roots that make up the 'third dimension) or 'aquatic vegetation' (phytoplankton, floating vegetation, macrophytes and epiphytes). Together this last group corresponds to the 'other vegetation' in the graminoid system. For the most part, the terrestrial vegetation is of less importance to consumers than is the aquatic vegetation. Important exceptions are the terrestrial higher predators (see below). Considerable densities of aquatic vegetation can be observed in the middle of domes and strands, where many big ponds cause holes in the canopy of the cypress (Ulanowicz et al., 1997). These open aquatic zones were considered to be part of the forest wetland model and provide important resources to the associated fauna (Bondavalli et al., 2000). Terrestrial vegetation is broken down into detritus, which is then used by the heterotrophs, and thereafter is recycled as detritus. This latter route is even more important than aquatic vegetation to some components, such as bacteria, shrews, bats, deer, bobcats, panthers and terrestrial birds.

Periphyton is more important to the aquatic species of the cypress than any other form of producer or detritus. The aquatic invertebrates, fish, aquatic herpetofauna, snakes, lizards, alligators, raccoons, otters, mink and aquatic birds in the cypress all depend on periphyton for ca. 30% of their sustenance (Fig. 3). This magnitude is dramatically less, however, than the 80% figure that prevails in the graminoids (Fig. 2). According to Ulanowicz et al. (1997), the importance of primary producers other than cypress (periphyton and other sub-canopy vegetation) waxes considerably during the dry season, when the canopy is negligible. Bondavalli et al. (2000) found, however, that heterotrophs depend heavily on non-cypress primary producers, even during the wet season, when canopy vegetation is dense.

3.2. Lindeman trophic analysis

The Lindeman trophic analysis section of NETWRK apportions compartments according to trophic levels. The results reveal that there are as many as 15 trophic levels in the graminoid network and 11 in the cypress. Thus, at least one non-redundant trophic pathway with 15 links can be found in the graminoid network. As usual, however, not much carbon persists beyond the fifth trophic stage, and the amounts calculated to reach the 15th level are absolutely infinitesimal (of the order 10^{-32} g). The first six trophic levels of the graminoid and cypress systems are depicted in Fig. 4.
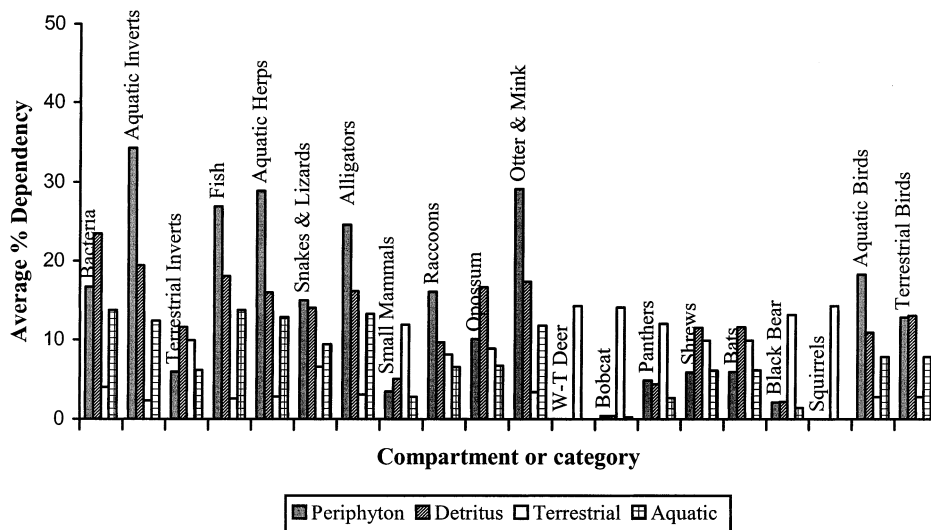

Fig. 3. The dependency on periphyton, detritus, aquatic and terrestrial vegetation in the cypress.
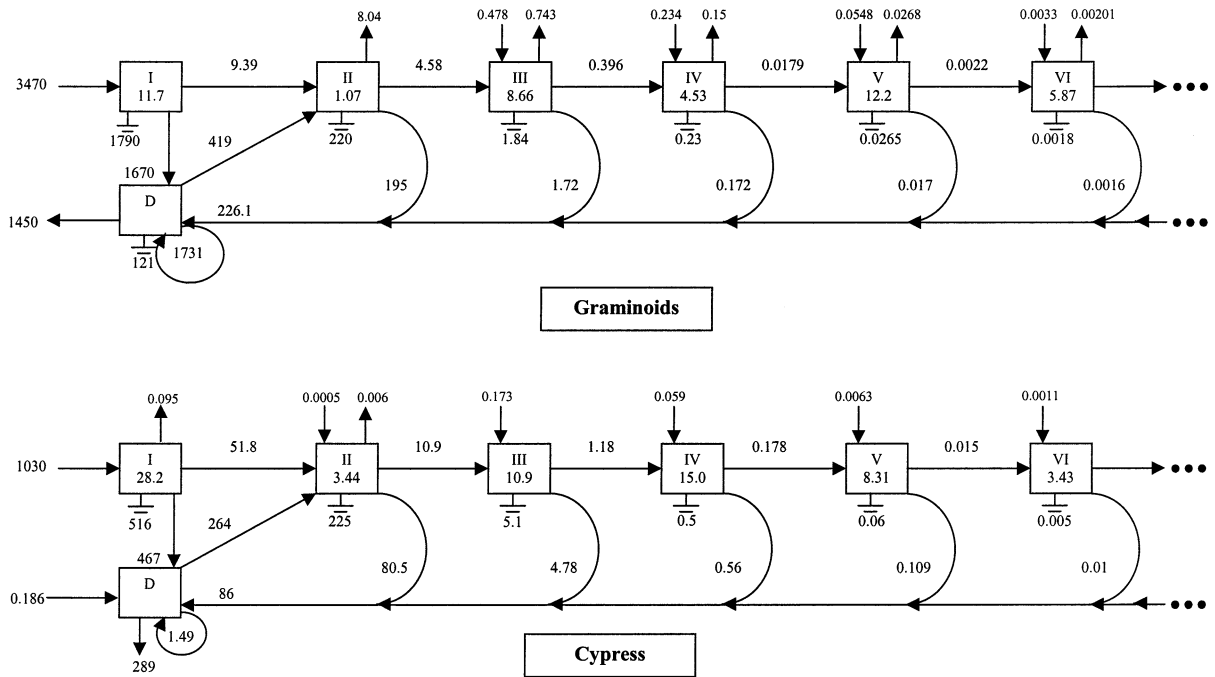
Fig. 4. Lindeman Spine for graminoids and cypress habitats.

Overall, the efficiencies between the graminoid trophic levels are lower than those observed in the cypress system. The efficiencies of trophic levels V and VI in the graminoids, however, are higher than the trophic efficiencies of levels V and VI of the cypress system (Fig. 4). It is also noteworthy that the activities surrounding the first trophic level and detritus are much higher in the graminoids than in the cypress. Recycling within detritus, export from detritus, and detritivory are much higher in the graminoids (Fig. 4). This is also reflected in the detritivory:herbivory ratios of the two systems. The ratio of detritivory:herbivory is ca. 45:1 in the graminoids—one of the highest such ratios ever observed and much higher than the 5:1 calculated for the cypress ecosystems.

This elevated detritivory suggests that the recycling of carbon is enormously important in the graminoid system. This result stands in marked contrast, however, to the total dependency analysis, which showed that most compartments depend mainly on periphyton, and dependencies on detritus appear to be decidedly secondary. This apparent contradiction may be explained by the fact that most excretion and mortality from living compartments becomes refractory detritus and carbon in the sediment (Detritus in Fig. 4), which in turn is utilized overwhelmingly by bacteria (TL2) in the sediment and in the water column (i.e. detritivory by TL2).

Similarly, much of the production by aquatic vegetation (periphyton, macrophytes, floating vegetation and *Utricularia*) is not consumed by herbivores, but rather is broken down into labile and refractory detritus, which then is utilized by bacteria in the sediment and the water column (again detritivory). This bacterial activity augments the magnitude of detritivory and reveals that much of primary production in the graminoids is not utilized by the higher trophic levels, but rather is recycled into the detritus and subsequently deposited as peat. The high dependencies by most heterotrophs on periphyton is due to the fact that the bulk of what is consumable among the primary producers consists of periphyton, thereby demonstrating how extremely important periphyton is to the graminoid system. Conversely, the

existence of terrestrial vegetation in the cypress system and the increased importance there of both aquatic and terrestrial vegetation to most heterotrophs (Fig. 3) increases the relative amount of herbivory in that system.

3.3. System level indices

Systems level indices are useful for comparing the total activities of ecosystems and the organization inherent in their structures. Activity is measured by the 'total system throughput', which is simply the sum of all the processes occurring in the system. According to this index, the graminoid system is far more active than the cypress system (Table 1). Its total system throughput (10 978 gC m^{-2} per year) is four fold that of the cypress system (2952 gC m^{-2} per year). The development capacity of an ecosystem is gauged by the product of the diversity of its processes as scaled by the total system throughput. The development capacity of the graminoid system (39 799 gC-bits m^{-2} per year) is significantly higher than that of the cypress (14 659 gC-bits m^{-2} per year), a difference that one might be inclined to attribute to the disparity in the scalar factor (total system throughput) between the systems. When one regards the normalized ascendancy, however, (as-

cendancy is a measure of the constraint inherent in the network structure), one notices that the fraction of the development capacity that appears as ordered flow (ascendancy/capacity) is 52.5% in the graminoids. This is markedly higher than the corresponding fraction in the cypress system (34.3%).

The graminoid system has been stressed by a number of modifications to the patterns of its hydrological flow, which have resulted in the loss of transitional glades, reduced hydroperiods, unnatural pooling and over-drainage (Light and Dineen, 1994). In comparison with the cypress community, however, the system has exhibited fewer changes in its faunal community and is sustained by an abundance of flora and microbiota. The cypress ecosystem, like that of the graminoids, is limited by a dearth of phosphorus, which remains abundant in marine and estuarine waters and sediments. The graminoid system compensates for this scarcity of nutrients with a profusion of periphyton. Periphyton exhibits a high P/B ratio, even under oligotrophic conditions.

The natural stressors that affect the cypress ecosystem appear to have far greater impacts, in that they modulate the rates of material and energy processing to a far greater extent in that system. This analysis is phenomenological and

Table 1
Information Indices for both the graminoid and cypress systems

Index	Cypress		Graminoids	
	Index	% of C	Index	% of C
Total system throughput (gC m^{-2} per year)	2952.3		10 978	
Development capacity = C (gC-bits m^{-2} per year)	14 659		39 799	
Ascendancy (gC-bits m^{-2} per year)	4026.1	34.3	20 896	52.5
Overhead on imports (gC-bits m^{-2} per year)	2881.6	19.7	3637	9.1
Overhead on exports (gC-bits m^{-2} per year)	75.4	0.5	606	1.5
Dissipative Overhead (gC-bits m^{-2} per year)	2940	20.1	4932	12.4
Redundancy (gC-bits m^{-2} per year)	3735.8	25.5	9728	24.4
Internal capacity (gC-bits m^{-2} per year)	5443.4		18 122	
Internal ascendancy (gC-bits m^{-2} per year)	1707.5	31.4	8394	46.3
Redundancy (gC-bits m^{-2} per year)	3735.8	68.6	9728	53.7
Connectance indices				
Overall connectance		1.826		1.586
Intercompartmental connectance		3.163		1.807
Foodweb connectance		2.293		

there is no clear reason why the modulation of rates of material and energy occur in the cypress. Thus, even though these systems are (1) adjacent to one another, (2) share many of the same species and (3) some of the heterotrophs of the cypress feed off the graminoid system, the characteristic indices of the graminoid system remain distinct from those of the cypress community.

Calculating and ranking 'relative sensitivities' proves to be an interesting exercise. For example, when the average trophic levels of the 66 compartments of the graminoid wetland ecosystem were calculated, lizards, alligators, snakes and mink were revealed to be feeding at trophic levels higher than some of the 'charismatic megafauna', such as the snail kite, nighthawk, Florida panther or bobcat (Table 2). The relative contributions to ascendancy by the latter actually outweighed those of the former, however. The relative values of these sensitivities thus seemed to accord with most people's normative judgments concerning the specific 'value' of the various taxa to the organization of the system as a whole (Table 2). Similarly, in the cypress system white ibis, large fish, alligators and snakes feed at high effective trophic levels, but the system performance seemed to be enhanced more by the activities of the vultures, gray fox, bobcat and panthers (Table 2).

In comparing the component sensitivities in the graminoid and cypress systems, one discovers numerous similarities between the taxa of the two systems (Table 2). For example, the avian and feline predators ranked high in both systems. The contributions of snail kites and nighthawks to the performance of the graminoid system were highest (at ca. 14 bits), while that of the bobcat and panther were highest in the cypress (at ca. 13 bits). Both bobcat and panther seem to be more sensitive in the cypress than in the graminoids.

The low sensitivity of crayfish (0.99 bits) in the graminoids was not repeated in the cypress, although aquatic invertebrates generally had a low sensitivity in that system, too (2.01 bits). The sensitivity of labile detritus was similar in both systems (around 1.5 bits), while refractory detritus was more sensitive in the graminoid (1.59 bits), indicating a greater importance in that system. The sensitivities of the primary producers are lower in the cypress (1.51 bits) than in the graminoids (1.66 bits) and are uniform within both systems, except for *Utricularia* in the graminoids. *Utricularia* are carnivorous plants, and, therefore, both its effective trophic level and its sensitivities are higher than those of the other primary producers (Table 2).

3.4. Cycling analysis

With 66 compartments in the trophic flow network, the number of potential pathways for recycling carbon becomes roughly proportional to 66-factorial—an immense number! The fact that the network is not fully connected reduces the number of potential cycles considerably. Nonetheless, the number of simple cycles in the graminoid network remains enormous. Using a variation of the cycle counting routine in NETWRK 4.2a, it was determined that approximately 24 billion cycles are present in the graminoid network and approximately 27 million in the cypress system.

The first stage in the cycle analysis is the removal of the cycles comprised entirely of living compartments. Such loops are generally rare in most ecosystems (Pimm, 1982). There were only 16 such cycles in the graminoids, although the cypress had 68. The major routes for recycling within the graminoids were found among the detritus compartments (both in the water column and in the sediment) and the bacteria that feed on the detritus (Fig. 5).

Recycling among the detritus compartments included carbon cycled from living sediment to sediment carbon (104 gC m^{-2} per year), to refractory (25 gC m^{-2} per year) and to labile (58 gC m^{-2} per year) detritus and from labile and refractory detritus to sediment carbon. The two next largest cycles, are between living POC and labile detritus (± 2.6 gC m^{-2} per year not shown in Fig. 5) and among mesoinvertebrates, sediment carbon and living sediment (0.7 gC m^{-2} per year). Thus, the linkage between the detrital cycle and the higher trophic levels in the graminoids is via mesoinvertebrates feeding on living sediments and sediment carbon, and it is a very small link, indeed. Since the detritivory:herbivory ratio is so large in the graminoids, one would expect that

Table 2
Ascendancy Sensitivity Coefficients (Sens. in bits) and effective trophic levels (ETL) for both the graminoid and cypress systems

	Graminoids			Cypress		
	Compartment	ETL	Sens.	Compartment	ETL	Sens.
1	Crayfish	2.14	0.99	Liable detritus	1.00	1.42
2	Mesoinvertebrates	2.15	1.12	Refractory detritus	1.00	1.45
3	Other macroinvertebrates	2.12	1.15	Phytoplankton	1.00	1.51
4	Flagfish	2.00	1.27	Float. Vegetation	1.00	1.51
5	Poecilids	2.20	1.47	Periphyton/Macroalgae	1.00	1.51
6	Labile detritus	1.00	1.55	Macrophytes	1.00	1.51
7	Refractory detritus	1.00	1.59	Epiphytes	1.00	1.51
8	Apple snail	2.12	1.60	Understory	1.00	1.51
9	Tadpoles	2.03	1.63	Vine leaves	1.00	1.51
10	Periphyton	1.00	1.66	Hardwoods leaves	1.00	1.51
11	Macrophytes	1.00	1.66	Cypress leaves	1.00	1.51
12	Floating vegetation	1.00	1.66	Cypress wood	1.00	1.51
13	*Utricularia*	1.03	1.69	Hardwood wood	1.00	1.51
14	Lizards	3.83	1.79	Roots	1.00	1.51
15	Freshwater prawn	2.27	2.12	Aquatic invertebrates	2.20	2.01
16	Ducks	2.20	2.32	Tadpoles	2.16	2.29
17	Bluefin killifish	2.57	2.34	Anseriformes	2.05	2.38
18	Other small fishes	2.48	2.44	Crayfish	2.26	2.46
19	Sediment carbon	1.00	2.44	Terrestrial invertebrates	2.00	2.55
20	Living sediments	2.00	2.58	Living sediment	2.00	2.64
21	Mosquitofishes	2.47	2.64	Squirrels	2.00	2.72
22	Living POC	2.00	2.80	Apple snail	2.26	2.74
23	Chubsuckers	2.50	2.86	Prawn	2.26	2.91
24	Shiners & Minnows	2.68	3.60	Rabbits	2.00	2.97
25	Gruiformes	2.01	3.76	White tailed deer	2.00	2.97
26	Muskrats	2.00	3.83	Living POC	2.00	3.08
27	W-T Deer	2.00	3.83	Black Bear	2.26	3.30
28	Terrestrial inverts	2.00	3.91	Small herb. & omni. Fish	2.60	3.48
29	Rabbits	2.00	5.10	Galliformes	2.33	3.58
30	Killifishes	2.81	5.13	Mice & Rats	2.37	3.77
31	Turtles	2.74	5.57	Wood stork	3.24	3.82
32	Large aquatic insects	2.96	5.63	Raccoon	2.74	3.84
33	Salamander larvae	2.57	5.64	Great blue heron	3.24	3.85
34	Grebes	2.63	5.79	Egrets	3.23	3.90
35	Other centrarchids	3.02	6.59	Hogs	2.44	3.96
36	Rats & Mice	2.27	6.66	Other herons	3.21	4.10
37	Raccoons	2.59	6.72	White ibis	3.58	4.19
38	Opossum	2.45	6.77	Turtles	2.82	4.28
39	Pigmy sunfish	3.09	6.79	Woodpeckers	2.52	4.43
40	Bluespotted sunfish	3.09	6.83	Omnivorous passerines	2.53	4.45
41	Dollar sunfish	3.09	6.87	Hummingbirds	2.53	4.45
42	Seaside sparrow	2.57	7.10	Small carnivorous fish	3.07	5.56
43	Passerines	2.96	7.16	Opossum	2.35	5.61
44	Topminnows	3.10	7.47	Kites & Hawks	3.37	6.10
45	Redear sunfish	3.13	9.09	Owls	3.36	6.10
46	Catfish	3.11	9.21	Mink	3.25	6.21
47	Spotted sunfish	3.16	9.32	Otter	3.25	6.23
48	Warmouth	3.21	9.42	Medium frogs	3.21	6.24
49	Mink	3.41	9.53	Small frogs	3.21	6.24
50	Snakes	3.32	9.66	Salamanders	3.28	6.32
51	Otter	3.34	9.71	Large frogs	3.32	6.38

Table 2 *(Continued)*

	Graminoids			Cypress		
	Compartment	ETL	Sens.	Compartment	ETL	Sens.
52	Bitterns	3.25	9.75	Gruiformes	3.35	6.53
53	Alligators	3.39	9.96	Armadillo	2.90	6.54
54	Large frogs	3.29	10.19	Pelecaniformes	3.40	6.61
55	Small frogs	3.17	10.33	Large fish	3.42	6.99
56	Other large fishes	3.27	10.69	Lizards	3.00	7.64
57	Largemouth bass	3.24	10.92	Caprimulgiformes	3.00	7.64
58	Medium frogs	3.16	10.93	Bats	3.00	7.64
59	Gar	3.45	10.96	Predatory passerines	3.00	7.64
60	Cichlids	3.22	10.98	Shrews	3.00	7.65
61	Fishing spider	3.27	11.77	Alligators	3.78	8.30
62	Bobcat	3.02	12.01	Snakes	3.79	8.58
63	Salamanders	3.32	12.29	Salamander larvae	3.20	8.62
64	Panthers	3.17	12.33	Vertebrate detritus	1.00	8.82
65	Snailkites	3.13	14.38	Vultures	2.00	10.03
66	Nighthawks	3.00	14.69	Gray fox	3.41	10.29
67				Bobcat	3.03	12.96
68				Florida panther	3.36	13.48

feeding in the aquatic habitat on living POC, labile- and refractory detritus would form a substantial part of the recycling in this system. The largest such loop, however, is along the cycle mesoinvertebrate–*Utricularia*–labile detritus– mesoinvertebrate and has a magnitude of only 0.4 gC m^{-2} per year.

Recycling in the cypress system is much more diverse, although the magnitude of recycling is smaller (Fig. 6). There are various bilateral cycles—for example, between living sediment and refractory detritus (18 gC m^{-2} per year), between living sediment and labile detritus (37 gC m^{-2} per year), between living POC and labile detritus (4.7 gC m^{-2} per year), and between labile detritus and terrestrial invertebrates (4.4 gC m^{-2} per year). The multi-compartment cycle with greatest magnitude is among labile detritus, living POC and prawns (2.7 gC m^{-2} per year) and between refractory detritus, living sediment, labile detritus and terrestrial invertebrates (2.6 gC m^{-2} per year). The cycling among the invertebrates seems to be of greater magnitude in the cypress than in the graminoids, and the recycling among terrestrial invertebrates is enhanced by the three-dimensionality of the cypress biome.

The aggregate activity devoted to cycling in the graminoid ecosystem is 476.8 gC m^{-2} per year, which puts the FCI at only 4.3%. The FCI is that fraction of all the total activity in the system that consists of cycling (Finn, 1976). By way of contrast, although only 177.2 gC m^{-2} per year is devoted to recycling in the cypress, this amount represents a higher FCI of 6%. The low FCI in the graminoids is due to the fact that not much detritus is making its way to the higher trophic levels there. Most of the carbon is being shunted
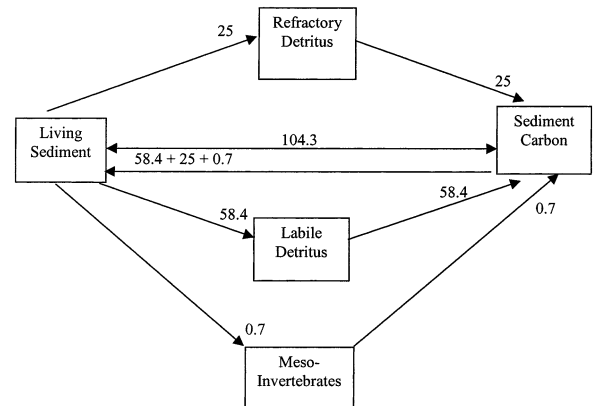

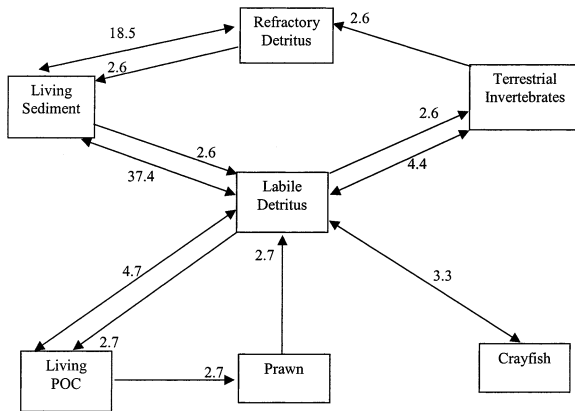Fig. 5. Carbon cycling within the graminoid detritus (gC m^{-2} per year).

Fig. 6. Carbon cycling within the cypress detritus (gC m^{-2} per year).

into the detritus, although the periphyton remains quite important to the higher trophic levels.

Bondavalli et al. (2000) suggest that the low FCI in the cypress owes to the fact that carbon reaching the bottom in the cypress is less likely to be ingested and fed back up the trophic chain, than is the case in, say, the Chesapeake Bay. The situation seems to be similar in the graminoids. Figs. 5 and 6 show that the magnitude of recycling between the detritus compartments and the invertebrates in the graminoids is small compared to what is occurring in the cypress.

4. Discussion

Considerations of scale have changed how we look at basic ecosystem properties, such as stability (Turner et al., 1993). O'Neill and King (1998) found that if disturbances are large and rapid compared to the responses of the system of interest, the ecosystem tends to become unstable, but it could remain stable at a larger spatial scale (or in this study, vertical extent). In this study the effect of spatial difference, or vertical extent, appears at the ecosystem level and is revealed using Ulanowicz (1986) theory of ascendancy.

The cypress system exhibits an additional spatial dimension in comparison with that of the graminoids. The third, vertical (terrestrial) dimension of cypress vegetation provides both additional habitat and food for the higher trophic levels. Even though terrestrial vegetation in the cypress was not the most important primary producer (as regards dependency—see Fig. 3), it nonetheless does seem to have increased the diversity of primary producers that can be utilized by higher trophic levels. The cypress system, therefore, appears more stable, because the increased diversity would become an important locus for feeding in the event of a drought, fire, or some catastrophic event, such as a parasitic infestation of the periphyton or aquatic *Utricularia*.

Conversely, in the graminoids the strong dependency of most higher-level components on periphyton (Fig. 2) makes that ecosystem more efficient (viz. the high ascendancy/capacity ratio), but at the same time more fragile. This fragility already can be seen in the northern parts of the Everglades, where increased nutrient loading has caused the displacement of sawgrass marshes with its accompanying periphyton and *Utricularia* by cattails (*Typha*) and has totally changed the character of the ecosystem.

The high dependency on graminoid periphyton would lead one to expect that herbivory would be far more important than detritivory in that system. The detritivory:herbivory ratio in the graminoids, however, does not support this expectation In fact, the ratio is markedly higher in the graminoids (45:1 vs. 5:1 in the cypress). This discrepancy could be explained by the fact that, although periphyton is important to the heterotrophs, much of the 1280 gC m^{-2} per year produced by periphyton (as well as production by other aquatic vegetation) is not consumed by herbivores, but is broken down instead into labile and refractory detritus. Bacteria in the water column (living POC) then consume the detritus; however, most of what is produced by the living POC is either recycled back into the detritus or exported, and very little makes its way to the higher trophic levels.

In the cypress, the appearance of terrestrial vegetation affords increased herbivory by terrestrial fauna such as mammals, birds and terrestrial invertebrates. Furthermore, much of what is produced by the bacteria is consumed by the higher trophic levels, and less production is recycled

back into the detritus. This is evident also from the cycle analysis, where the linkage in the cypress between recycling in the detritus and the higher trophic production is larger than in the graminoids. The amount of carbon recycled in the graminoid detritus is, however, markedly higher than in the cypress (Figs. 5 and 6). Similarly, the FCI for the cypress network is higher than that for the graminoids, indicating that the former is a more highly developed system.

With the addition of the arboreal dimension in the cypress, one would expect that system to be more productive than its graminoid counterpart, and that the total systems throughput (and, consequently, other systems properties) would be higher in the cypress as well. This is not the case, however. In fact, the throughput of the graminoids exceeds that of the cypress by some four-fold. Although the total biomass in the cypress is three times greater than that in the graminoids, the cypress systems P/B ratio is four times lower there than in the graminoids, thereby yielding the greater throughput in the graminoids. The increase in throughput in the graminoids ramifies as an increase in its development capacity and ascendancy.

The relative ascendancy, which excludes the effects of the throughput, is perhaps a better index with which to compare these two systems. The relative ascendancy of the graminoids is exceptionally high. For example, Heymans and Baird (2000) found that upwelling systems have the highest relative ascendancy of all the systems they compared (which were mostly estuarine or marine in origin), but the relative ascendancy of 52% for the graminoids is higher than any such index they had encountered. Unfortunately, very few other freshwater systems have been studied using NA and those given in Christensen and Pauly (1993) were studied using ECOPATH. There are some differences in the data when using ECOPATH instead of NETWRK (see Heymans and Baird, 2000); and, therefore, comparisons with these models would not be prudent. The relative ascendancy of 34% reported for the cypress is lower than most of the relative ascendancies calculated by NETWRK and reported by Heymans and Baird (2000). There is a general inverse rela-

tionship between the FCI and relative ascendancy (Heymans and Baird, 2000), which is also seen in the cypress and graminoid systems: The higher FCI and lower relative ascendancy in the cypress is in contrast to the lower FCI and higher relative ascendancy in the graminoids.

Some reasons behind the higher relative ascendancy of the graminoids can be explored with reference to the relative contributions of the various components to the community ascendancy (Table 2). The highest such 'sensitivity' in the cypress is more than one bit lower than its counterpart in the graminoids, and on average most higher-trophic level compartments that are present in both models exhibits higher sensitivity in the graminoids than in the cypress. It is noteworthy also that 41 compartments in the cypress show sensitivities of less than 5 bits, while only 28 compartments lie below the same threshold in the graminoids. The higher sensitivities in the graminoids owe mainly to the greater activity among the lowest trophic compartments, which causes the other compartments to seem rare by comparison. Thus, in the graminoids, community performance seems sensitive to a larger number of taxa, which accords with our analysis of dependency coefficients and stability discussed above.

Pahl-Wostl (1998) suggested that the organization of ecosystems along a continuum of scales derives from a tendency for component populations to fill the envelope of available niche spaces as fully as possible. This expansive behavior is seen in the cypress system, where the arboreal third dimension of the cypress trees fills with various terrestrial invertebrates, mammals and birds not present in the graminoids. The graminoid system, however, appears to be more tightly organized (higher relative ascendancy) than the cypress in that it utilizes primary production with much higher turnover rates. This confirms Kolasa and Waltho (1998) suggestion that niche space is not a rigid structure but rather co-evolves and changes in mutual interaction with the network components and the dynamical pattern of the environment. The graminoid system is more responsive, because it utilizes primary producers with higher turnover rates, and has, therefore, been able to track more closely

environmental and anthropogenic changes. The cypress system on the other hand, should have more resilience over the long term due to its higher overhead, especially its redundancy (Table 1).

According to Bondavalli et al. (2000) a high value of redundancy signifies that either the system is maintaining a higher number of parallel trophic channels in order to compensate the effects of environmental stress, or that it is well along its way to maturity. Even though these authors suggest that the cypress system is not very mature, in comparison to the graminoids, one would have to conclude that the cypress is more mature. (A slower turnover rate, as one observes in arboreal systems, such as the cypress is indicative of a more mature ecosystem). Furthermore, the third dimension of terrestrial vegetation affords the system a greater number of parallel trophic channels to the higher trophic levels than exists among the mainly periphyton dominated graminoid system. Although the graminoid system has a large throughput of carbon and a substantial base of fast-producing periphyton, it appears relatively fragile in comparison to the cypress system, which is more resilient over the long run and has more trophic links between the primary trophic level and the heterotrophs. In conclusion, scale, in the guise of the vertical dimension of the cypress makes that system more resilient as a whole, and less sensitive with respect to changes in material processing by many of its composite species.

Acknowledgements

Appendix A. Definitions pertaining to NA (Ulanowicz and Kay, 1991)

Ascendency: A measure of system size and organization. The product of a factor of the size of the system (the total systems throughput) times a factor representing the coherence of the flows (the average mutual information of the flow structure).

Dependency or dependency coefficients: The i–jth entry to the dependency matrix is the fraction of the total ingestion by j, which passed through compartment i along its way to j. Each column of the dependency matrix portrays the extended diet of that species, and because material is reused at various steps along the way, the coefficients sum to $> 100\%$.

Development Capacity: Upper boundary to the ascendancy.

Finn cycling index (FCI): The fraction of all the flow in the system that is due to recycling (Finn, 1976). The FCI is calculated from the relationship Tc:TST where Tc is the amount of system activity devoted to recycling and TST is the total systems throughput.

Lindeman Spine: Illustrates the net amount each integer trophic level receives from the preceding level, as well as the amount it creates through respiration, exports, detritus for recycling, and the net production available for transfer to the next higher level.

Overhead: The difference between the realized structure (ascendancy) and its upper boundary (development capacity) and an indicator of potential resiliency.

Throughput: The amount of medium flowing through each compartment in a steady state.

Total systems throughput: Measures the extent of the total activity in the system. It is measured as the sum of all flows occurring in the system.

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