

Insights into the processing of carbon in the South Florida Cypress Wetlands: a whole-ecosystem approach using network analysis

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Abstract

Aim The aim of this research was to investigate the potential of the South Florida Cypress Wetlands as a carbon-accumulating system.

Location This ecosystem is part of the Big Cypress Natural Preserve, located in the south-west part of Florida (USA) between the Mangrove Swamps that border the Gulf of Mexico and the Everglades.

Methods This investigation was carried out by constructing networks of carbon exchange between the living and nonliving components that comprise this ecosystem. By means of these networks potential for carbon accumulation has been assessed by identifying and quantifying pathways for the transfer of carbon, assessing the efficiency between trophic levels, and evaluating the importance of material cycling. These analyses are commonly referred to as network analysis.

Results Results obtained show that dependency on detritus by higher trophic levels is rather low and so is the trophic efficiency. Yet, less than 10% of the carbon that flows through the system is recycled and the magnitude of internal ascendancy reaches only 40% of the total system ascendancy.

Main conclusions All these results support the hypothesis that the South Florida Cypress Wetlands are predominately flow-through in nature and that carbon accumulation in this environment is noticeable.

Keywords

Global warming, carbon-accumulating system, cypress wetlands, network analysis, carbon processing.

INTRODUCTION

To mitigate the current trend in climate change, it is necessary to reduce drastically the concentration of carbon dioxide in the atmosphere. Toward this end, action must proceed along two lines: (I) past emissions must be reassimilated into storage and (II) the release of carbon from existing stocks must be reduced insofar as possible. As regards the first

option, different strategies have been recommended, most of them focusing on forestry management (Dixon *et al.*, 1994; Houghton, 1996). The potential of forests to serve as sinks for carbon is well recognized (Kolchugina & Vinson, 1995; Phillips *et al.*, 1998), however, the effectiveness of various ecosystems to sequester carbon differs widely with respect to the species involved, the ambient climate and the prevailing management practices (Costa, 1996). The feasibility of relying on ecosystems to sequester carbon will depend upon the inherent patterns of land use, which, in turn, are affected by demographic, economic and technological factors (Dixon *et al.*, 1994). Simulations aimed at predicting future trends in carbon storage by forests are based upon climate information

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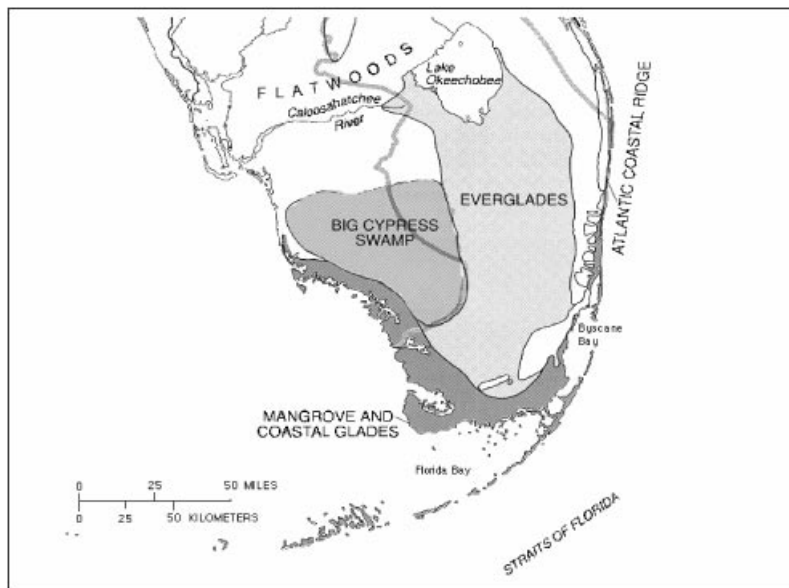


Figure 1 Study area, map modified from McPherson & Halley (1997).

and land use changes and have revealed that in coming years it remains uncertain whether or not the amount of carbon stored globally will exceed the quantity released back into the atmosphere (Dixon *et al.*, 1994). Under such an uncertain outlook, identifying and protecting sinks of carbon takes on an urgent priority.

This study focuses on the South Florida cypress wetlands. It is well known that ever wet conditions favour carbon sequestering (Spicer, 1993), and that peat-forming wetlands have great influence on the global balance of carbon in the atmosphere (Sjors, 1980; Maltby & Immirzi, 1993; Franzen *et al.*, 1996). These characteristics are shared also by the South Florida cypress wetlands (Ewel & Wickenheiser, 1988; Mitsch & Gosselink, 1993) so that one can hypothesize that these ecosystems may act as carbon-sequestering systems. Yet, being characterized by 'strands' or 'domes'—two major types of swamp forests, they bear some similarity to the peat swamp forests of Indonesia, one of the few recognized carbon sinks (although the contributions of the Indonesian wetlands toward banking global carbon have been reduced significantly through drainage and conversion to agricultural lands (Sorensen, 1993)). Given the importance of carbon-sequestering systems assessing the potential of the South Florida cypress wetlands in this respect has become an interesting issue.

One common, very useful approach is to analyse these systems through their carbon budgets. Using long-term monitoring data in connection with simulation models, the release of carbon to the atmosphere incurred by both human activities and natural processes can be compared with carbon uptake at the planetary (Fan *et al.*, 1998; Phillips *et al.*, 1998), regional (Houghton, 1993), country (Turner *et al.*, 1997) and ecosystem (Costa, 1996) scales.

Another approach is possible as well. For the cypress swamps properly to sequester carbon, it is necessary that matter reaching the sediment not be recycled back into the trophic

exchange system. To obtain clues about this issue the carbon budget can be considered in terms of network of exchanges: one can assess potential for carbon accumulation by identifying and quantifying preferential pathways for the transfer of carbon, assessing the efficiencies between trophic levels, and evaluating the importance of material cycling.

These analyses, that are commonly referred to as network analysis (Patten, 1985; Ulanowicz, 1986; Higashi & Burns, 1991), have been applied to a network model of the South Florida cypress swamps in order (1) to understand patterns of carbon exchange in the South Florida cypress wetland ecosystem, and (2) to assess the potential of this same ecosystem as a sink for carbon—a task with obvious implications for the management of this habitat.

STUDY AREA

The 295,000 hectare wetlands of the Big Cypress Natural Preserve and the adjacent Fakahatchee Strand State Preserve in south-west Florida (Fig. 1) have been described by the US Forest Service (1996) as a flat, gently sloping limestone plain. During the rainy season (June through November) 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 south-westward 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 1–10 hectares and consist of poorly drained to permanently wet depressions that are dominated by pond cypress. 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 centre outward. But a definite reason for this profile has not been determined yet, nor do all domes display the characteristic shape (Mitsch & Gosselink, 1993). During periods of low water levels, water is impounded in numerous ponds. Elevation ranges from 3.6 to 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 1500 mm, 80% of which falls from June to November, creating distinct wet and dry seasons. Precipitation received in 1 year has ranged from 760 to 2540 mm.

METHODS

Network construction

The creation of an ecosystem trophic network begins with the identification of the key components that comprise the ecosystem. The intention in depicting the kinetics of the cypress wetland ecosystem was to retain in the network only those taxa believed to actually inhabit this specific area for feeding and/or breeding. Duever *et al.* (1986) assembled most of the literature available on the use of habitat by animals in the cypress area, and this information has proved to be a solid foundation for constructing the networks. Only those reptiles, amphibians, birds and mammals that Duever found common to the cypress forest and mixed swamp forests appear in the final list of species. (save for a few additional species suggested by other experts.)

Once the list of species had been completed (Taxonomy follows Peterson, 1980, 1991a,b and Pritchard, 1978a,b,c), entries were then aggregated according to various criteria. For example, living compartments were taken to represent populations, guilds, or groups of populations that exhibit common trophodynamics, i.e. only those organisms with very similar sets of predators and prey were grouped into the same compartment. This trophic aggregation has been widely applied in ecosystem ecology (Teal, 1962; Moloney & Field, 1991; Stone & Berman, 1993; see the interesting discussion about these issues in Hannon *et al.*, 1991) although selecting the optimal level of resolution for representing large ecosystems in mathematically tractable models is a problem that is far from being resolved (see more about this in the discussion).

Adhering to the above criteria was not always possible, because detailed qualitative and quantitative information about particular species was often lacking. (In such cases clustering adhered closely to taxonomic distinctions.) Species with definite need for conservation measures, such as Florida panther (*Felis concolor*) and black bear (*Ursus americanus*)

(De Angelis *et al.*, 1998) were given separate compartments. Fully 68 compartments resulted from this aggregation procedure, as listed in Table 1.

One significant lexical question was how to treat the manifold species that comprise such functional groups as heterotrophic microorganisms or benthic meiofauna—groupings for which data were not available at the level of individual species. The scheme finally followed was to create two catchall compartments called 'living POC (Particulate Organic Carbon)' and 'living sediment' to represent these poorly resolved elements of the ecosystem. The 'living POC' includes bacteria, microprotozoa and zooplankton; while 'living sediment' combines bacterioplankton, microfauna and meiofauna.

Most of the other compartmental names are self-explanatory, but a few words of explanation need to be mentioned concerning the three detrital groups. 'Refractory detritus' was defined to encompass organic matter that decomposes at a relatively slow rate (*c.* 0.17 years⁻¹, according to Dierberg & Ewel, 1986). 'Labile detritus' is characterized by a faster decomposition rate (*c.* 5.7 years⁻¹). Because some of the species found in this ecosystem feed almost entirely on carrion, a third detrital compartment, consisting of very fresh vertebrate carrion, was created to avoid giving these saprovores (i.e. vultures) the appearance of being top-predators.

The next step in the construction of an ecosystem network is to designate a medium of exchange and to connect the compartments one to another via feeding and detrital pathways. The work reported herein followed carbon as the medium of exchange, and any information available on the diet of each taxon was used to specify the topology of the trophic connections. The connections of the ecosystem to the surrounding environment consist of migration, advection, primary production, respiration and harvest. Compartmental biomasses were quantified in terms of grams carbon per square metre (gC m⁻²), and flows in grams carbon per square metre per year (gC m⁻² years⁻¹).

The stocks and activities of all sixty-eight compartments vary over the course of the year, mostly driven by seasonal changes in water level. Accordingly, the kinetics of the cypress wetland ecosystem have been depicted in the form of two separate networks—one pertaining to the wet, high-water season (June through November) and a second to the dry season (December through May), when water levels are relatively low. A complete and detailed description of all source data and the calculations used to estimate the cypress ecosystem flows can be found on the World Wide Web at <http://www.cbl.umces.edu/~atlss>.

Network analysis

Network analysis is comprised of several techniques for the systematic analysis of ecological flow networks. Ulanowicz assembled the four primary methods used in Network Analysis into a single software package, NETWRK (Ulanowicz & Kay, 1991), including input-output analysis, trophic level analysis, cycling analysis and the calculation of indices that characterize the entire system. The constituent algorithms are based upon linear algebra and information theory and

Table 1 List of compartments in the cypress wetland network. Small fish 1 = herbivorous and omnivorous small fishes; Small fish 2 = primarily carnivorous small fishes; Passeriformes 1 = omnivorous passerine; Passeriformes 2 = predatory passerine.

No.	Compartment	No.	Compartment	No.	Compartment
1	Living POC	24	Turtles	47	Woodpeckers
2	Living sediment	25	Lizards	48	Passeriformes 1
3	Phytoplankton	26	Snakes	49	Passeriformes 2
4	Floating vegetation	27	Salamanders	50	Opossum
5	Periphyton	28	Large frogs	51	Shrews
6	Macrophytes	29	Medium frogs	52	Bats
7	Epiphytes	30	Small frogs	53	Black bear
8	Understory	31	Salamander larvae	54	Grey fox
9	Vines (leaves)	32	Tadpoles	55	Raccoon
10	Hardwood (leaves)	33	Pelecaniformes	56	Mink
11	Cypress (leaves)	34	Anseriformes	57	Otter
12	Cypress (wood)	35	Vultures	58	Florida panther
13	Hardwood (wood)	36	Kites & Hawks	59	Bobcat
14	Roots	37	Galliformes	60	Squirrels
15	Crayfish	38	Egrets	61	Mice & Rats
16	Apple snail	39	Great blue heron	62	Rabbits
17	Prawn	40	Other herons	63	White-tailed deer
18	Aquatic invertebrates	41	Woodstork	64	Hog
19	Terrestrial invertebrates	42	White ibis	65	Armadillo
20	Small fish 1	43	Gruiformes	66	Refractory detritus
21	Small fish 2	44	Owls	67	Liable detritus
22	Large fish	45	Caprimulgiformes	68	Vertebrate detritus
23	American alligator	46	Hummingbirds		

are explained in detail elsewhere (Ulanowicz, 1986). Below we provide quick thumb-nail sketches of the basic ideas behind each method.

(1) Input-output analysis allows one to quantify how any one compartment depends on any other compartment to obtain its requisite carbon. In particular, a total dependency matrix (Szymer & Ulanowicz, 1986) provides information on the fraction of the total amount ingested by compartment j (column designation) that has been provided by compartment i (row designation) over all pathways, both direct and indirect. To create the total dependency matrix, one starts with the matrix of diet coefficients (also called partial feeding coefficients) $[G]$, whose elements g_{ij} each designate the ratio between the flow from i to j and the sum of all direct flows to j in other words it's the fraction of the total input to compartment j that comes directly from i . To help illustrate g 's coefficients meaning and calculation an example, using a subset of the full 68 compartment network, is described in Fig. 2.

Multiplying $[G]$ by itself yields the matrix $[G]^2$, wherein the i - j th component represents the fraction of total input to j that comes from i over all pathways of exactly two trophic steps. In other words such coefficients quantify the material that i transfers to j by means of all pathways made of two links, that is pathways that connect i to j by crossing one intermediate variable. In Fig. 2 one such pathway connects Small Frogs with Snakes passing through Alligator. $[G]^3$ measures transfers of exactly three steps. By referring to Fig. 2 all the coefficients of the $[G]^3$ matrix are identically

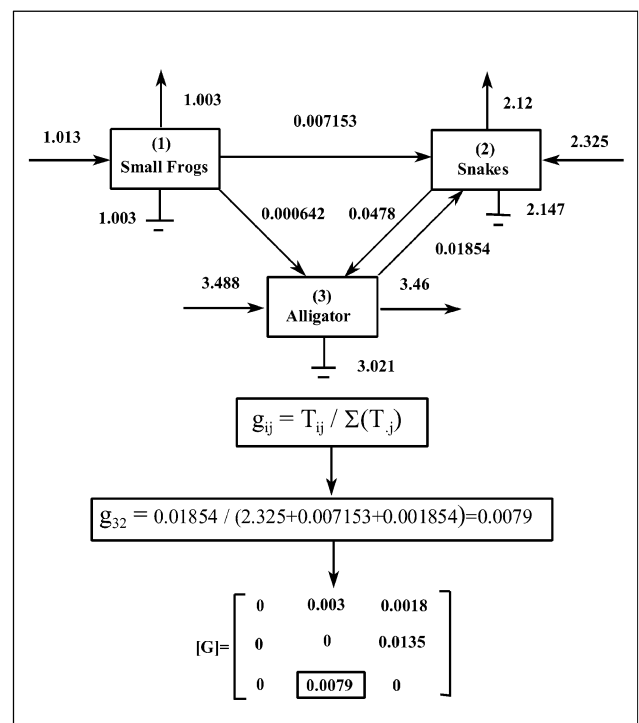
**Figure 2** Partial network of cypress wetland ecosystem, comprising only three compartments (all values are $\text{gC m}^{-2} \text{ years}^{-1}$) along with its matrix of partial feeding coefficients $[G]$. An example of calculation is given.

Table 2 Lizard indirect diet coefficients.

No.	Diet items	%	No.	Diet items	%
1	Living POC	1.660000	35	Vultures	0.161000
2	Living SED	5.880000	36	Kites & Hawks	0.004350
3	Phytoplankton	15.300000	37	Galliformes	0.088700
4	Floating vegetation	3.980000	38	Egrets	0.075400
5	Periphyton	5.470000	39	Great blue heron	0.014100
6	Macrophytes	3.790000	40	Other Herons	0.076300
7	Epiphytes	0.166000	41	Wood stork	0.090000
8	Understory	24.400000	42	White ibis	0.068700
9	Vines (leaves)	11.300000	43	Gruiformes	0.000885
10	Hardwood (leaves)	18.700000	44	Owls	0.007820
11	Cypress (leaves)	12.100000	45	Caprimulgiformes	0.001950
12	Cypress (wood)	1.080000	46	Hummingbirds	0.000008
13	Hardwood (wood)	1.020000	47	Woodpeckers	0.005430
14	Roots	2.040000	48	Passerines (omnivorous)	0.003970
15	Crayfish	1.090000	49	Passerines (predatory)	0.002300
16	Apple Snail	0.053300	50	Opossum	0.083600
17	Prawn	1.200000	51	Shrews	0.001590
18	Aquatic Inverts	1.450000	52	Bats	0.000001
19	Terrestrial Inverts	100.000000	53	Black Bear	0.003150
20	Small Fish (omnivorous)	3.190000	54	Grey fox	0.007570
21	Small Fish (carnivorous)	0.210000	55	Raccoon	0.038300
22	Large Fish	0.102000	56	Mink	0.002990
23	American alligator	1.160000	57	Otter	0.037700
24	Turtles	0.822000	58	Florida panther	0.000521
25	Lizards	0.231000	59	Bobcat	0.001480
26	Snakes	0.493000	60	Squirrels	0.031000
27	Salamanders	0.132000	61	Mice & Rats	0.012100
28	Large Frogs	0.080000	62	Rabbits	0.039600
29	Medium Frogs	0.129000	63	White-tailed deer	0.063400
30	Small Frogs	0.026200	64	Hog	0.001700
31	Salmander larvae	0.002340	65	Armadillo	0.007970
32	Tadpoles	0.004660	66	Liable Detritus	7.590000
33	Pelecaniformes	0.005030	67	Refractory detritus	32.200000
34	Anseriformes	0.000398	68	Vertebrate detritus	6.080000
				Sum	264.07

zero, as there are no pathways of length three in that subsystem.

Each power of the [G] matrix quantifies the fraction of carbon transferred from i to j through all the pathways whose length is equal to the power of the matrix. The total amount of carbon from i to j (which represent the g element in the total dependency matrix) can be calculated by summing up all the contributions of the successive integer powers of matrix [G]. This is a very intuitive way to explain the meaning of total dependency coefficients but because of the way in which [G] was normalized, this summation converges to what is called the total dependency matrix, $[I-G]^{-1}$. NTWRK4 use this equation for total dependency matrix calculation.

The sum of the contributions down a column in the total dependency matrix usually exceeds 100%, because material is visiting more than one compartment on its way through the network. As an example of indirect diet coefficients, we

consider the compartment for lizards found in the cypress swamps (see Table 2).

These reptiles feed entirely on terrestrial invertebrates, hence the total dependency coefficient of lizards on invertebrates is 100%. Because terrestrial invertebrates feed, among other things, upon compartment 8 (the understory foliage), production by the understory during the dry season will contribute 24.4% to the lizards by way of the invertebrates. That is, some of the material that was present in the understory first spent time incorporated in terrestrial invertebrates and then was transferred to lizards. Considering all (direct and indirect) pathways that reach lizards, one discovers that the indirect dependency coefficients for the lizard sum to 264%, signifying that the lizard feeds on average at trophic level 2.64.

(2) Trophic analysis reinterprets the cypress swamps network in terms of the linear trophic chain concept of Lindeman (Lindemann, 1942). As it is impossible to relegate

omnivorous heterotrophs entirely to a single trophic level, input-output techniques can be used to apportion the activities of omnivores among a series of hypothetical integer trophic levels (Ulanowicz & Kemp, 1979; Ulanowicz, 1995). As with input-output analysis, the trophic procedure begins with matrix [G] and its subsequent algebraic powers. If, for example, the [G] matrix is multiplied on the left by a row vector whose j -th element represents the fraction of the total input to compartment j that comes from outside the system (i.e. the degree to which this compartment acts as primary producer), the result is a row vector whose j -th element represents the fraction of j 's total input that arrives after a single step, i.e. it measures the degree to which that compartment is acting as a herbivore. Multiplying this row vector successively by the integer powers of [G], yields a succession of row vectors, the m -th of which estimates the activity of each compartment at trophic level m . The consecutive row vectors can be stacked upon each other to form what is termed the Lindeman transformation matrix. Each column of this composite matrix represents the apportionment of the corresponding species among the integer trophic levels. Calculating the Lindeman transformation matrix for the small model of Fig. 2 the result is:

$$[L] = \begin{bmatrix} 1 & 0.978 & 0.642 \\ 0 & 0.0215 & 0.0565 \\ 0 & 0 & 0.00122 \end{bmatrix}$$

The first row of this matrix reveals that 100% of the activity (throughput) of the first compartment, 97.8% of compartment 2's throughput, and 64.2% of compartment 3's activity occurs at the first trophic level. The second trophic level includes activity by only compartments 2 and 3, while the third level consists solely of 0.1% of the activity of species 3. The Lindemann transformation matrix allows one to think of the web-like network as being mapped into a concatenated sequence of integer trophic levels, the so-called Lindemann spine.

(3) Most networks of ecosystem flows contain cycles of material or energy, and the magnitude and structure of these cycles are analysed in detail by NETWRK. The program enumerates all the simple cycles in the given matrix of exchanges and then calculates the fraction of total activity that is devoted to cycling—what is known as the Finn Cycling Index (Finn, 1976). By normalizing the matrix of direct transfers by the total output of the compartment from which it originates, one obtains the matrix [F], a matrix whose i - j th element represents the fraction of the throughput of i which flows directly to j . All the integer powers of matrix [F] sum to give the output structure matrix, $S = [I-F]^{-1}$. Any diagonal entry of this matrix which exceeds unity implies that the designated compartment engages in cycling. Calling S_{ii} the diagonal element of the output structure matrix, the fraction of the i 's throughput devoted to cycling becomes $(S_{ii} - 1)/S_{ii}$. Multiplying each such fraction by its corresponding throughput and summing over all components yields the Finn index—the portion of the total system throughput T that is attributable to cycling:

$$T_c = \sum_i \{T_i (S_{ii} - 1)/S_{ii}\}.$$

(4) System-level indices quantify global attributes of the ecosystem. The activity level of the ecosystem is measured by the Total System Throughput (T), that is the total amount of medium flowing through the network. It is calculated simply by adding up all flows in the network. Multiplying this total throughput by the system indeterminacy, or diversity of the flow structure (as calculated using the Shannon information formula) (Ulanowicz, 1986), yields what is called the Development Capacity of the system. This quantity serves as an upper bound on how much the flow structure can be organized, which in turn is gauged by the system Ascendency, which also serves as a measure of network's performance in processing medium (Ulanowicz, 1986). The difference between this actual amount of flow structure and the theoretical upper bound on organization (the capacity) is called the system's Overhead. Overhead has conflicting interpretations. On one hand, it is a catchall for the system's inefficiencies at processing material and energy. What is a disadvantage under benign conditions, however, can turn to the system's advantage whenever the community is perturbed in some novel way. Under such circumstances the overhead comes to represent a 'strength-in-reserve' of degrees of freedom which the system can call upon to adapt to a new threat. A complete description of how one calculates these system-level indices and a detailed discussion about their meaning are available elsewhere (Ulanowicz, 1986; Ulanowicz, 1998).

RESULTS AND DISCUSSION

A system that sequesters carbon will reveal many compartments with low dependency coefficients on detritus; hence, the fate of detritus in the system is of particular interest. In order to gain an overview of how the major trophic groups are dependent upon detritus, an aggregated network was first analysed. The aggregated network was comprised of nine compartments: (1) Living detritus (that is mainly, the microbial community associated with the detritus (orig. boxes 1 and 2)); (2) Primary producers (orig. 3–14); (3) Invertebrates (orig. 15–19); (4) Fish (orig. 20–22); (5) Reptiles (orig. 23–26); (6) Amphibians (orig. 27–32); (7) Birds (orig. 33–49); (8) Mammals (orig. 50–65); and (9) Detritus (orig. 66–68). This network is depicted in Fig. 3, and the results of input-output analysis for both wet and dry season are summarized graphically in Fig. 4. (Primary producers were not included, as their dependencies upon detritus were all identically zero.)

The results reveal that, with the exception of living detritus, whose dependency on carbon passing through the detrital pool is high (88% during the wet season and 89% in the dry), the only other group to depend on detritus for more than 50% of its intake was the bird compartment during the dry season. As much as 59% of total consumption of carbon by birds had previously been detritus, although this percentage is much lower during the wet season (32%). Mammals in particular, but also reptiles, amphibians and fish, all exhibit low dependencies on detritus.

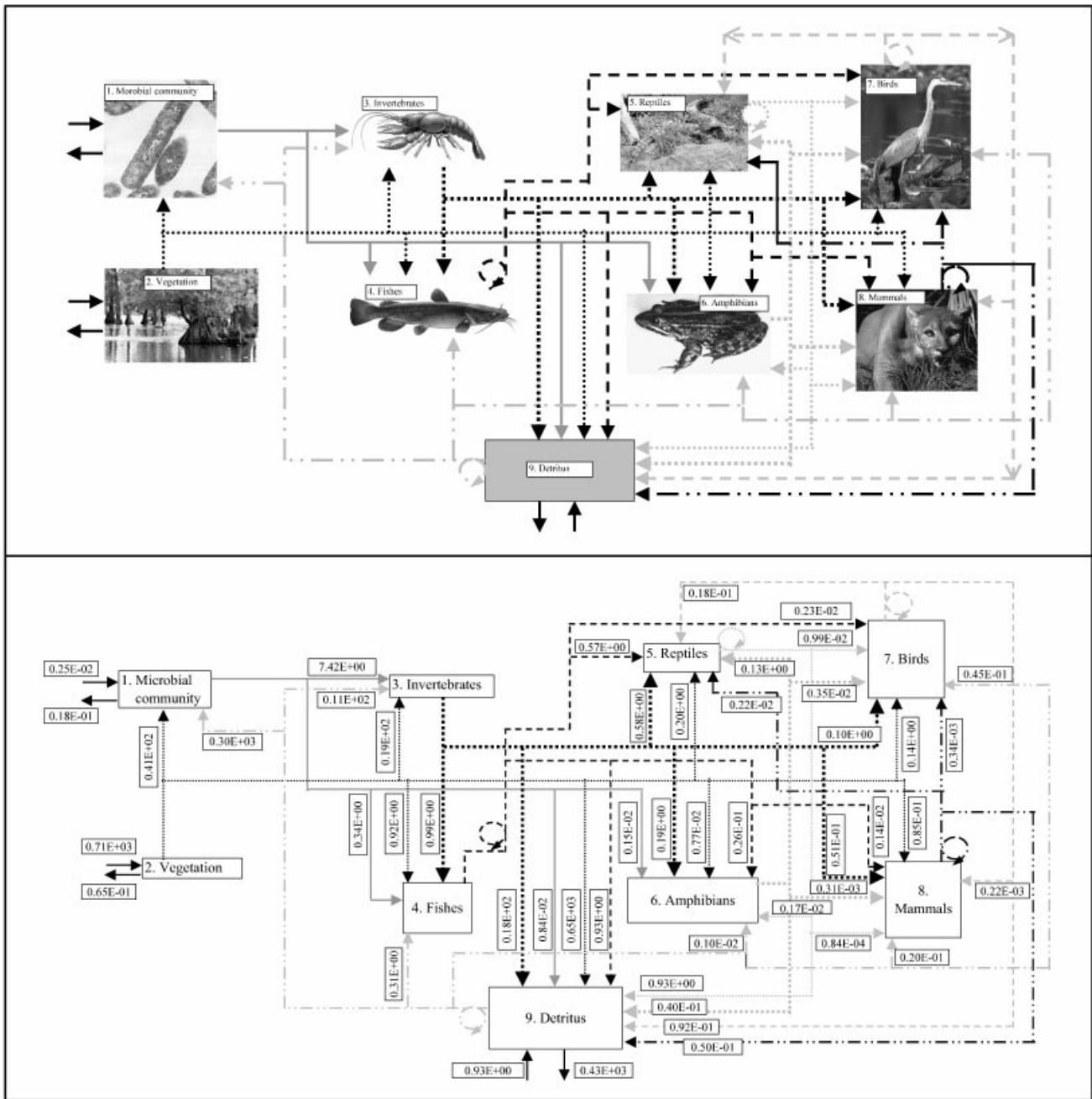


Figure 3 Aggregated network representing the major trophic groups considered in the cypress wetland network.

Looking in more detail at the original network (Fig. 5), one discovers that the high dependency by birds on detritus is due mainly to compartment 35, Vultures.

These feed 100% directly on detritus, and their aggregate dependency on all forms of detritus is higher than 100% (123% in the wet season and 141 in the dry).

Only twenty-one compartments depend indirectly on detritus over both seasons for more than 50% of their intake, and among them only eight receive a subsidy greater than 60%.

Among the latter eight are microorganisms and benthic meiofauna (the Living POC and Living Sediment compartments), several aquatic invertebrates (crayfish [*Procambarus alleni*], apple snail [*Pomacea paludosa*]), salamander larvae and opossum (*Didelphis marsupialis*).

White-tailed deer (*Odocoileus virginianus*), squirrels and rabbits receive almost no material via the detrital compartments and rely entirely upon primary production (compartments 3 through 14). In addition to these herbivores, most top

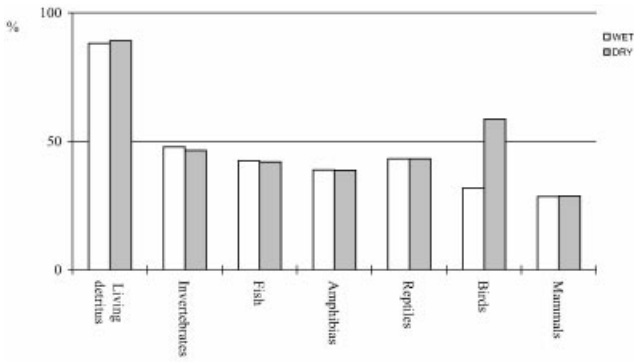


Figure 4 Results of input-output analysis for the aggregated network of Figure 3 (primary producers are not included, as their dependency upon detritus is identically zero).

predators display very low dependence upon detritus. Panther and grey fox (*Urocyon cinereoargenteus*) depend upon detritus for less than 15% of their intake, and the figure for bobcats (*Lynx rufus*) is far lower (2% in both seasons.) This indicates that top predators participate mostly in the grazing chain and show little need for detrital intermediaries. As one can observe in Table 3, top level species receive most of their energy from understory and hardwood leaves.

These constitute the two fundamental items in the diets of rabbits and deers, which in turn constitute the most important elements in the diets of the panthers. Rabbits represent 41% of the grey fox diet, and deers comprise 44% and 72% of the food for panthers and bobcats, respectively.

Cypress domes and strands, like many other wetland types, traditionally have been characterized as detritus-based ecosystems (Mann, 1972; Odum & Heald, 1975; Whipple & Patten, 1994; but see Moran *et al.*, 1988). This depends on the fact that primary productivity in wetlands generally is dominated by vascular plants, rather than by phytoplankton, and the bulk of primary production, made of material that is indigestible to animals, must be utilized first by microorganisms and subsequently made available to higher order consumers (Polis & Strong, 1996).

If this were true also for the South Florida cypress swamps, input-output analysis would have revealed most compartments to have dependencies on detritus close to 100%. The total dependency coefficients calculated in this study show instead dependencies of various heterotrophs upon detritus that are much lower. The reason why Cypress Swamp ecosystems have hither to been regarded as based upon detritus was that the dense tree canopy should not allow for significant growth of the other types of vegetation. It had not been taken into consideration, however, that during the dry season the tree canopy is negligible (cypress trees are deciduous), and the primary producers, such as periphyton, phytoplankton and other subcanopy vegetation, gain in relative importance. This advantage to subcanopy producers notwithstanding, input-output analysis reveals that heterotrophs depend heavily on noncypress primary producers during the high water period

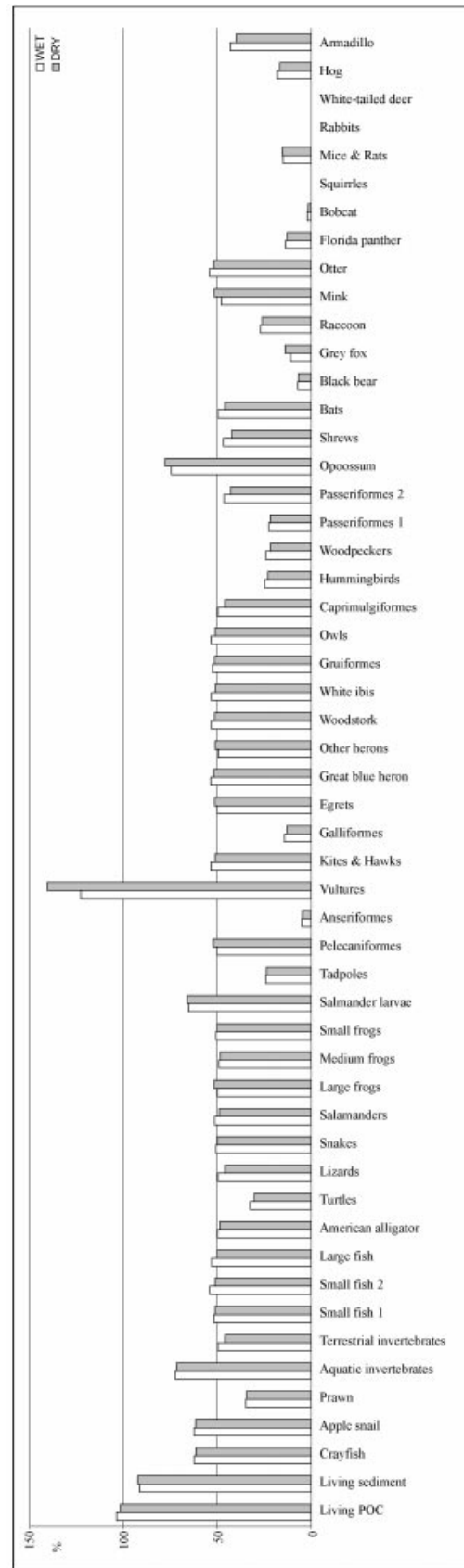


Figure 5 Results of input-output analysis for the 68-compartment network of the cypress wetlands (primary producers are not included, as their dependencies upon detritus is identically zero).

Table 3 Top species diet coefficients; each item is represented as a percentage of the total consumption.

Diet items	Black bear	Grey fox	Panther	Bobcat	Squirrels	Rabbits	Deer
Understory	53.2	3.4			57.4	64.1	64.1
Vine (leaves)					0.4		
Hardwoods (leaves)	29.8	1.9			32.2	35.9	35.9
Cypress (leaves)					10.0		
Terrestrial invertebrates	12.0	16.1					
Turtles	1.5						
Snakes	0.5						
Galliformes		1.4		5.4			
Egrets		2.1					
Great blue heron		0.4					
Other herons		2.1					
Woodstork		2.6					
White ibis		1.9					
Gruiformes							
Passerines 1		0.1		0.3			
Passerines 2		0.1		0.2			
Shrews		0.8		0.2			
Raccoon			20.0				
Mink		2.1		0.7			
Squirrels		22.5		7.0			
Mice & Rats		1.4	0.2	1.6			
Rabbits		41.0	3.5	12.6			
White-tailed deer	1.0		43.8	72.0			
Hogs	1.0		23.0				
Armadillo	1.0		9.5				

as well, even when the canopy of cypress is dense. A considerable amount of aquatic vegetation can be found in the middle of domes and strands, where big ponds often provide holes in the canopy. Also included in the ecosystem are the ecotonal edges of the domes and strands, areas where low-growing vegetation dominates primary production. These features give ample opportunity for nondetriral trophic pathways to become established within the Cypress Swamp ecosystem.

Low dependencies by heterotrophs upon detritus was the first signal that material passing through the detritus might not play as significant a role in ecosystem trophic exchanges as had once been thought. In order to explore this hypothesis further, it is helpful to take into account the analysis of how carbon cycles within the ecosystem. Such analysis demonstrates that the structure of pathways for recycle is exceedingly complex. The network for the wet season, for example, possesses exactly 3,975,514 simple cycles of carbon, while that for the dry season is even more complicated (27,084,903 simple cycles). Despite such a complicated structure, the values for the Finn Cycling Index (Table 4) were not impressive, indicating that only 4.7% of carbon activity during the wet season is devoted to recycle, and 5% during the dry.

The reason why there are so many more cycles during the dry season is beyond the scope of this paper and will be discussed elsewhere. Important here is the fact that, despite the great complexity of recycle pathways in the cypress communities, only a small fraction of total activity is devoted to cycle of carbon. Interestingly, the percentage of recycle

Table 4 System level indices, for both wet and dry season.

Indices	Wet	Dry
Cycling analysis		
Number of cycles	3,975,514	27,084,903
Finn cycling index (FCI, %)	4.7	5
Information indices		
Total system throughput (T)	2535	1842
Development capacity (C)	11,752	8651
Ascendency (A)	5076	3781
Internal ascendency (Ai)	2063	1593

activity is less than half the corresponding fraction occurring in physically more open ecosystems, such as the well flushed Chesapeake estuary, where recycling ranges from 15 to 25% (Baird & Ulanowicz, 1989). This difference between swamp and estuary seems to be related to the relative availability of detrital material in each habitat after it falls to the sediment. In Chesapeake Bay, carbon reaching the bottom is more likely to be ingested and fed back up the trophic chain; whereas in the cypress network, material reaching the bottom most probably will stay buried.

Further evidence to support the view that cypress ecosystems primarily pass carbon from primary production directly into the sediment comes from aggregated trophic analysis. The Lindemann spines obtained from this method are depicted in Fig. 6.

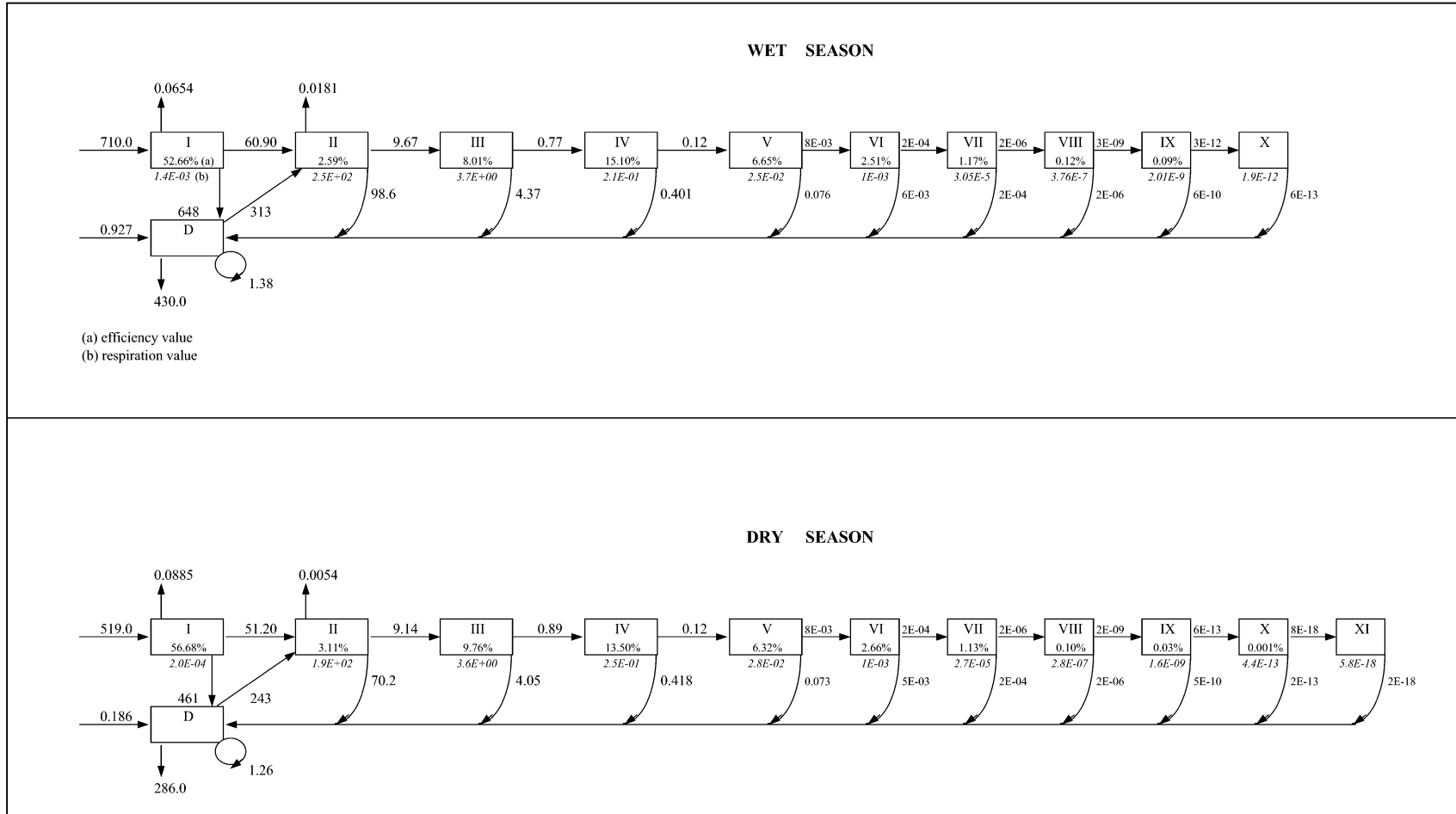


Figure 6 Results of trophic aggregation (Lindeman spine representation) for both wet and dry season for the South Florida cypress wetlands (all values are $\text{gC m}^{-2} \text{years}^{-1}$, where not differently specified).

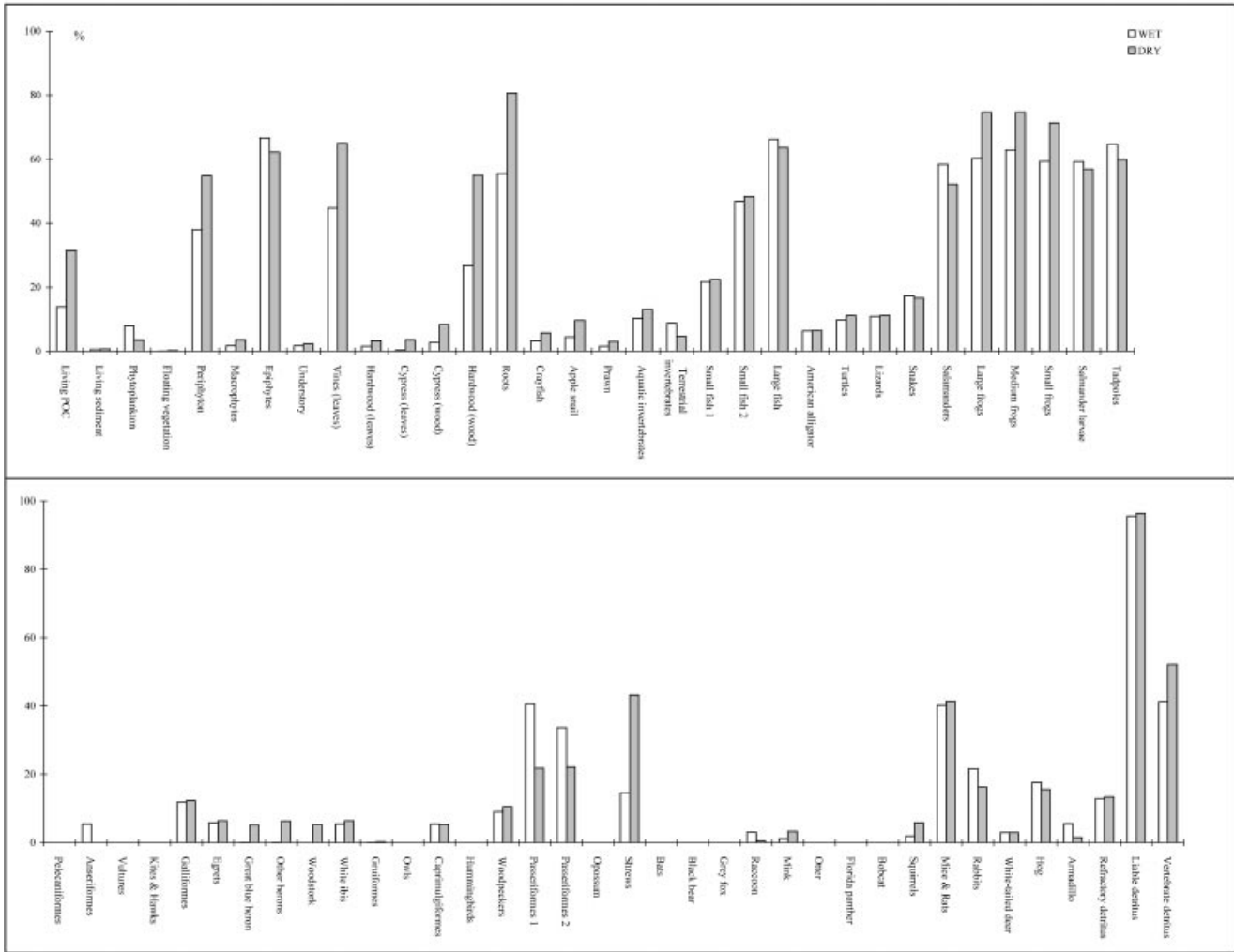


Figure 7 Efficiency coefficients for all the compartments considered in the two networks (wet and dry season) of the cypress wetlands.

They reveal that, of the total amount of carbon entering the system at the first trophic level, only 1.4% reaches the third trophic level during the wet season and 1.8% during the dry period. In both seasons a large fraction of the total primary production passes directly into detritus. Yet, of the total amount of material entering the second trophic level, fully 90% passes through living sediment. Part of this material is dissipated and part becomes detritus. Efficiency analysis (Fig. 7), describing compartments ability in transferring carbon to higher levels, helps confirm these trends.

Primary producers and living sediment appear to be very inefficient in passing carbon to upper trophic levels.

Again, in the Lindemann spines one reads that 60% (wet season) and 55% (dry season) of the total input of carbon is exported directly from the detritus compartment. This amount is not fed back into the system. The overall picture, then, is of an ecosystem that sequesters most of the carbon it fixes and passes only the small amount of production by auxiliary plants further up the food web. Further confirmation of

scenario is provided by global indices of network development, as quantified by information theory. (One must be circumspect, however, given the conflicting interpretation of some of these measures.) The whole-system measures are listed in Table 4. The total system throughput in the cypress wetland falls by some 27% from wet to dry seasons, and because this measure is used to scale all the other measures, the same drop is reflected in virtually all the other indices. Although the absolute magnitudes of trophic indices changed over the course of the year, the kinetic relationships among them remained essentially constant.

The magnitude of internal ascendancy (the formula for ascendancy applied only to internal system flows) is only 40% of that of the overall system ascendancy, supporting the conclusion that this system is predominately flow-through in nature. Because the horizontal flow of water through the cypress ecosystem is exceedingly slow, one might expect the cypress wetlands to function more as a closed system, with material recycling within it for a long time. But such does

not seem to be the case. A lot of material enters the system, and most of it immediately leaves the system to be buried in the sediment—whence the low value of internal ascendancy. Thus the major elements of system organization appear to be the exogenous exchanges.

Ascendency during both seasons reaches 35% of the development capacity. Given the very low magnitudes of dissipative overhead and overhead on exports, one is left to concentrate upon the overheads on imports and redundancy (based on quantification of parallel pathways proceeding between any two nodes). In particular, redundancy is calculated to be a considerable fraction of development capacity. A high value for redundancy signifies either that 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. Immature ecosystems tend to possess higher capabilities to sequester carbon in comparison to mature ecosystems. For example, in a mature forest, growth rate is largely balanced by wood decay. In the cypress ecosystem, however, only a small fraction of organic matter is retained in the system via cycling, so the system's value as a carbon sequestering system is only marginally related to its maturity. It remains however, an open ecological question whether one should classify the Cypress Swamp ecosystem as a young immature system and further investigation is needed to clarify this aspect.

Network models are simplifications of the cypress wetland ecosystems. One serious problem with describing webs is deciding how many and which groups of organisms should be included for the web to meaningfully represent the ecosystem. This issue has long been debated in the ecological literature and it is now clear that aggregation may affect the robustness of the outcomes (Strong, 1988; Martinez, 1991). To consider the effect of aggregation, the original sixty-eight-compartment network (XL, extra-large), and the nine-compartment model (S, small) described in Fig. 3 have been compared with two other networks obtained through a procedure of progressive lumping based on similar diets and taxonomic similarity. One such networks was comprised of thirty-four compartments (L, large), and the other counted eighteen variables (M, medium).

The comparison has been done by considering the Finn Cycling Index (FCI), which measures the fraction of the total activity that is devoted to cycling, calculated on the network related to the dry season. This choice depends on the fact that among all ecosystem functions, cycling seems particularly sensitive to aggregation (Ulanowicz, 1984). Results of this comparison are shown in Fig. 8. In the most resolved network, that which comprises sixty-eight components, the fraction of matter recycled is 5% and increases to 6–7% when the number of compartments decreases to thirty-four (network L). For a lower resolution recycling increases further, reaching 12% for structure S. This trends suggests that a more realistic model, one that assigns each species a compartment, could recycle even less than 5%, further supporting the conclusion that the South Florida cypress swamps tend to accumulate carbon.

Flow networks presented here have been constructed based on data gathered from the literature and on information

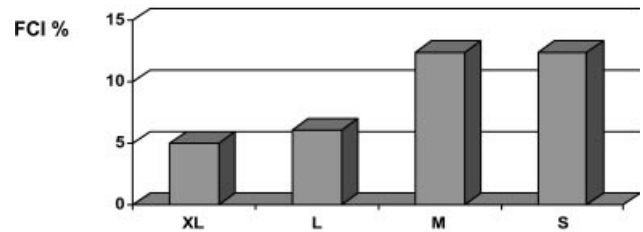


Figure 8 Finn Cycling Index (FCI) as a function of aggregation. The four networks characterized by different aggregation are labelled as follows: XL comprises sixty-eight compartments, L comprises thirty-four compartments, M counts eighteen compartments, and S identifies only nine compartments.

provided by experts in different fields (all listed in the web page). Yet, results of lab experiments (i.e. measures of primary production for phytoplankton and chemical analysis of sediments; Bondavalli, unpublished data) were used to fill some informational gap. All such information constitutes an heterogeneous data set as for sampling locations (spatial variability) and time periods (temporal variability). Accordingly, it was not possible to build networks representative of the state of the ecosystem at specific points in space and time; rather, by averaging the data, overall networks that reflect mean conditions of the ecosystem over time have been obtained.

Static models certainly are not appropriate tools to investigate within-season dynamics or effects of perturbation on ecosystem processes (Ulanowicz & Tuttle, 1992); however, they have been proved credible portraits when the aim was to investigate general properties of ecosystems (Baird & Ulanowicz, 1989; Wulff *et al.*, 1989; Bondavalli *et al.*, 1998): models discussed here must be intended in this perspective. To better understand the dynamical aspects of the South Florida cypress wetlands either multiple networks representative of different point in space and time should be built and analysed (Baird *et al.*, 1999), or static networks should be coupled with dynamical models (Ulanowicz & Tuttle, 1992; De Angelis *et al.*, 1998).

As stated above the networks presented in this article describe average conditions for the South Florida cypress swamps. Averaging, however, is not per se sufficient to compensate for the high heterogeneity that characterizes the data set utilized for quantifying the networks. A precautionary approach would suggest not to consider the flux rates as exact estimates of average material exchanges in the ecosystem. Some uncertainty must be associated to the coefficients and this requires a sensitivity analysis be performed to test the robustness of the results.

The sixty-eight-compartment network of trophic exchanges developed for the South Florida cypress wetlands is the most highly resolved and complicated trophic budget ever to be assembled. Given the exceedingly high number of paths and cycles in a network of this size the cycle analysis required a Sun-SPARC ultra™ working over 177 h to strip the 27 million cycles from the network. In these conditions performing a sensitivity analysis remains a daunting task.

With fewer cycles sensitivity analysis would become a feasible option but this imposes to reduce the network dimension, that is less compartments should be considered. This can be done by lumping variables, but aggregation generates further uncertainty, as it has been discussed for the Finn Cycling Index. Moreover this study has been carried out within a program of the US Geological Survey called ATLSS (Across Trophic Level System Simulation), whose aim is to predict the responses of a suite of higher trophic level species to human intervention on the ecosystems of South Florida. As this project focuses at the species level, ecosystem networks, originally conceived as calibration standards for more sophisticated dynamic models, should carry the same level of resolution required by the overall project. This approach however, has been followed in the understanding that adequate simulation procedures for testing the robustness of results in highly resolved networks must be developed in the near future to improve our ability to studying these and other ecosystems.

CONCLUSIONS

Global warming represents one of the world's most debated environmental problems, and finding ways to keep carbon dioxide out of the atmosphere has become a pressing issue. Carbon-accumulating systems could contribute decisively towards this end. Ecosystems that share a potential for carbon accumulation are present in many regions of the world; they are more numerous in boreal and arctic regions of the northern hemisphere, but their presence is consistent also at temperate latitudes of both northern and southern hemisphere (Moore & Bellamy, 1974). However their extension is shrinking alarmingly because of the great agricultural pressure and the growing centrifugal urbanization. Much effort should be devoted to preserving these environments but their significance to global climate change, necessary to justify their protection, will not be fully recognized until the processes that contribute to their carbon budget are understood and quantified.

In this work the potential of the South Florida cypress wetlands for carbon accumulation has been investigated using the methods of network analysis, which incorporates input-output analysis, trophic analysis, cycling analysis and system level indices. Through these analyses the kinetics of the overall ecosystem with regard to carbon processing has been elaborated. The low dependency on detritus shown by upper trophic levels, combined with the low recycling activity and the low internal ascendancy favour the hypothesis that the cypress wetlands act to conserve carbon through the burial of cypress litterfall. Further research is needed however, to substantiate this main conclusion. In particular temporal and spatial variability should be included in the networks in order to gain insight about dynamics processes that characterize these ecosystem as for the carbon budget.

Because the Florida cypress swamps are being subjected to increasing impacts by humans, and due to the intrinsic ecological value of these areas (suffice it here to mention that many rare and endangered species, such as the Florida panther (*Felis concolor*), are found in this environment) special efforts are being made to protect these ecosystems,

such as the creation of the Big Cypress National Preserve. If ecological studies should happen to demonstrate the value of these areas in accumulating carbon, further momentum should be given to efforts at protecting them.

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