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

Abstract

Global warming represents one of the world's most pressing 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, and the South Florida Cypress Wetlands appears to be a prime example of such systems. The potential of this ecosystem to sequester carbon can be explored through a quantitative examination of carbon fluxes transpiring in the system. Using the methods of network analysis, which incorporates input-output analysis, trophic analysis, cycling analysis and system level indices, one may elaborate the kinetics of the overall ecosystem with regard to carbon processing. The results of the analysis favor the hypothesis that the cypress wetlands act to conserve carbon through the burial of cypress litterfall. Contrary to prevailing opinion, cypress litter seems to contribute relatively little to higher trophic level production, which seem to depend more on production by understory plants.

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: (1) past emissions must be reassimilated into storages and (2) 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 (1,2). The potential of forests to serve as sinks for carbon is well recognized (3,4), 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 (5). 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 (1). Simulations aimed at predicting future trends in carbon storage by forests are based upon climate information 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 (1). Under such an uncertain outlook, identifying and protecting sinks of carbon takes on an urgent priority.

It is well known that the South Florida cypress wetlands sequester carbon as long as they remain continually flooded (6), and the significance of all peat-forming wetlands to the global balance of carbon in the atmosphere has been emphasized by several studies (7-9). The South Florida Cypress Wetlands are not homogenous, however, and are characterized by "strands" or "domes" --two major types of swamp forests. In this respect 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 [10]). 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, are found in this environment) special efforts are being made to protect these ecosystems, such as the creation of the Big Cypress National Preserve (BCNP). 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.

One common, very useful approach is to analyze 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 (4,12), regional (11), country (13) and ecosystem (5) scales. Emphasis is placed upon the exchanges of carbon, because it is only by understanding the interplay of carbon between plants, animals and non-living detritus that one can gain an appropriate perspective on ecosystem behavior and its ability to accumulate carbon. By analyzing the carbon budget as if it were a network of exchanges, one can identify and quantify preferential pathways for the transfer of carbon, assess the efficiencies between trophic levels, and evaluate the importance of material cycling. These methods, taken as a whole, are commonly referred to as network analysis. Each of the individual analyses can contribute in its turn towards assessing the potential of these South Florida forested wetlands for sequestering carbon, and, at the same time, highlighting the roles that their rich biodiversities and interactive structures play in this regard.

There is evidence that hydrological ground conditions affect the process of carbon accumulation in peat-forming ecosystems (14). In the cypress wetland region of South Florida there are two distinct hydrological seasons, and thus two networks were constructed for analysis.

In summary, the goals of this analysis are: 1) to understand the seasonal 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.

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. (15) 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, 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. Adhering to these 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 and White-tailed deer (Ecosystems, DeAngelis 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 particulate organic matter" (POC) 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 (ca. 0.17/yr, according to Dierberg and Ewel [1986]). "Labile detritus" is characterized by a faster decomposition rate, (ca. 5.7/yr.) 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 migrations, advections, primary productions, respirations and harvests. Compartmental biomasses were quantified in terms of grams carbon per square meter (gC/m^2), and flows in grams carbon per square meter per year ($gC/m^2/yr$).

The stocks and activities of all 68 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, highwater 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 <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 (16), 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 are explained in detail elsewhere (17). Below we provide quick thumb-nail sketches of the basic ideas behind each method.

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 (18) 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 partial feeding coefficients [G], whose elements g_{ij} each designate the fraction of the total input to compartment j that comes directly from i. 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. $[G]^3$ measures transfers of exactly three steps, and so forth. The total amount of carbon from i to j can be calculated by summing up all the contributions of the successive integer powers of matrix [G]. Because of the way in which [G] was normalized, this summation converges to what is called the total dependency matrix, $[I-G]^{-1}$. To help illustrate the dependencies, a subset of the full 68- compartment network has been extracted and depicted in Figure 2 along with its [G] matrix and the corresponding total dependency matrix.

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 foilage), 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.

Trophic analysis reinterprets the Cypress Swamps network In terms of the linear trophic chain concept of Lindeman (19). 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 (20,21). 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 an herbivore. Multiplying this row vector successively by the integer powers of [G], yields a succession of row vectors, the mth 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. In the example from Figure 2, the first row of the Lindemann transformation 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.

System-level indices quantify global attributes of the ecosystem. The activity level of the ecosystem is measured by the total system throughput, 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) (17), 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 (17). 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 disucssion about their meaning are available elsewhere (17,22).

Most networks of ecosystem flows contain cycles of material or energy, and the magnitude and structure of these cycles are analyzed in detail by NETWRK. The program enumerates all of 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 (23) 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 -- that portion of the total system throughput T that is

attributable to cycling: $T_c = \text{SUM} \{$

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Results and Discussion

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. Hence, the fate of detritus in the system is of particular interest. Translated into the variables used in input-output analysis, a system that sequesters carbon will reveal many compartments with low dependency coefficients on detritus In order to gain an overview of how the major trophic groups are dependent upon detritus, an aggregated network was first analyzed. The aggregated network was comprised of 9 compartments: (1) Living detritus (that is, the microbial community associated with the detritus [orig. boxes 1 and 2]); (2) Primary producers (orig. 3 to 14); (3) Invertebrates (orig. 15 to 19); (4) Fish (orig. 20 to 22); (5) Reptiles (orig. 23 to 26); (6) Amphibians (orig. 27 to 32); (7) Birds (orig. 33 to 49); (8) Mammals (orig. 50 to 65); and (9) Detritus (orig 65 to 68). This network is depicted in Figure 3, and the results of input-output analysis for both wet and dry season are summarized graphically in Figure 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. (Looking in more detail at the original network [Figure 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 21

compartments depend indirectly on detritus over both seasons for more than 50% of their intake, and among them only 8 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, Apple snail), salamander larvae and opossum.

White-tailed deer, squirrels and rabbits receive almost no material via the detrital compartments and rely entirely upon primary production (compartments 3 through 14). In addition to such herbivores, most top predators display very low dependence upon detritus. Florida panther and grey fox depend upon detritus for less then 15% of their intake, and the figure for bobcats 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 deer, which in turn constitute the most important elements in the diets of the panther. Rabbits represent 41 % of the grey fox diet, and white-tailed deer comprise 44 and 72% of the food for Florida panthers and bobcat, respectively.

Cypress domes and strands traditionally have been characterized as detritus-based ecosystems. If this were true, input-output analysis would have revealed most compartments to have much higher dependencies on detritus (close to 100%). The total dependency coefficients calculated in this study show dependencies of various heterotrophs upon detritus to be appreciable but nowhere as high as expected. Several prominent and interesting compartments rely significantly on the grazing chain. The reason why Cypress Swamp ecosystems have hitherto 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 non-cypress primary producers during the high water period 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 dominate primary production. These features give ample opportunity for non-detrital 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 8.8% of carbon activity during the the wet season is devoted to recycle, and 9.2% 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 activity is less than half the corresponding fraction occuring in physically more open ecosystems, such as the well flushed Chesapeake estuary, where recycling ranges from 15 to 25% (24). This difference between swamp and estuary seems to be related to the relative availabilities 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 Figure 5. 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, summarized in Figure 6, helps confirm these trends. Primary producers and living sediment appear to be very inefficient in passing carbon to upper trophic levels. 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 auxilliary plants further up the food web.

Further confirmation of this scenario is provided by global indices of network development, as quantified by information theory. (On 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 ascendency (the formula for ascendency applied only to internal system flows) is only 40% of that of the overall system ascendency, 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 ascendency. 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. 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. Failing long- term drought and associated fires, this system should continue to accumulate peat due to the particular conditions that prevail in cypress domes and strands.

It remains an open ecological question whether one should classify the Cypress Swamp ecosystem as a young immature system. One possible explanation for the high redundancy in the network may relate to the frequency of stressors, in particular fire. Fires periodically rake the Big Cypress, mainly during the dry season. The rate of peat accumulation decreases significantly as the frequency of fires rises. In those parts of domes and strands where peat remains in direct and continuous contact with water, the frequency and severity of fires is reduced. But as one moves toward the edge of these cypress "islands", the peat is not saturated with water for more frequent and longer intervals, so that the risk of fires increases.

Although fires reset ecological succession, it must not be overlooked that they also release significant amounts of carbon back into the atmosphere. Fires thus reduce the efficacy of the Big Cypress to sequestor carbon, and represent a major problem to managing the habitat. Furthermore, considering that global warming increases the level of evapotranspiration and thus lowers the water table, the outlook seems to be for an increasing probability of fire. The overall outlook, therefore, is for a kind of positive feedback that results in a progressive degradation of the habitat as a locus of peat formation -- all to the detriment of the global carbon balance.

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