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Overview Article

Species diversity in the Florida Everglades, USA: A systems approach to calculating biodiversity

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Abstract. The Everglades, a complex wetland mosaic bounded by human development at the southern tip of the Florida Peninsula, is home to a wide array of species, including 68 threatened or endangered animal species. Species richness within Everglades National Park, at the southern extreme of the Greater Everglades ecosystem, is 1033 plant taxa, 60 reptile taxa, 76 mammal taxa, 432 fish taxa, 349 bird taxa and 38 amphibian taxa. This paper briefly introduces the flora and fauna of the Greater Everglades, focusing on species of special conservation concern and those non-native species that are altering native ecology. While there is conservation utility in cataloging biodiversity, we argue that counts of species alone are inadequate descriptors of ecosystem condition because they fail to effectively indicate emergent ecosystem properties (resilience, productivity). We develop an approach to calculating biodiversity based on systems theory that can be applied across trophic levels to provide a condition benchmark that accounts for food web interactions. The Everglades, for which detailed flow data between ecosystem components have been compiled as part of ongoing modeling efforts (DeAngelis et al., 1998), is among the few ecosystems globally for which this technique is currently feasible. Flow data are coupled with exogenous forcing energies (in emergy units – Odum, 1996) to compute transformity values (Odum, 1988) for biotic and abiotic components of an Everglades graminoid marsh community. We calculate across-trophic level biodiversity using the Shannon information equation applied to ecosystem emergy flows. Results suggest that the graminoid marsh is operating at 42% of theoretical maximum ecosystem flow diversity. By comparing observed flows with theoretical maximum flows, we provide a measure of component conservation value; we observe strong overlap between species with lower than expected emergy-based importance and those known to be currently threatened or endangered. A significant positive association between this conservation value and transformity in the marsh suggests systematic upper-trophic level biodiversity degradation.

Key words. Biodiversity; Everglades; transformity; emergy; network analysis; ecosystem.

Introduction

At approximately 26 degrees north latitude, the Everglades of south Florida occupies the tip of the Florida Peninsula, a limestone plateau that is the southeastern extension of the North American continent (Fig. 1). The Everglades is the only subtropical preserve in North America, the largest sawgrass prairie in the world, the largest mangrove complex in the Western Hemisphere, and home to 68 threatened or endangered animal species. As a result of this unique biological value, the Everglades is currently the focus of a major restoration effort (www.evergladesplan.org) aimed, in part, at alleviating the effects of numerous impacts from surrounding land

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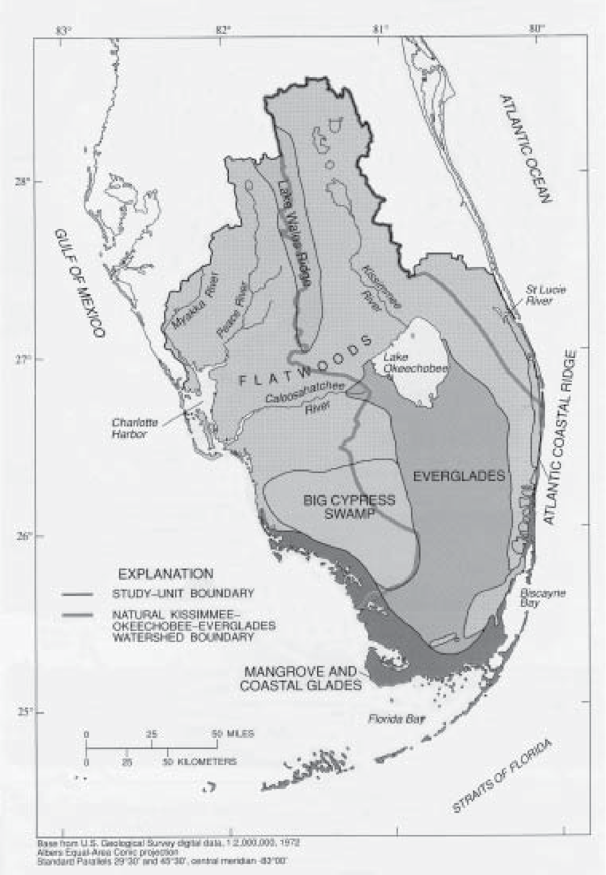

Figure 1. Major physiographic areas of south Florida, showing wide, arching Everglades slough bounded on the east by the Atlantic Coastal Ridge and on the west by the Big Cypress Swamp. To the north of the Everglades is Lake Okeechobee, the second largest inland freshwater lake in the USA. The Everglades' watershed is more than twice its size extending more than 350 km from north to south (from McPherson and Halley, 1997).

uses. Cumulative impacts over the last century have culminated in the system's natural flow of water being controlled by 1,000 miles of manmade canals, 720 miles of levees, 16 pump stations and 200 gates that divert 6.4 million m^3 of water daily from the Everglades to the surrounding seas. The biological consequences of hydrologic and water quality modification have been dramatic: approximately 90–95 % of the wading bird population has been lost since the 1930's (Ogden, 1997) and major changes in ecosystem composition, structure and function have been widely documented (Davis and Ogden, 1997; Forys and Allen, 2002).

The Everglades National Park (ENP), established Dec. 6th 1947 as the first park in the national system selected primarily for biological attributes, lies within the larger Everglades system (Greater Everglades). In addition to its federal protection status, the park, which covers an area over 600,000 hectares at the extreme southern tip of the Florida peninsula, is recognized as a Natural World Heritage site and a Ramsar Convention site, and forms the heart of a group of protected areas in the South Florida ecosystem (including Big Cypress National Preserve, Biscayne Bay National Park, Dry Tortugas National Park, Key Largo National Marine Sanctuary, several National Wildlife Refuges and the Florida Keys National Marine Sanctuary).

We begin with an ecological characterization of the Everglades and an overview of the historic and current system with a short discussion on the restoration efforts. Next, we present a literature review of biodiversity in the Everglades and provide an extensive species list for plants and major animal groups. Finally, we introduce a systems approach to calculating biodiversity across trophic scales using one Everglades community as the case study, ending with a discussion on integrating trophic interactions into biodiversity calculations.

Ecological characterization of the Everglades

The Florida peninsula is the result of several alternating episodes of submergence and emergence in response to the rise and fall of sea level over the past 40 million years. At high sea level the plateau acted as a marine shelf and limestone was deposited. During times of low sea level, acidic freshwaters from decomposition of organic matter dissolved and eroded the limestone creating the riddled solution features that characterize the limestone underlying the Everglades (Lane, 1994; Randazzo and Jones, 1997). Overlaying the limestone in the central portions of the Everglades is a thin veneer of organic peat of varying depth, generally decreasing from about 4–5 m in thickness in the northernmost parts of the Everglades, south of Lake Okeechobee, to only several centimeters deep at its southern extreme. The age of these peats (about 5,000 years) suggests that only recently conditions have been favorable for the establishment of the current vegetative communities (Gleason and Stone, 1994). Soils in nearly half of the Everglades, along both the east and west margins, are characterized as calcitic muds that resulted from deposition from calcareous blue-green algae periphyton associations in the alkaline waters of the Everglades (Gleason, 1974).

The climate of southern Florida is described as subtropical and humid. Average temperatures range in the mid 20s °C with lows in the winter averaging 15 °C and highs in the summer averaging about 27 °C. Average annual rainfall over the Everglades is between 100 and 165 cm (Duever et. al, 1994). The rainfall pattern (Fig. 2) generally is characterized by a dry season that extends from November to April or May and a wet season from June to September or October (Fernald and Purdum, 1998). The wet season usually accounts for more than half of yearly rainfall and is dominated by convective systems, while storms in the winter months are usually

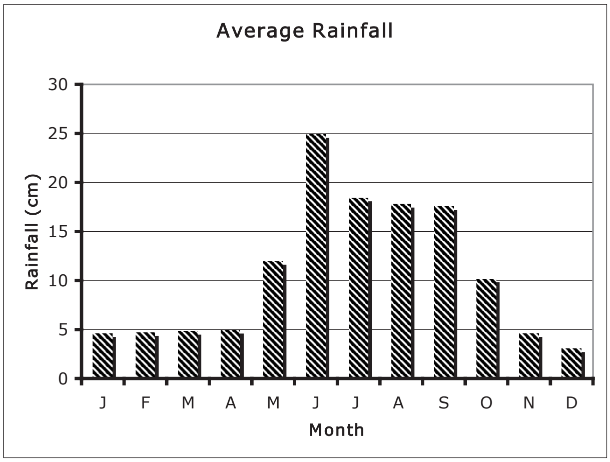

Figure 2. Average monthly rainfall (1961–1990) in the central Everglades (Fernald and Purdum, 1998).

the result of frontal activity. Rainfall is highly variable both from season to season and year to year, often punctuated by very dry years corresponding to El Niño events and hurricanes that can bring as much as 50 cm of rainfall in a short period of time (Fernald and Purdum, 1998).

The historic Everglades system. The historic Everglades was a wide arching, sawgrass (*Cladium jamaicense*) dominated "River of Grass" (Douglas, 1947), centrally located within the southern portion of the Florida peninsula (Fig. 1). The Everglades "River of Grass" covered approximately 10,100 km^2 and was the lower segment of a much larger drainage system (the Greater Everglades watershed) of approximately 23,300 km^2 (Gleason and Stone, 1994) stretching about 350 km from central Florida to the southern tip at Florida Bay. The southern region of the Everglades had nearly imperceptible slope from Lake Okeechobee southward to Florida Bay, averaging around 3 cm/km. On the east, the Everglades was bounded by a low sand-covered limestone ridge dominated by pine and tropical hardwood forests known as the Atlantic Coastal Ridge. The ridge was approximately 8–10 km in width with elevations averaging less than 10 m, and was breached in numerous locations by drainage ways carrying rainy season waters eastward to the Atlantic Ocean. To the west was the region known as the "Big Cypress Swamp", presumably named because of the dominance of cypress trees (*Taxodium* spp.) intermixed with sawgrass prairies. As Figure 1 suggests, the Big Cypress Swamp area was a separate hydrologic unit from the Everglades except during extremely wet years when waters may have flowed from one system to the other in either direction.

To the north of the Everglades, Lake Okeechobee (surface area = 1,732 km^2) received surface inflows from a drainage area of about 9,600 km^2 that extended from the central Florida highlands through a drainage way dominated by nearly level marshy wetlands and the meandering Kissimmee River (SFWMD, n.d.). The Lake was hydrologically connected to the Everglades and as lake levels rose in response to wet season rains, lake water would over-top the natural levee on its southern shore and sheet flow into the river of grass. Parker (1974) suggested that the timing of water levels in the overall Kissimmee-Everglades system was such that as the dry season approached in South Florida, the previous wet season rains in the northern portions of the basin were just arriving in Lake Okeechobee, which would then over-top the southern levee and sheet-flow into the Everglades maintaining water levels through the dry season.

The water that sheet-flowed across the Everglades was derived primarily from rainfall and thus was very low in nutrients. Nutrients from upland areas that entered the system in runoff were quickly taken up by vegetation or immobilized by soils. The result was that vast expanses of the Everglades were considered oligotrophic (nutrient poor) wetlands that developed under conditions of severe phosphorus (P) limitation (McCormick et al., 1998).

The Everglades system functioned as an interconnected mosaic of wetland habitats interspersed with seasonally saturated "tree islands" and pinelands, covering nearly 90 % of southern Florida (Odum and Brown, 1975). Minor variation in topography created a highly heterogeneous landscape mosaic and influenced the diversity of both flora and fauna. The alternating periods of wet and dry seasons regulated the life cycles of animal populations, while depths and duration of inundation resulting from the varying topography regulated primary production.

The Everglades system today. The Everglades of today bears little resemblance to the historic system. The spatial extent of the original Everglades has been reduced by approximately 50 % (Fig. 3). Over 4,000 km^2 of the Everglades south of Lake Okeechobee have been converted to agricultural lands. Areas along the eastern edge of the Everglades have been converted to various urban uses, including rock quarries, commercial and residential development, and agriculture. In all, approximately 12,000 km^2 of the original Greater Everglades (including the Kissimmee River watershed) have been converted to human uses (USACE and SFWMD, 1999).

Surrounded by developed lands and crisscrossed by roads, canals, and dikes, water no longer flows unobstructed from Lake Okeechobee to the Florida Bay and the Gulf of Mexico. Instead, water flow is highly managed through a series of canals, locks, and pumps which direct it to controlled Water Conservation Areas (WCA), thus altering the basic flows and storages of water and

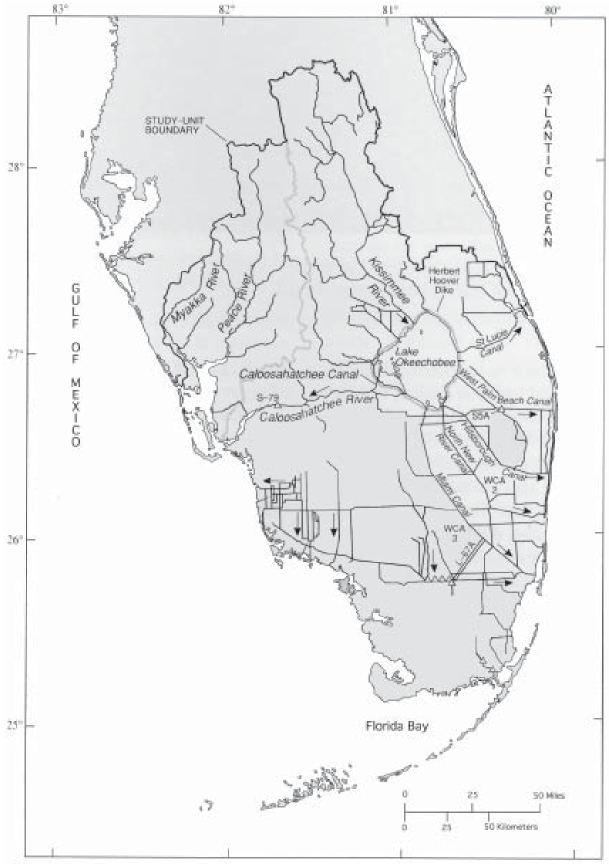

Figure 3. South Florida today. After more than 100 years of human "management" the hydrology of the greater Everglades systems is controlled by a network of canals and control structures that direct the flows of water (indicated by arrows) (from McPherson and Halley, 1997).

causing serious impact on both flora and fauna. Water management has also affected nutrient regimes with the release of urban stormwater and nutrient laden runoff from agricultural areas, increasing nutrient concentrations in the once oligotrophic Everglades and resulting in shifts in plant community structure. Stober et al. (1996) listed 6 critical issues facing the Florida Everglades including eutrophication, mercury contamination, habitat alteration and loss, hydropattern modification, and endangered and exotic species. They suggest that "the greatest threat to the Everglades ecosystem is to assume the issues are independent" (Stober et al., 1996).

The Comprehensive Everglades Restoration Plan. Recognizing that the Everglades was in peril, the United States federal government in partnership with the State of Florida developed a plan to reverse trends, restore the viability of the Everglades, and assist the recovery of several targeted species (Table 1) . The Comprehensive Everglades Restoration Plan (CERP) was implemented in 1998 for the restoration of the Greater Everglades ecosystem (USACE & SFWMD, 2005). Described as the world's largest ecosystem restoration project, the CERP includes restoring the natural flows of water and historical hydroperiods and improving water quality within the remaining natural areas of the Everglades system. In addition, the program will address water supply and flood protection needs in the urban and agricultural regions of south Florida surrounding the Everglades system. The estimated cost of the restoration effort is $7.8 billion; with annual operation and maintenance costs, including assessment and monitoring, of about $182 million (USCAE and SFWMD, 1999).

Biodiversity of different plant and animal groups

While "River of Grass" is an apt description for much of the ecosystem, where vast, predominantly monotypic stands of sawgrass (*Cladium jamaicense*) are common, much of the celebrated diversity of the ecosystem results from a landscape mosaic that also contains sloughs, wet prairies, cypress swamps, mangrove swamps, pinelands and tree islands. The Everglades represents a unique interface between sub-tropical species and those more characteristic of the Caribbean tropics. With a legendary capacity to support bird and fish life, and by providing a home for an array of charismatic mega-fauna (e.g. alligators, Florida panthers, snail kites), the biological value of the Everglades system is widely cited in efforts to protect and restore this ecosystem.

The Everglades is home to numerous species spanning the breadth of its heterogeneous ecosystem-types. Species richness has not been reliably quantified for the system as a whole, but within Everglades National Park there are 1033 species of plants, 60 species of reptiles, 38 species of amphibians, 76 species of mammals, 432 species of fish, and 459 species of birds (Table 2; ICE, 2004). The diversity of the Greater Everglades is substantially higher when one considers the cypress (*Taxodium* spp.) systems in Big Cypress National Preserve, the tree island systems of the northern Everglades (the Water Conservation Areas – Fig. 3), the preserved areas of Lake Okeechobee and the Kissimmee River, and the coastal marine preserves, including Florida Bay, Biscayne Bay and the Florida Keys.

Plants. The flora of the South Florida ecosystem was a primary factor in the original creation of Everglades National Park (ENP) (Robertson, 1959). Of the estimated 1600 species that are found in South Florida, more than 1000 have been cataloged in Everglades National Park alone (Avery and Loope, 1983). Over 150 families are represented, with Poaceae (124 taxa), Asteraceae (81), Fabaceae (69), Cyperaceae (53), Euphorbiaceae (45) and Orchiadeae (42) the most diverse; 111 families are represented by fewer than five taxa. Of the flora richness in

ENP, the majority (664) are dicotyledons, with 316 monocotyledons; over 45 ferns (and fern allies) have also been cataloged (Avery and Loope, 1983). While the plant diversity of Everglades is large, it is distributed unevenly in space. The diverse ecosystem mosaic (at both landscape and regional scales) leads to high β-diversity (Whittaker, 1975) even where α-diversity may be low in many of the particular patches.

Much of the plant life (>60 %) in the South Florida ecosystem is of tropical affinity, and local endemism rates are high (65 taxa are endemic, mostly concentrated in the rocky pinelands on the eastern Everglades) (Long and Lakela, 1976). Most of the communities found in the region are unique to North America, with closer analogs throughout the Caribbean, and many of the tropical species found are at the northward extent of their habitat range.

Table 1. Targeted Species in the CERP's South Florida Multi-Species Recovery Plan (MSRP).

Status	Species	Scientific name
Mammals		
E	Key deer	*Odocoileus virginianus clavium*
E	Key Largo cotton mouse	*Peromyscus gossypinus allapaticola*
E	Key Largo woodrat	*Neotoma floridana smalli*
Birds		
T	Audubon‘s crested caracara	*Polyborus plancus audubonii*
E	Cape Sable seaside sparrow	*Ammodramus (= Ammospiza) maritimus mirabilis*
E	Snail kite	*Rostrhamus sociabilis plumbeus*
E	Florida grasshopper sparrow	*Ammodramus savannarum floridanus*
Reptiles		
E	American crocodile	*Crocodylus acutus*
T	Bluetail (blue-tailed) mole skink	*Eumeces egregius lividus*
T	Sand skink	*Neoseps reynoldsi*
Invertebrates		
E	Schaus swallowtail butterfly	*Heraclides (= Papilio) aristodemus ponceanus*
T	Stock Island tree snail	*Orthalicus reses*
Plants		
E	Avon Park harebells	*Crotalaria avonensis*
E	Beach jacquemontia	*Jacquemontia reclinata*
E	Beautiful pawpaw	*Deeringothamnus pulchellus*
E	Carter‘s mustard	*Warea carteri*
E	Crenulate lead-plant	*Amorpha crenulata*
E	Deltoid spurge	*Chamaesyce (= Euphorbia) deltoidea*
E	Florida perforate cladonia	*Cladonia perforata*
E	Florida ziziphus	*Ziziphus celata*
E	Four-petal pawpaw	*Asimina tetramera*
E	Fragrant prickly-apple	*Cereus eriophorus var. fragrans*
T	Garber's spurge	*Chamaesyce (= Euphorbia) garberi*
E	Garrett's mint	*Dicerandra christmanii*
E	Highlands scrub hypericum	*Hypericum cumulicola*
E	Key tree-cactus	*Pilosocereus (= Cereus) robinii*
E	Lakela's mint	*Dicerandra immaculata*
E	Lewton's polygala	*Polygala lewtonii*
E	Okeechobee gourd	*Cucurbita okeechobeensis ssp. okeechobeensis*
T	Papery whitlow-wort	*Paronychia chartacea (= Nyachia pulvinata)*
T	Pigeon wings	*Clitoria fragrans*
E	Pygmy fringe-tree	*Chionanthus pygmaeus*
E	Sandlace	*Polygonella myriophylla*
E	Scrub blazing star	*Liatris ohlingerae*
E	Scrub mint	*Dicerandra frutescens*
E	Short-leaved rosemary	*Conradina brevifolia*
E	Small's milkpea	*Galactia smallii*
E	Snakeroot	*Eryngium cuneifolium*
E	Tiny polygala	*Polygala smallii*
E	Wireweed	*Polygonella basiramia (=ciliata var. b.)*

Source: "Notice of Availability of a Technical/Agency Draft Implementation
Schedule for the South Florida Multi-Species Recovery Plan" [Federal Register:
April 2, 2004 (Volume 69, Number 64)]

Table 2. Species richness in Everglades National Park.

Group	# Species	Location
Invertebrates	590	WCA 1-3 and ENP[1]
Plants	1033	Everglades National Park[2]
Reptiles	60	Everglades National Park[2]
Mammals	76	Everglades National Park[2]
Fish	432	Everglades National Park[2]
Birds	349	Everglades National Park[2]
Amphibians	38	Everglades National Park[2]

1 – Shuford, R., SWFWMD, unpublished data.
2 – ICE, n.d. – note that the lists include anomalous, extirpated species, and those for which presence is listed as unreliable.

The flora can be divided into several structural community-types, driven largely by exogenous factors, including hydroperiod and inundation depth, fire frequency, soil substrate (peat or marl soils, the distribution of which reflects hydrology and water source), anthropogenic nutrient enrichment and salinity. Small differences in surface elevation can result in dramatic shifts in community type, composition and richness. Davis (1943) classified the vegetation into seven communities ranging from high pinelands along the eastern ridge to coastal beach and dunes systems along the Florida Bay and Gulf of Mexico coast. Long (1974) identified 13 communities and tabulated the approximate number of plant species in each as follows: scrub vegetation, 76 species; hammocks/tree islands, 306; freshwater swamps, 188; dry pinelands, 303; seasonally wet pineland, 361; mangrove, 13; salt marsh, 23; wet prairies, 172; dry prairies, 303; coastal strands and dunes, 115; ruderal or disturbed lands 250; aquatic marshland, 119; and marine waters, 5. The total richness was estimated to be 1,647 species of vascular plants representing 177 families, though Gunderson (1994) citing Avery and Loope (1983) suggested the number in the southern Everglades was closer to half that number (830 species). Long (1974) further suggested that the vegetation that makes up these plant communities could be categorized into four main groups based on their origin: tropical species, non-tropical species, endemic species, and exotic and introduced species. Gunderson (1994) hierarchically grouped floral assemblages based on what he termed hydro-edaphic conditions (soil saturation and salinity) and growth form (forested versus graminoid). His classification contained nine classes including rockland pine forests, tropical hardwood hammocks, bayheads, willow heads, cypress forests, sawgrass marshes, wet prairies, ponds and creeks, and slough (having little or no emergent vegetation).

Of particular interest for biodiversity, tree islands, which persist on topographic high points within the wetland mosaic, support a wide diversity of tropical woody species and facultative herbaceous species (Sklar and Van der Valk, 2003); these systems act as ecological centers, attracting wildlife from areas with longer inundation. They are also particularly vulnerable to replacement by introduced species. Tree island or hammocks are dominated by hardwood species of both tropical and temperate affinities, including mahogany (*Swietenia mahogoni*), gumbo limbo (*Bursera simaruba*), and cocoplum (*Chrysobalanus icaco*) and more temperate species of live oak (*Quercus virginiana*), red maple (*Acer rubum*), and hackberry (*Celtis laevigata*). Also present are royal palm (*Roystonea alata*), cabbage palm (*Sabal pametto*) and 12 other palm species. Bayheads, which exist in saturated but rarely inundated areas, contain isolated stands of Carolina willow (*Salix caroliniana*) on slight elevations, or bald-cypress (*Taxodium distichum*) in organic matter filled depression. The warm, humid environment within tree islands and bayheads is ideal for supporting numerous orchids, bromeliads and ferns, some of which are endemic to the region.

The marsh complex that is the most well-known image of the Everglades is comprised of some 100 species, primarily graminoid, that are adapted to extended inundation (>200 days/year). Sawgrass (*Cladium jamaicense*) tends to dominate in shallower regions, often in the absence of any co-dominants. Historic sawgrass communities were responsible for the deposition, over 5000+ years, of deep peat soils south of Lake Okeechobee; the farming of these soils over the last 50 years has led to serious oxidation of those peat stocks. In areas with anthropogenically-elevated levels of nutrients (phosphorus in particular) and extended hydroperiod, sawgrass is being replaced by monotypic stands of cattails (*Typha domingensis*).

Ridges of sawgrass are interspersed with flow-oriented, deeper (30 60 cm) channels, called sloughs, which support only those macrophytes adapted to deeper water and longer inundation. Along the gradient of mean water depth and inundation period, wet prairies fall between ridges and sloughs. A typical slough is dominated by water lilies (*Nymphaea odorata*) and bladderworts (*Utricularia* spp.), while Tracy's beaksedge (*Rhynchospora tracyi*), spikerush (*Eleocharis cellulosa*), muhley grass (*Muhlenbergia filipes*) and maidencane (*Panicum hemitomon*) are co-dominants in the wet-prairie habitat. Also critically important to local biogeochemical cycling are periphytic algal mats, which are a complex assemblage of photosynthetic algae, bacteria, and zooplankton that are central in carbon, calcium and phosphorus cycling and strongly sensitive to nutrient enrichment.

Other ecosystem types persist in the Greater Everglades, largely driven in composition, productivity and geography by prevailing hydrologic patterns/elevation and geologic substrate. Among these other ecosystems are the cypress swamps of the Big Cypress National Preserve, an oligotrophic wetland mosaic dominated by *Taxodium* spp. (cypress). Within Big Cypress, the character of the woody vegetation varies from hat-rack cypress (dwarf trees due to nutrient limitations) to large luxurious strands (e.g. Fakahatchee Strand) in landscape depressions where nutrients and water accumulate. Another geographically significant ecosystem is the rocky pinelands of the southeastern Everglades, which is also nutrient poor, and in many cases exhibits limited soil development due to flood-drought cycles and frequent fire. Pinelands are dominated by South Florida slash pine (*Pinus elliottii* var. *densa*), with saw palmetto (*Serenoa repens*) a common understory dominant, but are the most diverse habitat in the Everglades, consisting of over 300 varieties of primarily tropical plants (Loope et al., 1979).

The freshwater ecosystems of the Everglades grade slowly into tidally-influenced ecosystems as water generally flows from north to south. Mangrove forests present throughout the coastal areas in the region (forming the largest mangrove complex outside of Australasia) are dominated by three species of mangroves (red – *Rhizophora mangle*, black – *Avicennia germinans*, and white – *Laguncularia racemosa*) that compete along an increasing salinity gradient. A complement of herbaceous wetland and dune species also persists in the tidally-influenced region that provides critical ecosystem services as a fish and shrimp nursery.

Thirty-five species of plants are listed as rare, threatened, endangered or of special concern by various monitoring agencies in and around the Everglades system. Twenty-eight of these have been identified as specific management targets by the CERP (Table 1); most are herbaceous and threatened by nutrient enrichment, hydrologic change, fire suppression and introduced species.

Invertebrates. Unlike most of the vertebrates, little is known about the richness of invertebrates in the Everglades. With the exception of a few key species, data related to the ecological relationships and autecology of terrestrial and aquatic invertebrates is scarce. It is fairly well known that aquatic invertebrates play an important role in freshwater food webs. Schomer and Drew (1982) suggested that periphyton communities tended to have high concentrations of invertebrates because of high food availability and dissolved oxygen (DO) concentrations. Yet, Turner et al. (1999) found that standing stocks of invertebrates in the Everglades were among the lowest when compared with values from the literature as averages over large spatial areas and across seasons.

Gunderson and Loftus (1993) suggested that invertebrates have had little, if any, basic systematic inventory in the Everglades, with most information collected for the larger terrestrial and aquatic invertebrates. They further suggested that, generally, the Everglades was depauperate in aquatic invertebrates. Lodge (1994) proposed that the Everglades does not have a great diversity of freshwater invertebrates because of limits on habitat types and possibly historically fluctuating climate. Table 3 lists composition and richness of major aquatic invertebrates native to the Everglades. Of the larger aquatic crustaceans and mollusks, only one species each of crayfish (*Procambarus alleni*), freshwater prawn (*Palaemonetes paludosus*) and amphipod (*Hyalella azteca*) have been found (Gunderson and Loftus, 1993). In their book the *Mayflies of Florida*, Berner and Pescador (1988) show no stoneflies and only two mayflies in the Everglades, compared to 16 species found in South Florida (Table 4). The

Table 3. Composition and richness of invertebrates native to the Everglades*.

Group	Total Species	Species Rich Taxa	Depauperate Taxa
Crustaceans	Unknown	Cladocerans (~37) Copepods (>10)	Crayfishes (1) Prawns (1)
Insects	Unknown	Odonates (~40) Water beetles (~55) Midges (~76)	Mayflies (2)
Snails	Aquatic (21)	Physids (5) Planorbids (7)	Pilids (1) Hydrobiids (2)

* After Gunderson and Loftus (1993)

Table 4. Family, genus and species for 5 insect orders in South Florida (compiled from Lenkzewski, 1980; Opler et al., 1985; Ferguson et al., 1999; Kondratieff, 2000a and 2000b; Hoback et al., 2001)

Order	Family	Genera	Species
Dragonflies and Damselflies	Aeshnidae	7	11
	Calopterygidae	2	3
	Coenagrionidae	7	25
	Corduliidae	3	5
	Gomphidae	6	8
	Lestidae	1	4
	Libellulidae	19	39
Butterflies	Hesperiidae	26	35
	Lycaenidae	8	12
	Nymphalidae	19	27
	Papilionidae	3	7
	Pieridae	8	14
	Riodinidae	1	1
Tiger Beetles	Cicindelae	2	13
Moths	Arctiinae	15	21
	Lithosiinae	7	10
	Notodontidae	14	24
	Pericopinae	1	1
	Saturniidae	9	12
	Sphingidae	29	50
	Syntominae	8	10
Mayflies	Baetidae	5	8
	Caenidae	2	3
	Ephemerellidae	1	1
	Ephemeridae	1	1
	Heptageniidae	1	1
	Leptophlebiidae	1	1
	Metretopodidae	1	1

Florida applesnail (*Pomacea paludosa*) deserves special mention as an important freshwater mollusk in the Everglades due to its predation by a variety of wildlife including young alligators and numerous birds (Kushlan, 1975). The most notable of these birds is the snail kite, which feeds exclusively on the applesnail (Lodge, 1994). It is generally held that the chydorid, cladocerans, odonates, and dipterans are diverse (Gunderson and Loftus, 1993).

Freshwater invertebrates are critical in transfer of energy through the Everglades system. The invertebrate community operates at several trophic levels in the wetlands, some as primary herbivores of plant material and consumers of detritus and others as carnivores. Some species, such as the crayfish and apple snail, are major prey for fishes and other predatory species, including some endangered animals. Factors that influence invertebrate numbers, biomass, and even community composition therefore may have significant effect on energy transfer through the Everglades. Obviously, the ecology and life histories of aquatic invertebrates are affected by the hydrology of the Everglades marsh, which has increasingly been altered and managed by human practices. The distributions and overall abundance of invertebrates appear to be adversely affected by changes in flood releases, diversion of water, and impoundments (Science Subgroup, 1996). Compound these changes by natural disturbances such as hurricanes and droughts, and the net result is dramatically reduced standing stocks of invertebrates, sometimes for years following the events (Science Subgroup, 1996).

Fishes. The Everglades National Park is home to 432 species of fish from 91 families; approximately 260 species are observed frequently. The most diverse families are Cyprinidae (minnows and shiners – 32 species), Centrarchidae (bass/sunfish/crappie – 24), Sciaenidae (drum/kingfish – 18), Percidae (darter/perch – 17), Clupeidae (shad – 16), Cyprinidontidae (topminnows/killifish – 16) and Gobiidae (gobys – 16) (Table 5). A large fraction of the regional fish diversity inhabits the marine and estuarine waters; only 30 species are native to fresh water. Of those, there are several important game species that attract thousands of anglers to the park each year, including tarpon (*Megalops atlantica*), and largemouth bass (*Micropterus salmoides*). The latter is particularly in peril due to bioaccumulation of mercury and crowding out by exotic species. Several smaller fish species are extremely important as food source for wading birds and larger fish. Mosquitofish (*Gambusia holbrooki*) are the most common freshwater fish in the Everglades and are found throughout the park. Several marine species are also important for recreational fishing, including snook (*Centropomus undecimalis*), red drum (*Sciaenops ocellatus*), and spotted seatrout (*Cynoscion nebulosus*)(Schmidt et al., 2002).

Currently, no fish species are listed as threatened or endangered. However, a health advisory is in effect for six species of marine fish found in northern Florida bay, including the spotted seatrout, gafftopsail catfish (*Trachinotus goodei*), crevalle jack (*Caranx hippos*), ladyfish (*Elops saurus*), and bluefish (*Pomatomus saltatrix*), as their average mercury level is in excess of the state limit for human consumption (Schmidt et al., 2002).

Amphibians and reptiles. Among the more emblematic features of the Everglades ecosystem is the presence of the American alligator (*Alligator mississippiensis*). However, the Everglades is home to almost 100 other species of amphibians and reptiles, many of which are threatened by the large-scale changes in ecosystem dynamics and habitat that have occurred with development pressure and water management. The breakdown into groups of species found in Everglades National Park shows 60 reptile taxa, with snakes (both Viperidae and Colubridae), skinks, anoles, geckos, and freshwater turtles the richest families (Table 6). Of the 38 amphibian taxa, the salamander (Plethodontidae) and frog (Hylidae and Ranidae) families are the richest.

The list of threatened and endangered species in this group includes several large species that receive global conservation attention (sea turtles – Hawksbill, Kemp's Ridley, Green, Loggerhead, Leatherback; American alligator; American crocodile – *Crocodylus acutus*), some that receive state-wide attention (gopher tortoise – *Gopherus polyphemus*, Eastern indigo snake – *Drymarchon corais couperi*) and others that are highly specific to the Everglades (Florida snapping turtle – *Chelydra serpentine*, Alligator snapping turtle – *Macroclemys temminckii*, bluetail mole skink – *Eumeces egregius lividus, sand skink – Neoseps reynoldsi) (Table 7)*. Over 30 exotic species have been catalogued in the South Florida ecosystem, and are becoming increasingly significant as agents of ecosystem change.

Birds. The large and heterogeneous area of protected habitat, subtropical climate, and position as a gateway between North and South America contribute to making the Everglades a hotspot for bird biodiversity. The official Everglades National Park (ENP) birdlist records 349 species (Table 2 – after Robertson et al., 1994), though richness across the entire South Florida region is undoubtedly higher (estimated greater than 400 – ENP, n.d.). Many of these birds, including ducks (Anseriforms), rails (Gruiforms), wading birds (Ciconiiformes), skimmers (Charadriiformes), plovers, avocets, oystercatchers, sandpipers, gulls, and terns, depend on wetland areas for their survival (Table 8). The winter season is the period of greatest bird abundance in the Everglades, with 294 winter resident species in the ENP, many of which migrate from the eastern United States and Canada to exploit the concentrated food source that occurs during the dry season. Less than half of the wintering species stay in the Everglades year-round. Others are neotropical migrants that only stop temporarily before crossing over the Gulf of Mexico to other regions in the Caribbean, Central and South America in the fall season, or while returning to North America in the spring.

The Everglades has historically served as a haven for wading birds (Ciconiiformes), with 16 residents found in ENP. While wading birds are abundant in the region today, population numbers were significantly higher 150 years ago. Despite having suffered enormous losses due to plume hunters at the end of the 19th and early part of the 20th century, the abundance of birds was still remarkable and in 1930 the number of wading birds nesting in the Everglades was estimated as 300,000 (McCally, 1999). However, changes in the hydrologic regime stemming from the Central and South Florida Project of 1949, which created compartmentalization of water flows that is presently being restored, have and continue to reduce wading birds populations. By the early 1990s, only 10,000–50,000 wading birds were estimated to nest in the Everglades (Ogden, 1997).

Due to alteration of the water flows and resulting shifts in plant community, two habitat specific residents of the Everglades are now endangered. The endemic Cape Sable seaside sparrow (*Ammodramus maritima*) breeds only in marl prairies covered with select marsh grasses (*Muhlenbergia* spp. or sparse *Cladium jamaicense*) (Nott and Comiskey, n.d.). The snail kite (*Rostrhamus sociabilis plumbeus*), a resident of subtropical

Table 6. Families and species counts for reptiles and amphibians of the Everglades.

Reptile Families	Count	Amphibian Families	Count
Alligatoridae	2	Ambystomatidae	3
Anguidae	3	Amphiumidae	2
Cheloniidae	1	Bufonidae	3
Chelydridae	1	Hylidae	10
Colubridae	17	Leptodactylidae	2
Crocodylidae	1	Microhylidae	1
Emydidae	5	Plethodontidae	8
Gekkonidae	5	Proteidae	1
Iguanidae	2	Ranidae	6
Kinosternidae	1	Salamandridae	1
Phrynosomatidae	2	Sirenidae	1
Polychridae	5		
Rhineuridae	1		
Scincidae	6		
Teiidae	2		
Testudinidae	1		
Trionychidae	1		
Tropiduridae	2		
Viperidae	2		

Table 5. Species (n = 431) in each of 90 fish families in the Everglades. Numbers in parentheses indicate the number of species (n = 256) in each family for which the record in the region is considered reliable.

Family	Species	Family	Species	Family	Species
Cyprinidae	32 (8)	Sparidae	5 (5)	Sphyraenidae	2 (2)
Centrarchidae	24 (3)	Belonidae	4 (1)	Stromateidae	2 (2)
Sciaenidae	18 (18)	Centropomidae	4 (3)	Synodontidae	2 (1)
Percidae	17 (7)	Cichlidae	4 (4)	Albulidae	1 (1)
Clupeidae	16 (4)	Lepisosteidae	4 (1)	Amiidae	1 (0)
Cyprinodontidae	16 (1)	Ophidiidae	4 (3)	Anguillidae	1 (0)
Gobiidae	16 (15)	Scombridae	4 (4)	Antennariidae	1 (1)
Carangidae	14 (13)	Batrachoididae	3 (0)	Aphredoderidae	1 (0)
Syngnathidae	13 (7)	Dasyatidae	3 (2)	Aplocheilidae	1 (1)
Serranidae	12 (9)	Echeneidae	3 (1)	Callionymidae	1 (1)
Bothidae	11 (11)	Eleotridae	3 (1)	Chaetodontidae	1 (1)
Ictaluridae	10 (2)	Labridae	3 (3)	Clariidae	1 (0)
Poeciliidae	9 (1)	Sphyrnidae	3 (2)	Coryphaenidae	1 (1)
Scaridae	9 (9)	Triglidae	3 (3)	Ephippidae	1 (1)
Atherinidae	8 (4)	Acipenseridae	2 (1)	Gobiesocidae	1 (0)
Haemulidae	8 (8)	Apogonidae	2 (2)	Lobotidae	1 (1)
Balistidae	7 (7)	Ariidae	2 (0)	Loricariidae	1 (0)
Catostomidae	7 (1)	Bythitidae	2 (2)	Mobulidae	1 (1)
Blenniidae	6 (6)	Elopidae	2 (0)	Molidae	1 (1)
Carcharhinidae	6 (3)	Esocidae	2 (0)	Polynemidae	1 (1)
Characidae	6 (0)	Lamnidae	2 (2)	Pomatomidae	1 (1)
Engraulidae	6 (1)	Muraenidae	2 (2)	Priacanthidae	1 (1)
Exocoetidae	6 (4)	Myliobatidae	2 (1)	Pristidae	1 (1)
Gerreidae	6 (6)	Ogcocephalidae	2 (1)	Rachycentridae	1 (1)
Lutjanidae	6 (6)	Ostraciidae	2 (2)	Rajidae	1 (1)
Ophichthidae	6 (5)	Percichthyidae	2 (0)	Rhinobatidae	1 (1)
Tetraodontidae	6 (6)	Petromyzontidae	2 (0)	Torpedinidae	1 (1)
Clinidae	5 (5)	Pomacentridae	2 (2)	Trichiuridae	1 (1)
Mugilidae	5 (4)	Rhincodontidae	2 (2)	Umbridae	1 (1)
Soleidae	5 (4)	Scorpaenidae	2 (2)	Xiphiidae	1 (1)

marshes, eats only snails of the genus *Pomacea* (apple-snails) which are themselves restricted to subtropical graminoid marshes (Alsop, 2001). Other endangered bird species include the Florida grasshopper sparrow (*Ammodramus savannarum floridanus*), the Kirtland’s warbler (*Dendroica kirtlandii*), the wood stork (*Mycteria ameri-*

Table 7. Federally Protected Species in the Everglades region (USFWS, 1994).

Common Name	Scientific Name	USFWS Status[1]
Amphibians And Reptiles		
American alligator	*Alligator mississippiensis*	T-S/A
Atlantic loggerhead turtle	*Caretta caretta caretta*	T
Atlantic green turtle	*Chelonia mydas mydas*	E
American crocodile	*Crocodylus acutus*	E
Leatherback turtle	*Dermochelys coriacea*	E
Atlantic hawksbill turtle	*Eretmochelys imbricata imbricata*	E
Gopher tortoise	*Gopherus polyphemus*	C2
Southern hognose snake	*Heterodon simus*	C2
Atlantic ridley turtle	*Lepidochelys kempii*	E
Gulf salt marsh snake	*Nerodia clarkii*	C2
Island glass lizard	*Ophisaurus compressus*	C2
Florida pine snake	*Pituophis melanoleucus mugitus*	C2
Gulf hammock dwarf siren	*Pseudobranchus striatus lustricolus*	C2
Florida crawfish frog	*Rana capito aesopus*	C2
Florida scrub lizard	*Sceloporus woodi*	C2
Miami black-headed snake	*Tantilla oolitica*	C2
Birds		
Cape Sable seaside sparrow	*Ammodramus maritima*	E
Florida grasshopper sparrow	*Ammodramus savannarum floridanus*	E
Florida scrub jay	*Aphelocoma coerulescens coerulescens*	T
Piping plover	*Charadrius melodus*	T
White-crowned pigeon	*Columba leucocephala*	T
Kirtland‘s warbler	*Dendroica kirtlandii*	E
Reddish egret	*Egretta rufescens*	C2
Arctic peregrine falcon	*Falco peregrinus tundrius*	T
Southeastern American kestrel	*Falco sparverius paulus*	C2
Bald eagle	*Haliaeetus leucocephalus*	T
Migrant loggerhead shrike	*Lanius ludovicianus migrans*	C2
Wood stork	*Mycteria americana*	E
Red-cockaded woodpecker	*Picoides borealis*	E
Audubon‘s crested caracara	*Polyborus plancus audubonii*	T
Snail kite	*Rostrhamus sociabilis plumbeus*	E
Roseate tern	*Sterna dougallii*	T
Mammals		
Sherman‘s short-tailed shrew	*Blarina carolinensis (=brevicauda) shermani*	C2
Florida mastiff bat	*Eumops glaucinus floridanus*	C1
Florida panther	*Felis concolor coryi*	E
Round-tailed muskrat	*Neofiber alleni*	C2
Florida mouse	*Peromyscus (= Podomys) floridanus*	C2
Southeastern big-eared bat	*Plecotus rafinesquii*	C2
Englewood mole	*Scalopus aquaticus bassi*	C2
Mangrove fox squirrel	*Sciurus niger avicennia*	C2
West Indian manatee	*Trichechus manatus latirostris*	E
Key Largo woodrat	*Neotoma floridana smalli*	E
Key deer	*Odocoileus virginianus clavium*	E
Silver rice rat	*Oryzomys argentatus*	E
Key Largo cotton mouse	*Peromyscus gossypinus allapaticola*	E
Lower Keys marsh rabbit	*Sylvilagus palustris hefneri*	E
Southeastern beach mouse	*Peromyscus polionotus niveiventris*	E
Florida black bear	*Ursus americanus floridanus*	C2
Invertebrates		
Schaus’ swallowtail butterfly	*Heraclides aristodemus ponceanus*	E
Stock Island tree snail	*Orthalicus reses*	T
Bartram‘s hairstreak butterfly	*Strymon acis bartrami*	C2

1 – E: Endangered; T: Threatened; C1: A candidate for Federal listing, with enough substantial information on biological vulnerability and threats to support proposals for listing; C2: A candidate for listing, with some evidence of vulnerability, but for which not enough data exist to support listing; T-S/A: Threatened due to Similarity of Appearance

cana) and the red-cockaded woodpecker (*Picoides borealis*) (Table 7).

Mammals. Mammalian distributions, evolution, and ecology (like those of the other vertebrates) are influenced by the geographic, geological, and environmental characteristics of South Florida (Robertson and Federick, 1994). Geographic factors affecting mammalian distributions and abundances include: 1) the relative isolation of south Florida from the main North American land mass because of its location at the end of a long peninsula, 2) the fact that it is the only subtropical area on the continent, cut off from direct land contact with other tropical and subtropical areas, and 3) the relative close proximity of the Caribbean Islands just off the coast. Means and Simberloff (1987) have suggested a fourth factor contributing to species numbers; the reduced area of uplands in southern Florida (known as "the Everglades effect"). South Florida's geologically recent emergence from the sea has direct bearing on its present assemblage of land mammals, as do the landscape mosaic of vegetative communities, marked seasonal fluctuations in water levels, and pulsing events like fires and hurricanes. In recent times, human influences, through both direct and indirect resource use, have been a major force affecting the distribution and abundance of many of the mammals of the region. Encroaching urban development, agricultural expansion, drainage, water diversion, and the introduction of pollution and nonnative species have had deleterious effects on many species. In all, thirty-five species of native land mammals have been regularly recorded in south Florida and the Everglades (Layne, 1974; Stevenson, 1976; Brown, 1997); an additional 41 species have either been recorded outside the wetland areas of the Everglades (e.g., seals, whales), have been so infrequently observed to be considered unreliable records (e.g., spotted skunk, river otter), or have been locally extirpated (e.g., bison, wolves). In addition to the native land mammals, about ten introduced species are known to be established and about eight others have been recorded (Layne, 1974). Table 9 lists mammals of Everglades National Park and indicates their status.

In general, raccoons (*Procyon lotor*) and marsh rabbits (*Sylvilagus palustris*) are the most common mammals in the Everglades and rodents the most abundant. The opossum (*Didelphis virginiana*) is the only marsupial in North America and is found throughout the Everglades. White-tailed deer are common throughout the Everglades (Miller, 1993). Lynne (1978) suggested that the Everglades mink (*Mustela vison evergladensis*), while rare, is found in the Everglades region of South Florida. The rarest mammal in the Everglades is the Florida panther (*Felis concolor coryi*), whose preferred habitat may be the drier portions of the western Everglades and Big Cypress (Smith and Bass, 1994), regions also preferred by the bobcat (*Lynx rufus*) (Labisky and Boulay, 1995).

Layne (1974) identified four major patterns of mammal distribution in the mainland of South Florida: cosmopolitan, east coastal, divided, and disjunct. Cosmopolitan species, or those that are widespread throughout

Table 8. Birds of Everglades National Park.

Order	Common Name(s)	Aquatic	Transient	Permanent
Anseriforms	Ducks, Swans, Geese	32	1	5
Apodiformes	Swifts, Hummingbirds	0	1	1
Caprimulgiformes	Nightjars, Poorwills	0	0	2
Charadriiformes	Gulls, Terns, Plovers, Sandpipers	61	7	30
Ciconiiformes	Herons, Ibises, Bitterns	19	1	20
Columbiformes	Doves	6	0	6
Coraciiformes	Kingfishers	1	0	1
Cuculiformes	Cuckoos	0	0	4
Falconiforms	Hawks, Eagles, Kites, Falcons	1	1	6
Galliformes	Turkey, Quail	0	0	2
Gaviiforms	Loons	2	0	0
Gruiformes	Rails, Limpkin, Cranes	12	0	7
Passeriformes	Warblers, Sparrows, Mimics, etc.	14	21	28
Piciformes	Woodpeckers	7	0	5
Pelecaniforms	Pelicans, Boobies, Comorants	8	0	5
Phoenicopteriformes	Flamingos	1	0	1
Podicipediformes	Grebes	3	0	1
Procelliiforms	Shearwaters, Storm-petrels	2	0	0
Psittaciformes	Parrots	0	2	0
Strigiformes	Owls	0	0	4
	TOTAL	169	34	128

List from Robertson et al. (1994). Classification based on Alsop (2001). *Aquatic* species are found predominantly in open water or wetland habitat. *Transient* species are neotropical migrants that occur only in Fall or Spring. *Permanent* species are non-migratory year-round residents.

the landscape, include: opossum (*Didelphis virginiana*), cotton rat (*Sigmodon hispidus*), bobcat (*Lynx rufus*), white-tailed deer (*Odocoileus virginia*), and raccoon *(Procyon lotor*). Species that are confined to the east coast include oldfield mouse (*Peromyscus polionotus*) and Florida mouse (*P. floridanus*). Many of the land mammals are more terrestrial in their affinity for habitat types and thus do not occur in great numbers throughout the wetland portions of the Everglades. A considerable number of species have divided ranges, with populations on the east and west sides of the Everglades in the more terrestrial environments. Examples include short-tailed shrew (*Blarina brevicauda*), eastern cottontail (*Sylvilagus floridanus*), grey squirrel (*Sciurus carolinensis*), southern flying squirrel (*Glaucomys volans*), cotton mouse (*Peromyscus gossypinus*) and marsh rabbit (*Sylvilagus palustris*). The Everglades mink (*Mustela vison evergladensis)* is the only mammal having two well-separated disjunct populations.

There is only limited information on population trends and population ecology of most Everglades mammals. While presently there is little or no empirical data to document population trends of most species of mammals in the Everglades basin, it is widely speculated that several species dependent on freshwater marsh habitats have substantially declined as a result of human induced changes (Science Sub-group, 1996). Two species of principal concern are the round-tailed muskrat (*Neofiber alleni*) and the river otter (*Lutra canadensis*). Two endangered species with habitat within Everglades National Park are the Key Largo wood rat (*Neotoma floridana smalli*) and the Key Largo cotton mouse (*Peromyscus gossypinus allapaticola*). Other more upland species such as the three native squirrels (gray (*Sciurus carolinensis*), fox *(Sciurus niger)*, and southern flying (*Glaucomys volans*)) and the black bear (*Ursus americanus floridanus*) have become greatly reduced in numbers and range as a result of human development activities (Table

Table 9. Mammals of Everglades National Park.*

Species	Status
Opossum (*Didelphis virginiana*)	Locally common
Short-tailed shrew (*Blarina brevicauda*)	Locally common
Least shrew (*Cryptotis parva*)	Locally common
Eastern mole (*Scalopus aquaticus*)	Hypothetical
Seminole bat (*Lasiurus seminolus*)	Hypothetical
Florida yellow bat (*Lasiurus intermedius*)	Hypothetical
Evening bat (*Nycticeius hymeralis*)	Hypothetical
Brazilian free-tailed bat (*Tadarida brasiliensis*)	Hypothetical
Florida mastiff bat (*Eumops glaucinus*)	Hypothetical
Marsh rabbit (*Sylvilagus palustris*)	Common
Eastern cottontail (*Sylvilagus floridanus*)	Rare to common
Gray squirrel (*Sciurus carolinensis*)	Rare to locally common
Fox squirrel (*Sciurus niger*)	Uncommon
Southern flying squirrel (*Glaucomys volans*)	Uncommon
Rice rat (*Oryzomys palustris*)	Common
Cotton mouse (*Peromyscus gossypinus*)	Common
Cotton rat (*Sigmodon hispidus*)	Common
Roundtail muskrat (*Neofiber alleni*)	Locally common
Grey fox (*Urocyon cineroargenteus*)	Rare
Black bear (*Ursus americanus*)	Rare
Raccoon (*Procyon lotor*)	Common
Everglades mink (*Mustela vison*)	Uncommon
Long-tailed weasel (*Mustela frenata*)	Hypothetical.
Eastern spotted skunk (*Spirogale putorius*)	Hypothetical
Striped skunk (*Mephitis mephitis*)	Rare
River otter (*Lutra canadensis*)	Uncommon.
Florida panther (*Felis concolor*)	Endangered subspecies (F.c.coryi).
Bobcat (*Lynx rufus*)	Common
White-tailed deer (*Odocoileus virginianus*)	Common
Nine-banded armadillo (*Dasypus novemcinctus Linnaeus*)	Introduced. Somewhat common
Roof rat (*Rattus rattus*)	Introduced. Uncommon
House mouse (*Mus musculus*)	Introduced. Common
Norway rat (*Rattus norvegicus*)	Introduced. Hypothetical.
Red fox (*Vulpes vulpes*)	Introduced. Rare
Coati (*Nasua narica*)	Introduced. Rare.
Domestic dog (*Canis familiaris*)	Introduced. Rare
Domestic cat (*Felis domesticus*)	Introduced. Rare
Domestic pig (*Sus scrofa*)	Introduced. Rare

* after Florida National Parks & Monuments Association (n.d.)

7). The ecological consequences of increasing population of introduced feral cats, dogs, and pigs, while of minor consequence on mammal populations, may have significant consequences to other wildlife populations.

Introduced species. The South Florida ecosystem, and the Florida Everglades in particular, is a regional hot-spot for invasive exotic taxa. The orientation and length of the Florida peninsula result in many of the species native to the South Florida region being at the southward extent of their habitat range. An estimated 221 species of introduced plants have growing or naturalized populations in the region, perhaps as a result of this geographic condition coupled with the substantial changes in regional hydrology and the large human population. Listed in Table 10 are some of the more significant adventive plant taxa. Among the most expensive, both with respect to ecological and financial costs, are melaleuca (*Melaleuca quinquenervia*) and Brazilian pepper (*Schinus terebinthifolius*); both are increasing coverage, particularly in disturbed areas of the South Florida ecosystem.

A number of non-native mammal species have been accidentally or intentionally introduced in South Florida. Layne (1974) listed the following species as known or suspected to have become established in south Florida: Nine-banded armadillo (*Dasypus novemcinctus Linnaeus*), red-bellied squirrel, (*Sciurus aureogaster*) black rat (*Rattus rattus*), coyote (*Canis latrans*), red fox *(Vulpes vulpes*), and jaguarundi (*Herpailurus yaguarondi*). In addition, along the fringes of the Everglades, the feral dogs *(Canis familiaris)* and cats *(Felis domesticus)* are somewhat common.

Exotic fishes, of which there are 32 established species and 43 additional observed species in the State of Florida (found at http://myfwc.com/Fishing/Fishes/Exotic%20List.html on Mar. 7, 2005; P. Shafland), include the walking catfish (*Clarias batrachus*), blue and spotted tilapia (*Oreochromis aurea* and *Tilapia mariae*), oscar *(Astronotus ocellatus)*, and Mayan cichlid *(Cichlasoma urophthalmus).* These species pose a threat to native fish populations through predation and competition for nesting sites (McCann et al., 1996). Similarly, the introduced house finch (*Carpodacus mexicanus*), house sparrow (*Passer domesticus*), European starling (*Sturnus vulgaris*), monk parakeet (*Myiopsitta monachus*), iguana (*Iguana iguana*), Cuban tree frog (*Osteopilus septentrionalis*) and wild hog (*Sus scrofa*) are causing both physical damage and community shifts in the native ecosystems. Other organisms whose impact is less well documented include Burmese pythons (*Python molurus bivittatus)*, vervet monkeys (*Cercopithecus aethiops*), and boa constrictors (*Constrictor constrictor*).

Table 10. Most Dominant Invasive Plants (Thayer et al., 2000).

Scientific Name	Common Name
Melaleuca quinquenervia	Melaleuca tree
Lygodium microphyllum	Old World climbing fern
Schinus terebinthifolius	Brazilian pepper
Casuarina equisetifolia	Australian pine
Colubrina asiatica	Latherleaf, Asian snakeroot
Eichhornia crassipes	Water hyacinth

A systems approach to calculating biodiversity

Richness and diversity. Assessments of biodiversity at the ecosystem scale typically rely on counts of species in different classes (e.g., avian richness or herbivore richness). Our introduction to the diversity of the Everglades illustrates the critical need for conservation, but raises several conceptual and practical problems related to describing and comparing ecosystems and setting conservation priorities. First, biodiversity databases assembled from a variety of sources can be misleading when different areas have been sampled with different sampling intensities, which leads to inherent collection bias, or observations reported with different confidence (Peet, 1974; Fagan and Kareiva, 1997). Further, while some correlation can be found between plant species richness and animal species richness, areas rich in plant species diversity do not always coincide with richness at other trophic levels (Mares, 1992). Consequently, biodiversity hotspots identified based on richness at one trophic level alone may miss areas of major conservation importance (Mares, 1992; Harcourt, 2000; Kareiva and Marvier, 2003). Finally, when designing conservation strategies using diversity as the indicator of ecosystem service, there is ambiguity in the definition of diversity (e.g., cladistics, species, genetic), which can lead to confounded conservation priorities (Angermeier and Karr, 2004).

In addition, the effort to equate the number of different actors in an ecosystem with the functional value of that ecosystem is a perilous one: empirical studies have uncovered limited evidence to support this hypothesis (although see Tilman and Downing, 1994), and modeling studies suggest that ecosystem function can be maintained with only a fraction of the species varieties (Grime, 1997; Schwartz et al., 2000). Smith et al. (1993) suggest that conservation programs designed according to species richness, and not evolutionary processes, will fail to protect the most critical habitat with respect to genetic information. Further, and possible most important, simple counts of organism variety in a region fundamentally fail to capture the networks of ecological interactions and feedbacks that produce ecosystem properties (e.g., productivity, stability) (Ulanowicz, 2001; Worm and Duffy, 2003), which are frequently cited as one motivation for biodiversity conservation. Angermeier and Karr (1994) discuss problems with associating ecological diversity with ecological integrity, arguing that the latter is the goal for which the former is a poor indicator.

To address the information limitations of species richness as an ecosystem indicator, ecologists frequently turn to diversity indices, derived originally from information theory. Such indices, well known in the ecological literature, are adaptations of information theory used to describe the organization of ecosystems which began with MacArthur (1955), who used the Shannon diversity formulation (Eq. 1) to compare flows within an ecosystem. The use of physical stocks (biomass, abundance, cover, frequency) of system actors as a metric of ecosystem condition began with Margalef (1961), and is now a standard component of ecological theory and practice (Peet, 1974; Krebs, 2000). The typical formulation is:

$$H = -\sum_{i=1}^{j} p_i * \log[p_i] \tag{1}$$

where H is the diversity, p_i is the probability of observing component i in a system of j components. Observation probabilities (p_i) are typically measures of relative physical stocks for each ecosystem component. Ulanowicz (2001) suggests that the application of information theory to ecosystems using Eq. 1 with physical stocks has met with mixed success; no consistent association between Shannon diversity and ecosystem function or stability has been demonstrated. As a result, some ecologists have tended to disregard the tools of information theory for the description of ecosystems (Ulanowicz, 2001).

There are two limitations of conventional application of the Shannon diversity index that lead to its failure to effectively predict ecological properties (condition, stability, resilience, productivity). The first is that the original conceptualization of Shannon diversity was directed at the determinacy of flows within a system (MacArthur, 1955), theorizing that the flows of energy and materials between components was indicative of information transfer between components. Yet, subsequent applications of Shannon diversity replaced flows with physical stocks. The reasons and drawbacks for this convenient but unfortunate tangent are discussed in detail in Ulanowicz (2001).

A second limitation of the standard Shannon diversity metric is that it ignores ecosystem food web hierarchy. Given a fixed number of ecosystem components, the Shannon equation (Eq. 1) is maximized (H_{max}) when the probability of observing each component (p_i) is equal; that is, evenness in physical stocks increases diversity. However, given typical trophic transfer efficiencies (i.e., Lindeman efficiencies), and even differences in efficiency between organisms within the same trophic level, this benchmark of maximum ecosystem condition at maximum evenness in ecosystem physical stocks is erroneous. The result is that Shannon diversity using physical stocks is appropriate only within a single trophic level and cannot be used at the ecosystem scale or even within groups (e.g., avifauna) populating multiple trophic levels. While we advocate the replacement of stocks with flows as per Macarthur's (1955) original intent, a similar argument for computing diversity using physical flows (energy, carbon) can be made. That is, evenness of physical flows is not the expected condition for an entire food web because the energy/carbon throughput decreases geometrically with increasing trophic level.

To address these two limitations, we propose that a diversity index is necessary that: 1) accounts for the expected hierarchical distribution in the magnitudes of physical stocks across trophic levels and 2) accommodates the observed hierarchical distribution of flows in ecosystem food web networks. In the following sections we use energy systems theory (Odum, 1994) to develop modifications of the Shannon diversity index that incorporate "quality adjusted flows" (defined below) to compute an ecosystem scale diversity index for the Everglades.

An ecosystem application – the Florida Everglades. The Florida Everglades has been the focus of detailed ecological enumeration for many years, and data compiled for the Across Trophic Level Systems Simulation (ATLSS – DeAngelis et al., 1998) and matrix synthesis provided by Ulanowicz et al. (2000 and 1997; http://cbl.umces.edu/%7eatlss/ATLSS.html) represent perhaps the most disaggregated and complete ecological network data available. Using carbon as the network numeraire, bilateral interactions between system components (i.e., species, groups of species or abiotic compartments) have been described using published data and field measurements organized into material flow input/output matrices. Bilateral interactions are defined as the allocation of available energy between biotic and abiotic compartments; cybernetic feedbacks are excluded from this definition, a point we return to later. While flow matrices have been compiled for four ecosystem types in the Everglades, graminoid marsh, cypress swamp, mangrove swamp, and Florida Bay, we focus on the graminoid marsh in this study, employing the data presented in Heymans et al. (2002) and Ulanowicz et al. (2000), and integrating emergy theory (Odum, 1996) with flow matrices to develop an ecosystem-scale measure of biodiversity.

Emergy synthesis and ecosystem networks. Network analysis, where a standard physical quantity (e.g., carbon, available energy) is used to describe bilateral interactions, implicitly assumes that the energy in all those interactions is directly comparable. Emergy theory (Odum, 1994; Odum, 1996) suggests that this assumption is an ecological oversimplification; different forms of energy have different qualities that reflect their differential abilities to perform work within an ecosystem. For example, insolation and carnivore metabolism may be reported in similar units (Joules per time), but have dramatically different properties and potentials within an ecosystem. Odum (1996) concludes that energy alone is an insufficient numeraire for describing the flows in self-organizing complex systems.

Emergy, formally defined as the energy of one form (usually solar energy) required through all processes and transformations to make a product or flow, provides a numeric framework for comparison of species contributions to ecosystem organization in directly comparable units (solar emjoules, or sej). Emergy is often referred to as energy memory, reflecting that this system synthesis approach is effectively a form of accounting that traces energy flow and dissipation back through all necessary transformations to scale all flows relative to a common energy benchmark (solar equivalent energy). Emergy synthesis allows comparison of energy flows of different form; Odum (1996) argues that different forms of energy have different qualities that arise from the energy required to make them. In a self-organizing adaptive system, he argues, forms of energy that require larger investment per unit available energy (i.e., exergy) must provide commensurate higher quality cybernetic work in the form of feedback control. Transformity is an index of quality and quantifies the emergy invested per unit available energy produced (i.e., emergy per exergy, sej/J) for each flow in a system of interest. Direct comparison of energy flows, both within and across the system boundary, is misleading until physical flows have been adjusted by their transformity values that reflect the work necessary for their production.

In the context of evaluating ecosystem biodiversity, the emergy framework suggests that evaluating species importance based on biomass or available energy throughput alone, without adjusting for transformity, will tend to dramatically underestimate the system-scale control potential of energy flows in upper trophic levels, where only a small fraction of total system physical throughput is incorporated. That is, the importance of upper trophic levels with respect to carbon or energy throughput is small compared with their actual role in ecosystem function, which includes cybernetic control (e.g., control of population at lower trophic levels, seed dispersal, commensal relationships, ecosystem structural attributes). For example, Terborgh et al. (2001) show dramatic changes in vegetative community composition in the absence of predators, suggesting top-down ecosystem control. Pandolfi et al. (2003) similarly illustrate the influence of removing upper trophic level consumers in coral reef degradation. Odum (1996) argues that methods for energy flow analysis should incorporate the relative energetic contributions (i.e., importance value) of each component by adjusting for transformity (quality) to avoid misrepresenting their influence.

Biodiversity index at the ecosystem scale. The Shannon diversity index (Eq. 1) disaggregates diversity into two components: 1) richness or variety and 2) evenness or dominance. That is, more taxa variety or more evenness among the taxa present will increase H (the index quantity); the maximum value of H (H_{max}) is observed when observation probabilities (p_i) are equal across all taxa. When p_i are defined based on physical stocks, the implicit assumption is that a basis for ecosystem condition can be inferred from the deviation a system displays from maximum evenness of all compartments. Since the intent of p_i for ecosystem evaluation is to capture the importance of each component within the ecosystem (not within a single trophic level), physical stocks are a poor surrogate for the functional role any actor plays. In particular, the expectation of evenness in physical stocks or flows is inappropriate when comparing across trophic levels; the sequential reduction in energy (or biomass, cover, abundance) through repeated transformations (Fig. 4) serve to make higher trophic level importance values increasingly small relative to lower trophic levels. The association between richness (component 1) and trophic level is complex (e.g., typically, richness of insects > plants > mammals; this does not hold for the Everglades graminoid marshes that are strongly monotypic in their plant community), but the effect of trophic dynamics on dominance (component 2), when measured using either physical stocks or flows, is dramatic.

To compensate for this problem, we depart from the standard Shannon diversity implementation in two ways. First, by applying the index to network flows rather than standing stocks, we follow the original intent of the information theoretic approach in ecology (MacArthur, 1955). Since only flows can actually transmit information within an ecosystem setting, their determinacy is of considerably more ecological interest than the distributions of biomass compartments (Ulanowicz, 2001). A second departure, following Odum (1996), is that the Shannon diversity should be computed based on flows that have been scaled by appropriate scaling values (transformities) to adjust for the expected decline in physical stock dominance with sequential energy transformation (Fig. 4).

A transformity-adjusted index of compartment importance offers informative characteristics with respect to the balance of emergy flows throughout a system only when provided in contrast to some theoretical benchmark. The Shannon diversity computation in ecology is benchmarked against the maximum possible value given the number of species observed, a condition obtained when compartments are equally important. When evaluated with respect to the emergy throughput for each component, this corresponds with the condition postulated to exist in adaptive systems that maximize power during ecological succession (Odum, 1996). The maximum power principle (Odum and Pinkerton, 1955; Odum,

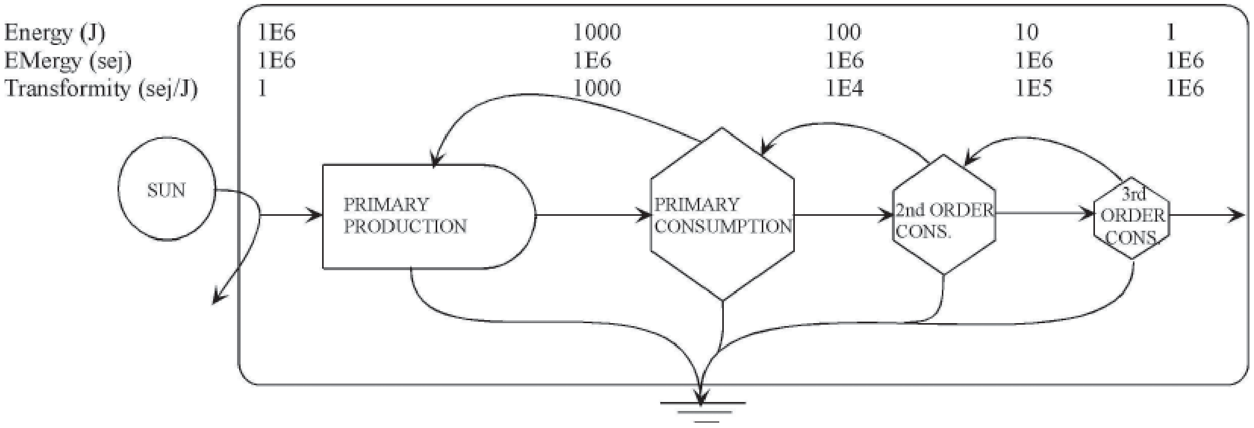

Figure 4. Energy, emergy and transformity in a typical food chain. The maximum empower principle predicts that feedback controls from a component (inferred from transformity) are commensurate with the emergy invested in supporting that component. If emergy flows on each pathway are equal, quality-adjusted diversity is maximized.

1994; and restated as the maximum empower principle in Odum, 1996) postulates that network systems will develop component interconnections that make maximum use of available energy gradients, adjusted to reflect their energy quality. In adaptive systems, this means that higher energy quality translates into increased feedback control potential because systems maximizing emergy throughput will select those components whose service to whole-system function are commensurate with what was required to make them, while selective pressure will tend to remove those components that fail to provide such service. The expected result is that adaptive systems will exhibit approximately equal emergy flows on all pathways. The standard Shannon diversity benchmark (H_{max}) becomes more meaningful as a basis for evaluating system condition (with degradation indicated by deviation from the maximum) when applied across trophic levels in light of this expected emergy flow equality.

On a component-wise basis, this also allows comparison between observed emergy flows and those expected at the theoretical optima. Those compartments that are more or less important than expected given the benchmark of emergy flow evenness can be identified, and systematic trends in importance can be examined. We view deviation from emergy flow expectation to be a measure of conservation value; that is, species processing less emergy than expected are those which may warrant conservation attention, and, further, that the magnitude of the deviation prioritizes that attention. While it is clear that, even in healthy ecosystems, some organisms will be more and other less abundant than expected, we hypothesize that healthy ecosystems will show no systematic trend of deviation from expectation with trophic level.

Our specific objectives in this paper are to compute transformity values from complex network data in order to assign component importance adjusted for energy quality, develop an index of biodiversity at the system-scale that accounts for energy quality, and develop an index that allows inference of each components deviation from expected ecosystem importance.

Materials and methods

Network data

Network data, consisting of carbon flows (g C/yr) were compiled from published data for both wet and dry season conditions for the Everglades graminoid marsh system (details for accounting, aggregation and assumptions in Ulanowicz et al., 1997; Ulanowicz et. al, 2000). There were 66 ecosystem compartments in the graminoid marsh. Not all of these compartments are living; ecosystem pools include labile and refractory detritus. Further, the primary production pools were partitioned into root, and leaf compartments. Many of the lower trophic level compartments represent aggregations of species (due to lack of data); for example, mesoinvertebrates, macroinvertebrates, centrarchid fish, snakes and passerine birds are lumped categories for the marsh system.

The original data were presented in a "To… From" matrix of carbon exchanges from one component (i.e., species or group of species where aggregations were necessary) of the network to another, where each cell in the matrix represents a material transfer. An energy systems depiction (Fig. 5a) of a generic energy/material network containing biotic and abiotic components includes organisms feeding at multiple trophic levels and on both photosynthetic and detrital food chains. Cybernetic feedbacks are not included in the matrix data, and are omitted from this figure. For each component in Fig. 5a, five flows describe bilateral interactions (e.g., consumption, gross production, net production/transfer, respiration and

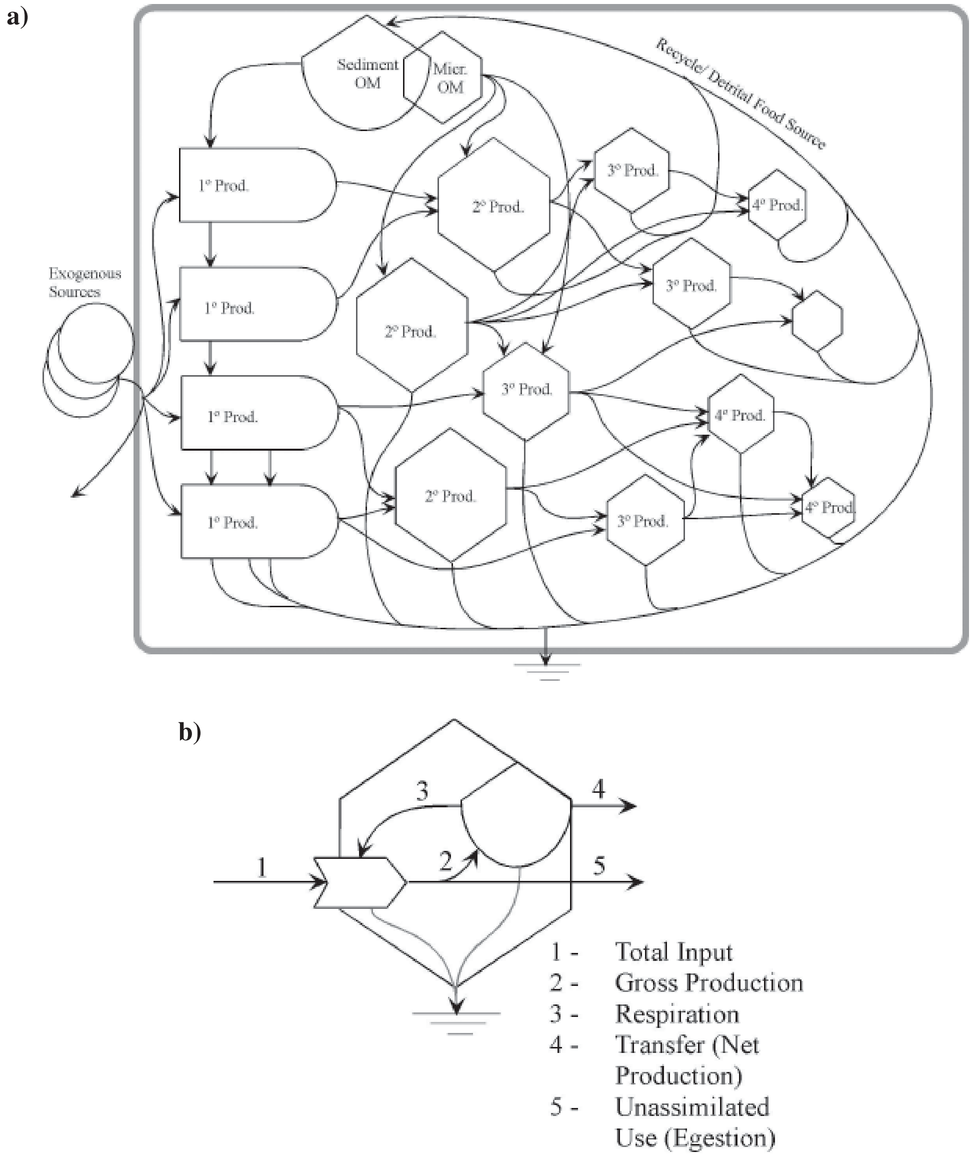

Figure 5. a) Energy systems diagram of a generic ecosystem. b) Diagram of bilateral and internal energy pathways compiled for each compartment within the input-output matrix.

egestion) with other components in the system (Fig. 5b). Energy or material inputs (1) arrive from exogenous sources (e.g. sunlight, rainfall and wind driving photosynthetic production) or from components within the network (e.g., plant biomass supporting production of white-tailed deer, apple snails and marsh rabbits). Gross production (2) quantifies the portion of that energy that is assimilated, while the complimentary fraction (egestion – 5), though required for production and partially processed during digestion, is not incorporated. Respiration (3) represents the metabolic work of each compartment (i.e., internal feedbacks to secure energy), while Transfer (Net Production – 4) is the energy that is eventually used by other components in the food web. Note that matrices of bilateral interactions such as those used herein assume a steady-state condition – seasonal effects are presented by developing steady-state matrices for wet and dry season biomass and energy flow. The "heat sink" symbol (Fig. 5) represents energy unavailable to do work (i.e., entropy).

Our analysis required network matrices with the following attributes (see Odum and Collins, 2003). First, flows should be reported in energy units (e.g., Joules), with flows in each cell directed from column component to row component. Second, along the main diagonal, net production (total transfer to all other components), should be reported as a negative number; other entries represent bilateral interactions between specific components. The original material flow matrices (Ulanowicz et al., 2000; Ulanowicz et al., 1997) were processed to achieve these requirements as follows:

1) Flows, initially reported in g C/m^2/yr were converted to J/m^2/yr assuming an energy content of 18.8 J/g C (organic).
2) The matrices were transposed (inputs, or energy flows, to each component along rows, allocation of net production, or transfer, from each component along columns)
3) Component steady state net production values (Flow 4 in Fig. 5b) were assigned to the main diagonal as negative numbers. This precluded any component (e.g. alligators) securing any portion of its diet from other individuals of the same component.
4) Emergy flows were added as inputs. Exogenous emergy flows were split between primary producers based on steady-state standing stocks (g/m2) of photosynthetically active material (i.e. leaves, but not wood and roots). These emergy inputs were inferred from Brown and Bardi (2001), and were 5.2×10^{11} and 1.3×10^{11} sej/m^2/yr for the wet and dry seasons for the graminoid marsh.
5) Flows of egested material were introduced in the matrix (they were omitted from the original matrices because that carbon was unassimilated; it is, however, a necessary component of each compartment's production). To do this, each bilateral flow was multiplied by 2.5; it was assumed that an organism's assimilation efficiency (gross production/total input) was constant across its sources of food. The sensitivity of the method to this assumption was not tested within the scope of this work.

Transformity calculations

To compute transformities from these network flow data, we used a linear optimization technique that manipulates a set of unknowns (transformity values) to meet a set of constraints (emergy inflow = emergy outflow). This particular set of constraints makes the tacit assumption that there are no co-production modules in the ecosystem; the method can be extended to allow co-production, but this was unnecessary for the current data set.

An example optimization table is given in Figure 6. Each row in Figure 6 represents a system component. The constraints to the right of each row follow from the equality of emergy inflow and emergy outflow. Specifically, the energy inputs multiplied by appropriate transformity values (unknowns in this case) equal the net production or transfer of energy multiplied by its transformity:

$$Emergy\ Inflow_j = \sum_i X_{ij} * \tau_i = \sum_i X_{ji} * \tau_j = Emergy\ Outflow_j \quad (2)$$

where X_{ij} is the energy transfer from component i to component j, and τ_i is the transformity value of respective flows.

To avoid artificial overestimation of the transformity of fecal/senescent biomass contributions to detritus from high-quality components, we applied the following rules:

1) The transformity (sej/J) of a compartment is the emergy (sej) from incoming flows driving biotic production (Flow 1, Fig. 5b) divided by the energy (J) remaining for trophic transfer (Flow 4 in Fig. 5b).
2) Where flows converge to abiotic components (e.g. detrital pools), the transformity of the incoming flow is adjusted to the level of the detrital pool storage.

A simple linear optimization method (Bardi et al., 2005) was applied to the processed matrix to estimate unknown transformities (sej/J) for each component. Hillier and Lieberman (1990) discuss the potential for "guess-and-check" methods to locate non-global solutions; because input/output matrices used herein are square (# rows = # columns) and no linearity assumptions are violated, this was considered impossible. The identification of feasible solutions for the large number of constraints for all analyses required slight relaxation of the default precision for the Microsoft Excel Solver (Bardi et al., 2005).

We compared transformity values across season (wet and dry) and examined the stability of computed transformities by statistically comparing an estimated regression slope to unity using standard inferential techniques.

System-level diversity index

Quality-adjusted Shannon diversity is computed using Eq. 1 in the typical manner in ecology, except relative importance value (p_i in Eq. 1) is defined as the proportion of total system emergy flow (sej/yr) allocated to each component. We refer to relative value calculated in this manner as the Emergy Importance Value (EIV) and compute it as follows:

$$EIV_i = \frac{NP_i * \tau_i}{\sum_j NP_j * \tau_j} \quad (3)$$

where NP_j is the net production (J/yr) and τ_j (sej/J) is the computed transformity of component i. In this formulation, importance value is the relative contribution of each component to the total emergy flow through all biotic components (i.e., denominator of Eq. 3), computed by summing net production times derived transformity over all components.

Transformities			Tr1	Tr2	…	Trn	
To ⇓	From ⇒	Solar Emergy	Comp. 1	Comp. 2	…	Comp. n	Constraints
Comp. 1			- P_1				Σ_{Comp1} (Flows$_i$*Tr$_i$) = 0
Comp. 2			C_1 -to- C_2	- P_2		C_n -to- C_2	Σ_{Comp2} (Flows$_i$*Tr$_i$) = 0
…					..		…
Comp. n			C_1 -to- C_n	C_2 -to- C_n		- P_n	Σ_{Comp3} (Flows$_i$*Tr$_i$) = 0

P_i values are total component production minus respiration

Ci -to- Cj values are energy transfers from comp. i to comp. j

Objective	Σ Contraints = 0

Figure 6. Schematic of input/output matrix form. Transformity values (top row) represent unknowns in the simultaneous equations defined by the constraints. For fully specified systems (i.e. # equations = # unknown transformities) the objective function is redundant.

It follows that an ecosystem Shannon diversity index (following Eq. 1) is:

$$Biodiversity = -\sum_{i=1}^{j} EIV_i * \log[EIV_i] \qquad (4)$$

The maximum possible value for this index occurs when the emergy on each pathway, and therefore each component's EIV, is equal.

A deviation from H_{max} for the conventional application of the Shannon index indicates some degree of dominance structure in the community. When physical flows are adjusted for quality, flow evenness across all ecosystem components is expected; indeed, it is the postulated goal condition for network systems that are maximizing power (Odum, 1994). Across all components in a healthy ecosystem, therefore, we expect to see no association between emergy throughput and trophic level. We therefore use the fractional diversity index (observed diversity: maximum diversity) as a measure of an ecosystems condition. It is also informative to see which particular components deviate from the expected importance. To measure this deviation from expectation, we compute a ratio between expected and observed emergy throughput (EOET) for each component:

$$EOET_i = \frac{TET / N}{NP_i * \tau_i} \qquad (5)$$

where TET is total emergy throughput in the entire system, N is the number of biotic compartments and NP and τ are as in Eq. 3. The resulting values are natural log transformed to linearize the response; consequently, values larger than 0 indicate a component less important than the expected value of 1 (i.e., equal emergy flows on all network pathways). EOET values were compared qualitatively with normative judgments of species importance (e.g., conservation value), and systematic variability in EOET values (e.g., association with transformity or trophic level) was examined using regression analysis.

Results

Transformity values for the graminoid a system are given in Table 11. These values represent an average between wet and dry seasons. While there was a strong correlation between seasons (r = 0.81) (Fig. 7), higher transformities were observed in the wet season coincident with greatly increased emergy input without commensurate response in biomass production (5.2×10^{11} and 1.3×10^{11} sej/m^2/yr for wet and dry, respectively; contrasted with primary production of 6.27×10^3 g C/m^2/yr in the wet season vs. 3.47×10^3 g C/m^2/yr in the dry season).

Table 12 summarizes quality-adjusted diversity, the theoretical maximum diversity and the relative diversity as a percent of maximum for the graminoid marsh. We observe that the marsh ecosystem is operating at 42 % of its maximum potential diversity.

Figure 8 shows that as component transformities increase, the Expected-to-Observed Emergy Throughput of a component becomes increasingly small relative to the expected value, thus yielding a higher EOET ratio; the

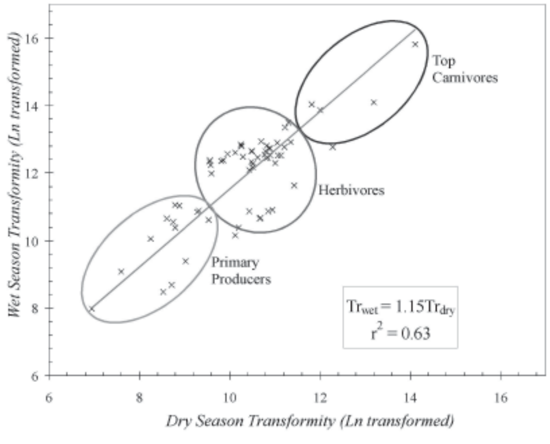

Figure 7. Seasonal association of computed component transformity values. Transformity values are consistently higher in the wet season (Pr [slope = 1.0] < 0.001), during which emergy inflows are substantially increased.

association is strongly statistically significant (p<0.001). Those organisms that exhibit lower than expected emergy throughput coincide substantially with normative judgments of rarity and high conservation value (Bobcats, Florida panthers, Kites and Hawks, Minks, Black Bears all have high EOET values; conversely, Vultures, Detritus, Invertebrates, Ibis and Periphyton are more important than expected with low EOET values).

Discussion

Biodiversity assessments at the ecosystem scale have traditionally taken the form of species catalogs, sorted by different classes, but without addressing important trophic interactions that actually stimulate the emergence of ecosystem properties. This study presents a new way to calculate across trophic level ecosystem diversity that takes into account trophic interactions and derives energy quality adjusted importance values of each species or component. In so doing, we hope to bridge the gap between biological diversity assessments and the ultimate objective of assessing ecological function (Angermeier and Karr, 1994).

Table 12. System scale indices of biodiversity for the Everglades graminoid marsh. Indices are computed in this study; exogenous emergy inputs are from Brown and Bardi (2001).

Quality Adjusted Diversity (bits)	1.73
Theoretical Maximum Diversity (bits)	4.14
Relative Diversity (%)	42%
Exogenous Emergy Inputs (sej/ha/yr)	5.2E11 (wet), 1.3E11 (dry)

The method described cannot be applied in a large number of cases; in fact, the required level of compartment specificity and flow detail is somewhat unprecedented in ecosystem studies. However, the original effort to link information theory (MacArthur, 1955) with ecosystem phenomenology requires this level of detail. Our approach follows that original effort by both making use of flows, not stocks, and extends it by recognizing the need to adjust flows by their energy quality to better reflect their cybernetic role in ecosystem function.

Transformity offers a useful indicator of this cybernetic role within an ecosystem. However, the accuracy of our computation is dependent on the validity of the source data. One area that poses potential theoretical problems is the dramatically different transformities observed within a given system between seasons. Specifi-

Table 11. Computed transformity values for graminoid marsh matrix in rank order by transformity.

Ecosystem Component	Transformity (sej/J)	Ecosystem Component	Transformity (sej/J)
Periphyton	3.56E+03	Small frogs	1.07E+05
Labile Detritus	6.43E+03	Muskrats	1.08E+05
Flagfish	1.24E+04	Medium frogs	1.09E+05
Floating Vegetation	1.25E+04	White Tailed Deer	1.10E+05
Utricularia spp.	1.51E+04	Salamander larvae	1.11E+05
Living Sediments	1.59E+04	Catfish	1.18E+05
Other Macroinvertabrates	1.91E+04	Gruiformes	1.28E+05
Apple snail	1.97E+04	Large frogs	1.30E+05
Mesoinverts	2.02E+04	Alligators	1.34E+05
Macrophytes	2.08E+04	Spotted sunfish	1.36E+05
Poecilids	2.23E+04	Cichlids	1.36E+05
Lizards	2.67E+04	Warmouth	1.38E+05
Tadpoles	2.91E+04	Rabbits	1.41E+05
Crayfish	3.04E+04	Other Large Fishes	1.45E+05
Freshwater Prawn	3.87E+04	Turtles	1.51E+05
Bluefin killifish	4.14E+04	Largemouth Bass	1.52E+05
Chubsuckers	4.26E+04	Snailkites	1.62E+05
Mosquitofishes	4.35E+04	Raccoons	1.63E+05
Other Small Fishes	4.37E+04	Grebes	1.76E+05
Shiners & Minnows	5.35E+04	Salamanders	1.79E+05
Killifishes	5.68E+04	Cape Sable Seaside Sparrow	1.85E+05
Large Aquatic Insects	6.37E+04	Fishing spider	1.99E+05
Terrestrial Inverts	6.74E+04	Passerines	2.13E+05
Topminnows	7.51E+04	Gar	2.17E+05
Bluespotted Sunfish	8.38E+04	Rats&Mice	2.28E+05
Pigmy Sunfish	8.42E+04	Bitterns	2.40E+05
Opossum	8.63E+04	Otter	4.00E+05
Dollar Sunfish	8.71E+04	Mink	4.38E+05
Redear Sunfish	8.83E+04	Nighthawks	5.39E+05
Snakes	9.62E+04	Panthers	1.35E+06
Ducks	1.01E+05	Bobcat	3.30E+06
Other Centrarchids	1.03E+05		

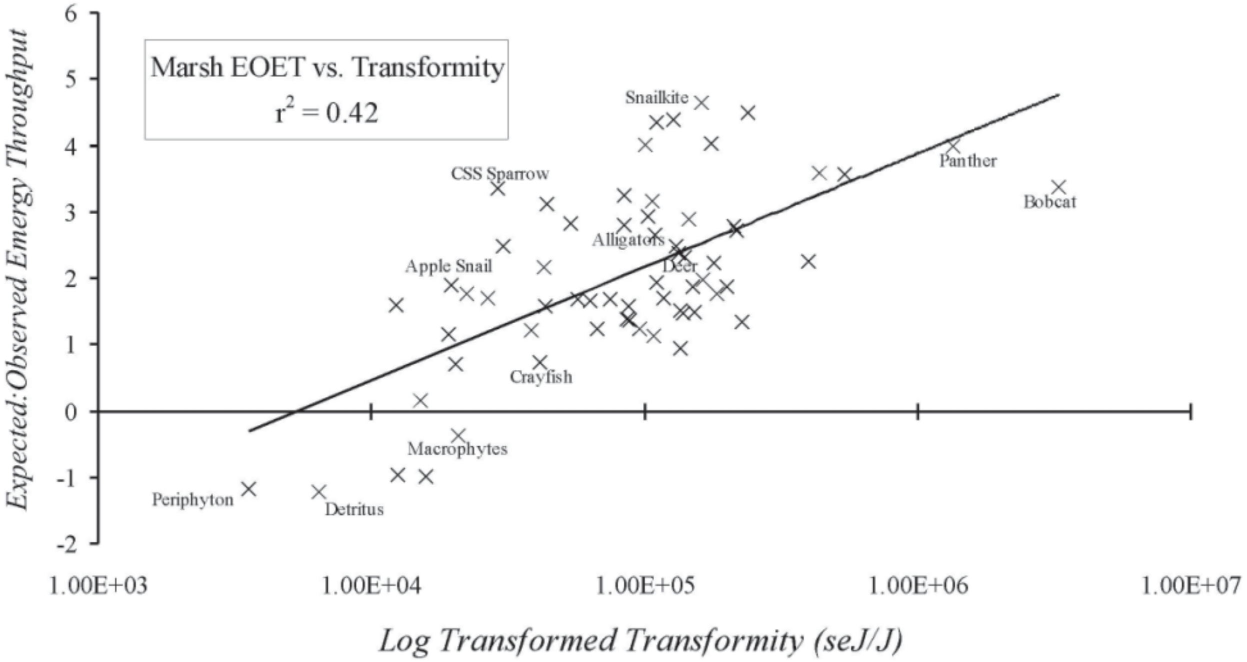

Figure 8. Expected-to-Observed Emergy Throughput (EOET) vs. Transformity for the graminoid marsh.

cally, the nearly order of magnitude difference between wet and dry season transformities – with dry seasons exhibiting significantly lower transformity values – indicates dramatic differences in resource consumption rates and process efficiencies that may be artifacts of the data used. While there is considerable uncertainty in the specific values computed for each component, we note that the transformity values obtained are in strong agreement with similar calculations made using other techniques (Odum, 1996).

While network analyses (Ulanowicz, 1986; Dame and Patten, 1981) and emergy refinements proposed herein offer little insight into the particular cybernetic controls provided by each species in the system, transformity has been proposed as an informative measure of the expected importance of each component (Odum, 1996). Ulanowicz (1980), in developing the ecosystem concept of ascendency, recognized the need to scale flow diversity at the system scale by total system throughput to adequately compare between systems. We propose that system-scale flow diversity further requires adjustment for energy quality (transformity) before meaningful cross-trophic comparisons of importance and between-system comparisons of development or stress can be achieved. As such, we propose an emergy-based ascendency framework as an avenue of further research (see Christensen, 1994, for a preliminary effort).

Deviance from the Shannon index maximum, as applied herein, may be a useful indicator of system condition. This may be true at the ecosystem scale and at the scale of particular ecosystem component. Our effort to identify specific organisms that exhibit deviation from expected importance (EOET, measured as a fraction of expected productivity adjusted for quality) showed increases in EOET with transformity. This observation suggests that the ecosystem is systematically depauperate in the upper trophic levels, a conclusion consistent with the documented losses in wading bird populations, alligators and top carnivores. Notably, those species with high normative value in society (i.e., those for which wildlife management plans and on which considerable public scrutiny are focused) are generally those with high EOET values, indicating their rarity relative to expected emergy flow contributions. For purposes of evaluating ecosystem condition, we would expect that during recovery the trend of EOET with transformity would tend towards no association ($r^2 \sim 0$). However, were the ecosystem to continue to degrade, we would expect an increasingly significant positive association between EOET and transformity as lower quality ecosystem components are selected for, and ecosystem hierarchy and organization diminish.

While we would not postulate that all components of an ecosystem would be present in equal importance (and therefore there might be significant variability in EOET even in healthy ecosystems), we do expect that intact ecosystems would demonstrate approximately equal emergy at all trophic levels, and consequently no systematic association between EOET and transformity. If this were not the case, net production at one trophic level would be failing to generate production at the next trophic level.

The overlap between an emergy based approach to ecosystem evaluation and network analysis/ascendency is fertile ground for ongoing research. It is critical that the findings of this paper be extended in two ways. First, coupling emergy and ascendency should be viewed as a priority as a result of the implicit assumption in ascendency analysis (and other ecological flow analyses – e.g. Dame and Patten, 1981) that energy flows on all bilateral pathways are directly comparable (i.e., equal quality), a conclusion at odds with energy systems theory. This can be achieved using simple systems that have already been carefully examined as part of previous research efforts (see Ulanowicz, 1997; Odum and Collins, 2003; Bardi et al., 2005 for widely cited examples).

Second, we believe this technique should be extended to numerous systems with varying levels of disturbance and successional state, and in so doing, additional metrics of system development and status should be quantifiable. Wetlands differ in their capacity to support higher trophic level organisms (e.g., the Okavanago has a much higher grazer and predator biomass than the Everglades) and it is currently unknown how the EOET responds in other ecosystems, nor how effective the cross-trophic level diversity indices are at capturing whole system condition. The data required to develop these indices are not widely collected; in particular, acquiring the necessary level of compartment specificity and flow detail is resource intensive. However, as part of a global effort to understand and quantify the condition of large wetland ecosystems like those described in this volume, the necessary data are identifiable and methods for their estimation could be easily standardized.

Summary

A brief overview of the rich biota of the Greater Everglades system was given across groups (plants, mammals, insects, fish, birds). While these are considered vital for conservation prioritization, we argue that such catalogs are of limited value for assessing ecological systems. An alternative approach is the application of information theoretic indices, an endeavor with a long history in ecology. We present two critical limitations of the conventional application of the Shannon diversity equation, and offer energy-quality adjustment of ecosystem flows as a theoretical advance that allows application of this index at the ecosystem scale. This revised index has the additional value of making the index benchmark of maximum evenness more realistic within an ecosystem context. When applied to individual ecosystem components (EOET), the index can be contrasted with the condition of maximum flow evenness to yield a measure of conservation value for each ecosystem component. We observed that deviation from expected importance corresponded well with normative judgments of conservation value. We observed a significant positive association between transformity and EOET for the graminoid system and suggested that this relates to ecosystem-degradation.

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