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The consequences of the aggregation of detritus pools in ecological networks

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Abstract

Ecological networks are quantitative, graph-based descriptions of ecosystems, consisting of compartments (trophospecies and nutrient pools) that exchange fluxes of nutrients or energy. Previous research pointed out how the model's design is a crucial task that can heavily influence analyses results, and how merging compartments for the purpose of comparing two or more different ecosystems can significantly alter the indices on which the comparison is based. All these works have been focused on the aggregation of trophospecies, whereas networks may comprise several nutrient compartments that may be lumped as well, either for lack of information or for comparison constraints.

We show how the aggregation of these non-living compartments can have a greater influence on network analysis results than trophospecies clustering. This problem should on the one hand encourage modelers to make an effort to test the possible effects of aggregations, and on the other show how the role of non-living compartments could be very important in determining network dynamics.

1. Introduction

In ecosystem modeling, food web design is a central task. Identification of the elements that comprise the ecosystem and the connections between these elements represents critical assumptions that have proven influential upon results of further analysis (Goldwasser and Roughgarden, 1997; Martinez et al., 1999; Abarca-Arenas and Ulanowicz, 2002).

Numerous and diverse are the variables that influence and guide the modeler in this crucial part of building the network representing an ecosystem: living compartments can represent either a single population or a group of populations with common

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trophodynamics (Yodzis and Winemiller, 1999; Luczkovich et al., 2003; Krause et al., 2003) and decisions about the degree of resolution are driven, generally, by the amount of available information together with the purpose of the study (Jordán, 2003).

In many studies, even when a resolution at species level is desirable, adhering to this species-resolution criterion may not be possible, because no detailed information is accessible and/or the hypothetical sampling effort is unaffordable (Gaedke, 1995; Martinez et al., 1999). In such scenarios, species are lumped together according to various criteria such as common diet and life history characteristics (Pielou, 1984; Yodzis, 1984; Abarca-Arenas and Ulanowicz, 2002). Commonly only species with definite relevance for the project are given separate compartments (Baird and Ulanowicz, 1989; Christensen and Pauly, 1993; Heymans and Baird, 2000; Heymans et al., 2002).

Project goals together with the modeler's background are two additional variables that may influence the ecosystem representation, underlining some particular aspects of the food web (e.g. primary production, fisheries, microbial loop, etc.) while overlooking others.

Aggregation of species is a controversial issue (Martinez, 1991, 1993, 1994) and several studies point out how in binary food web analysis the investigated properties may strongly depend on the degree of aggregation (Goldwasser and Roughgarden, 1997; Martinez et al., 1999). The same is true for weighted (or quantified) networks, where several of the calculated properties depend strongly on the choice of compartments and degree of aggregation (Ulanowicz and Kemp, 1979; Abarca-Arenas and Ulanowicz, 2002).

Ecological network analysis (ENA) (Ulanowicz, 1986, 2004; Christensen and Pauly, 1992; Fath and Patten, 1999) requires representing systems as diagrams where boxes embody the major components of the system and weighted arrows indicate the amount of transfers of material or energy.

In comparative studies, where flow networks are examined by means of ecological network analysis, the degree of aggregation among the components must essentially be the same (Wulff and Ulanowicz, 1989; Baird et al., 1991; Ulanowicz and Wulff, 1991; Baird and Ulanowicz, 1993) in order to avoid analysis results that state artificial dissimilarities. An aggregation into trophospecies hides real system differences that are due

to real disparities in species absence/presence. Were information available on all or most species in a system, the different structures of the systems would represent real differences. In general, the limited data availability leads to choose the less resolved system as a benchmark and to reduce model complexity for the other systems to adapt models to this simpler common topology. As a consequence of this procedure, the two models are now comparable but we stress that the new topological structure produces outputs different from the original one.

In order to study, control and, possibly, reduce the effects of all this variability in system topology, some authors try to give suggestions and rules for food web construction (Cohen et al., 1993) while others evaluate the role of aggregation upon study results and conclusions (Hall and Raffaelli, 1991; Martinez, 1991; Goldwasser and Roughgarden, 1997; Sugihara et al., 1997; Abarca-Arenas and Ulanowicz, 2002).

Abarca-Arenas and Ulanowicz (2002) estimated the effects of taxonomic aggregation in ecological network analysis. They studied the effects of aggregation in the Chesapeake Bay ecological network. Starting from the complete 50 compartments model, 19 distinct less resolved systems were produced and analyzed. Results emphasize the role of species lumping upon system level indices such as Ascendency, Development Capacity, and Overhead (for a description see Section 2). In particular, they found that "the reduction of system components not only decreases the information inherent in the system, but may also affect the structural and functional representation of the system" (Abarca-Arenas and Ulanowicz, 2002).

In studying and debating about aggregation consequences in ecological studies, attention has been devoted mainly to combination of living components: species or group of species. But what are the consequences of aggregating the non-living components of the system? Non-living compartments comprise nutrient pools, detritus, inorganic and organic compounds, etc.

Among the published ecological networks, aquatic models largely predominate. These model can be ascribed principally to two classes, for what concerns the presence of non-living components: there are models that compact detritus into a single compartment (e.g. Monaco and Ulanowicz, 1997; Arreguin-Sanchez et al., 2002; Ortiz and Wolff, 2002; Zetina-Rejon et al.,

2003) and others showing two or more compartments for detritus pool (e.g. Baird and Milne, 1981; Wulff and Ulanowicz, 1989; Baird and Ulanowicz, 1989; Almunia et al., 1999; Hagy, 2002).

In this work we analyze the effects of aggregation on ecological network results focusing on the non-living components. Eleven aquatic ecosystems networks were selected and analyzed. All the models have carbon as currency and three separate non-living compartments for C pools: dissolved organic carbon (DOC), suspended particulate organic carbon (suspended POC) and sediment particulate organic carbon (sediment POC). We investigate and evaluate the results before and after the aggregation of the three non-living compartments, and compare the outcomes with living compartment aggregation in ecological networks.

2. Materials and methods

2.1. Networks and network analysis

Ecological network analysis, the modeling approach utilized in this work, requires one to represent ecosystems as species or trophospecies (Yodzis and Winemiller, 1999) connected by directed flows (weighted edges) of matter. Special flows connect the compartments with the world exterior to the system: imports, exports and dissipations (or respirations). Compartment standing stocks and fluxes can be calculated using different currencies, according to the purpose of the research (e.g. mass of carbon or nitrogen or phosphorus, etc., per unit area per unit time).

The systematic analysis of the ecosystem flow network is comprised of several techniques. Ulanowicz assembled the primary methods used in network analysis into a single software package, NETWRK (Ulanowicz and Kay, 1991); a new windows compatible version of this software (WAND: windows application for network analysis digraphs) has been recently realized (Allesina and Bondavalli, 2004) and was utilized for this study. Among the several types of analysis performed by the software, our attention focuses upon the calculation of indices that characterize the entire system: total system throughput (TST), ascendency (ASC), development capacity (DC), redundancy (RED), and the Finn cycling index (FCI).

Table 1
This squared $(N+2) \times (N+2)$ (N = number of compartments) matrix embeds all the fluxes between system compartments and the outside environment

	0	1	…	N	N+1	N+2
0	Imports				0	0
1 … N	Fluxes Between Compartments				Exports	Respirations
N+1	0	…	…	0	0	0
N+2	0	…	…	0	0	0

The $N \times N$ part is the internal fluxes matrix, while in the 0, $N+1$th, $N+2$th rows and columns the exchanges with the outside are stored.

All indices are calculated from a flow matrix as shown in Table 1.

2.2. Total system throughput—TST

Total system throughput is a measure of ecosystem size. The definition of TST varies among authors: in Finn's (1976) original work it stood for the sum of the internal transfers plus the imports whereas Ulanowicz (1986) and Patten and Higashi (1984) defined TST in more comprehensive fashion as the sum of all fluxes occurring in the ecosystem. We will adopt this latter definition in what follows.

Mathematically, if we represent the network with a matrix where each coefficient t_{ij} is associated with a flux from i to j compartments (Table 1), we can compute the TST as

$$\text{TST} = \sum_{i=0}^{N+2} \sum_{j=0}^{N+2} t_{ij} = t_{..}$$

where N is the number of compartments, compartment 0 (zero) stands for *imports*, compartment $N+1$ stands for *exports* and $N+2$ for *respirations*. We can rewrite this formula using "contractions" (Zorach and Ulanowicz, 2003) as $t_{..}$ (the first dot stands for summation among all the rows of the matrix while the second one for summation among columns).

2.3. Ascendency—ASC

Ascendency is a measure of the development reached by a studied system and it takes into account both the size of the fluxes (the TST) and their organization (the average mutual information index (AMI)). The average mutual information is defined as a decrease of uncertainty about the organizational level of an ecosystem Ulanowicz (1995). This index, derived from information theory, tells us what we know about the fate of a quantum of energy that enters the system in terms of pathways. The more the system is constrained (less pathways), the higher the information is on realized pathways. Likewise, the AMI is higher when the amount of material transferred is concentrated on a few pathways, whereas other existing pathways transfer only a comparatively small amount. The maximum organization is achieved when the network looks like a chain (one incoming flow and one outgoing for each compartment), while the minimum AMI is obtained for completely connected networks where a quantum entering a compartment will leave it for any other with equal probability. It is scaled by the total system throughput to arrive at the ascendency:

$$\text{ASC} = \text{TST} \times \text{AMI}$$

where

$$\text{AMI} = \sum_{i=0}^{N+2} \sum_{j=0}^{N+2} \frac{t_{ij}}{t_{..}} \log\left(\frac{t_{ij} t_{..}}{t_{i.} t_{.j}}\right)$$

High values for ascendency represent a mature food web where species are specialized, exchanges are structured and internal cycling and transfer efficiencies are high. In case an ecosystem is developed and organized to its fullest potential, the ascendency would equal the development capacity, which forms the upper bound of the ascendency (even if this is just a theoretical limit that cannot be achieved due to the dissipative nature of the system and the instability resulting from a high degree of specialization and organization of pathways).

2.4. Development capacity—DC

This index defines the maximum level for development in the studied ecosystem. The development capacity is calculated by multiplying the TST by the entropy generated by the flows (i.e. how diverse compartments are used by other living compartments as food sources). The flow diversity (H) increases with the number of compartments and the evenness of the flows. Referring to the matrix reported in Table 1, DC is mathematically determined as

$$\text{DC} = -\text{TST} \times \sum_{i=0}^{N+2} \left(\left(\frac{t_{i.}}{t_{..}}\right) \log\left(\frac{t_{i.}}{t_{..}}\right)\right)$$

2.5. Redundancy—RED

The amount of the development capacity still unorganized is called *overhead* and it is equal to the differences between DC and ASC:

$$\text{DC} - \text{ASC} = \text{overheads}$$

The overheads occur due to both the magnitudes and diversity of pathways of imports and exports (as a measure of self-reliance) to and from the systems, and of the dissipation of energy (respiration). Another component of the overhead is the *redundancy*, which reflects parallelisms in trophic pathways. High values of redundancy reflect a high proportion of parallel pathways in the system.

2.6. Internal ascendency, development capacity and redundancy

The internal indices are calculated like the general ones, but consider only internal exchanges between the 1st and the Nth compartments ($N \times N$ portion in the matrix depicted in Table 1), excluding flows exchanged with the outside of the system: imports, exports and dissipations. Internal Redundancy does coincide with redundancy *tout court*, so the values were not examined separately in what follows.

2.7. Finn's cycling index—FCI

FCI (Finn, 1976) is the fraction of all flow in a system that is recycled and it ranges from 0 to 1: two values are representative of the two extreme situations in which no currency is recycled (FCI = 0), and the entire amount is fed back into the system (FCI = 1). Even if this index was found to underestimate the real contribution of cycles to total flows (Allesina and Ulanowicz, 2004), for the comparison we want to

Table 2
The 11 aquatic networks analysed: Nickname is the label associated to the systems, NC is the number of compartments, Liv is the number of living compartments

Description	Nickname	NC	Liv	Reference
Aggregated Baltic Sea ecosystem	AGGBALTIC	15	12	Wulff and Ulanowicz (1989)
Charca de Maspalomas	CHARCA	21	18	Almunia et al. (1999)
Chesapeake Bay in Summer	CHESAPEAKE	36	33	Baird and Ulanowicz (1989)
Kromme Estuary	KROMME	25	22	Scharler and Baird (2005)
Lago Scuro Parmense	LAGOSCURO	25	22	Bondavalli (unpublished data)
Lower Chesapeake Bay	LOWER	34	31	Hagy (2002)
Middle Chesapeake Bay	MIDDLE	34	31	Hagy (2002)
Sundays Esturay	SUNDAYS	25	22	Scharler and Baird (2005)
Swartkops Estuary	SWARTKOPS	25	22	Scharler and Baird (2005)
Upper Chesapeake Bay	UPPER	34	31	Hagy (2002)
Ythan Estuary	YTHAN	13	10	Baird and Milne (1981)

perform the FCI is reliable, as we will analyze it in its normalized form (FCI after aggregation − FCI before aggregation divided by the original FCI value).

2.8. Analyzed systems

In this study eleven aquatic networks (Table 2) have been selected and analyzed. The number of system compartments range from 13 to 36 but all the networks, in their original form, comprise three non-living compartments. These are identical for all investigated models and are identified as: dissolved organic carbon (DOC), suspended particulate organic carbon (suspended POC), sediment particulate organic carbon (sediment POC).

2.9. System analysis and aggregation

The 11 selected systems were analyzed at first in their original form and again with the three original detritus compartments aggregated into one. All the system indices described above were determined before and after aggregation to estimate the effect of this procedure and test results variability.

To lump together the three detritus compartments we applied an algorithm by Ulanowicz and Kemp (1979), a procedure that, summing all inputs and outputs of single compartment to be aggregated, rearranges only the organization of fluxes, while it leaves the magnitude untouched, providing a check on mass conservation and preserving the TST unchanged (see also Appendix A for details on the algorithm). At the same time the procedure minimizes changes in the amount of

information, and as a direct consequence the reduction of the ascendency value is the lowest possible (Hirata and Ulanowicz, 1985). Because the procedure leaves the TST untouched, we can compare directly the indices for the two versions of the network. Further, relative indices and weighted indices will have the same behavior.

3. Results

Results for all system indices calculated before and after aggregation are reported in Table 3. TST was not considered in the analysis because, as specified above, the aggregation procedure works to leave this value unchanged.

DC and ASC show lower values in the new aggregated form than in the resolved one with three separate detritus compartments. Observed patterns are the same for internal indices (internal ascendancy and internal capacity), with slightly lower values due to the smaller number of compartments.

Observed trends in DC are predictable and in agreement with the definition of these indices. Because development capacity is maximized if all compartments handle the same fraction of flux, we can state that a diminution in the number of compartments can only diminish the maximum entropy as well. For example, having a $t_{..} = 1$ and 4 compartments handling one fourth of the flux each, we would have $DC = -4E(0.25 \log_2 0.25) = 8$, while having two compartments with half of the flux each DC would become $DC = -2E(0.5 \log_2 0.5) = 2$. In this case halving the number of compartments reduces the DC to one third.

Table 3
System level indices for the selected ecosystems before (upper) and after (lower) detritus compartments aggregation

Nickname	ASC 3	ASC 1	DC 3	DC 1	RED 3	RED 1	FCI 3	FCI 1	INTASC 3	INTASC 1	INTDC 3	INTDC 1	INTRED 3	INTRED 1
AGGBALTIC	1.63E+03	1.19E+03	4.24E+03	4.11E+03	1.56E+03	1.83E+03	2.31E-01	2.93E-01	1.03E-03	6.39E+02	2.58E+03	2.47E+03	1.56E+03	1.83E+03
CHARCA	6.16E+06	5.13E+06	1.46E+07	1.44E+07	5.04E+06	5.90E+06	2.46E-01	3.10E-01	4.14E-06	3.17E+06	9.18E+06	9.06E+06	5.04E+06	5.90E+06
CHESAPEAKE	3.44E+07	2.25E+07	7.86E+07	7.67E+07	2.29E+07	3.27E+07	2.12E-01	3.29E-01	2.35E-07	1.28E+07	4.63E+07	4.55E+07	2.29E+07	3.27E+07
KROMME	7.48E+03	5.68E+03	2.15E+04	2.08E+04	8.43E+03	9.17E+03	4.08E-01	4.74E-01	4.23E-03	3.05E+03	1.26E+04	1.22E+04	8.42E+03	9.17E+03
LAGOSCURO	2.61E+03	1.62E+03	5.96E+03	5.21E+03	2.29E+03	2.28E+03	2.39E-01	3.24E-01	1.13E-03	5.42E+02	3.42E+03	2.82E+03	2.29E+03	2.28E+03
LOWER	1.19E+07	9.07E+06	3.09E+07	2.98E+07	1.10E+07	1.29E+07	2.09E-01	2.43E-01	8.08E-06	5.39E+06	1.91E+07	1.83E+07	1.10E+07	1.29E+07
MIDDLE	1.55E+07	1.13E+07	3.73E+07	3.57E+07	1.29E+07	1.13E+07	2.58E-01	2.95E-01	1.05E-07	6.79E+06	2.35E+07	2.19E+07	1.29E+07	1.51E+07
SUNDAYS	1.14E+04	7.93E+03	2.65E+04	2.51E+04	7.19E+03	8.62E+03	2.02E-01	2.59E-01	5.69E-03	3.39E+03	1.29E+04	1.20E+04	7.20E+03	8.62E+03
SWARTKOPS	6.90E+03	5.17E+03	1.83E+04	1.76E+04	5.68E+03	6.34E+03	2.62E-01	3.41E-01	3.50E-03	2.40E+03	9.19E+03	8.74E+03	5.69E+03	6.34E+03
UPPER	7.29E+06	5.49E+06	1.83E+07	1.76E+07	6.27E+06	7.32E+06	2.77E-01	3.62E-01	5.18E-06	3.52E+06	1.15E+07	1.08E+07	6.27E+06	7.32E+06
YTHAN	8.66E+03	3.48E+03	2.34E+04	2.07E+04	7.37E+03	1.04E+04	2.70E-01	3.74E-01	5.44E-03	1.20E+03	1.28E+04	1.16E+04	7.37E+03	1.04E+04

That is to say maximum development decreases with the number of compartments, and with the differences in flow distribution among compartments.

The topic becomes more complicated if we account for ascendency changes. It has been demonstrated (Hirata and Ulanowicz, 1985) that the aggregation process can only diminish the ascendency value, but predicting the extent of the decrease by glancing at the exchange matrix is not so easy. In fact, we can say that if all the fluxes exiting (or entering) a compartment are equal, then the contribution to ascendency is 0 for those coefficients, while when they are not all equal some will contribute positively and some negatively, and that the positive contribution will be greater than the negative ones. If we have a preponderant self-loop, as usually happens when we lump detrital compartments (see example in Appendix A), this will contribute positively to the ASC value, making other fluxes negative contributors. Since the TST is invariant between the original and aggregated networks, changes in ASC and DC are to be addressed to changes in AMI and H, respectively (Hirata and Ulanowicz, 1985).

The ratio ASC/DC takes the different capacity for development according to its flow structure and the magnitude of flows in the diverse ecosystems into account. Even this "standardized" measure decreases significantly with the aggregation of detritus compartments (one-tailed paired t-test ASC/DC: $t = 9.0045$, d.f. = 10, $p = 2.060E-06$) since the two indices involved changed not homogeneously due to the aggregation process. For example, in the Baltic Sea model the change for ascendancy is about 27%, whereas the DC changed only by about 3%. The same results originate from the analysis of Internal ASC/Internal DC where the change reached a maximum of 76% and was statistically significant ($t = 7.4932$, d.f. = 10, $p = 1.040E-05$).

An opposite pattern to that found for ASC is followed by the FCI where higher values were determined for the aggregated version of the analyzed systems. We can say that the lumping of detrital compartments usually creates new cycles leading to an increase of this index (for the role detrital compartments play in cycling see also Allesina et al., 2005).

The trend for Redundancy is ambiguous; results are higher for nine of the aggregated networks but lower for the "Lago Scuro" and "Middle Chesapeake Bay" models. Aggregation of compartments can create more parallel pathways, but also delete existing ones.
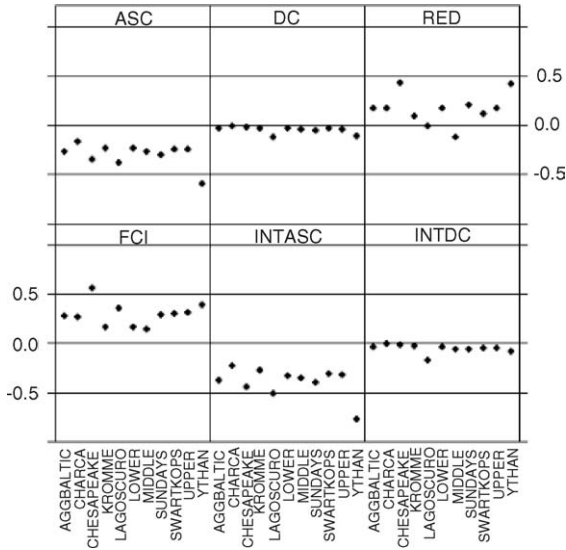
Fig. 1. Percentage change of system level indices due to aggregation of detritus compartments. The *y*-axis represent index (three compartments)/index (one compartment) − 1. Values below 0 are found when the index decreases after the aggregation.

In order to illustrate trends and quantify changes for the studied indices, differences between indices computed for the original networks and the transformed models with a single aggregated compartment for detritus are expressed as relative ratio of changes calculated as [index for 3 detritus]/[index for 1 detritus] − 1. The results are depicted in Fig. 1.

Interpreting results in terms of percentages, differences for the ASC, always negative (ASC decreasing), showed changes always greater than 15%. The main variation was found for the Ythan estuarine system where the ASC showed a change of about 60%. Also, the DC shows differences always negative but never exceeding 12%. Identical patterns are depicted for internal ASC and DC but with larger variations; e.g. maximum changes for internal ASC range from 23 to 78% for the 11 systems.

For redundancy both positive (maximum positive change is about 42%) and negative (maximum negative change is about 13%) variations were detected, confirming the ambiguous behavior of this parameter. The general trend seems to be a decrease in redundancy in the aggregated networks, which was the observed behavior in 9 out of 11 systems. Values for

internal redundancy are identical (and not separately represented in Fig. 1).

Values calculated for the FCI were always positive with amounts reaching the 55% for the Chesapeake Bay (in summer).

In order to test if the differences in those indices were significant, we compared the values statistically with single tailed *t*-tests for paired samples. We found significant decreases for ASC ($t = 2.1445$, d.f. = 10, $p = 0.0288$), internal ASC ($t = 2.1437$, d.f. = 10, $p = 0.02884$), DC ($t = 2.6847$, d.f. = 10, $p = 0.01145$) and internal DC ($t = 2.6847$, d.f. = 10, $p = 0.01145$); the increase for FCI was significant ($t = -9.1729$, d.f. = 10, $p = 1.743\mathrm{E}{-}06$). There was no significant decrease, using one-tailed *t*-test, for RED ($t = -1.5761$, d.f. = 10, $p = 0.07304$).

4. Discussion

Aggregation of detritus compartments in the eleven studied ecosystem networks showed strong consequences in the magnitude of the analyzed system level indices. These indices, representing a synthetic way to describe global attributes of ecosystems, are defined to gauge the pattern of development (Ulanowicz, 1986, 1997), and are used in numerous cases for whole ecosystem comparison studies (e.g. Baird and Ulanowicz, 1993; Baird and Heymans, 1996; Baird et al., 2004; Christensen and Pauly, 1993; Monaco and Ulanowicz, 1997; Wulff and Ulanowicz, 1989).

In particular, ascendency as a measure of growth and system development has great value in indicating advanced maturity and in the comparison of ecosystems, but it reveals major changes as a consequence of aggregating detritus compartments. This trend is confirmed even if we use an adimensional measure such as the fraction of realized ascendency ASC/DC, and internal ASC/internal DC, a frequently utilized metric for comparing the developmental status of ecosystems. A similar decreasing trend for internal ascendency and development capacity was observed in Abarca-Arenas and Ulanowicz (2002) where effects of trophic aggregation were investigated for the Chesapeake Bay trophic network. In this study the original 50 compartments were differently lumped to generate a series of 19 derived sub-systems, ranging from a maximum of 50 compartments to a minimum of 22, and aggregation

involved living compartments only. Internal indices (in particular ascendency and development capacity) were calculated and compared with the original ones, finding a decrease in values of about 2.7% for internal ASC and 6.1% for internal DC at maximum, which are really small compared to the percentages when aggregation involved detritus compartments (78% for INTASC and 12% for INTDC) (Fig. 1). This pattern suggests the numbers or resolution of non-living compartments to have a greater impact upon system characteristics than living compartments topology. This is marked in particular for internal ascendancy. INTASC, and in general ASC, depends more on the magnitude of fluxes and their distribution rather than on the number of compartments. DC, on the other hand, relies more on the latter. Detrital compartments are usually characterized by large size and a high number of connections in comparison to most living compartments. Moreover, ASC is very sensitive to the presence of self-loops. The lumping of detrital compartments usually creates self-cycles, embedding all the exchanges occurring between the three compartments before aggregation (see Appendix A). These self-cycles, being relatively "heavy" if compared to the total system throughput of the system, lead to a decrease in ASC.

Self-loops cause further variations by increasing the internal recycling and the FCI. For this index higher values were determined for the aggregated networks, but this increase is not due only to self-cycles: lumping compartments could lead to direct connections missing in the original network. To give an example we go back to the configuration of the Baltic Sea model (Wulff and Ulanowicz, 1989; Ulanowicz and Wulff, 1991) where, by analyzing the structure of cycles, the authors did not find an overlap between flows within the planktonic community and the circulation related to deposit feeders (and nekton). The cycles present in the two sub-systems are disjointed. In grouping detrital compartments into one, the two sub-systems became one with new and different cycles connecting pelagic and benthic communities. Consequences of this procedure are not limited to changes in system indices but in a significant loss of information. In fact when considering detritus as compacted into one single compartment, we would neglect important information about system functioning not highlighting the two separate sub-system involved in internal recycling (see for example Allesina et al., 2005).

Although consistency in resolution is essential in system comparison due to a lack of information on all taxonomic species, and reachable through aggregation, it is not a perfect solution. Let us make an example starting from the self-cycles generated by detrital compartment lumping. In this study we started our analysis with systems characterized by three distinct detritus compartments that were combined into one. This procedure generated a self-loop upon this new compacted component since the algorithm applied (Ulanowicz and Kemp, 1979) leaves the TST unchanged and preserves all flows, including those among the original detritus compartments: the flows that were intra-detritus in the original network were therefore combined in the self-cycle of the new aggregated detritus compartment. Let us assume we are interested in comparing these networks with others originally built with just one detrital compartment: in the majority of these models we do not find a self-loop upon this component (e.g. Browder, 1993; Rosado-Solórzano and Guzmán del Próo, 1998; Vega-Cendejas and Arreguín-Sánchez, 2001; Zetina-Rejon et al., 2003) because, in many cases, self-loops are neglected in network construction due to a lack of information. In this case, even if all models chosen for a comparative study have the same number of compartments, comparison is still problematical because of the presence/absence of the detritus self-loop that will change the quantity of material/energy passing through the system and consequently the TST together with all the other systems indices (TST is involved in the calculation of all considered system indices, see Section 2).

5. Conclusions

Level of resolution, as a key variable influencing ecosystems structure and characteristics, has been broadly debated (Martinez, 1991, 1993, 1994; Goldwasser and Roughgarden, 1997; Martinez et al., 1999). Many investigations focused upon the effects of taxonomic aggregation on food web properties: e.g. resolution can reach the species level for top predators but others (e.g. algae) are grouped into a single compartment (Yodzis and Winemiller, 1999; Jordán, 2003; Luczkovich et al., 2003; Krause et al., 2003).

In binary food web analysis, debate is active and investigators focus on characteristics that are more robust to data resolution and less sensible to aggregation,

so that they represent real features of food webs and not modelers artifacts (Martinez, 1991, 1993, 1994; Martinez et al., 1999; Sugihara et al., 1997). Analogously, taxonomic aggregation effects for weighted trophic networks are beginning to be explored (Ulanowicz and Kemp, 1979; Abarca-Arenas and Ulanowicz, 2002).

In this work, we analyzed patterns suggesting that the resolution of non-living compartments has a greater impact upon system characteristics evaluation than living compartments topology. We propose that two systems with a different number of detrital pools are incommensurable with each other even when all the other compartments are built with the same resolution. This has obvious consequences for network building and comparative network analysis. It is generally not possible to have a fully resolved network where all species are identified and all flows have been measured. Therefore, it is the amount of available data and the researchers' ability to fill any data gaps dictating the quality of the networks. Besides such obvious and unavoidable shortcomings, there is as yet no consensus among researchers about how to best resolve a network. In general, the most resolved version is chosen, and seldom is a strategy for identifying compartments used (but, see e.g. Luczkovich et al., 2002). In inter-system comparisons, the most aggregated network usually serves as a reference point to aggregate other networks, with all the implications discussed above. When comparing the same system over time, the network is generally constructed in the same fashion, unless known species extinctions, invasions or migrations occur. With these simple constraints, a comparative analysis of ecosystems can render useful results. It is suggested to verify results using a sensitivity analysis, where the number of compartments, number of links and amounts transferred can be changed in accordance to data reliability. Due to the nature of the indices discussed here (i.e. their dependence on the number of compartments, number of links and amount transferred), it is not possible to find a network structure which makes them 'robust' indices for comparison.

Another issue addressed by the present work is the enormous importance of detritus pools in ecosystems' networks. The non-living compartments, coupled with the microbial loop, are essential to a full understanding of ecosystem's dynamics. This

is particularly true in ecological networks, which present weighted links. In fact, the detritus pools are not just hubs for the system, holding the majority of connections, but also manage a great part of the total flow of matter inside the system. This question is extremely important if one considers that the majority of ecological network analysis products (e.g. by using ECOPATH) allow just a single detritus compartment. This characteristic may lead to the deletion of important ecosystem features, such as the cycle structure (for example see Allesina et al., 2005) which in turn has consequences for the indices discussed above. Other compartments with a throughput that has to be redistributed over many links might of course have a similar influence on the ecosystem indices. Whether it is the size, turnover, or connectivity (number of links and the pattern of material transfer) that influences above discussed indices the most remains to be explored.

Our findings open the discussion for debate upon network construction rules which will need a further specific study to be properly analyzed. However, results so far suggest that consistency in compartment models resolution is essential in ecosystem comparison (locally and temporally) and this pertains especially to detritus compartments.

Appendix A. Aggregating detritus compartments

The aggregation technique utilized in the text has been described in Ulanowicz and Kemp (1979) and Hirata and Ulanowicz (1985). The algorithm is very simple: let T be a $N+2$ by $N+2$ matrix of transfer as the one depicted in Table 1. For simplicity's sake, let the detritus compartments be represented in the last three rows and columns excluding exports and

Table A1
The matrix of transfers T

	Imports	1	2	3	4	Exports	Respirations
Imports	0	100	0	0	0	0	0
1	0	0	80	0	0	0	30
2	0	0	0	70	0	0	40
3	0	0	0	0	50	0	20
4	0	10	30	0	0	0	10
Export	0	0	0	0	0	0	0
Respirations	0	0	0	0	0	0	0

See also Table 1. The compartments 2–4 represent exchanges from (rows) and to (columns) detritus compartments.

respirations (N, $N-1$, $N-2$). Aggregating the three compartments into a single detritus pool involves the construction of an aggregation matrix as follow: let I be the $N+2$ by $N+2$ identity matrix. We just change the coefficients: $I[N-1, N-1] = I[N-2, N-2] = 0$ and $I[N, N-1] = I[N, N-2] = 1$ and we call the resulting matrix A. Now, the aggregated version of the network T, called T' is obtained by multiplying the matrix A for T and the resulting matrix for the transposed matrix A^{T}. As an example, take Table A1, representing a small network where a living compartment (1) receives 100 units of currency from outside the system. Eighty units are passed along to a detrital loop composed by compartments 2–4.

The network is in steady state, as the inflow balances the outflow for any compartment. In order to aggregate the three detritus compartments into a single detritus pool, one builds the aggregation matrix A (Table A2): the three compartments will be lumped into the single compartment 2.

This is done performing $T' = ATA^{T}$ (Table A3). Note that the aggregation left the TST (sum of all flows) unchanged (conservation of mass) and that the process formed a self-loop of 150 units (coefficient [2, 2]).

Table A2
The aggregation matrix A

	Imports	1	2	3	4	Exports	Respirations
Imports	1	0	0	0	0	0	0
1	0	1	0	0	0	0	0
2	0	0	1	1	1	0	0
3	0	0	0	0	0	0	0
4	0	0	0	0	0	0	0
Export	0	0	0	0	0	1	0
Respirations	0	0	0	0	0	0	1

This matrix is obtained, starting from the identity matrix, swapping coefficients $[i, i]$ and $[i, j]$ where i is the compartment that one wants to aggregate to compartment j.

Table A3
The aggregated matrix of transfers T'

	Imports	1	2	3	4	Exports	Respirations
Imports	0	100	0	0	0	0	0
1	0	0	80	0	0	0	30
2	0	**10**	**150**	**0**	0	0	**70**
3	0	0	0	0	**0**	0	**0**
4	0	**0**	**0**	0	0	0	**0**
Export	0	0	0	0	0	0	0
Respirations	0	0	0	0	0	0	0

It is obtained performing $T' = ATA^{T}$. Note that the rows and columns 3, 4 are composed of zeroes only, and can be eliminated. The values that have been changed by the aggregation procedure are presented in bold.

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