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Ecological validation of soil food-web robustness for managed grasslands



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ARTICLE INFO ABSTRACT Keywords: The actual relationship between biodiversity and ecosystem functioning is a challenging and intriguing issue Soil food webs which always fascinated many ecologists. In this study the detrital soil food webs of three temperate sandy Ecological networks ecosystems have been compared in the attempt to quantify the extent to which anthropogenic action affects Carrying capacity them. The structure of the corresponding food webs was analysed and their topological robustness was calculated Complexity through the use of a dynamic model, which is briefly introduced. Our Alteration Index has been used here for the Hubs first time to enable a direct comparison between different food-web architectures. The results show that all soil networks have a disassortative nature, as expected for theoretical food webs. The values of the clustering coefficient, of the connectance and of the complexity, together with the calculation of the robustness suggest that the fallowed pasture with low pressure management is more robust than the other two grasslands under middle intensity management. The robustness shown by ecological networks could be useful elsewhere for evaluating the sustainability of agricultural practices to which the soil system is subject.

1. Introduction

Ecological indicators are either biological assemblages or single taxa that indicate by their occurrence something about the environmental conditions. In most cases, single taxa are used as bioindicators, but the food-web architecture of biological assemblages, also called ecological networks, is according to us a strong and much more comprehensive ecological indicator. As concerns the topology, a study carried out by Montoya and Solé (2002) suggested as first that food webs show a smallworld and scale-free structure, showing high values of the clustering coefficient and a power-law degree distribution. Instead other studies have highlighted a deviation from the small-world and scale-free topology founding that most food webs display low clustering coefficients, similar to random expectations, and less skewed exponential and uniform distributions especially, in the case of food webs with high connectance values (Dunne et al. 2002a, Camacho et al. 2002). On the contrary, as regards the degree correlation, the disassortative nature of ecological networks seems to have been ascertained: nodes with many links are mostly connected with nodes with a low number of links (Newman 2002, 2003, Stouffer et al. 2005). However, to what extent do these phenomena mirror the soil environmental conditions?

Research on ecological networks concerns topics of great interest,

like their robustness in response to external anthropic perturbations depending on the food-web architecture. Before biodiversity loss and the Sixth Mass Extinction became global issues, Solé and Montoya (2001) found that food webs were more vulnerable to targeted attacks to hubs than to random attacks to hubs and spokes, characteristic generally found in scale-free networks (Strogatz 2001, Barabasi 2016). Other studies found that even without highly skewed degree distributions, food webs were much more robust to random loss of species (mostly spokes) than to loss of highly connected species (hubs), suggesting that any substantial skewness in degree distribution will tend to alter the response of a network to different kinds of node loss (Dunne et al. 2002b, 2004). Moreover Dunne et al. (2002b) also found that the robustness of the food web increased with increasing connectance and this result applies both for targeted removals of hyper-connected species (hubs) and for random removals of nodes in space (Boit et al. 2012, Mulder et al. 2012) and time (Maia et al. 2019).

Even if the amount of studies on ecological networks is constantly increasing (Hines et al., 2015; de Vries et al., 2013; Sechi et al., 2015), one of the most controversial debates in the context of ecological networks remains the relationship between stability and complexity of an ecological system (Mulder et al. 2012, Sechi et al. 2015, Brose et al. 2019, Galiana et al. 2022). Briefly reviewing the XXI Century literature

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Fig. 1. From the 8362 document results obtained running SCOPUS on the query TITLE-ABS-KEY "food webs" AND "trophic relations" (2002–2022), 512 studies addressed the food-web metrics in relation to the environment (accessed June 10, 2022). Even for novel networks, the majority of the trophic information has been derived from existing literature.

from 2001 to 2022, we see that food-web indicators, such as connectance, complexity and vulnerability, are quite popular, despite the need to increase further the knowledge of who-eats-whom interactions (Fig. 1).

The predominant idea that the stability of ecological communities would increase with their complexity (Elton 1958, MacArthur 1955) was questioned by May (1973) who, using methods related to dynamic models, came to the conclusion that the stability of an ecosystem decreases with increasing number of species and interactions. May's criterion suggested that a community remains stable if a decrease in connectance C is accompanied by an increase in diversity S, so that SC remains a constant quantity (Pascual and Dunne 2006, Mulder et al. 2006). Several studies, starting with Cohen and Newman (1985) and Cohen et al. (1986), at first seemed to corroborate May's hypothesis and found approximately constant values of linkage density $SC \approx 2$, although more detailed empirical data, exhibited a higher degree of interaction between species, namely $SC \approx 10$ (Martinez 1991, Mulder et al. 2006), and a positive relationship between C and S contrary to what predicted by May's criterion (Sugihara et al. 1989). But, with all the ongoing pressures on species and ecosystems, to which extent do biodiversity and connectance matter for the ecosystem functioning of the environment?

The aim of this paper is to analyse the topology and the robustness of three networks corresponding to reference soil systems, highlighting similarities and differences. Through the use of a model whose dynamics is dictated by an extension of the Lotka-Volterra equations, we studied what may be the consequences of artificial perturbations induced in the system. Unlike previous studies, that are often based on a purely topological network analysis despite the availability of so many software tools (Hudson et al. 2013, Marzidovšek et al. 2022, Petchey et al. 2008, Vaughan et al. 2018, Williams, 2010), this study derives the robustness of the food webs through a strictly dynamical analysis. This represents an upgrade considering that the structure of a given network has a strong impact on the outcomes of dynamics, as highlighted in Pimm and Lawton (1978), McCann and Hastings (1997), Hastings (1996), and Jordán et al. (2002). In this regard, already Dunne (2006) stated that the dynamics of species in complex ecosystems is more tightly connected than conventionally thought, which has profound implications for the impact and spread of perturbations, surely now during the Anthropocene.

Several studies have investigated the varying structural characteristics shown by food webs representative of different types of habitats, area and environments (Bascompte and Jordano, 2007, Briand 1983, Briand and Cohen 1987, Chase 2000, Cohen 1994, Link 2002, Dunne et al. 2004, Mulder and Elser 2009, Mulder et al., 2011, 2012, Brose et al. 2019, Galiana et al. 2022). Also land-management practices and environmental changes affect belowground communities, influencing the overall stability and productivity of the food webs (Clay 2004, Powell 2007, Mulder and Elser 2009, Wall et al. 2015). Unravelling the alteration due to stress addressing the extent to which and the way how anthropogenic action affects soil systems can be helpful in establishing among others the sustainability of agricultural methods, promoting applied ecological implications of soil biodiversity.

2. Material and methods

2.1. Data sampling and construction of the food webs

The data used in this study derived from sampling and monitoring activities performed in the framework of the Dutch Soil Quality Network (Mulder et al. 2006, 2011). Thanks to this survey, we have available data on the taxonomy, abundance, body size, and general feeding habits of soil invertebrates for several sites in The Netherlands (Mulder and Elser, 2009, Cohen and Mulder 2014). The trophic height, derived from the feeding behaviour of these invertebrates, is based on the main feeding preferences, as explained later in this section. We have chosen a pristine site and two (chemically as different as possible) sites from the dozen downloadable from Mulder and Elser (2009).

The first ecosystem considered (site 247) is one fallowed pasture that shares a belowground biomass distribution equal to the energetic equivalence rule (Mulder and Elser 2009, Conti et al. 2020). According to the Eltonian rule (Elton 1927), being the lumped dry weight of all the sampled soil invertebrates of the first trophic level (first order consumers) exactly 10.28 times the lumped dry weight of all the sampled soil invertebrates of the second trophic level (second order consumers), we can consider this Dutch ecosystem as a reference ecological network (Mulder and Elser 2009, Conti et al. 2020).

The other two ecosystems (sites 225 and 230) are organic farms certified by the Agricultural Economics Research Institute of the Netherlands (LEI) (Mulder et al. 2011). These meet all the legal requirements for this type of agriculture (using compost/farmyard manure and no biocides, averaging 1.7 livestock units per hectare) and are periodically monitored by the LEI. Due to liming, both soils are much less acid than the previous site (pH equals 4.4 for site 247 and 5.5 and 5.4 for sites 225 and 230, respectively), although the soil quality is much



Fig. 2. A sketch of the ecological networks for the reference site 247 (a, upper panel, as circular network depicting prey-predator interactions at the left and stretched network depicting the hierarchy of trophic group at the right), site 225 and site 230 (b and c, respectively, both lower panel). Nodes/species are organized in five main groups of different colours (see Figs. 3–5) and placed in a circular layout, with the nodes/species numbered consequently. The size of each node is proportional to the base-10 logarithm of the abundance of the corresponding species (log X_i). Direct links between the organisms belonging to trophic level 1 (primary consumers, being they herbivorous, fungivorous or bacterivorous invertebrates, hereafter preys) and the organisms belonging to trophic level 2 (secondary consumers, either carnivorous or omnivorous invertebrates, hereafter prey-predator connections, each one going from the prey node to the predator node.

lower due to agricultural management as evident from their soil carbon: nitrogen:phosphorus ratios (soil C:P and N:P ratios equal 70.6 and 4.0 for site 247, but 49.8 and 3.5 for site 225, and only 31.4 and 2.7 for site 230, respectively). Also organic matter is decreasing, from 5.9% (site 247) down to 5.6% (site 225) and 4.4% (site 230), all dry matter.

Regarding the sampling of soil invertebrates, three replicate samples of about 5 m² from the upper 10 cm of soil for the fauna were taken. Bulk samples of 50 soil cores (diameter 2.3 cm) were used to extract the microfauna and two soil cores (diameter 5.8 cm) were used to extract the mesofauna. Extraction of free-living nematodes was performed within one week of core sampling using Oostenbrink funnels, and all the elutriated nematodes were collected; ecto- and endoparasitic nematodes were recovered with centrifugal flotation. All nematode individuals were counted, and \sim 150 randomly chosen specimens were identified at

species level and measured under a light microscope to derive their body length, and, hence, their body mass (Mulder and Vonk, 2011). Enchytraeid worms were sampled by wet extraction and microarthropods by dry extraction: in both laboratory protocols, heat was increased gradually with incandescent bulbs, and the invertebrates escaped by moving downward. All sampling protocols were extensively described in Mulder et al. (2011).

For all the taxa we know the abundance X_i , the body mass M_i , the biomass B_i (given by $B_i = X_iM_i$) and the value of the growth rate r_i in condition of mutual interaction, with i = 0; 1;:::; n (n is the number of species detected in the ecosystem). Within each guild, we used the overall r_i value as in Moore et al. (1993) and De Ruiter et al. (1995). All identified soil invertebrates fell into five guilds (herbivorous, bacterivorous, fungivorous, carnivorous, and omnivorous) and the

independent trophic links among taxa (from any prey to its consumer, hence from any first order consumer to its second order consumer) were inferred from the matrix in Mulder and Elser (2009). Specifically, we used their complete inventory of multitrophic interactions of soil food webs (Supporting Table S2 in Mulder and Elser 2009) for all trophic links consistent with literature-derived guilds (the common practice as shown in Fig. 1). These authors included in fact one comprehensive summary listing all hundred papers from which these guilds were derived, although it should be kept in mind that most attention was paid to feeding preferences. For instance, some rare panphytophagous oribatids like *Galumna elimata* have a certain degree of omnivory, but given their gut content these mites were labeled as "herbivorous" (Mulder and Elser 2009).

We postulated constant allochthonous resources as "consumers benefit from but do not affect resource renewal rate" (Polis et al. 1997) and kept in our simulations microbial and plant biomasses (trophic level 0) constantly available for grazing by basal (specialized) species (i.e., trophic level I, first order consumers, hereafter preys) and nonbasal (omnivore) species (i.e., trophic level 2, second order consumers, hereafter predators). As in Conti et al. (2020), our assumptions will be:

- In the absence of predators, the population of the prey would grow proportionally to its size.
- In the absence of prey, the population of the predator would decline proportionally to its size, meaning extinction of that population.
- When both predator and prey are present, the interspecific effect of the predation has to be represented as a decrease in the population of the prey and an increase in the population of the predator.

Using the data obtained from the sampling, we have built three direct and unweighted food webs for soil organisms (trophic interactions are set at either 1, if present, or 0, if absent). In Fig. 2 the representative networks of the three ecosystems are showed, with the numbered nodes/ species placed in a circular layout, where each group of species (the aforementioned guild) is distinguished by a different colour. The size of each node is proportional to the base-10 logarithm of the numerical abundance of the corresponding species (Log*X*).

2.2. Simulation within the ecosystems

The dynamics of the soil system after the removal of some groups of species was simulated using the model and applying the same methodology described in Conti et al. (2020). Simulations have been carried out within NetLogo, a multiagent fully programmable modelling environment suitable for the simulation of complex systems (Wilensky 1999, Novak and Wilensky 2006). In the model we combine the Lotka-Volterra model (Lotka 1920, Volterra 1926, 1939) with the logistic equation (Verhulst 1838) in order to take into account intra-specific and interspecific competition (i.e., between the individuals belonging to the same population and between the populations). The dynamical equations describing the variation in species abundances are given by.

$$\frac{dX_i}{dt} = \left[r_{i0} + \alpha \sum_j A_{ij} X_j \right] X_i \left(1 - \frac{X_i}{K_i} \right) (i = 1, 2, ..., n)$$

$$\tag{1}$$

where r_{i0} is the growth rate of the *i*-th species in absence of interaction and K_i its carrying capacity. Coefficients A_{ij} weigh the food interaction among pairs of species and depend on the biomass of the prey species. In particular, $A_{ij} > 0$ when species *i* preys species *j* and $A_{ij} < 0$ when species *j* preys species *i*. The parameter α is a coupling coefficient that can be considered as a measure of the interaction strength of a given species within the rest of the food web. For details on how the values of A_{ij} , r_{i0} , K_i and α were obtained, we refer to the methodology described in Conti et al. (2020: Supporting Information). Here we just point out that the formula has the same form of a logistic equation in which instead of the growth rate without interaction r_{i0} , the term inside the square brackets in equation (1) is used. This term is the growth rate r_i in case of interaction between species and considers, in addition to the intra-specific interaction an inter-specific interaction, i.e. the effect due to predation.

$$r_i = r_{i0} + \alpha \sum_j A_{ij} X_j \tag{2}$$

All the simulations were done by choosing the initial abundance of the species in the interval:

$$X_i(0) \in \left[K_i - \frac{K_i}{2}; K_i\right]$$
(3)

so that they cannot exceed their carrying capacity.

For each considered food web, starting from the initial conditions (3), at each time step the populations $X_{i(l)}$ of all species are updated by numerically integrating equation (1) and all the species reach the steady state established by their carrying capacity. Any removal of one or more species will induce a disturbance within the system which could lead to a variation in the abundance or, possibly, to the extinction of some species. In order to quantify structural changes and to compare one single simulation to others, we used the Alteration Index (AI) introduced in Conti et al. (2020) and defined as:

$$AI = \sum_{K} \frac{|X_{sk} - X_{fk}|}{X_{sk}} = \sum_{k} \frac{|\Delta X_k|}{X_{sk}}$$
(4)

where X_{sk} and X_{fk} are, respectively, the abundance of species *k*-th calculated after 100 time steps, i.e. in the steady state, and the abundance of the same species calculated at the end of the simulation. In other words, AI considers the sum of the absolute variations in abundance that the species undergo due to the forced removal of some other species, normalized with respect to their abundance in the steady state. It is therefore a measure of the alteration of the ecosystem due to the introduced perturbation, and as such a novel ecological indicator.

3. Theory and calculation

3.1. Biodiversity, connectance and complexity

In the case of ecological networks, the number of nodes/species defines the biodiversity *S* of the ecosystem. By calling *L* the number of trophic links between the species, each graph is distinguished by the value of the connectance *C*, which gives the ratio between the number of connections actually present on the possible ones. Therefore we have $C = L/S^2$ in the event that loops (i.e. connections of a node with itself) are taken into consideration, which, in the case of food webs, is equivalent to consider the phenomenon of cannibalism. Otherwise, if we do not consider the presence of loops, we have C = L/S(S - 1). Thereby connectance gives a measure of the probability that two species interact with each other within a graph. The complexity *c* of a network, and in particular in this case of an ecosystem, is closely connected to the concept of connectance. Complexity *s* of the ecosystem and corresponds to the linkage density *L/S* of the web: c = CS = L/S.

3.2. Network topology

The topology of a network is strongly determined by two characteristic quantities: the average path length $\langle d \rangle$ and the average clustering coefficient $\langle C \rangle$. The average path length $\langle d \rangle$ is given by the average of the distances d_{ij} between all pairs of nodes in the network. For a direct network this quantity is given by.

$$\langle d \rangle = \frac{1}{S(S-1)} \sum_{\substack{i,j=1,S\\i\neq i}} d_{ij}$$
(5)

The average clustering coefficient $\langle C \rangle$ gives an idea of how strong the

aggregation between the nodes is. For a single node i with degree k_i , the local clustering coefficient is given by.

$$C_i = \frac{2L_i}{k_i(k_i - 1)} \tag{6}$$

where L_i represents the number of links that connect the k_i neighbour nodes of node *i*. Basically C_i gives the probability that two neighbours of a node are in turn connected and it is a quantity between 0 and 1. The degree of clustering of the entire network is determined by the average clustering coefficient.

$$\langle C \rangle = \frac{1}{S} \sum_{i=1}^{S} C_i \tag{7}$$

In random graphs the average path length and the average clustering coefficient are both low. Watts and Strogatz (1998) proposed the Small World graph that can be built from a regular graph by replacing some of its links with random links. This type of graph presents a low average path length and, as opposed to the random graph, a high average clustering coefficient: all features that are simultaneously present in the structure of many real networks. To say that a network is a small world, it is necessary to ensure that it has a low value of the average path length and at the same time a high value of the clustering coefficient compared to that of a random network comparable to it, that is, with the same number of links and nodes. In egalitarian small world networks all nodes have about the same number of links. However, many real networks do not follow a Poisson degree distribution and are aristocratic, i.e. consisting of a majority of nodes with few links and a minority of hyperconnected nodes, called hubs. Examples of real networks of this type are known since decades, like the Internet (Faloutsos et al. 1999), the World Wide Web (Albert et al. 1999), the network of scientific collaborations (Newman 2001), the protein networks (Jeong et al. 2001) or the metabolic networks (Jeong et al. 2000). Since they do not have a typical scale, they are called scale-free networks. Their degree distribution follows a power law, namely:

$$pk \sim k^{-\gamma} \tag{8}$$

The different nature of the systems which, if described in terms of complex networks, shows the scale-free property makes it an almost universal feature, as shown by the recent comparison of differentlyscaled networks located worldwide (Galiana et al. 2022). Montoya and Solé (2002) compared the properties of real networks with those obtained for random networks with the same number of links and found that the average path length is very similar and very short, but the clustering coefficient is much greater for real food webs compared to random ones. This, as already mentioned, is a characteristic aspect of small-world behaviour. In addition, they obtained a strongly non-Poissonian link distribution P(k) which seems to follow a power law. Camacho et al. (2002) contradicted these results by stating that the clustering coefficient of real food chains is lower than that observed in small-world networks and therefore more similar to that of a random network. Furthermore, according to them, link distribution does not appear to be scale-free. However, they found that, when link distribution is normalized for link density L/S, it shows a universal functional shape given by an exponential decay instead of by a power law one. Also the clustering coefficient and the average path length follow a universal functional form that scales with the density of the links.

3.3. Network robustness

Some natural and social systems show a great capacity in maintaining basic functions despite the failure or lack of some of its components. The percolation theory studies the robustness of networks by assessing the impact of removing nodes or, alternatively, links. Robustness is inferred from the percentage of nodes that must be removed to completely break up the system (Mulder et al. 2012, Conti et al. 2020). In percolation theory, to get an idea of the degree of disintegration of the system, the measure of the largest component of the network (giant component) is considered. Alternatively, Dunne et al. (2002b) define the robustness of the food web as the fraction of primary species removed which induces a total loss of at least 50 % of the species (primary and secondary extinctions). In this study robustness calculation will be carried out according to this definition. The removal or failure of one node is not independent of the others because the activity of each node depends on the activity of its neighbouring nodes.

Therefore, cascading failures could be observed in which the failure of a missing node induces the failure of the nodes connected to it, in a comparable way to the domino effect in which a local variation propagates throughout the whole system. For this reason it is important to perform the calculations of the robustness of the network, not only from a structural point of view, but simulating the dynamics resulting from the removal of the nodes, as is done in the present study. The topology of the graph, and in particular the presence of hubs in scale-free networks, strongly influences its resistance to external attacks, determining the robustness of the system.

The greater robustness of scale-free networks compared to random ones, in response to the random removal of links, is due to the presence of hubs. Being random, removal will be much more likely to involve nodes that have a low degree because these are much more numerous than hubs (e.g. Barabasi 2016). On the contrary, hubs will be removed with an extremely lower probability and this is what allows the network to remain intact. The question is different in the case of targeted attacks on the system rather than random removals. Assuming to know in detail the topology of the network, attacks aimed at removing nodes with a high degree can be perpetrated. The removal of even a small fraction of hubs is sufficient to disrupt a scale-free network. To our knowledge, it is the first time that evidence is provided that ecological systems with a scale-free networks are very tolerant of random errors or failures, but, like communicative and social networks, they are very vulnerable to targeted attacks on the hubs (cf. Colizza et al. 2006, Cota et al. 2019). The hubs matter much more than expected in the soil biome.

Solé and Montoya (2001) studied the response of some food chains by simulating the loss of nodes and looking at the level of secondary extinctions. They came to the conclusion that the removal of highly connected species causes a very high rate of secondary extinctions compared to a random removal of species. It would therefore seem that ecological networks are more vulnerable to targeted attacks to hubs than to random attacks, characteristic generally found in scale-free networks (Strogatz 2001, Barabasi 2016). As mentioned previously, however, ecological networks do not seem to have a scale-free structure. According to Dunne et al. (2002b, 2004), the degree distribution still being fat tailed, even if not properly with a power law slope, alters the response to targeted and random removals so that the first modality is more effective than the second, similarly to what happens in scale-free networks. As specified by Dunne (2006), in the specific case of food webs, the removal of the most interconnected species is not always the best strategy to carry out targeted attacks affecting the integrity of the ecosystem.

In particular, Allesina and Bodini (2004) have shown that the most important species for the integrity of the system are the dominant species, that is those that pass energy to other species along the food chain. It is precisely the removal of these species that causes a greater number of secondary extinctions. The dominant species, although probably having a high out-degree value, are not necessarily the ones most interconnected if ingoing links are also considered. For this reason, in this study, the criterion for the removal of species in targeted attacks is the elimination of those nodes with a high closeness centrality value. The closeness centrality of a node is defined as the inverse of the average of its distances to all other nodes. It measures how close a node is to the others and quantifies how rapidly an effect that generates from that species can spread in the food web (Rocchi et al. 2017). It should be noted that, in the food webs studied here, the species with the highest



Fig. 3. Average Clustering Coefficient and Average Path Length. The dark grey columns represented the real networks and the light grey columns the average results for 10 comparable random networks with confidence interval. Please note the base-10 log-scaled vertical axes.

closeness centrality value are also the dominant ones, that is, the most abundant ones and those with a high out-degree value.

3.4. Degree correlation

Degree correlation is a property of graphs that regard the tendency of nodes to connect with other nodes of similar or completely different degrees. Based on this characteristic, three types of networks are distinguished. In neutral networks nodes link to each other randomly, so the number of links between the hubs coincides with what predicted by chance. In assortative networks nodes with comparable degree tend to link each other: small-degree nodes to small-degree nodes and hubs to hubs. Finally, in disassortative networks the hubs avoid each other, linking instead to small-degree nodes. A simple way to quantify the degree correlation makes use of the degree correlation function (Barabasi 2016). For each node i we can measure the average degree of its neighbours:

$$k_{nn}(k_i) = \frac{1}{k_i} \sum_{j=1}^{S} A_{ij} k_j$$
(9)

The degree correlation function computes all nodes with degree k.

$$k_{nn}(k) = \sum_{k'} k' P(k'|k)$$
 (10)

where $P(k^{*}|k)$ is the conditional probability that by following a link of a degree k node, we reach a degree-k' node (Barabasi 2016). Therefore, $k_{nn}(k)$ is the average degree of the neighbours of all degree-k nodes. If we approximate the degree correlation function with.

$$k_{nn}(k) = ak^{\mu} \tag{11}$$

the nature of the degree correlation is determined by the sign of the correlation exponent μ : positive for assortative networks, negative for disassortative networks and almost zero for neutral networks. There are many studies investigating the properties of networks that derive from their degree correlation, among which Murakami et al. (2017), D'Agostino et al. (2012), Tanizawa (2013), Thedchanamoorthy et al. (2014) and Neal (2019). According to these studies, assortative networks have the capacity to be more robust against targeted attacks, while disassortative networks have greater efficiency in the transport of information.

This would explain why communication-oriented networks, i.e. networks whose primary function is the exchange of information, have evolved a disassortative structure. In assortative networks, hub removal in targeted attack causes less damage because the hubs form a core group, hence many of them are redundant. Hub removal is more damaging in disassortative networks, as in these the hubs connect to many small-degree nodes, which fall off the network once a hub is deleted (Colizza et al. 2006, Cota et al. 2019). Real world networks display assortative hubs in some instances, particularly when high robustness to targeted attacks is a necessity (Thedchanamoorthy et al. 2014). The disassortative nature of ecological networks (Newman, 2002, 2003, Gross and Cardinale, 2005, Stouffer et al., 2005) could explain their weakness towards targeted attacks to the most interconnected nodes, more than their degree distribution.

4. Results and discussion

4.1. Topology of the food webs

To check if the three ecological networks considered in this study have a small world structure we calculate their average path length and their average clustering coefficient and we compare these results with the average values of the same quantities obtained from 10 random networks with the same number of nodes and the same average number of links. Since the considered direct networks are disconnected, for the calculation of the average path length it was preferred to take into account the corresponding indirect graph.

Fig. 3 shows that the average clustering coefficient of real networks is much greater than that obtained for random networks. Instead the average path length assumes a value similar, if not equal, to that of the random counterpart. These results are in line with those obtained by Montoya and Solé (2002) for other types of food webs. The low values of the average path length and the great difference between the average clustering coefficient of real and random networks can be considered a confirmation of the small world nature of the three networks analysed (Fig. 3). By comparing the values of the average clustering coefficient of the three real networks, we observe that networks 225 and 230, both organic farms, have very similar and, evidently, lower clustering coefficients than network 247, an uncultivated land. A higher clustering coefficient could indicate a greater robustness of the system, since the presence of clusters within the network guarantees the presence of alternative routes in the event of disappearance of nodes, and these results validate our computational approach given the lower soil quality of the sites 225 and 230 in comparison to the reference 247 (Material and methods). For all three networks the values of the connectance are 0.27, 0.21 and 0.24 (for sites 247, 225 and 230, respectively). Therefore, also in this respect, network 247 (C = 27%) seems to be more robust.

The study of the degree distribution of the links did not show particular trends in any network: hence it cannot be said that they have a scale-free structure. On the other hand, all three networks have a disassortative nature, as historically expected for food webs (Newman 2002, 2003, Stouffer et al. 2005): nodes with many links are mostly



connected with nodes with a low number of links. In this calculation, the total number of links, given by the sum of the incoming and outgoing links, was considered for each node. The results are shown in Fig. 4 in which is plotted the node degree vs. the average degree of neighbour nodes for the three networks. The assortativity values are deduced from the slope of the lines that fitted the data in the log-log plot. All three networks have highly similar and negative assortativity values: -0:387 \pm 0:011, -0:388 \pm 0:057 and -0:390 \pm 0:064 SD for networks 247, 225 and 230, respectively, despite the very different environmental conditions.

4.2. Robustness of the three food webs

We calculated the value of the robustness of the networks according to the definition provided by Dunne et al. (2002b). Using the model described in Conti et al. (2020), random and targeted attacks to the species with the highest closeness centrality (for the same values of the closeness centrality it has been chosen to remove the species that is most abundant), were simulated. We proceeded in the following way: starting from the undisturbed system, the closeness centrality was calculated for all nodes and the one with the highest value was selected and removed. The dynamics of the system and the possible occurrence of secondary extinctions were therefore observed. Once the system has reached a condition of stability, the closeness centrality values were recalculated for all nodes and once again the one with the highest value was selected and removed. This process ends when half of the species have disappeared from the ecosystem (both because of removals and because of secondary extinctions).

In Fig. 5 the values of the Alteration Index show to be as a function of the robustness that the three networks have if subjected to targeted and random attacks. The tables embedded below the plot show the robustness and the Alteration Index for the three networks, in the case of targeted attacks and random attacks. The values for random attacks were the average values simulated ten times. From the results obtained, some observations can be made. The first concerns the comparison between networks. Network 247 proves to be the most robust both in the case of targeted attacks and in the case of random attacks, confirming what already suggested by the values of the clustering coefficient and by those of the connectance; network 225 follows and finally network 230. This sequence closely reflects the ecological stoichiometry of the three soils, as described in Material and methods.

The second observation concerns a comparison between types of attacks: all three networks are more robust against random attacks rather than targeted attacks. The last consideration concerns the relation between the Alteration Index and the robustness of the system. The alteration suffered by the ecosystem depends on the robustness of the food-web architecture, hence the Alteration Index proves to be a good parameter for measuring the disaggregation of the system.

As expected, in the tests carried out, when robustness is greater, the Alteration Index is smaller, with the only exception of the case in which network 247 is subject to targeted attack. In the next paragraph we explain this apparent contradiction by focusing on the hubs. Fig. 6 shows the trend of the Alteration Index, the connectance, the complexity and species richness, as the nodes with the highest closeness centrality were removed for the calculation of the robustness against targeted attacks.

We note that connectance and complexity have similar trends: these decrease much more gradually and ultimately have higher values for network 247 than for the other two networks. The most robust network (our reference 247) is therefore the one that has higher values of connectance and complexity both at the beginning and at the end of the simulation. From the decreasing trend of species richness we can see the moments in which secondary extinctions occurred. Note that only a small fraction of secondary extinctions occurred in the reference 247 network, although earlier than in the other two networks. In contrast, the poor-quality soil networks 225 and 230 undergo a greater increase in the Alteration Index at the beginning, when only a small fraction of

Node Degree

40 50 60 70 80 90

35

30

tativity values.



Robustness vs Alteration Index

Fig. 5. The values of the Alteration Index reported as a function of the robustness that the three networks show when subjected to attacks either targeted (mostly to hubs) or random (mostly to spokes).

NETWORK 230

0.43

44.96

secondary extinctions occurs, and less when secondary extinctions are more (Fig. 6).

NETWORK 230

0.26

At the time of the major secondary extinctions, a low functional redundancy occurs and although fewer species undergo an alteration, the collapse is dramatic, confirming the rivets hypothesis (Ehrlich and Ehrlich 1981) that likens taxa to rivets holding together a complex system, and postulates that ecosystem functioning will be impaired as its rivets (species) fall out. Hence, all three networks have a disassortative nature as expected for food webs in general (Newman 2002, 2003, Stouffer et al. 2005), and for detrital soil food webs in particular.

It is remarkable that the cascading effect on biodiversity occurs much earlier in the network 225 than in the network 230, possibly due to the lack of hubs like omnivorous mites (*Pyemotes, Tarsonemus* and Stigmaeidae) connecting the bacterial and the fungal pathways, hubs that were recorded only in the latter network. Differences were found in the values of the clustering coefficient, of the connectance and of the complexity. These values were greater for network 247 and this suggested a greater robustness of this network than those depicted by the other two. The calculation of the robustness through a dynamic model confirmed this hypothesis. It therefore appears that the ecosystem related to the fallowed pastures with low pressure is much more robust than the two ecosystems related to organic farms subject to middle intensity management.

There are also differences between the two sites dedicated to organic agriculture, that are connected to the anthropic liming action that increased the soil pH of almost one order of magnitude (pH = 4.7 for site 247 and 5.4 < pH < 5.5 for the two other sites). The value of the clustering coefficient and the calculation of robustness suggest that network 225 is more robust than network 230, probably due to the higher soil organic matter content of site 225 in comparison to site 230 (5.6% and 4.4%, respectively). This result is in sharp contrast with what Dunne et al. (2002b) affirmed about the positive relationship between connectance and robustness, and can in our case be explained by a more dominant omnivory in edaphic communities, a phenomenon theoretically claimed (Pimm et al., 1991; Mulder et al., 2005, 2012; Sechi et al.,

2015; Brose et al., 2019; Thakur et al. 2020), but here demonstrated for the first time.

37.80

It is quite intuitive to say that the nutrients of the soil and its composition affect the resources available to soil organisms. This affects the type and abundance of invertebrates present in the soil and therefore the structure of the network from the lowest to the highest trophic levels of the food web (Clay, 2004; Powell, 2007; Mulder et al., 2013; Sechi et al., 2015; Wall et al., 2015). Despite this, in order to fully ascertain the correlations existing between the robustness of the ecological network and the type of management to which the site is subject, further studies would be required in order to shed light on the real anthropic impact have on the robustness of soil systems. If the computational evidences suggested by this study will to be confirmed by more empirical observations (possibly linked to ongoing valuable data repositories actions), the robustness shown by soil networks could be useful for evaluating, from an ecological point of view, the sustainability of agricultural practices. Our results provide hints towards both the realistic modelling of observational networks (i.e., empirical food webs) as well as computational evidence for an entirely novel way to assess ecosystem health.

CRediT authorship contribution statement

Letizia Stella Di Mauro: Formal analysis, Software, Visualization, Writing – original draft. Alessandro Pluchino: Formal analysis, Investigation, Project administration, Software. Erminia Conti: Conceptualization, Methodology, Resources, Validation, Writing – original draft. Christian Mulder: Conceptualization, Data curation, Investigation, Methodology, Resources, Project administration, Supervision, Writing – original draft, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence







the work reported in this paper.

Data availability

Data will be made available on request to C. Mulder, Section of Animal Biology "Marcello La Greca", Via Androne 81, 95124 Catania, Italy (christian.mulder@unict.it).

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