Structural divergence of terrestrial arthropod food webs in time and space

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Contents

Abstract

Climate change and landscape modification by agricultural intensification and rapid urbanization are two of the processes threatening biodiversity at a global scale. Our knowledge about the effects of this global changes on biodiversity are mostly based on findings at the species level. In this context, it is broadly accepted that agricultural intensification, climate change or pollution modify the number of species and individuals reducing or enhancing biodiversity. However, little attention has been paid to the effects on species interactions; on who interacts with whom and the strength or frequency of those interactions. Modifications at the food web structure can modify its stability and functionality even when species composition remains unaltered. Moreover, some of these interactions such as pollination or pest control sustain ecosystem services and contributes to the benefit of humans. In this essay, I examine how global change drivers impact interaction intensity, diversity and stability among food webs over time and space. In doing so, I explicitly target terrestrial food webs, with a focus on invertebrate networks. Mostly, I will target variation due to global changes such as land management, landscape complexity or climate change. Parasitism in invertebrates and mutualism between plants and pollinators are two networks that have been analyzed quantitatively for variation in their interaction structures in relation to global changes. Some of the variation in the food web complexity where shown to be driven by landscape complexity, geographical distance and time. Interactions, therefore, are dynamic processes and future research needs to take into account this aspect and include the food webs approach when investigating global change effects on natural communities. Thus, new data on how interactions vary the complexity of a network, is a current need to develop new knowledge about effects of global change on species interactions and to improve our predictions about the future of the ecosystems under the continuous changes induced by human activities.

1. Introduction

We are experiencing a deep ecological crisis. Global changes are threatening our ecosystems by altering the physical environment through changes in the temperature, nutrient inputs to the soil, changes in the landscape or destruction of natural habitats. This new scenario is, as well, the main cause of an increasing biodiversity loss (Butchart et al., 2010).These negative trends in biodiversity might affect overall functioning of ecosystems (Hooper et al., 2005). Therefore, biodiversity loss and species turnover have been for many years a central theme for conservation biologists. However, the link between species diversity and ecosystem functioning is not straightforward. Species are not independent organisms, they are part of networks where they interact with other species and these interactions are affected by the environment. Thus, it is realistic to expect a change in the interactions occurring between species when biodiversity is directly affecting the species pool. However, only because two species occur in the same place and at the same time does not mean that they will interact or they will do it with the same frequency everywhere. This network approach, thus, needs to be considered when connecting biodiversity and ecosystem functioning. The functionality of an ecosystem is a direct result of its network structure (Tylianakis et al., 2008). Therefore, assessing future changes in ecosystem functioning by only studying community composition is a not always valid approach. Therefore the study of species interactions in terms of food web structure needs to be taken into account when predicting the future of ecosystems.

In this essay I review recent findings about how species interaction networks vary in time and space and which are the factors that have been found to have an effect in the structure of ecological food webs. This approach is of great value for describing possible future scenarios regarding ecosystems functioning due to the current global change.

2. What is a food web

A food web is a representation of species interactions. Depending on the type of interactions we can distinguish between predator-prey, competition or mutualist food webs. For two species to interact we have to account for some simple but basic requirements. First, species must match in their phenology, they have to occur at the same time and at the same place. And second, there must be traits that allows the interaction, for example, a predator might need to be bigger in size than its prey or have specific abilities that will permit the interaction, for example hunting mode (Poisot et al., 2015).

Species inhabiting a certain habitat and the interactions occurring between them establish an interaction network where species are the nodes and the interaction linking each of them are the edges. With this approach, we can describe every network, from the simplest to the more complex and species rich communities. In a general way we could say that the number of species interacting and the number of interactions are the basic “building blocks” to describe any food web (Poisot et al., 2012). Figure 1 represents two simple food web with two primary producers, two consumers and one predator where the arrows represent the interactions. However in Fig. 1a) not every species interacts with every other. A way to quantify the differences between food web structures is to compare the relation and ratio between the species that define the network and the interactions that link them (see below).

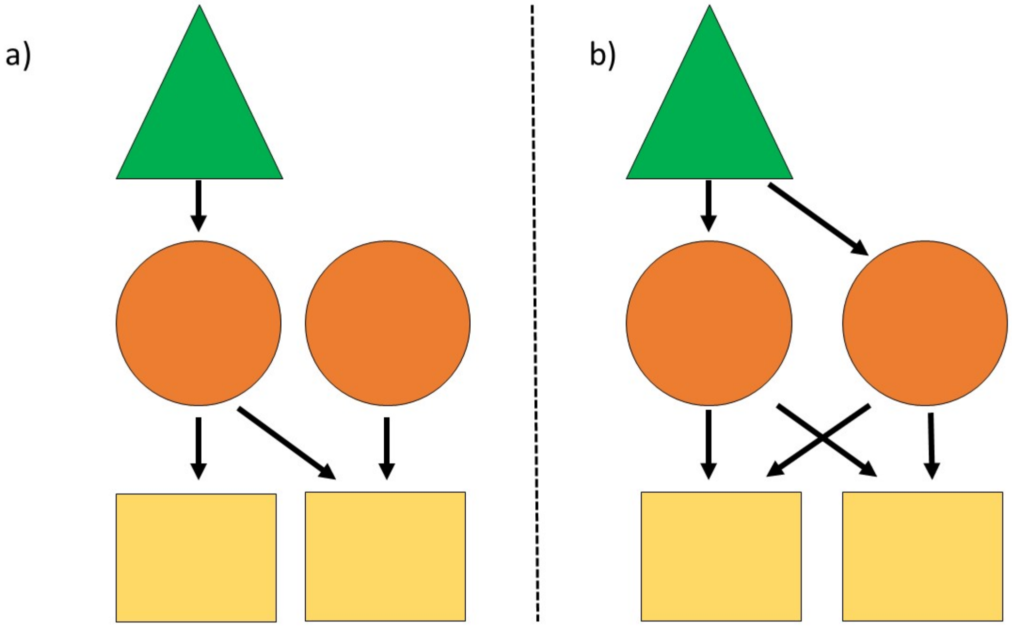

Figure 1. Example of two food webs with different structure. Squares represent primary producer species, circles represent consumer species (herbivores) and triangles represent predator species.

2.1. Food web structure and complexity

As mentioned before, the complexity of a food web is given by both, the number of interactions (links) in the network and the number of species or taxa (nodes) involved in those interactions. The more species, the more possible interactions can occur in a network. But for a real measurement of complexity we need to consider the evenness of the distribution of the interactions among species. In Table 1, I included some the most common attributes that are used for describing food webs (Thompson et al., 2012). These terms give an approach to how the food web is structured. For example, a high linkage density indicates that on average most species interact with many others. In Figure 1b network has a higher linkage density than Fig 1a. Figure 1b, thus, represents a food web dominated by generalist species where predators will feed on a larger variety of prey species than specialists.

In general terms, food webs that enclose a high number of generalist species have high linkage density and are classified as complex networks. Other metrics as connectance, generality or vulnerability represent different ratios of prey/predator, host/parasitoid or plant/pollinator that can be useful to understand how mechanisms as pollination or pest control work beyond species richness and composition. For example, a high vulnerability in a host-parasitoid network would indicate a high number of parasitoids per host species, giving us a great overview of how the network is assembled. Therefore, several of these food web descriptors have been used when describing specific networks (Trøjelsgaard et al., 2015; Tylianakis et al., 2007).

Food web attribute	**Definition**
Linkage density	Number of links per taxon.
Connectance	Proportion of potential tropic links that do occur.
Generality	Mean number of prey per consumer.
Vulnerability	Mean number of consumer per prey.
Robustness	Minimum level of secondary extinction that occurs in response to a perturbation.
Network Specialization	Deviation between observed and expected interactions if they were random.

Table 1. Definitions for the most common terms used when describing food web characteristics. Modified from Thompson et al. (2012).

2.2. Food webs structure: Stability and robustness against disturbances

But why does the network structure matters? Linkage strength affects the stability of the network. In other words, the strength of the interactions that builds the network modifies the capability of a network to maintain its main structure unaltered after the loss of a species. Stable food webs are expected to contain many weak interactions and few strong ones (McCann et al., 1998; Wootton and Stouffer, 2016). Here, it is important to remark that the strength of a link is negatively related to the degree of generalization of the species. Links connecting a specialist predator and its prey will be stronger than those connecting a generalist predator with one of its prey. In practice, the strength of a link can be used as a way of describing the influence of both interacting species on each other. A specialist predator will likely go extinct if its prey is lost, while a generalist predator will be almost unaffected by the same process. Meanwhile, a prey species will be highly affected by the feeding rate of a specialist predator while generalist predators will slightly affect its growth rate (Montoya et al., 2006).

As a result, the more complex an interaction network is, the weaker are the links between species, which ultimately will conceive a greater stability to the web. Examples of these stability can be found both in the temporal and spatial scale in the study of food webs of herbivore insects and their natural enemies on oaks (parasitoids) (Kaartinen and Roslin, 2012, 2011). Both studies found great changes in the community composition at the species level both, in space and time. Yet, this difference was not observed in the interaction structure of the food webs. The reason behind these results is that the networks were complex and most of the species turnover could be explained by the extinctions or colonizations of rare species, while common generalist species typically persisted across the food webs (Kaartinen and Roslin, 2012, 2011). In other words, the high generality of the networks kept a stable structure in time and space.

When a species is lost or extinct in an ecosystem, its absence can drive the extinction or loss of other related species, this is what we call secondary extinctions. Clear examples of secondary extinctions show how the absence or low density of a top predator can negatively affect the primary producer level by increasing the negative effect of the herbivores (Estes et al., 1989). Robustness against secondary extinctions (see Table 1) is directly related with the generality of the network. Higher connectance (the realized proportion of possible links; calculated as the linkage density by the number of species in the network) increase the robustness in a species interaction network (Dunne et al., 2002). Therefore, the more generalist species in a community, the more stable it will be against extinction processes. When extinction processes target specialist species a smaller fraction of a network will be affected but those few links may be hard to recover. In this line of reasoning, ecological networks will be robust against random losses of species but really fragile when keystone species are the target of this losses (Solé and Montoya, 2001). These keystone species are normally highly connected nodes within the species interaction network, therefore their loss would affect a great proportion of the network (Solé and Montoya, 2001).

Redundant interactions are important for the stability of a network. Networks where this phenomenon is observed are characterized a high number of interactions per species (linkage density), therefore the addition or removal of one species will not affect the overall functioning of the network (Peralta et al., 2014). For example, a food web with high species redundancy will be secured in case of one species goes extinct since other species will cover the same interactions or function in the network as the extinct species (Borrvall et al., 2000). Contrarily, networks with really rare or specialized species may be really unstable against extinctions.

Therefore, recent findings on ecological networks are of great importance for conservation biology for several reasons. First, they provide valuable data to the task of linking ecosystem functioning with its components and structure (Thompson et al., 2012). Second, they give hope to maintaining the functionality of important ecosystem networks as pollination or pest control even when a biodiversity reduction has taken place (Kaartinen and Roslin, 2012). And finally, they are crucial to identify the keystone species whose extinction could lead cascading effect and disable the same services (Stouffer et al., 2012).

3. What has been explored so far?

Our knowledge about how a species interaction network is assembled, its importance or the role of its structure for the overall stability of the ecosystem is limited to certain specific interactions and organisms. In this essay I will review the available information concerning invertebrate food webs in terrestrial ecosystems. More precisely, I will target host-parasitoid and plant-pollinator food webs. To date these two food webs have been the most studied invertebrate and terrestrial webs, from a structural point of view. Both networks have been described using the same methodology and most of the reviewed literature shares basically the same approach where data on species interaction is based on direct observations. In the case of the pollinator-plant food webs, the network metrics are normally based on direct observations of interactions pollinator-plant during transect counts. In the case of host-parasitoid food webs, the interactions are normally described from data on the parasitoids found in the collected host species. Therefore, it is understandable that a general problem when studying predator-prey interactions between invertebrates in terrestrial ecosystems is the difficulty of directly observing every interaction to get a complete or “close to the real” food web. This may be the main reason for this type of network to be partially unstudied or being less commonly targeted in empirical studies. However, new molecular techniques like analyzing predator´s gut content are being tested and so far the obtained results are encouraging making the sampling of species interactions much easier and reliable (Roslin and Majaneva, 2016). From this raw data, composed of species at different trophic levels, the links that connect them and the frequency or strength of each link, metrics as linkage diversity, connectance, generality or vulnerability are calculated exactly in the same way for every type of network. This methodology, thus, creates a great opportunity to compare networks in a large geographical and temporal scale.

3.1. Host-Parasitoid food webs

Host-parasitoid networks are one of the most studied food webs in terms of its structure. Many examples of the temporal and spatial change of these networks can be found in recent work but also over the last decade. Here I present some of the drivers that have been on the focus of such studies.

3.1.1. Landscape complexity and structure

Landscape complexity and composition is one of the best studied factors affecting ecological communities. In terms of food web structure, landscape complexity has been shown to alter properties of host-parasitoid networks. Tylianakis et al 2007 studied the networks composed between cavity-nesting bees, wasps and their parasitoids in a gradient of landscape complexity that covered several land use types from forest (complex landscape) to pasture and rice fields (highly modified or simple landscapes). The results showed that parasitism in bees and wasps was higher in modified habitats and simple landscapes. If we consider parasitism rate as an ecosystem function this is a clear example of the relation between network structure and ecosystem functioning. In addition, pastures and rice fields had more specialized parasitoids, and therefore a higher vulnerability to species loss (Tylianakis et al., 2007). This may appear strange if we think about specialized parasitoids as rare parasitoids. However, this was not the case here, since the decrease in generality was driven by the specialization of generalist parasitoids. Thus, parasitoids with a large range of hosts in complex landscapes specialized on fewer hosts in the simple landscapes. These results have direct impact on the robustness of the network since it implies that the loss of a single species could alter the whole network structure if this is a keystone species (Solé and Montoya, 2001). One of the most interesting result by Tylianakis et al. (2007) is that all the observed changes occurred with almost no changes in the species richness or evenness across the complexity gradient, indicating that species richness may have little importance in terms of network structure. It also shows that the same species may interact differently depending on the habitat. Similar results have been found when studying host/prey-parasitoid/predator food webs structure in a gradient from intensively managed grasslands to restored meadows. Complex landscapes obtained the highest score in food web complexity in terms of linkage density (Albrecht et al., 2007). One may think that this results could partially be explained by restored meadows being richer habitats in their plant composition. However, even though biodiversity in the lower trophic level (producers) appears to affect more positively species in higher trophic levels, not all the differences in network structure can be explained without other factors as landscape diversity in this case.

However, one should not expect the same results for the structure of every food web when studying landscape complexity in different systems. Host-parasitoid food webs in agro-ecosystems have been found to be simpler in complex landscapes (Gagic et al., 2011). In this example, the proportion of pest individuals that where infected by parasitoids in cereal fields in complex landscapes was higher than the one in homogeneous landscapes. The explanation for this results was that one of the parasitoids species became particularly dominant in the complex landscape. Similarly, it was found that the agricultural intensification was positively related to the complexity of the networks (Gagic et al., 2011). Landscape complexity and its relationship with pest control or parasitism rate, thus offers some contradictory results. These contradictions appears to be even greater when comparing new food web structure studies (Albrecht et al., 2007; Gagic et al., 2011; Tylianakis et al., 2007) with previous literature comparing parasitoid richness and rates of parasitism (Montoya et al., 2003). However, these variation should not be consider as contradictions but as a warning to consider some important facts when analyzing food web structure as the difficulty to generalize results when comparing networks, the need for a unifying criteria and the non-lineal relation between diversity and network complexity.

A clear example about the sometimes wrongly assumed connection biodiversity and food web complexity was found when mapping food webs composed by herbivores and their natural enemies inhabiting oaks (Kaartinen and Roslin, 2011). The results showed how the networks kept most of their structural characteristics unaltered even if the differences in species richness and composition varied greatly across a landscape gradient (Kaartinen and Roslin, 2011). These results enhance the importance of studying network structure instead of basing the total of our environmental policies on information from species richness and inventories. A species richness approach in Kaartinen and Roslin (2011) could lead us into thinking that the functioning of such networks is under a threat if we would not find the expected species composition. However, a closer look from a food web structure approach would show that the observed changes in the species composition would not alter the overall structure of the network since species turnover affected mostly rare species.

3.1.2. Soil quality

Nutrient enrichment has been proposed to explain higher connectance in a host-parasitoid interaction network (Fonseca et al., 2005). Nonetheless, in this case the differences disappeared when accounting for the effect of the matrix size. The reason is that a larger matrix will contain a larger number of species and as a result a higher number of interactions, which will increase the network connectance (Fonseca et al., 2005). Yet, later findings suggests a relation soil quality – network structure. For example, differences were found in the connectance and vulnerability of host-parasitoid networks between organic and conventional farms (McFadden et al., 2009). Organic farms showed higher species richness but also a higher number of parasitoid species attacked the herbivore community. However, and contrarily to what one would expect the robustness of the network was not altered when the food web was exposed to simulated species loss (MacFadyen et al., 2009).

3.1.3. Invasive species

A priori we could hypothesize that pest control will be threatened by invasive species colonizing new habitats or expanding they range (Cannon, 1998). Therefore, knowledge about the effect of novel species on a host-parasitoid network is crucial for the future of pest control. However, this information is scarce or not available. One of the few examples available is an experiment were a new herbivore was introduced into a network with a rich parasitoid community (McFadden et al., 2009). The goal was to simulate an alien species invasion in the network hypothesizing that a rich parasitoid community would affect more negatively the invader´s performance. However, the results showed that the mortality of the new pest did not increased with species richness. This result remarks once again the fact that species richness and ecosystem functioning do not always correlates, however no network metrics where used to quantify the food web structure in both treatments so no conclusions can be established from the network structure point of view. Therefore, much more needs to be done if we want to predict the status of biological control under the threat of species invasions.

3.2. Mutualistic food webs involving plants and pollinators

The second type of ecological interaction food webs I am focusing on are mutualistic plant-pollinator networks. An increasing number of pollination studies is currently reporting food web metrics (Aizen et al., 2012; Olesen et al., 2008, etc.). Further, these networks have been usually presented as perfect models to study the future global change scenarios. The relationship between the plants and their pollinators is mediated by the phenology of both partners, therefore the effect of climate change in these networks can be easily assessed or predicted in short study periods (Memmott et al., 2007). Thus, pollination food webs have been the target of some recent work assessing the influence of drivers such as habitat loss, species invasion or changes in the temperature regime.

3.2.1. Habitat loss and fragmentation

Habitat loss can affect the structure of pollinator networks by reducing the habitat area or increasing its fragmentation, which would have a direct effect in the way species interact. The smaller the patch the simpler the network would become the interaction matrix would contain less species. Additionally, if the landscape is highly fragmented some species would have difficulties to keep their role in the network, for example making some resources/prey unreachable. Recent findings have shown how generality and frequency of interactions in a pollinator network decreased when reducing the patch size (Aizen et al., 2012). This could be explained by generalist species losing their main role when decreasing the patch size. The ultimate consequences of this reduction in generality is a decrease in the robustness of the system (cf. section “Stability and robustness against disturbances”). The reduction of the habitat quality can also affect the components of an ecosystem food web. Habitat restauration was found to recover pollination networks when evaluating grassland restoration in Sweden (Winsa, 2016).

Geographical distance between communities could explain differences between pollinator mutualistic networks (Trøjelsgaard et al., 2015). Networks geographically distant including plants and their pollinators are expected to present larger differences in their structure than geographically close networks. This hypothesis was tested in a system of islands and it was found indeed, that more distant pollinator communities were more different in their plant and pollinator species composition but also in their interactions (Trøjelsgaard et al., 2015). Each island presented a different set of organisms, so the turnover between islands was significant (mostly endemic species) but when the same species where present in more than one island, the fidelity or strength of their interactions decreased with the distance.

Altogether, these results can provide us with some valuable information about how habitat loss or fragmentation may affect plant-pollinators interactions under the current global changes. We could expect that reducing patch size we would decrease the robustness of the network (Aizen et al., 2012) and that increasing fragmentation (distance between habitable patches) we would modify the partner fidelity (Trøjelsgaard et al., 2015). Therefore, landscape complexity and configuration seem to be important factors altering these food webs. However, specific work focusing on these questions need to be conducted.

3.2.2. Temperature

We can hypothesize that rising temperatures will affect the network structures in time and space. Metabolic processes are partially controlled by temperature, thus, feeding rate or handling time are assumed to be directly affected by temperature (Brown et al., 2004). Similarly, theoretical models have shown that temperature can alter the mobility of both the predator and the prey, and thus their encounter rate – thereby having visible effects on food web functioning (Dell et al., 2014). Therefore, it seems likely that an increase on the average temperatures will have direct effects on the most basic mechanisms that regulates species interactions (Rall et al., 2010).

Apart from these effects at a metabolic or physiological level, there are other ways changes in temperature can affect networks. The mismatch in phenology accelerated by global warming is one the most obvious and well-studied problems (Hegland et al., 2009; Memmott et al., 2007). The natural cycle of some species can be seriously affected by a change in the temperature regime and the primary consequences can be observed in temporal mismatches between interacting species. Even though both, the onset of flowering plants and the emergence of the pollinator community are similarly affected by an increase in the mean temperatures, it is hard to expect exactly identical specific species responses by both groups (Hegland et al., 2009). This shifts in phenology have been broadly studied in mutualist networks, however it has been often addressed through a community composition approach. Thus, conservation biology has often conclude that pollination will be secured in ecosystems with a diverse pollinator community when facing these future changes. The reason behind this theory is that a richer pollinator community will offer a larger variation in the responses to changing temperatures. Therefore an overlap of responses or a higher complementarity will ensure that the pollinator community can provide the service (Blüthgen and Klein, 2011; Memmott et al., 2007). Thus, by extrapolating the results based in community composition data to a food web structure approach we can assume that is really likely that changes in the temperatures regime will affect the way organisms interacts. However, this relation remains to be clearly demonstrated. I included temperature as a factor affecting the food web structure of the plant-pollinator interactions because it is assumed to have a great importance. However, the existing data providing this theoretical framework needs to be supported by empirical work and a continuous data over the years. Therefore, we could draw conclusions about the effect of climate change in plant-pollinator networks.

3.2.3. Invasive species

Mutualist networks have been found to be highly affected by the introduction of new species. The work done by Aizen et al. (2008) is a perfect example to explain the transformation process suffered by the network across an invasion using data on networks at different invasion stages based on the incidence of alien species. At the beginning, when the non-native pollinator species are rare and limited in habitat, they will interact with the most generalist plant species, abundant and widely distributed (Olesen et al., 2002). But as the non-native pollinator species become more common, they turned into more generalist pollinators interacting with a broad range of species. Introduced species can even enhance the stability of the network with no changes in the overall connectivity (Aizen et al., 2008). The truth is that this benefits are masked by a decrease on the connectivity between native species. In other words, the invasive species will become a generalist that will overcome the loss of connectivity between native species. I may use this empirical example to remark that even if ecology agrees on considering the network structure as a conservation priority, species richness should not be completely ignored.

But not only invasive pollinator species have been targeted. The effect of invasive species on the pollinator network structure have been also studied from the plant perspective (Stout and Casey, 2014; Tiedeken and Stout, 2015). Quantitative network metrics were compared in two different periods, during the invasive plant was flowering and after the flowering period in Ireland. The results showed how the invasive *Rhododendrum ponticum* acted as a super-generalist in the network during its flowering period, monopolizing almost a 50% of the pollinator's visits. But interestingly, once its flowering period finished, the network structure remained stable and was almost unaffected (Tiedeken and Stout, 2015). This output is the result of native species occupying the empty space left in the network after Rhododendrum *ponticum* floral resources were not abailable. However, not every native species replaced the invasive plant and its dominant role in equal proportions. Instead, few plant species became more generalist than the rest of the native vegetation community (Tiedeken and Stout, 2015). From another perspective, pollinators did not replaced the floral resources of *Rhododendrum ponticum* with only one native species but expanded their range of plant used. Generality, to be understood as number of plants used per pollinator in this case, increased during the second period. From this results we can conclude that the degree in which an invasion will affect a mutualistic network may depend on the native vegetation composition and its phenology. In this case, even if the introduced plant became dominant and a highly connected generalist, the pollinator community was able to find floral resources after its flowering period so the network structure was not disturbed. An important point to account for is that, as the authors point at, the removal of highly connected invasive species could have a detrimental effect on the pollinator community if there are no native plants that would overcome the loss of floral resources.

Nevertheless, sometimes phenology does not explain the effect of an invasion. An invasive plant with a more overlapping flowering period can attract more pollinators to the whole native plant community, thus, benefiting the functioning of the network. While other plants with similar characteristics may had a negative effect in the visitation rate to native competing for pollinators (Bartomeus et al., 2008). Therefore, even though species invasion may be the most studied factor in terms of plant- pollinator food web structure, differences like the one found by Bartomeus et al. (2008) implied that generalizations cannot be easily drawn.

3.3. Similarities and dissimilarities between plant-pollinator and host-parasitoid networks

Interaction networks can be used to describe any type of interaction occurring between individuals, from mutualistic relations as pollination, to antagonistic ones as predation or parasitism. Thus, the general metrics of linkage, connectance, generality, vulnerability, network specialization etc. (cf. above, section “Food web structure, complexity and functionality”) can be used to describe the structure of any food web. For example, if we speak about “vulnerability” we will describe it as the number of parasitoids per host, number or pollinators per host plant or number of predators per prey depending on what type of network is the studied one. Therefore, an advantage of using this approach is that the theories and terminology used when studying any type of network are the same and generalizations can be done in order to find similar or dissimilar patters between different ecological processes. For example, if we are interested in understanding the interactions and processes occurring in a crop field we may need to account for three different systems: pollination, parasitism and predation. Based on our current knowledge, few generalizations can be done.

3.3.1. Robustness of plant-pollinator networks and variation in host-parasitoid

Mutualistic plant-pollinator networks appear to have a constant and common structure in most of the cases that this type of food webs have been analysed. First, pollinator networks have been found to be really complex. These food webs are normally built by a high number of plants and pollinators involved in a heterogeneous system with a high density of links (Olesen et al., 2007). Second, networks present a clear nested structure, which basically means that while generalist interact with a great set of species, specialist interact with smaller sub-sets within the generalist set (Bascompte et al., 2003). Third, it exists an asymmetry in the interactions, specialist pollinators will visit only a plant species, but this plant species is at the same time a generalist visited by a large set of pollinators or vice versa. (Bascompte et al., 2003). Overall, these characteristics result in really complex systems with high linkage and connectance which ultimately make plan-pollinator food webs a perfect example of stable and robust networks (Dupont et al., 2009). However, this positive statement from a network structure perspective does not change the reality of the worldwide declining pollinator populations (Potts et al., 2010).

Host-parasitoid networks instead appears to be more difficult to classify or generalize when it comes to the stability of their structure. In some cases they have been shown to have a great stability in structure along time and space (Kaartinen and Roslin, 2012, 2011; Peralta et al., 2014). But interestingly, it is possible to find the opposite results in the existing literature. Here, I have briefly discussed how sometimes the landscape simplification have a great effect simplifying the network structure (Tylianakis et al., 2007), while in other cases the food web structure showed a more complex structure in homogeneous landscapes (Gagic et al., 2011). A possible cause for these differences is that the chosen examples do not correspond to the same study systems and geographical areas, making harder the comparison. While Tylianakis et al., (2007) focus on tropical host-parasitoid food web composed by cavity-nesting bees, wasps and their parasitoids, Gagic et al., (2011) targets cereal aphids and their parasitoids in central Europe. However, this contradictory results point at the importance of studying the food web structure and understand the drivers for its variation, it may be that in tropical areas the drivers differ from the ones in central Europe.

3.3.2. Temporal variation: Network stability despite changes in community composition

As a general fact, it is interesting to point at the temporal dynamics of both network types. Temporal variation in pollinator networks have been observed even within a single season. The phenology of every single plant and pollinator specie create a great variation in the community composition throughout the season resulting in continuous changes of the network structure. The role of a single species, therefore, will be assigned by the length of its phenophase (Olesen et al., 2008). Thus, a pollinator with a wide phenophase will have to opportunity to interact with a larger set of flowering plants, becoming a generalist, while specialist will have a temporal constrain that will restrict the interaction with some of the earlier or later flowering plants. Changes in the plat-pollinator food web structure can be observed as well when looking at this networks in a geological time scale. For example, in a system of islands, the structure of the networks in older islands was characterized by interactions between specialists while generalist interactions had a higher representation in younger islands (Trøjelsgaard et al., 2015). Overall, pollinator networks have been described as robust networks over time even though their species composition can vary drastically.

Host-parasitoid networks, on the other hand have not shown a constant or clear response in their structure over time. At least there are not many examples of their temporal variation, so it is hard to generalize. There are, however, examples of networks with strong temporal stability between years in their structures despite a high species turnover rate (Kaartinen and Roslin, 2011). Complementarity or redundancy are normally used as predictors of food web stability but this has not been the case when testing it at some host- parasitoid networks over its temporal variation (Peralta et al., 2014). Therefore, despite sharing some common properties, we cannot say that plant-pollinator and host- parasitoid networks are completely similar in this aspect. Plant- pollinator food webs appear to be more constant in their structure and temporal stability than host- parasitoid webs. Plant-pollinator networks experience great temporal variations between years but also within a single season so maybe this is a reason for them to be specially robust and stable. However, more empirical works needs to be done if we really want to compare the temporal stability of both networks, especially in host- parasitoid networks.

4. Knowledge gaps

Biodiversity is the main focus in most of the research targeting global changes and the response of natural ecosystems. This approach target the nodes of the species interaction networks but it lacks a deeper understanding on how these networks are structured or how they respond to changes. Fortunately, food webs approaches and the importance of network structure are increasingly being considered over the last years. Yet, a first look to the literature covering empirical work in this field make visible several knowledge gaps.

Probably, the most visible knowledge gap is the fact that only few types of species interaction networks have been studied from a structural perspective. In this essay I review the recent literature about food web structure in terrestrial arthropod food webs. In this framework, plant-pollinator and host- parasitoid food webs have been the target of nearly all the empirical work during the last decade. Knowledge about predator-prey interaction networks, on the other hand, is scarce. Probably, one of the reasons for explaining this lack of information has to do with the complexity of predator-prey food webs and the difficulty to identify all the possible interactions, especially the second one. Species interactions in pollination can easily be assess by direct observations (see i.e. (Bartomeus et al., 2008; Olesen et al., 2008; Trøjelsgaard et al., 2015). Similarly, host-parasitoid food webs have been built based on information extracted from the host after their collection in the field (Hrček and Godfray, 2015). Therefore, describing predator-prey food webs can be a challenge when identifying all the possible interactions, direct observations are not always possible and so far the best solution is the use of molecular techniques (Roslin and Majaneva, 2016; Sheppard and Harwood, 2005).

Another area where our knowledge about food webs structure lacks of support is in empirical work. It exist an unbalanced proportion of papers targeting theoretical models and empirical research, the former ones being more abundant. The theoretical work cover a wide range of knowledge about structure variation and robustness of interaction networks (Berlow et al., 2004; Solé and Montoya, 2001). However, this theory can be considered insufficient and more empirical work is needed in order to validate our theory-based knowledge about how food web structure is affected by disturbances.

4.1. The importance of understanding the effect of global changes on network structure

Which drivers need to be prioritized when evaluating changes in food web structures? Global changes have direct effects on species interactions (Tylianakis et al., 2008), therefore, ecology should prioritize its effort by studying the effect of the most important and evident drivers for food web structure variation. Due to the evidently relation between food web structure and ecosystem functioning, most of the work in this field has focused in analyzing food webs providing ecosystem services. Therefore, most of the empirical work has been carried out in agro-ecosystems and semi-natural habitats. As a result, landscape composition, intensification and management practices are among the most explored topics (Gagic et al., 2011; Tylianakis et al., 2007). Information about the effect of other global change drivers as temperature, CO2 concentrations or soil enrichment and management can be found, but normally this work is far from a network perspective. Resource lack often limits the possibility to study species interaction. Therefore, the food web structure approach is commonly based in interactions between two trophic levels, or it focus on specific groups or species leaving unexplored the effects of such drivers in the whole food web structure (linkage density, connectance, generality, vulnerability etc). However, hypothesis can be drawn by basic assumption taken from these studies, even when their focus is not the structure of the food web itself. For example, even though the effect of rising temperatures have not been studied in predator-prey networks we can create hypothesis and possible scenarios from similar studies targeting pollinator networks or even species-specific interactions. For example, it is hard to expect that two plants cohabiting in the same community would have a similar response for each environmental factor: temperature, light, soil richness or water availability. Additionally it is difficult to anticipate that climate change will alter all these factors with the same strength and direction, therefore it is expected that some species will be more negative or positively affected by the future changes. Hence, species interactions are expected to change, especially in those cases where the interacting species are directly affected by climate change. For example, two pests, the nun moth (Lymantria monacha L. (Lepidoptera: Lymantriidae)) and the gypsy moth (L. dispar L), are expected to expand their norther distributions by 500-700 Km while retreating their southern limit by 100 to 900 Km (Vanhanen et al., 2007). This prediction have serious implications since predators for these two pests could be differently affected by rising temperatures or have a greater tolerance that would allow them to keep their geographical distribution. Therefore a shift in species distribution will have an effect in species interactions, but food web structure need to be analyzed if we want to say something about the implications for the functioning of the ecosystem.

CO2 rising levels have been shown to directly affect plant communities. Specifically, and among other effects, an increase in the CO2 levels can alter the growth rate and C:N ratio of the plant leaves. These modifications therefore, will directly affect the herbivore community. More precisely, insects from different feeding guilds may have different response, in terms of consumption rate and pupal weight, to an increase in CO2 levels (Bezemer and Jones, 1998). Mutualistic networks are expected to suffer similar changes due to phenological shifts driven by an increase of the atmospheric CO2. (Memmott et al., 2007) found that pollinators could lose up to 50% of the floral resources available due to this mismatch.

Yet, and to recapitulate, future research need to focus in the general food web structure in addition to specific interactions if we want to have a whole picture to predict the future of the ecosystems and the implication for the species relationship. This species-specific studies point at changes happening at some nodes or levels of the trophic network so it expected that the food web structure would be affected as well.

4.2. Conclusions and future directions

Networks are clearly dynamic in space and time and its variation includes not only species composition but also interaction diversity (Poisot et al., 2012). Even though the current knowledge about changes in trophic interactions is supported by many theoretical studies, it exists an important gap between the theory and empirical research where observations and experiments in nature need to back theory. A frequent position to exclude network structures in scientific research is the difficulty of tracking species interactions (Poisot et al., 2012). The sampling effort when targeting links between species can be even greater than the one for species composition and in some cases researchers lack in resources, data quality or a define methodology to study species interactions. Nevertheless, new opportunities are emerging. Recent theoretical work and empirical studies have shown that simple measurements are enough to quantitatively assess the structure of the sampled networks (Bersier et al., 2002; Poisot et al., 2012; Roslin and Majaneva, 2016). Sampling effort can be reduced if large or global scale studies would target the most common interactions, normally abundant and easy to sample, leaving a part the rest of the rare interactions with a smaller effect in the global differences.

Maybe the most important and relevant reason to turn our focus to the study of species interaction networks is that global changes are threatening our ecosystems and the loss of species and natural habitats is just the top of the iceberg. The future of conservation biology has to be led by an incorporation of new aims including the conservation of ecosystem network structures. Moreover, every ecosystems in the planet have direct effects on the human population welfare. Grasslands and meadows are habitats for species interaction networks intervening in the pollination and the natural pest control of our crop fields while soil communities are responsible for the recycling of nutrients and organic matter, etc. Therefore, the study of complex food webs with multiple levels opens an opportunity for better understanding ecosystem functioning and the effect of global changes (Albouy et al., 2014). Nevertheless, to be able to advance in this field, empirical studies where the structure of the network and its functionality are manipulated are needed (Thompson et al., 2012). It is important, however, to distinguish between different ecological problems and decide whether it is important to focus on network structure conservation or species conservation. If we think about it, a stable ecosystem may be also more uninteresting from a biodiversity point of view, since its network might be composed of many generalist species and only few rare ones (Tylianakis et al., 2010). Thus, the conservation of rare specialist species could move to a second position if the focus is on the preservation of the ecosystem network structure. On the other hand, managements with the goal of increasing the number of rare species could weaken the linkage density of the network, thus, decreasing its stability. It would be of great interest to have a guideline about whether to focus on one or another ecosystem aspect depending on the region, ecosystem type, threat, etc. For example, (Stouffer et al., 2012) propose to focus on species´ roles prioritizing the conservation of those species contributing in a greater way to the stability of the network. In other situations it may be of interest to target network modules, namely a group of species that interact more closely within the food web. Nevertheless, and indifferently if the aim should be to preserve network structure or species diversity, both aspects need to be taken into account to understand natural communities and assess their health or status. Ecology and conservation biology, thus, have now the challenge of integrating both approaches in the future research of natural ecosystems.

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