Disentangling Plant-Animal Interactions into Complex Networks: A Multi-view Approach and Perspectives

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Learning Objectives

After completing this chapter, you should have an understanding of the following:

- The terms: species interaction networks, nestedness, modularity, individual-based networks, multilayer networks.
- How stochastic and deterministic factors shape the organization of plant-animal networks.
- The ways in which interaction networks vary over space and time and are affected by environmental perturbations.
- The potential of ecological networks for understanding plant-animal interactions and their evolutionary and coevolutionary processes.

10.1 Introduction

Since the seminal book *On the Origin of Species* by Charles Darwin, modern ecologists have been aware that the origin, maintenance and function of biodiversity are products of biotic interactions among species (Darwin 1859; Ings and Hawes 2018). Particularly, the majority of animal and plant species are embedded in highly diverse trophic systems which include different types of organisms within a large and complex web of life (Herrera and Pellmyr 2002). The idea of a web of life has been used as a theoretical framework to study the complexity of these plant-animal relationships in species interaction networks (Dáttilo and Rico-Gray 2018). In these interaction networks, plant and animal species are denoted by nodes and their interactions by links describing the use of plants as resources by animals (Ings et al. 2009). By studying plant-animal interaction networks, researchers have provided new insights on how interactive communities are structured and the ecological and evolutionary dynamics of these systems (Bascompte et al. 2003; Bascompte and Jordano 2007; Vázquez et al. 2009).

In general, plant-animal interactions range from negative (e.g., parasitism and herbivory; Poisot et al. 2017; López-Carretero et al. 2018) to positive (e.g., pollination and seed dispersal; Vizentin-Bugoni et al. 2018; Anjos et al. 2020) interactions, all of which directly contribute to the functioning of ecosystems. For example, in the tropics, 90% of the woody plant species depend on animals to move their pollen and to disperse their seeds (Jordano 2000; Ollerton 2017). Without such mutualistic interactions, these plants would be unable to complete their life cycles, and their animal partners would be unable to feed themselves (Herrera and Pellmyr 2002). Recent evidence supports the idea that ecological interactions are the driving force of natural selection in nature, where all species reciprocally affect each other across their populations and communities (Guimarães et al. 2011; Medeiros et al. 2018). For example, a study performed by Galetti et al. (2013) showed that the loss of large-gape avian frugivores in forest fragments led to a reduction in seed size, highlighting the role of ecological interactions in the evolutionary trajectories and compositions of tropical forests. Despite the important role of biotic interactions in both ecological and evolutionary processes, there is still only limited use of biotic interaction theory to address ecological hypotheses.. Therefore, the incorporation of the diversity of biotic interactions into species interaction networks remains an important gap in our knowledge of biodiversity and ecosystem functioning (Luna et al. 2020).

Even though plant-animal interactions can be studied under several approaches and facets, here we aim to explain how plants and animals interact by forming non-random ecological networks, and how both stochastic and deterministic factors shape the organization of these networks across environmental gradients. Moreover, in this chapter, we will explain how ecological networks can be used to study not only how groups of individuals from different species and trophic levels interact with each other (i.e., interspecific networks) but also how individuals within groups vary in their interactions (i.e., individual-based networks). Finally, we will introduce a multi-layer view of ecological networks, and we will conclude by discussing the future of ecological networks and their robustness and stability to different environmental disturbances.

10.2 The Non-random Organization of Plant-Animal Interaction Networks

Historically most studies have focused on describing and explaining the ecological and evolutionary dynamics only between pairs of species (see Herrera and Pellmyr 2002). For this reason, ecological interactions among *groups* of species are one of the less understood and studied components of biodiversity (Luna et al. 2020). In fact, only in the past 20 years have we started to understand the role of ecological interactions in shaping biodiversity and ecosystem functioning (Ings and Hawes 2018). Now, ecological theory recognizes that ecological communities are groups of species that not only coexist but also depend on each other (Vellend 2016). For example, plants provide food resources for many animal species in exchange for positive services (e.g., pollination or seed dispersal; Escribano-Avila et al. 2018; Vizentin-Bugoni et al. 2018), but are also strongly affected by antagonistic partners (e.g., herbivores and seed predators; López-Carretero et al. 2018; Luna et al. 2018a). These plant-animal relationships are part of the evolutionary history of natural ecosystems, in which groups of species from both trophic levels have developed optimal strategies that maintain the complexity and functionality of biodiversity (Bascompte et al. 2003; Bascompte and Jordano 2007). Under a complex network approach, functionality arises from organization, and therefore disordered (i.e., random) networks might not be functional. To better understand the relationship between organization and functionality, imagine that you have a disassembled car: if you put all of its parts together in a random manner, you will end up with many important parts in the wrong places, and the final product will not be a functional car. However, if you assemble all the pieces of the car in an ordered manner, it will be much more likely to run and be functional. The same idea applies to plant-animal interactions. Species play different functional roles that allow some species to establish multiple interactions and maintain cohesive networks, providing functionality and robustness to the system (Jordano et al. 2003; Olesen et al. 2007; Dáttilo et al. 2016). As plant-animal interactions are key to maintaining the functionality of environments, the maintenance of functionality depends on spe-

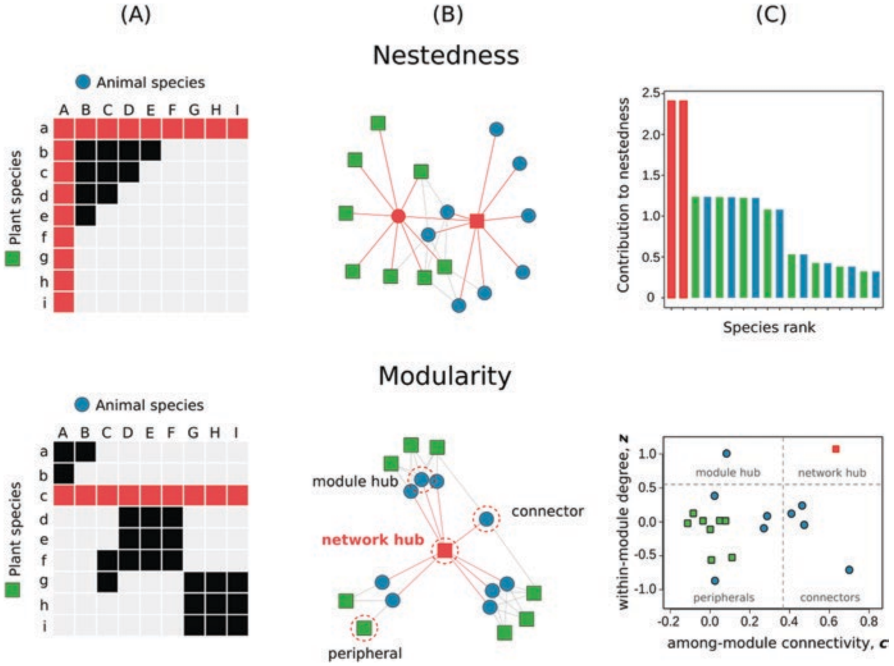

Fig. 10.1 **a** Matrices denoting the nested (top) and modular pattern of interactions (bottom) between plants (rows) and animals (columns). Black cells represent species pairs that interaction, gray cells represent species pairs that do not interact, and red cells represent interactions involving highly connected species. **b** Plant-animal interaction networks representing the interactions in **a**. Blue and green nodes represent animal and plant species, respectively. Red nodes denote highly connected species within both nested and modular pattern of interactions. **c** Plant and animal species contributions to nested and modular patterns of interactions (see text for detailed information)

cies interactions having an organized structure (i.e., interactions are not randomly assembled; Bascompte et al. 2003; Olesen et al. 2007).

Two main non-random structural properties have been frequently reported in interaction networks: nestedness and modularity (Dehling 2018). In nested networks, species that engage in few interactions (specialists) are connected to the rest of the community by their interactions with a subset of highly interactive species (generalists), while interactions between specialists rarely occur in nature (Fig. 10.1, Bascompte et al. 2003). Moreover, a core group of generalist plants and animals interact with virtually all other species in the network, performing similar roles and thereby lending high functional redundancy to the system (Bascompte and Jordano 2007). The other non-random structural property, modularity, describes a pattern in which a subgroup of species in one trophic level interacts more frequently with a group of species from another trophic level (Fig. 10.1, Olesen et al. 2007). Both nestedness and modularity occur along a continuum, and a network can be nested and modular at the same time, or even have nested modules (Dehling 2018).

In the classical literature, nestedness has been called the "*architecture of biodiversity*" since this organization promotes species coexistence by reducing competition and increasing biodiversity (Bascompte and Jordano 2007; Bastolla et al. 2009). But what generates nestedness in species interaction networks? Well, one of the main explanations for the emergence of nestedness in plant-animal networks is attributed to the natural structure of ecological communities. We know that about 60–70% of nested patterns can be attributed to differences in relative species abundances (i.e., few abundant and many rare species; Vázquez et al. 2007; Krishna Jr et al. 2008). In this case, abundant species should interact most frequently with each other as well as with less abundant species, while rare species are more likely to interact with more abundant species rather than with other rare species. This abundance-based process shaping plant-animal networks means that interactions with rare species become subsets of the interactions of the most abundant species and, consequently, result in nested interaction networks (Krishna Jr et al. 2008). However, stochastic factors structuring ecological communities (i.e., dispersal, drift and selection as proposed in the Unified Neutral Theory of Biodiversity; Hubbell 2001) also influence the ways in which species interact. The variability in nested networks can also be explained by deterministic factors, and elucidating which of and how these factors affect ecological networks has become one of the main challenges for field ecologists. One study performed by Dáttilo et al. (2014a) showed that ant dominance hierarchies can determine about 50% of the nestedness patterns found in ant-plant networks mediated by extrafloral nectaries. Specifically, these authors showed that an ant species' position within the nested network could be predicted only by differences among numerical dominance and recruitment of ant species. Therefore, both stochastic (i.e., neutral theory) and deterministic (i.e., niche-based theory) processes underlying nestedness have been proposed to explain the origin of structural patterns in ecological networks.

For modular networks, the presence of semi-independent groups of highly interactive species has been shown to be the result of multiple drivers of organization and functioning (Hintze and Adami 2008). Some of the most studied factors driving modularity are pollination and seed dispersal syndromes and spatio-temporal variation, which are well documented ecological filters (Vazquez et al. 2009; Donatti et al. 2011; Tylianakis and Morris 2017). The idea of pollination syndromes is based on observations suggesting that floral phenotypes reflect specialization toward certain groups of floral visitors (Fenster et al. 2004). In the case of seed dispersal syndromes, the hypothesis is based on the fact that fruits have a heterogeneous set of traits (i.e., different shapes, sizes and colors) and, therefore, different groups animals (e.g., birds, bats or ants) interact with particular sets of plant species (Donatti et al. 2011). Following this idea, ornithophilous flowers should only rarely be visited by insects or mammals, so humming birds and ornithophilous flowers should form a cohesive group within a larger plant-pollinator network (Olesen et al. 2007; Vazquez et al. 2009). This same reasoning can be extended to networks that include multiple groups of frugivores, in which large frugivores (e.g., mammals) eat bigger fruits while smaller frugivores (e.g. birds) eat smaller fruits, generating modularity (Donatti et al. 2011). In addition, the temporal and spatial co-occurrence of species is another factor affecting the presence of an interaction, and may also generate modularity. In a study performed by Araujo et al. (2018) in the Neotropical savanna, the authors found that plant species compositions along a spatial gradient were not the same (i.e., high species turnover) and that their floral traits and floral visitors also were exclusive to certain regions, resulting in isolated/modular networks. Moreover, modular networks may reflect phylogenetic clustering and divergent evolutionary histories (Schleuning et al. 2014), or even the simple spatial foraging of pollinators as demonstrated by Dupont et al. (2014). These findings indicate that, as with species occurrences, plant-animal interaction networks are context and scale dependent (Dáttilo et al. 2019). Despite the importance of considering the drivers of interaction network patterns, we are only beginning to understand the main mechanisms and processes behind the organization of plant-animal interaction networks.

Since interaction frequencies are highly heterogeneous and differ among species within a network, they also reflect variation in trophic specialization (i.e., trophic niche breadth; Devictor et al. 2010). Under a network approach, specialization has two components: (i) niche breadth, which is the number of other species with which an individual species interacts, and (ii) niche overlap, which is the similarity of interactions between species in a network (Blüthgen et al. 2006). Thereby, trophic specialization at the network level is a measure of the total number of interactions in a network and the similarity in interactions between species, which gives a complete overview of how the group of species interact (Blüthgen et al. 2006; Vázquez et al. 2007). Note that this approach based on network theory is different from the common interpretation of trophic specialization, in which if a bird just eats fruit from a few plant species it will be considered a specialist, but if it eats fruits from a large set of plant species it will be considered a generalist, without considering other species with which the plant or bird interacts. However, in ecological networks, the fact that an animal eats a small set of food resources might not reflect a true specialization, since such an animal might be a rare species, or those resources might also be eaten by many other species of animals. To avoid assuming that all rare interactions are specialized ones, measures of species specialization within interaction networks tend to consider the availability of partners (Blüthgen et al. 2006).

Until now we have explained network structure considering the network as a whole, but we can also explain network organization with a species-level framework. As the building blocks of ecological networks are individuals from different species, we can measure the contribution of each species to the overall structure previously described, namely nestedness or modularity (Olesen et al. 2007; Saavedra et al. 2011). For nestedness, we can measure how much the contribution of a given species to nestedness differs from that expected randomly (Saavedra et al. 2011). Such an approach is based on the idea that if species interactions are randomly sorted, one would not expect a network to remain cohesive and functional. Species play different roles in maintaining network structure, and studies have shown that only a few species contribute positively to maintaining nested structures (▣ Fig. 10.1c, Saavedra et al. 2011). This is a paradox, as in some cases the species that most contribute to the network structure are also those most vulnerable to extinction (Vidal et al. 2014). For modular networks, species also play different roles in holding the network together. To elucidate the role of each species within a modular network, we can compute the extent to which each species is connected to the other species in its module (i.e., within-module degree, z_i), as well as the degree to which the interactions of a given species are evenly distributed across modules (i.e., among-module connectivity, c_i; Olesen et al. 2007; Dehling 2018, ▣ Fig. 10.1c). Species can then be classified as peripherals (i.e., species with few interactions with other species), connectors (i.e., species connecting several modules to each other), module hubs (i.e., species with many interactions only within their own modules), or network hubs (i.e., species who have both many interactions within their own modules but also connect several modules to each other). Moreover, we also can think about the structural role of a species in maintaining a cohesive and resilient network. This species-level framework is extremely useful in obtaining additional information on how roles within plant-animal networks may act in complementary ways, ultimately allowing identification of potential network collapses and extinction cascades (Dáttilo et al. 2016).

10.3 Plant-Animal Networks Across Natural Gradients

Just as the composition, abundance and richness of species vary over environmental gradients, ecological interactions also vary over space and time (Poisot et al. 2015). The variation of ecological interactions is mainly due to the highly dynamic nature of species interactions (CaraDonna et al. 2017). For instance, species interactions can be assembled and disassembled over short periods of time (e.g., through the course of a day and even between day and night) (Luna et al. 2018b). Moreover, although two species can occur in the same place, simple co-occurrence does not automatically determine that two species will interact, as species must pass through ecological filters in order to establish an interaction (Dormann et al. 2017; Tylianakis and Morris 2017). In addition, with the current situation of global change, the introduction of an exotic species into an ecosystem may alter local trophic chains and create additional variation in ecological network dynamics (de M Santos et al. 2012). An important point we need to consider is that the high dynamism of species interactions has shaped their evolutionary and co-evolutionary history over natural gradients (Medeiros et al. 2018). For this reason, the study of interaction networks has attracted the attention of researchers working with the role of biotic interactions in maintaining biodiversity.

In the last section we pointed out that the encounter probability of a partner (i.e., stochastic factors) is one factor that determines how species interact. However, ecological filters related to environmental conditions can also change the way species interact, independently of species composition. For instance, landscapes with higher forest cover and landscape heterogeneity hold higher diversity of ant-plant interactions than landscapes with lower forest cover and landscape heterogeneity (Corro et al. 2019). Similar trends have been reported for plant-pollinator networks, where the number of interactions and network nestedness increase with increasing landscape heterogeneity (Moreira et al. 2015). In addition, Dalsgaard et al. (2011) showed that the specialization level in plant-hummingbird networks is

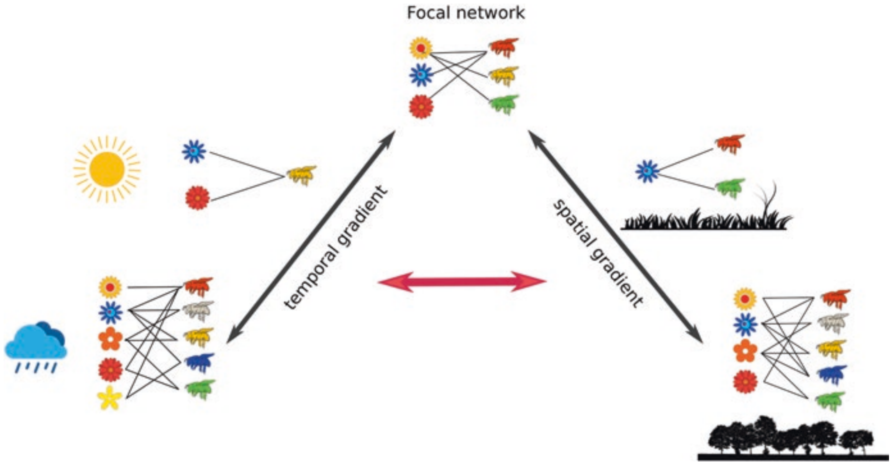

Fig. 10.2 Hypothetical representation highlighting how species and their ecological interactions within a focal pollination network observed in the field can change over temporal (here represented as dry and rainy seasons) and spatial (here represented as pasture and forest environments) gradients

associated with contemporary precipitation across the Americas. In these cases, the ways in which ecological networks vary are driven by changes in environmental conditions over space (Fig. 10.2). Furthermore, to better understand how environmental factors affect ecological networks at large spatial scales, we also need to consider elevational and latitudinal gradients.

Historically, both elevational and latitudinal gradients have been used as natural experiments to elucidate which environmental factors explain the distribution of biodiversity around the globe. We know that with increasing elevation, environmental conditions (e.g., lower temperature and higher solar radiation) change over very short distances, providing an excellent framework for studying ecological networks along these elevation gradients. As this field of study is quite new to involving ecological networks, only a few studies have assessed how environmental factors affect the organization of species interactions across elevations. However, we know that as elevation increases, the nestedness of plant-pollinator networks decreases, making them more susceptible to random extinctions (Ramos-Jiliberto et al. 2010). More recent evidence has also revealed that the trophic specialization of plant-pollinator networks decreases with increasing elevation in Mt. Kilimanjaro (Africa), highlighting the importance of environmental gradients in structuring species interactions (Classen et al. 2020). In the case of latitudinal gradients, one the most influential studies showed that trophic specialization of plant-pollinator and seed-dispersal networks is lower at tropical than at temperate latitudes (Schleuning et al. 2012). This trend is due to the greater climatic stability in the tropics, which generates higher resource diversity and, therefore, higher generalization of consumer species (Schleuning et al. 2012). Another study found that Quaternary climate-change (climatic shifts in the last 2.6 million years) is negatively associated with modularity and positively associated with nestedness (Dalsgaard et al. 2013). These findings indicate that both current and historical climate together offer a complementary explanation for the organization of biotic interactions that we find in nature today.

In addition to spatial variation, ecological networks are also driven by seasonal and temporal changes in environmental conditions. One study dealing with ants that visit plants bearing extrafloral nectaries showed that in periods of the year when plant extrafloral nectar production peaked, ant-plant interaction networks tended to be more nested and less specialized (Lange et al. 2013). Similarly, Ramos-Robles et al. (2016) found that in periods of the year with higher fruit availability, plant-frugivore networks also presented a more nested and generalized pattern of interactions (Ramos-Robles et al. 2016). For antagonistic networks, a recent study found that in the season with higher precipitation, harvester ants collected fewer seed species which led to less specialized networks (Anjos et al. 2019). It is important to mention that studies on the variation of plant-animal networks throughout time are not yet common when compared to studies on plant-animal networks along spatial gradients and, therefore, new studies should test the generality of these conclusions.

As environmental conditions fluctuate and affect plant-animal network properties, they also affect both species and biotic interactions. But how can we measure network variation over space and time? Poisot et al. (2012) proposed a new framework that considers another dimension of ecological networks: the interaction beta diversity. By mentioning the term *beta*, we refer to the turnover of species interactions and two additive components: interaction turnover (i.e., changes in the identities of interactions due to spatial/temporal changes in species composition) and interaction rewiring (i.e., changes in the identities of the interactions generated by the reassembly of interactions between the same species in different sampling sites/times; Poisot et al. 2012) (▣ Fig. 10.3). Studies dealing with interaction beta diversity have shown that despite evident changes in species composition over time or space, network properties such as nestedness or modularity do not change over both environmental gradients (Dáttilo et al. 2013a; Kemp et al. 2017). Therefore, to elucidate another aspect of network variation in relation to time or space we can consider the turnover of interactions. In recent years, network researchers have observed that species interactions tend to vary more frequently than species composition, and that abiotic factors can be a main driver of this interaction turnover (Carstensen et al. 2014; Poisot et al. 2017; Dáttilo and Vasconcelos 2019). Moreover, we now know that when geographic and environmental distances increase between habitats, species turnover has been identified as an important driver of the interaction beta diversity (Dáttilo and Vasconcelos 2019). Conversely, when we compare sites with highly similar species compositions, the main driver of interaction beta diversity tends to be interaction rewiring among species (Luna et al. 2018b). In addition to studying interaction beta diversity over spatial gradients, this framework also allows us to measure how ecological networks vary over time. For example, CaraDonna et al. (2017) showed that interaction rewiring was the main driver of interaction beta diversity in plant-pollinator networks across time, in this case between weeks. This ability of species to switch partners was mainly due to constant changes in the co-occurrence and abundance of species, directly influencing who could interact with whom (CaraDonna et al. 2017). Although current knowl-

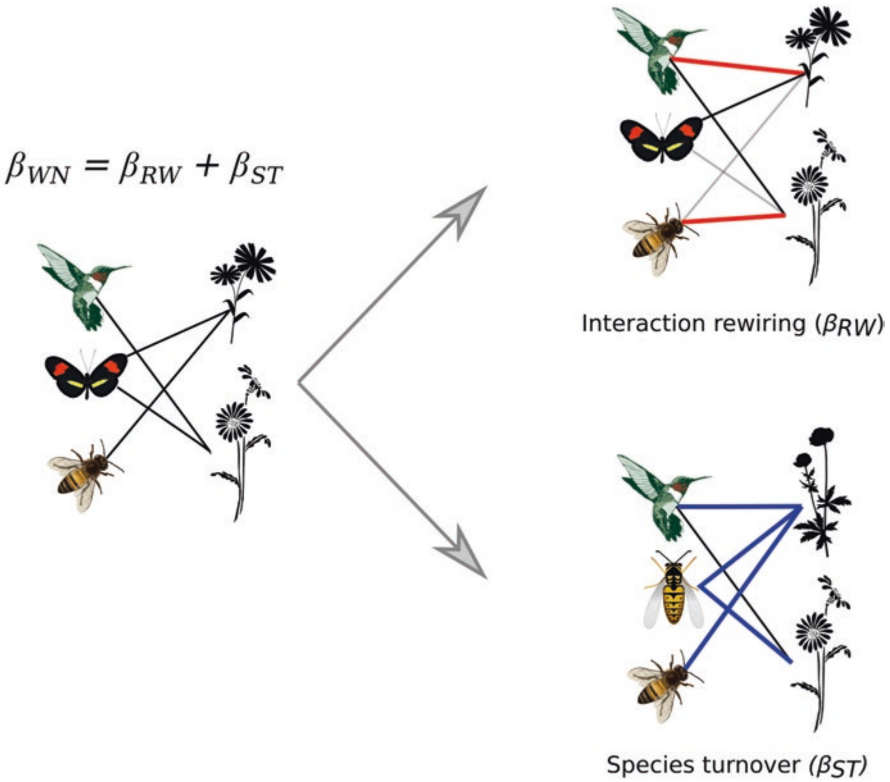

Fig. 10.3 Diagram illustrating the components of interaction turnover (i.e., beta diversity of interactions). The gray arrows indicate two possible paths of interaction change between the original plant-animal network on the left and the two alternative networks on the right. The top-right diagram shows an interaction rewiring, where gray links denote those interactions that are lost with respect to the network in the left side. Red links denote the new interactions between shared species and black links indicate the interactions that did not change between the two networks. In the bottom-right diagram, changes in the composition of species drive changes in species interactions as denoted by blue links, while the black link is the interaction that did not change between the two networks

edge allows us to hypothesize how environmental patterns can change ecological networks, there is still a lot of work to be done. Now, researchers working with interaction networks are seeking to understand how environmental factors affect the structure and the ecological and evolutionary dynamics of plant-animal interaction networks in different ecosystems around the world.

10.4 Individual-Based Networks: Linking Communities to Populations

In the previous section, we described how groups of plants and animals establish non-random patterns of organization within “species interaction networks” and how these networks vary through space and time. In those networks at the species level, we pool all records of the interactions of individuals of a species in the field and represent them as a single node in the network. However, species do not actually interact in nature. That is, individuals of species meet and interact with each other, rather than the "species" themselves interacting. In this sense, some studies have recently used tools and concepts derived from Graph Theory to study intrapopulation network variation (Pires et al. 2011; Dáttilo et al. 2013b). These individual-based networks use a set of mathematical abstractions to identify and connect interactions performed by individuals within a population, such as different feeding habits. It is worth clarifying that although the use of interspecific networks is now popular and widespread, it is still uncommon to use network analysis to assess the variation in interactions among individuals of a population. In order to unravel the details of individual-based networks, in this section we will present a biological and ecological framework for studying how populations interact amongst themselves by applying an intrapopulation network approach. Moreover, we will explain how such networks are non-randomly assembled similarly to the non-random patterns displayed by interspecific networks.

The variation in individual traits (i.e., phenotype) is a property of all populations and it is a key element of evolutionary processes, since natural selection can only act on variation within populations. These intraspecific trait variations are directly related to the ways in which different individuals of the same species interact, thereby affecting both population and community dynamics (Begon et al. 2006; Bolnick et al. 2011). Imagine a population of shrubs of the same species, all of them genetically similar but not phenotypically equal. In this theoretical shrub population, each individual has a different size, age and set of traits (e.g., number of flowers or fruits). Such differences among individuals of the same species might influence how many interactions each shrub can establish. For instance, if one shrub bears a higher number of fruits it might be more attractive to frugivorous birds compared to another individual with fewer fruits (◘ Fig. 10.4). Correspondingly, this could also be applied to animals. For example, the individual traits of each individual bird in a population (e.g., beak size, age, gender, body size and ecophysiological needs) are going to affect how many interactions each individual can establish (◘ Fig. 10.3). Therefore, intra-population variation and individual specialization are the cornerstones of individual-based networks.

As shown for interspecific networks, individual-based networks also display both nestedness and modularity as non-random structures. However, both measures have to be interpreted properly for individual-based networks to avoid any confusion with their interspecific counterparts. Thereby, the nestedness of an individual-based network reflects that the use of resources by individuals has a hierarchy, in which the set of resources used by individuals with few interactions represents a subset of the resources used by individuals with many interactions (Pires et al. 2011). Intraspecific modularity can show that there are individuals that use resources in a "selective" way, establishing more interactions with a set of resources than with others. Nestedness has been shown to be a property of both mutualistic (e.g., ant-plant protective systems and primate frugivory respectively; Dáttilo et al. 2014a, b) and antagonistic individual-based networks (e.g., seed predation by harvester ants; Luna et al. 2018a, b). The empirical evidence indicates that nestedness

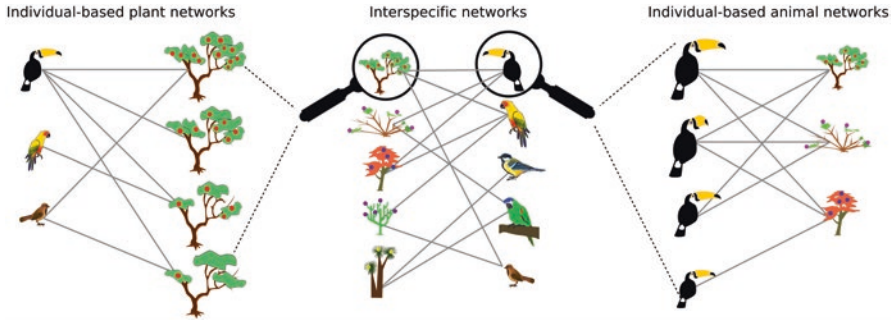

Fig. 10.4 Interspecific ecological networks involving plants and animals can be viewed as individual-based networks to assess interindividual variation. In these individual-based networks, plant (left) and animal (right) individuals are nodes, and their ecological relationships with species from the other trophic level are depicted by links (lines)

in individual-based networks also could be explained by both stochastic and deterministic factors. Under the framework of stochastic factors, Luna et al. (2018a) showed that resource abundance explains around 60% of the diet of harvester ants. Specifically, the authors found that the diets of ant nests located in sites with lower plant abundances represented subsets of the diets of ant nests located in sites with higher plant abundances. Intriguingly, the same authors observed that the variation that could not be explained by abundance was explained by the determinism of the Optimal Diet Theory (i.e., ant colonies tended to forage in more energetic resources at shorter distances) (Luna et al. 2018a). In other case, some studies have shown that for howler monkey-plant networks, the age and social role of an individual determine its role within the network. Such studies observed that older and dominant monkeys tended to access a greater number of resources, while the diets of younger and non-dominant monkeys were just subsets of the diets of dominant monkeys (Dáttilo et al. 2014c; Benitez-Malvido et al. 2016). On the other hand, modularity in individual-based networks has also been shown to be a property of mutualistic plant–pollinator (Dupont et al. 2014; Valverde et al. 2016). and antagonistic plant-herbivore interactions (Carvalho et al. 2021) For individual-based plant–pollinator networks, the modular pattern has been explained by the restricted movements of bumblebees in space, which generate isolated network compartments between patches of plants (Dupont et al. 2014). Other evidence has shown that modularity can be a consequence of plant phenology, since the alternating flowering of different plant species leads to animal individuals interacting more frequently with some plants during certain periods of the year (Valverde et al. 2016). The heuristic power of this individual-based network approach has already revealed new insights on the ecological and evolutionary dynamics of species interactions that cannot be detected using interspecific networks. For instance, one of the most interesting findings dealing with plant-pollinator networks is that plant individuals that have higher centrality in the network (i.e., nodes with high degrees that act as bridges maintaining cohesive networks) have higher fitness, and therefore should be favored by natural selection (Gómez and Perfectti 2012). Note that the previous examples show that by studying individuals we can assess the variation in the interactions of individual plants (i.e., producers) and animals, ultimately furthering our understanding of interspecific interactions (see Guerra et al. 2017). Despite the potential use of individual-based networks to evaluate the ecological and evolutionary dynamics of species interactions, the amount of theoretical and empirical information available is still limited. Therefore, we encourage researchers from around the world to employ an interspecific approach to link population dynamics to community structure.

10.5 Plant-Animal Multilayer Networks

The implementation of ecological networks to study plant-animal interactions has prompted the development of numerous scientific discoveries that have increased our understanding of the function and dynamics of species interactions (Dáttilo and Rico-Gray 2018). Despite ecological networks being a fundamental area of research in ecological theory, most of the knowledge generated by implementing such an approach only describes interaction patterns between two trophic levels (e.g., animals and the plants they use as food sources). This limited view of species interactions ignores the multiple relationships that a species can establish in an environment as well as any variation across time and space (Dáttilo et al. 2016). Thereby, when bipartite ecological networks are described through time and space, they are considered static entities isolated one from another, leading to posible biased conclusions. For example, we might consider a plant a specialist if we assess its interactions with herbivores, but the same plant could be a generalist if we assessed its interactions with pollinators. By integrating multiple interaction types and spatio-temporal variation into a single network, one could more accurately and thoroughly describe species interactions and reveal new insights into the complexity of species interactions (Genrich et al. 2017; Pilosof et al. 2017). Recent developments in the field of complex networks have provided a mathematical framework for studying networks with multiple layers, which include multiple types of vertices (e.g., herbivores, pollinators and plants) with multiple types of edges (e.g., mutualistic and antagonistic interactions). In fact, the implementation of multilayer networks in ecology has already made advances in understanding biotic interactions (Pilosof et al. 2017), and in this section we will explain how to use this multilayer-network framework to study plant-animal relationships.

A multilayer network is an approximation used to connect multiple entities/interactions into a single network, allowing the use of interlayer edges that connect different layers of a network. For instance, layers can be represented by networks of different interactions types (e.g., pollination, herbivory and seed dispersal) connected by shared species (e.g., plants). The interesting and heuristic part of this approach is that interlayer edges represent additional and more realistic ecological processes that are not considered in single bipartite networks (e.g., the effect of one interaction on the output of another interaction). However, this approach is not limited to merging multiple interaction types, since multilayer networks allow more elaborate scenarios like a network with multiple interaction types over time and space, something that we will explain in the next paragraph.

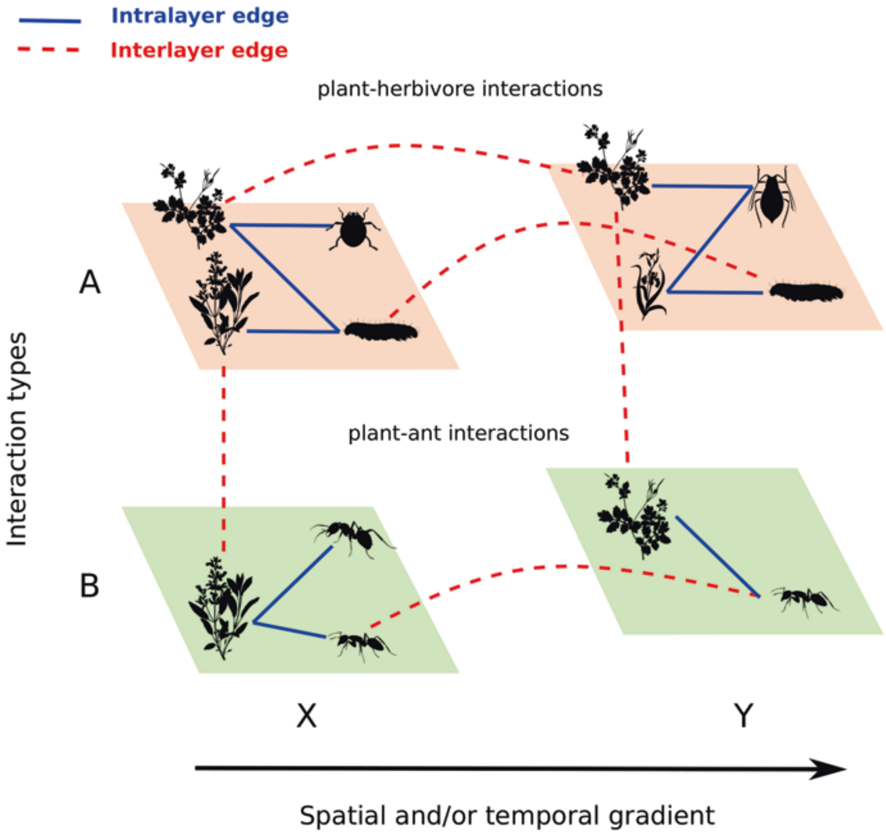

Fig. 10.5 A schematic plant-animal multilayer network. The first layer is represented by the interaction type (A = plant-herbivore interactions. B = plant-ant defensive mutualism). The second layer is represented by ecological interactions shared between spatial or temporal gradients (from X to Y). Intralayer edges are in blue, and interlayer edges showing different ecological and evolutionary processes across layers are in red dashed lines

Similar to bipartite networks, an ecological multilayer network (EMN) is also built by a set of nodes. However, we also need a set of layers, which can be different interaction types, networks in different periods of time or networks across space (Fig. 10.5). Note that these EMNs are not limited to only one set of layers. In other words, we can use an EMN representing one set of layers for different interaction types and another type of layer for periods of time. Each type of layer is called an aspect (e.g., an annual set of networks or a set of antagonistic and mutualistic interactions of a single system). Thus, to refer to each element of each aspect we refer to an elementary layer (e.g., the pollination network of a month). As species assemblages vary over space and time not all nodes can be found in all the elementary layers of an EMN. Thus, the nodes that are part of a specific elementary layer are called state nodes. Finally, to connect the network layers, we have intralayer edges (i.e., interactions within each layer, Fig. 10.5) and interlayer edges, which connect state nodes across elementary layers. Edges can be weighted or unweighted (binary, frequencies or abundances), which could affect interpretation of the results as previously showed for bipartite networks (Miranda et al. 2019). Moreover, it is worth mentioning that the nature of each layer is only limited by the imagination, and that there are more types of layering than those mentioned in this chapter.

But how can we describe the organization of EMNs? Initially, we can identify influential nodes or edges with three main descriptors: (i) eigenvector versatility (i.e., a species' importance depends on its connections within and across layers, and on the connections of its neighbors), (ii) betweenness versatility (i.e., how often the shortest paths between each pair of nodes go through a given node within and across layers) and, (iii) multidegree (i.e., the degree of each species across all layers). These descriptors can be used to assess how a group of species might be affected if certain species are removed or which species are relevant to main network cohesion. If species connect different layers in a non-random way, this could imply that there are nonrandom patterns of interactions across layers. Consequently, we can use a measure of modularity to identify which species are present in different layers and interacting with other species in those different layers (Pilosof et al. 2017). In addition, we can also identify motifs, which are small numbers of species/nodes that interact in repetitive and predictable ways (e.g., one plant always interacts with the same two pollinators, or one herbivore always predates the same three plants). By searching for motifs in networks, we can assess whether certain motifs appear more often within or across layers in order to answer questions such as: Are there certain types of interactions that are predictable or constant across space or time? Or, how different are interaction motifs between interaction types? Applying the above-mentioned descriptors could reveal the ecological dynamics of species interactions and even evolutionary consequences of biotic interactions in a more integrative way.

Current evidence shows that plants connect herbivores and pollinators between layers, suggesting that the dynamics of antagonistic and mutualistic communities are interconnected via plants (Sauve et al. 2016). This more comprehensive idea of species interactions could not be visualized using bipartite networks. For example, in a study performed by Timóteo et al. (2018), the authors used the different habitats as a layer along with plants and animals, to show that animals with wide-ranging movements (e.g., birds and elephants) disperse plants across habitats. In another study, by merging highly diverse mutualistic networks (a total of 390 species including pollinators, bird seed dispersers and ants), Dáttilo et al. (2016) showed that only a few species contributed to the maintenance of the whole network structure. This finding indicates that conserving interactions of keystone mutualists in interlinked mutualistic networks is crucial to the persistence of species-rich mutualistic assemblages. However, despite the possible applications of EMN for studying plant-animal interactions, ecologists must carefully study the underlying mathematical framework in order to fully understand and correctly use this approach. Moreover, the field of multilayer networks is still growing, and many of its descriptors and tools used are still in development and discussion. Thus, this is an open area of research which promises to provide new tools for understanding nature and its complexity.

Conclusion and Future Directions

To end this chapter, we would like to highlight that animals and plants are embedded in complex and species-rich interaction networks. Moreover, both stochastic and deterministic factors explain the organization of such plant-animal interaction networks. By using the complex network approach and by studying how biotic interactions vary between individuals of the same population, we can create a bridge between population and community ecology. As also observed in interspecific networks, individual-based networks are not randomly assembled. In fact, the structure and function of interaction networks vary over time and space and can be driven by environmental conditions. However, interaction networks are only an initial approach for studying the complexity of species relationships within the web of life and, therefore, multilayer networks hold promise for elucidating the real complexity of natural systems. Our planet is mega-diverse and there are regions in which you can find thousands of species at relatively small spatial scales (e.g., the Tropical Andes or Amazon rainforest), begging the question, how we can study and identify who interacts with whom when diversity is so high? In recent years, molecular techniques have started to help to solve this problem, such as DNA barcoding allowing us to analyze the gut content of herbivores and frugivores and identify the plants in different animals' diets (García-Robledo et al. 2013; González-Varo et al. 2014). Such techniques are still slow and expensive, but we hope that in coming years molecular techniques will become more accessible and commonplace, boosting the study of plant-animal interactions in the process.

Charles Darwin was aware of the high diversity of interactions that species establish, using the image of an "entangled bank" to call to mind this vast complexity in his seminal book *On the Origin of Species* (Darwin 1859). More recently, the variety of life forms and the interactions between them that caught Darwin's attention also inspired John N. Thompson to propose the Geographic Mosaic Theory of Coevolution (GMTC). This theory postulates that many of the co-evolutionary dynamics between groups of interacting species occur at a geographic scale above the level of populations (Thompson 2005). He hypothesized that a selection mosaic favors different evolutionary trajectories between populations, allowing some regions to be co-evolutionary hotpots (i.e., where the interaction affects the fitness of both partners) and coldspots (i.e., where selection is not reciprocal or there is no selection; Thompson 2005). Thanks to ecological networks, we now know that co-evolution is a diffuse process and that changes in one trait of a species can affect another species in a network without direct interaction, favoring similar traits at a community level (Guimarães et al. 2011, 2017). In another study, it was shown that ecological interactions promote gene flow across large geographical distances, favoring trait matching and thereby co-evolutionary dynamics (Medeiros et al. 2018). Likewise, some evidence suggests that the structure of pollinator and seed-dispersal networks (i.e., nestedness and modularity) could be a result of trait matching and exploitation barriers, both co-evolutionary processes (de Andreazzi et al. 2020). Thus, it is clear that interactions between animals and plants can drive selection, as both groups reciprocally affect each other across population and communities. On the other hand, many interactions have never been observed and studied, and

> with the current trajectory of global changes (e.g., global warming, habitat loss & biological invasions), if human lifestyles continue in the same way we might never be able to observe such natural wonders. Thus, we invite the reader to increase their efforts and collaborate to elucidate Darwin's intriguing and inspiring entangled bank.

Key Points

- Plant-animal interactions can be studied by implementing a complex network approach.
- Complex networks that arise from plant-animal interactions are non-randomly organized, which can be explained by stochastic and deterministic factors.
- The organization of plant-animal networks varies through space and time.
- Individuals are the building blocks of ecological networks.
- Plant-animal interaction networks can help us understand the complexity of evolutionary and co-evolutionary processes in interactive communities.

Questions

- What are the main benefits and limitations of studying interaction networks?
- What is a multilayer network?
- Could the use of molecular techniques change the current understanding of plant-animal networks?

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Further Reading/Additional Resources

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