Complexity and stability of ecological networks: a review of the theory

Pietro Landi1,2 · Henintsoa O. Minoarivelo1,3 · Åke Brännström2,4 · Cang Hui1,5 · Ulf Dieckmann2

Received: 20 April 2017 / Accepted: 29 June 2018 / Published online: 6 July 2018
© The Author(s) 2018

Abstract
Our planet is changing at paces never observed before. Species extinction is happening at faster rates than ever, greatly exceeding the five mass extinctions in the fossil record. Nevertheless, our lives are strongly based on services provided by ecosystems, thus the responses to global change of our natural heritage are of immediate concern. Understanding the relationship between complexity and stability of ecosystems is of key importance for the maintenance of the balance of human growth and the conservation of all the natural services that ecosystems provide. Mathematical network models can be used to simplify the vast complexity of the real world, to formally describe and investigate ecological phenomena, and to understand ecosystems propensity of returning to its functioning regime after a stress or a perturbation. The use of ecological-network models to study the relationship between complexity and stability of natural ecosystems is the focus of this review. The concept of ecological networks and their characteristics are first introduced, followed by central and occasionally contrasting definitions of complexity and stability. The literature on the relationship between complexity and stability in different types of models and in real ecosystems is then reviewed, highlighting the theoretical debate and the lack of consensual agreement. The summary of the importance of this line of research for the successful management and conservation of biodiversity and ecosystem services concludes the review.

Keywords Biodiversity · Community · Complex networks · Ecosystem · Resilience

Introduction
In the geological era of the Anthropocene, our planet is changing at paces never observed before (Millennium Ecosystem Assessment 2005). Pollution, natural resources exploitation, habitat fragmentation, and climate change are only some of the threats our biosphere is facing. Species extinction is happening at faster rates than ever, greatly exceeding the five mass extinctions in the fossil record. Even if sometimes we do not realize it, our lives are strongly based on services provided by ecosystems, thus the responses to global change of our natural heritage are of immediate concern for policy makers. As ecosystems are composed by thousands of interlinked species that interact directly or through their shared environment, such as nutrients, light, or space, a holistic perspective on the system as a whole is normally required to predict ecosystem responses to global changes (Wolanski and McLusky 2011). A systems-analysis approach is thus often crucial for acquiring an understanding of all the dynamical feedbacks at the ecosystem level and for accurately managing the biodiversity that we rely on in terms of ecosystem services. In particular, mathematical network models can be used to simplify the vast complexity of the real world, to formally describe and investigate ecological phenomena, and to understand how ecosystems react to stress and perturbations (Dunne 2006). Complex-networks models are composed of a set of compartments, describing either species or coarser functional groups, and a set of links that represent interactions or energy or biomass flows among compartments. Thus, such models can describe both biotic and abiotic interactions...
among species, i.e., both interactions among the species themselves and interactions with their external environment, and consequently they can often successfully be used to assess ecosystems stability to perturbations. Stability of an ecosystem can be understood as its propensity of returning to its functioning regime after a stress or a perturbation in its biotic components (e.g., decline in species abundances, introduction of alien species, and species extinction) or abiotic components (e.g., exploitation, habitat fragmentation, and climate change). A challenging and central question that has interested ecologists and systems analysts alike for decades is how the stability of an ecosystems depend on its complexity, as roughly measured by the ecosystems’ diversity in species and their interactions (Johnson et al. 1996; Worm and Duffy 2003; Dunne et al. 2005; Hooper et al. 2005; Kondoh 2005; Loreau and De Mazancourt 2013).

To appreciate the importance of this question, we first recollect and differentiate between the major different functions that ecosystems continuously provide. Natural ecosystems sustain life and provide services that can be divided into four areas (Millennium Ecosystem Assessment 2005): provisioning, such as the production of food and water; regulating, such as the control of climate and disease; supporting, such as nutrient cycles and crop pollination; and cultural, such as spiritual and recreational benefits. For the management and conservation of ecosystems services it is important to know how the complexity of an ecosystem is related to its stability, thus how the diversity of species in the ecosystem and the network of their interactions can contribute to maintaining a stable supply of services. This is especially important in an era in which the pressure exerted on natural ecosystems is becoming stronger and stronger, influencing their structure and functioning, while the services they provide are vital for a continuously increasing number of people. In particular, human activities, directly or indirectly, tend to simplify the composition and the structure of natural ecosystems. Therefore, understanding the relationship between complexity and stability of ecosystems is of key importance for the maintenance of the balance of human growth and the conservation of all the natural services that ecosystems provide. Using ecological-network models to study the relationship between complexity and stability of natural ecosystems is the focus of this review. We first introduce the concept of ecological networks and their characteristics, followed by central and occasionally contrasting definitions of complexity and stability. After that, we review the literature on the relationship between complexity and stability in different types of models and in real ecosystems, highlighting the theoretical debate and the lack of consensual agreement. We continue with describing the importance of considering the dynamic adaptation of species behaviour and the resulting changes in ecosystems structure, after which we conclude by summarizing the importance of this line of research for the successful management and conservation of biodiversity and ecosystem services in the current era of the Anthropocene.

Ecological networks defined

An ecological network describes interactions among species in a community (Pascual and Dunne 2006). There are different types of interactions, e.g., trophic interactions (feeding), mutualistic interactions (pollination, seed dispersal, etc.), and competitive interactions (interference for common resources). Ecological networks can be represented as a set of $S$ nodes, characterizing the species, connected by a set of $L$ links, characterizing possible interactions among each ordered pair of species (Newman 2010; Estrada 2012). Links can be described by either a binary variable (0 or 1, absence or presence of interaction) or by a real number characterizing the weight (or strength) of the interaction. In the first case the network is called unweighted, while in the second case it is called weighted. Moreover, interactions can be undirected (or symmetric), meaning that species $i$ affects species $j$ to a certain amount and equally vice versa, or directed (or asymmetric), meaning that species $i$ can affect species $j$ differently from how species $j$ affects species $i$ (Fig. 1). Moreover, interactions can be described by their sign (+ or −). For example, trophic networks (food webs) are characterized by the fact that one species is feeding on the other, thus the coefficients $a_{ij}$ (describing the effect of species $j$ on species $i$) and $a_{ji}$ (describing the effect of species $i$ on species $j$) will obviously have opposite signs (thus their product will be negative, $a_{ij}a_{ji} < 0$), i.e., one species is benefiting while the other is suffering from the interaction. In mutualistic networks both species are benefiting from the interaction, thus both coefficients $a_{ij}$ and $a_{ji}$ will be positive (and so their product, $a_{ij}a_{ji} > 0$), while in competitive networks both species are suffering from the interaction, thus both coefficients $a_{ij}$ and $a_{ji}$ will be negative (thus their product will be again positive, $a_{ij}a_{ji} > 0$) (Fig. 2). Notice therefore that trophic networks cannot be undirected (symmetric), since the two coefficients describing the interaction always have opposite sign (and typically also different absolute values).

The structure of the ecological network can be described by the $S \times S$ matrix $A = \{a_{ij}\}$, where each element $a_{ij}$ describes the link between species $i$ and species $j$, i.e., the effect that species $j$ has on species $i$. In the most particular case of unweighted and undirected network, matrix $A$ is symmetric (i.e., $a_{ij} = a_{ji}$) and its elements are either 0 or ± 1 (Newman 2010; Estrada 2012). In the most general case of weighted and directed network, matrix $A$ can have any composition of real values. For bipartite networks (i.e., those formed by two disjoint groups of respectively $m$ and $n$ species, $S = m + n$, with interactions only between two species of different groups), such as mutualistic networks of plants and their
pollinators or antagonistic networks of host-parasite interactions, the matrix $A = [a_{ij}]$ is a $m \times n$ matrix (Fig. 2).

Unfortunately, there is no unique quantification of the elements $a_{ij}$. Depending on the scope (theoretical vs. empirical), several measures and indexes have been used to quantify the matrix $A$. For example, theoretical studies mostly refer to $a_{ij}$ as the effect of a perturbation from equilibrium of the abundance of species $j$ on the population growth rate of species $i$ (elements of the Jacobian matrix describing the linearized dynamics of the model ecosystem around equilibrium, see also ‘Network stability’). In such cases, the matrix $A$ has been called community matrix (Novak et al. 2016). Another option is to define the elements of matrix $A$ as the effect of a single individual of species $j$ on the per-capita growth rate of species $i$: in such case, matrix $A$ has been called interaction matrix, and its elements are called interaction strengths (Kokkoris et al. 2002). Unfortunately, such coefficients are well defined in theory, but very hard to measure in the field or in lab experiments. On the other hand, empirical observations mainly quantify magnitude of energy and biomass flows between compartments in model ecosystems, or consumption rate for resource-consumer and prey-predator interactions, or visiting probabilities in pollination networks. Such quantities are relatively easy to be estimated empirically, but they are not directly related to elements of the theoretical Jacobian (community) matrix as they are independent of species equilibrium abundances. For example, in empirical studies of mutualistic interactions, the degree of species dependence on another species (see ‘Network complexity’ for a definition) has been used to quantify the link among involved species (Jordano 1987). See also Berlow et al. 2004, Wootton and Emmerson 2005, and Novak et al. 2016 for reviews on the different definitions of strength of interaction and of the matrix $A$.

**Network complexity**

*Species richness $S$, or the total number of interacting species in the network, also known as the network size, has been used as the simplest descriptor of network complexity (MacArthur 1955; May 1972, 1973; Pimm 1980a; Table 1). In the particular case of bipartite networks, species richness $S$ is expressed as $S = m + n$. In food-web studies, the use of trophic species (a functional group of species sharing the same set of predators and preys) as a replacement of taxonomic species (i.e., when species are distinguished based on morphological and phylogenetic criteria) is a widely accepted convention (Schoener 1989; Pimm et al. 1991; Goldwasser and Roughgarden 1993; Williams and Martinez 2000; Dunne et al. 2002a). The use of ‘trophic species’ has indeed been shown to reduce methodological biases in food web datasets because it reduces scatter in the data and avoids redundancy of interactions (Pimm et al. 1991; Martinez 1994). Sometimes, the use of morphospecies (species distinguished from others by only their morphologies) as a replacement of taxonomic species is also considered because of a lack of taxonomic distinction between species (Olito and...*
Fox 2014). Hence, network size often refers to the number of functional or morphological diversity in the system.

Another commonly-used indicator of complexity is the connectance $C$ (May 1972, 1973; Newman 2010; Estrada 2012), measuring the proportion of realised interactions among all the possible ones in a network (i.e., the total number of interactions $L$ divided by the square of the number of species $S^2$ or $L$ divided by the product $m \times n$ in the case of a bipartite network). It accounts intuitively for the probability that any pair of species interact in the network. It is probably

---

**Fig. 2** Examples of real-world ecological networks. First row: food web from the estuary river of St. Marks, Florida, USA (Baird et al. 1998). Second row: mutualistic network of pollination from the Flores Island, one of the Azores oceanic islands (Olesen et al. 2002). Left column: network representation. Second column: matrix representation. The food web is unweighted directed: in b the black entries in the matrix represent presence of interaction. The mutualistic network is weighted undirected: the link width in c and the shade of grey in d are proportional to the weight of the interaction which represents the number of pollinator visits.
| Network complexity | Definition | References |
|---------------------|------------|------------|
| **Species richness** (S) | Total number of species in the network | May (1972, 1973) Food webs: MacArthur (1955), Pimm (1979, 1980a), Cohen and Briand (1984), Cohen and Newmann (1985), Havens (1992), Martinez (1992), Haydon (1994), Borrvall et al. (2000), Dunne et al. (2002a, b), Dunne and Williams (2009), Banašek-Richter et al. (2009), Gross et al. (2009), Thébault and Fontaine (2010) and Allesina and Tang (2012) Mutualism: Okuyama and Holland (2008), Thébault and Fontaine (2010), Allesina and Tang (2012) and Suweis et al. (2015) Competition: Lawlor (1980), Lehman and Tilman (2000), Christianou and Kokkoris (2008), Fowler (2009) and Allesina and Tang (2012) |
| **Connectance** (C) | Proportion of realized interactions among all possible ones, \( \frac{L}{S^2} \) | May (1972, 1973) Food webs: De Angelis (1975), Pimm (1979, 1980a, 1984), Martinez (1992), Haydon (1994, 2000), Chen and Cohen (2001), Olesen and Jordano (2002), Dunne et al. (2002a, b), Dunne et al. (2004), Banašek-Richter et al. (2009), Gross et al. (2009), Thébault and Fontaine (2010), Tylianakis et al. (2010), Allesina and Tang (2012), Heleno et al. (2012) and Poisot and Gravel (2014) Mutualism: Jordano (1987), Rezende et al. (2007), Okuyama and Holland (2008), Thébault and Fontaine (2010), Allesina and Tang (2012), Suweis et al. (2015) and Vieira and Almeida-Neto (2015) Competition: Fowler (2009) and Allesina and Tang (2012) |
| **Connectivity** (L) | Total number of interactions | Mutualism: Okuyama and Holland (2008) Competition: Fowler (2009) |
| **Linkage density** | Average number of links per species, \( \frac{L}{S} \) | Food webs: Pimm et al. (1991) and Havens (1992) Mutualism: Jordano (1987) |
| **Interaction strength** | Weight of an interaction in the interaction matrix | Food webs: Paine (1992), McCann et al. (1998), Berlow (1999), Borrvall et al. (2000), Berlow et al. (2004), Wootton and Emmerson (2005), Rooney et al. (2006) and Otto et al. (2007) Mutualism: Okuyama and Holland (2008), Allesina and Tang (2012), Rohr et al. (2014) and Suweis et al. (2015) Competition: Lawlor (1980), Hughes and Roughgarden (1998), Kokkoris et al. (1999, 2002), Christianou and Kokkoris (2008) and Allesina and Tang (2012) |
| **Jacobian element** | Weight of an interaction in the community (Jacobian) matrix | Food webs: De Angelis (1975), Yodzis (1981), Haydon (1994), de Ruiter et al. (1995), Haydon (2000), Neutel et al. (2002, 2007), Emmerson and Raffaelli (2004), Emmerson and Yearsley (2004), Allesina and Pascual (2008), Gross et al. (2009), Allesina and Tang (2012), Jacquet et al. (2016) and van Altena et al. (2016) Mutualism: Allesina and Tang (2012) Competition: Lawlor (1980), Hughes and Roughgarden (1998), Kokkoris et al. (1999, 2002), Christianou and Kokkoris (2008) and Allesina and Tang (2012) |
| **Weighted linkage density** | Average number of links per species weighted by interaction strength | Food webs: Bersier et al. (2002), Tylianakis et al. (2007) and Dormann et al. (2009) |
Table 1 (continued)

| Network complexity       | Definition                                                                 | References                                                                 |
|--------------------------|---------------------------------------------------------------------------|---------------------------------------------------------------------------|
| Weighted connectance     | Weighted linkage density divided by species richness                       | Food webs: Haydon (2000), Bersier et al. (2002), Tylianakis et al. (2007), Dormann et al. (2009) and van Altena et al. (2016) Mutualism: Minoarivelo and Hui (2016) |
| Species degree           | Number of interactions (links) with other species                          | Food webs: Waser et al. (1996), Memmott (1999), Solé and Montoya (2001), Camacho et al. (2002), Dunne et al. (2002b), Montoya and Solé (2002); Vázquez and Aizen (2003) and Dunne and Williams (2009) Mutualism: Jordano et al. (2003) and Rohr et al. (2014) |
| Species strength         | Sum of weighted interactions shared by the species with others             | Mutualism: Bascompte et al. (2006), Feng and Takemoto (2014) and Suweis et al. (2015) |
| Dependence of species i on species j | Number of visits between i and j divided by the total number of visits between species i and all other partners | Mutualism: Jordano (1987), Bascompte et al. (2006), Feng and Takemoto (2014) and Vieira and Almeida-Neto (2015) |

one of the earliest and the most popular descriptors of ecological networks structure. Sometimes, a simpler measurement of interactions, known as connectivity, has been used instead of connectance. The connectivity of a network is simply its total number of interactions \( L \) (Newman 2010; Estrada 2012).

To understand the average level of specialization of the network, i.e., whether the network is dominated by specialists (species holding few interactions) or generalists (species holding many interactions), food web ecologists have introduced linkage density. It is calculated as the average number of links per species, or the connectivity divided by species richness, \( L/S \) (Montoya et al. 2006).

To increase the information value of these network metrics, some theoretical studies have incorporated the strength of interactions. Thus, quantitative counterparts of linkage density and connectance, called respectively weighted connectance and weighted linkage density, have been developed (Bersier et al. 2002; Tylianakis et al. 2007; Dormann et al. 2009). Weighted linkage density considers the proportion of biomass flow to weight the contribution of each link to and from all equivalent species. Equivalent species are defined using the Shannon metric (Shannon 1948) of entropy (or uncertainty). Weighted connectance is then computed as the weighted linkage density divided by species richness. There are several reasons for believing that networks metrics incorporating the strength of interaction are better suited to reflect salient ecosystem properties, among which the ability to give increased weight to strong interactions and the fact that weighted metrics change continuously with the change of link strength and even with the eventual removal of the link. The latter can be particularly important in empirical food-web studies in which the sampling effort typically dictates the number of links discovered, with greater effort often leading to many more additional weak links.

As connectivity and linkage density are only community-average descriptors of network structure, they do not inform on the relative importance of each species to the overall connectivity. Node degree distribution, i.e., the distribution of the number of interactions per species, is another widely used descriptor of network complexity (Newman 2010). The degree of a node (or a species) refers to the number of links to other interacting partners in the network. The distribution of node degree in ecological networks have been shown to differ from a Poisson distribution that characterises large random networks (Camacho et al. 2002; Dunne et al. 2002b; Montoya and Solé 2002; Jordano et al. 2003).

A generalization of the node-degree distribution is the interaction-strength distribution, taking into account the weights associated with each link (Newman 2010). The strength (or weighted degree) of each species is computed as the sum of all the weighted interaction strengths of that species (Feng and Takemoto 2014; Suweis et al. 2015). However, particularly for pollination and frugivory networks, interaction strengths are often approximated by the number of visits of an animal species to a plant species (Jordano 1987). A normalized index for this kind of networks is species dependence on another species. The dependence of a species \( i \) on a species \( j \) is defined as the fraction of interactions (e.g., visits or diet item) between \( i \) and \( j \) relative to the total number of interactions of species \( i \) (Bascompte et al. 2006; Vieira and Almeida-Neto 2015). In this context, species strength refers to the sum of dependences of the mutualistic partners relying on the species.

**Network architecture**

Beyond ecological patterns in interaction and strength distribution, interactions in ecological networks exhibit even more complex topological features, related to the
architecture of the network (Table 2). Among the most important of these features is the level of modularity or compartmentalization. Modularity depicts the extent to which a network is compartmentalized into delimited modules where species are strongly interacting with species within the same module but not with those from other modules (Olesen et al. 2007). Although a number of metrics have been developed to quantify the level of compartmentalization in a network, modularity (developed by Newman and Girvan 2004) has been the most widely accepted. This measure assumes that nodes in the same module have more links between them than one would expect for a random network and Modules are thus obtained by partitioning all nodes in the network in order to maximize modularity. However, see, e.g., Rosvall and Bergstrom (2007) and Landi and Piccardi (2014) for limitations of modularity and other metrics of compartmentalization.

Another important descriptor of ecological network architecture, especially for mutualistic networks, is nestedness. It is a pattern of interactions in which specialists can only interact with a subset of species with which more generalists interact. It means that in a nested network, both generalists and specialists tend to interact with generalists whereas specialist-to-specialist interactions are rare (Bascompte et al. 2003). To quantify the nestedness of a network, several metrics have been developed. Among the most commonly used are for example the ‘temperature’ metric by Atmar and Patterson (1993) and the NODF (Nestedness metric based on Overlap and Decreasing fill) metric by Almeida-Neto et al. (2008).

Despite the existence of several metrics and algorithms, they are all mainly based on measuring the extent to which specialists interact only with a subset of the species generalists interact with.

### Network stability

In theoretical studies, each entry \( a_{ij} \) of matrix \( A \) usually quantifies the change in population growth rate of species \( i \) caused by a small perturbation in the abundance of species \( j \) around equilibrium abundances (i.e., stationary regime, species abundances are constant in time). Thus matrix \( A \) is equivalent to the Jacobian matrix of the dynamical system that describes species abundance dynamics over continuous time, evaluated at equilibrium, and it is also called a community matrix. Such a matrix is very useful for studying the (local) asymptotic stability of the equilibrium. In fact, stability is defined by the real part of the leading eigenvalue of the Jacobian matrix (i.e., the eigenvalue with the largest real part). If the real part of the leading eigenvalue is positive, the equilibrium is unstable, i.e., any small perturbation from the equilibrium will be amplified until convergence to another ecological regime, at which some of the species in the community might be extinct. Otherwise, if the real part of the leading eigenvalue is negative, then small perturbations around the equilibrium will be dampened, and the system will converge back to its stationary regime. Therefore, the sign of the real part of the leading eigenvalue can be a binary indicator of stability. Moreover, if stable, the inverse of the absolute value of the real part of the leading eigenvalue gives an indication of the time needed by the system to return to its equilibrium. Systems that quickly return to equilibrium after perturbations are called resilient. Resilience is therefore often measured by the absolute value of the leading eigenvalue (if negative) of the community matrix. Notice that resilience is only defined for stable equilibria and it only gives information about the asymptotic behaviour of the system (see Neubert and Caswell 1997 for transient indicators). Global (vs. local) stability implies that any (vs. small) perturbation from the equilibrium will be dampened. Global

| Table 2 | Measures of network architecture |
|---------|--------------------------------|
| Network architecture | Definition | References |
| Modularity | Extent to which a network is compartmentalized into delimited modules | Food webs: Moore and Hunt (1988), Ives et al. (2000), Krause et al. (2003), Thébault and Fontaine (2010) and Stouffer and Bascompte (2011) Mutualism: Olesen et al. (2007), Mello et al. (2011) and Dupont and Olesen (2012) |
| Nestedness | When specialists can only interact with subset of the species generalists interact with | Food webs: Atmar and Patterson (1993), Neutel et al. (2002), Cattin et al. (2004), Thébault and Fontaine (2010) and Allesina and Tang (2012) Mutualism: Bascompte et al. (2003), Memmott et al. (2004), Almeida-Neto et al. (2008), Bastolla et al. (2009), Zhang et al. (2011), Campbell et al. (2012), James et al. (2012) and Rohr et al. (2014) |
stability usually refers to the case of a single equilibrium (typical of linear systems).

The notion of structural stability of a system is used when the system’s dynamical behaviour (such as the existence of equilibrium points, limit cycles or deterministic chaos) is not affected by small perturbations such as small changes in the values of its parameters (Solé and Valls 1992). However, Rohr et al. (2014) extended this definition to the notion of structural stability of an equilibrium which refers to the domain (or probability) of coexistence of all the species in the ecosystem. An equilibrium at which all the species \( S \) in the system coexist with positive abundances is called feasible. Structural stability usually refers to perturbations in the system itself (i.e., slightly changing one of its parameters) rather than perturbations in the state of the system (i.e., abundances, see previous paragraph). Assuming that a system is at a feasible equilibrium, a small perturbation in a parameter (e.g., species carrying capacity, intrinsic growth rate, predator conversion efficiency, handling time, …) will generically move the system to a slightly different (in terms of species abundances) feasible equilibrium, unless the system is close to a bifurcation point for that parameter. A bifurcation is indeed a qualitative change in the asymptotic behaviour of a system driven by a perturbation in one of its parameters. Such qualitative change could, for example, be a switch to a non-feasible equilibrium (where one or more species go extinct), to a non-stationary (e.g., periodic) orbit, etcetera. The region in parameter space for which the system has a feasible equilibrium is its domain of stable coexistence, and gives an indication (or probability) of its structural stability. The bigger the domain, the more structurally stable the system (Rohr et al. 2014).

In addition to this, the number of coexisting species at an equilibrium could trivially be an indicator of stability. This number will be \( S \) at a feasible equilibrium, and will be smaller than \( S \) at an equilibrium at which some species have gone extinct. If this number is standardized to the total number of species \( S \) we obtain the proportion of persistent species once equilibrium is reached, that is, persistence (Thébault and Fontaine 2010).

The notions of asymptotic stability and structural stability can of course be generalized in the case of non-stationary asymptotic regimes (such as cycles, tori, and chaotic attractors), using, e.g., Lyapunov exponents. In such cases, or in the study of empirical time series, other stability indicators can however be more useful. For example, temporal stability (the reciprocal of variability) quantifies the stability of fluctuating variables. It is usually defined as the ratio of the mean over its standard deviation (the inverse of the Coefficient of Variation). A high mean contributes to temporal stability, as it contributes to values far from 0 (extinction), as well as a low standard deviation that describes fluctuations around the mean.

Another approach to stability considers the effect of removing target species from a system. The extinction cascade measures the loss of additional species after the removal of one target species. Robustness (Dunne et al. 2002a)—or deletion stability or resistance (Borrall et al. 2000)—is indeed the ability of a system to resist extinction cascades. Species removal can be random or targeted (e.g., the most connected species or species with low or high trophic level).

Instead of removing target species, invisibility describes the propensity of a system (or a resident community) to be invaded by new species (Hui and Richardson 2017). Non-invadable systems are thought to be more stable than systems that are easily invaded by introduced alien species. Thus, resistance to invasion can be a measure of system stability. Invasion can simply bring the system in a new stable and feasible configuration, or in the worst case it could lead one or more species to extinction (see Hui et al. 2016 for a recently proposed measure of invisibility).

A summary of the different introduced measures for network stability is given in Table 3. See Pimm (1984), Logofet (2005), Ives and Carpenter (2007), Donohue et al. (2013), and Borrelli et al. (2015) for additional reviews on different stability concepts.

### Complexity–stability debate

Before the 1970s, ecologists believed that more diverse communities enhanced ecosystem stability (Odum 1953; MacArthur 1955; Elton 1958). In particular, they believed that natural communities develop into stable systems through successional dynamics. Aspects of this belief developed into the notion that complex communities are more stable than simple ones. A strong proponent of this view was Elton (1958), who argued that “simple communities were more easily upset than richer ones; that is, more subject to destructive oscillations in populations, and more vulnerable to invasions”. In fact, both Odum (1953) and Elton (1958) arrived at similar conclusions based on repeated observations of simplified terrestrial communities that are characterized by more violent fluctuations in population density than diverse terrestrial communities. For example, invasions most frequently occur on cultivated land where human influence had produced greatly simplified ecological communities; outbreaks of phytophagous insects occur readily in boreal forests but are unheard of in diverse tropical forests; and the frequency of invasions is higher in simple island communities compared to more complex mainland communities. These observations led Elton (1958) to believe that complex communities, constructed from many predators and parasites (consumers), prevented populations from undergoing explosive growth (e.g., pest outbreaks).
| Network stability | Definition                                                                 | References                                                                                                                                 |
|-------------------|----------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------|
| Asymptotic stability | Perturbations from the ecological regime are dampened. The system return to its ecological regime after a perturbation in the state of the system | May (1972, 1973)  
Food webs: De Angelis (1975), Yodzis (1981), De Ruiter et al. (1995), Haydon (2000), Neutel et al. (2002, 2007), Emmerson and Raffaelli (2004), Emmerson and Yeadley (2004), Rooney et al. (2006), Otto et al. (2007), Allesina and Pascual (2008), Gross et al. (2009), Allesina and Tang (2012), Visser et al. (2012) and van Altena et al. (2016)  
Mutualism: Feng and Takemoto (2014)  
Competition: Lawlor (1980), Christianson and Kokkoris (2008) and Fowler (2009)  
Food webs: Thébault and Fontaine (2010)  
Mutualism: Okuyama and Holland (2008)  
Competition: Lawlor (1980) and Christianson and Kokkoris (2008)  
Food webs: Haydon (1994), McCann et al. (1998), Krause et al. (2003), Kondoh (2003, 2006, 2007), Thébault and Fontaine (2010), Stouffer and Bascompte (2011) and Heckmann et al. (2012)  
Mutualism: Ferrière et al. (2002), West et al. (2002), Bascompte et al. (2006), Bastolla et al. (2009), Olivier et al. (2009), James et al. (2012), Valdovinos et al. (2013) and Song and Fledman (2014)  
Competition: Kokkoris et al. (2002) and Christianson and Kokkoris (2008) |
| Resilience | Return time to ecological regime after a small perturbation | Elton (1958)  
Food webs: McCann et al. (1998), Ives et al. (2000) and Kondoh (2003, 2006, 2007)  
Competition: Hughes and Roughgarden (1998), Lehman and Tilman (2000) and Fowler (2009) |
| Persistence | Proportion of coexisting species (over the total number of species) at ecological regime. In case of a feasible regime the persistence is equal to 1 (i.e., coexistence of all species in the community) | Elton (1958)  
Food webs: Pimm (1979, 1980b), Borrvall et al. (2000), Dunne et al. (2002a) and Dunne and Williams (2009)  
Mutualism: Memmott et al. (2004), Campbell et al. (2012) and Vieira and Almeida-Neto (2015)  
Food webs: Dunne et al. (2002a) and Dunne and Williams (2009)  
Mutualism: Ramos-Jiliberto et al. (2012) |
| Structural stability | Domain or probability of feasible existence of an ecological regime w.r.t. system perturbations | Elton (1958)  
Food webs: De Angelis (1975), Haydon (1994), Kondoh (2003, 2006, 2007) and Allesina and Tang (2012)  
Mutualism: Rohr et al. (2014)  
Competition: Christianson and Kokkoris (2008) |
| Temporal stability | The reciprocal of temporal variability. It quantifies the stability of fluctuations in time. It is the ratio of the mean value of the variable in time over its standard deviation (the inverse of the Coefficient of Variation) | Elton (1958)  
Food webs: McCann et al. (1998), Ives et al. (2000) and Kondoh (2003, 2006, 2007)  
Competition: Hughes and Roughgarden (1998), Lehman and Tilman (2000) and Fowler (2009) |
| Deletion stability (extinction cascade) | Loss of additional species after the removal of one target species | Elton (1958)  
Food webs: Pimm (1979, 1980b), Borrvall et al. (2000), Dunne et al. (2002a) and Dunne and Williams (2009)  
Mutualism: Memmott et al. (2004), Campbell et al. (2012) and Vieira and Almeida-Neto (2015)  
Food webs: Dunne et al. (2002a) and Dunne and Williams (2009)  
Mutualism: Ramos-Jiliberto et al. (2012) |
| Robustness | Resistance of a system against additional extinction after species removal | Elton (1958)  
Food webs: Hui et al. (2016)  
Competition: Kokkoris et al. (1999) |
| Resistance to invasion | Resistance of a system to be invaded by new species | Elton (1958)  
Food webs: Hui et al. (2016)  
Competition: Kokkoris et al. (1999) |
and would have fewer invasions (see Hui and Richardson 2017 for background in invasion science). His ideas were closely related to MacArthur’s (1955), who hypothesized that “a large number of paths through each species is necessary to reduce the effects of overpopulation of one species.” MacArthur (1955) concluded that “stability increases as the number of links increases” and that stability is easier to achieve in more diverse assemblages of species, thus linking community stability with both increased trophic links (e.g., connectance $C$) and increased numbers of species ($S$). In other words, multiplicity in the number of prey and predator species associated with a population freed that population from dramatic changes in abundance when one of the prey or predator species declined in density. Additionally, Paine (1966) also showed that species diversity in food webs is related to the number of top predators, and that increased stability of annual production may lead to an increased capacity for systems to support such high-level consumer species, thus resulting in increased species diversity.

These early intuitive ideas were challenged by the work of May (1972, 1973). He used mathematics to rigorously explore the complexity–stability relationship (see a first review by Goodman 1975). By using linear stability analysis (asymptotic stability of the Jacobian matrix) on models constructed from a statistical universe (that is, randomly constructed Jacobians with randomly assigned elements), May (1972, 1973) found that complexity tends to destabilize community dynamics. He mathematically demonstrated that network stability decreases with diversity (measured as the number of species $S$), complexity (measured as connectance $C$), and the standard deviation of the Jacobian elements $\sigma$. In particular, he found that more diverse systems, compared to less diverse systems, will tend to sharply transition from stable to unstable behaviour as the number of species $S$, the connectance $C$, or the average Jacobian element $\sigma$ increase beyond a critical value, i.e., the system is stable if $\sigma \sqrt{SC} < 1$, unstable otherwise.

In his seminal study on community stability, May (1972, 1973) measured asymptotic local stability. In this analysis, it is assumed that the community rests at an equilibrium point where all populations have constant abundances. The stability of this equilibrium is tested with small perturbations. If all species return to the equilibrium—monotonically or by damped oscillations—it is stable. In contrast, if the population densities evolve away from the equilibrium densities—monotonically or oscillatory—they are unstable. In a community of $S$ species, this approach is based on the $S \times S$ Jacobian matrix, whose elements describe the perturbation impact of each species $j$ on the growth of each species $i$ at equilibrium population densities. The $S$ eigenvalues of the Jacobian matrix characterize its temporal behavior. Specifically, positive real parts of the eigenvalues indicate perturbation growth, while negative real parts indicate perturbation decay. Accordingly, if any of the eigenvalues has a positive real part the system will be unstable, i.e., at least one of the species does not return to the equilibrium. The mathematical proposition, thus, contradicts the ecological intuition.

**Food webs**

The use of random community matrices in May’s (1972, 1973) work has attracted much criticism (Table 4). It was shown to be extremely unlikely that any of these random communities could even remotely resemble ecosystems with a minimum form of ecological realism, such as containing at least one primary producer, a limited number of trophic levels and no consumers eating resources that are two or more trophic levels lower (Lawlor 1978, but see; Allesina and Tang 2015 for a review on the random matrix approach). The non-randomness of ecosystem structure has been demonstrated in detail by more recent food-web topology studies (e.g., Williams and Martinez 2000; Dunne et al. 2002a, b, 2004, 2005; Dunne 2006). Accordingly, subsequent work added more structural realism to those random community matrices by including empirical patterns of food web structure and Jacobian elements distributions (see Allesina and Tang 2012; Allesina et al. 2015; Jacquet et al. 2016 for the most recent advances and; Namba 2015 for a review). Several simple models have played an important role in characterizing the non-random structure of food webs, including the cascade model (Cohen et al. 1990), the niche model (Williams and Martinez 2000), and the nested-hierarchy model (Cattin et al. 2004). The niche and nested-hierarchy models have been able to capture several structural properties of empirical food webs.

**Species richness**

In general, food web features vary with species richness. Although empirical datasets of ecological networks do not display any consistency regarding their size, it has been observed that ecological networks have much smaller size than other published real-world network datasets, such as co-authorships between scientists or the World Wide Web (Dunne et al. 2002b).

Haydon (1994) discussed some of May’s hypothesis (such as the measure of stability, the consideration of unfeasible models, and the self-regulatory terms on the diagonal of the community matrix describing intraspecific interactions) but still found that (asymptotic) stability and feasibility of (generalized Lotka–Volterra) model ecosystems is reduced by the number of species. Gross et al. (2009) found that smaller model ecosystems follow other rules than larger ecosystems. Indeed, they studied artificial food webs generated by the niche model and considering nonlinear functional responses of different kinds. Thus, adding more details to
| References | Complexity–stability measures | Methods and assumptions | Additional results |
|------------|-------------------------------|-------------------------|--------------------|
| Negative complexity–stability relationship | | | |
| Haydon (1994) | S-Asymptotic, feasibility | Lead eigenvalue of random and plausible model Jacobian at feasible equilibria | Stability is reduced by donor control interactions |
| Pimm (1979, 1980b) | S, C-extinction cascades | Simulation of plausible food web model (generalized Lotka–Volterra) | If carnivores are removed |
| Gross et al. (2009) | S, C, Jacobian elements-Asymptotic | Lead eigenvalue of Jacobian of realistic food web model (niche) | Increasing strength of interaction destabilizes large networks |
| Allesina and Pascual (2008) and Allesina and Tang (2012) | S, C-Asymptotic | Lead eigenvalue of random, empirical, and model (cascade and niche) Jacobian of antagonistic interactions | |
| Krause et al. (2003) and Thébault and Fontaine (2010) | C, interaction strength-Resilience, persistence | Simulations of model and real food webs (nonlinear functional responses in Thébault and Fontaine 2010) | Stability is enhanced in compartmentalized and weakly connected architectures |
| van Altena et al. (2016) | Jacobian elements-Asymptotic | Lead eigenvalue of Jacobian of model obtained from real food web data | Skew toward weak interactions enhances stability |
| Neutel et al. (2002, 2007) and Emmerson and Yeansley (2004) | Jacobian elements-Asymptotic, resilience, feasibility, persistence | Lead eigenvalue of Jacobian of model (cascade) and real food webs | Weak interactions in long feedback loops of omnivorous species is stabilizing |
| McCann et al. (1998) | Interaction strength-Persistence, temporal stability | Nonlinear models away from equilibrium | Weak links and intermediate interaction strengths are stabilizing |
| Positive complexity–stability relationship | | | |
| Ives et al. (2000) | S-Temporal stability | Simulation of model community under environmental variation | Increasing the number of modular subcommunities increases stability |
| Pimm (1979, 1980b) | S, C-Extinction cascades | Simulation of plausible food web model (generalized Lotka–Volterra) | If herbivores are removed |
| Stouffer and Bascompte (2011) | S, C-Persistence, extinction cascade | Simulation of model (niche) | Compartmentalization increases stability |
| De Angelis (1975) | C-Asymptotic | Lead eigenvalue of Jacobian of plausible food web model | Stability is increased by donor control interactions |
| Dunne et al. (2002a) and Dunne and Williams (2009) | C-Robustness | Simulation of model obtained from real food webs | Skewness of degree distribution increases robustness |
| Haydon (2000) | Weighted C-Asymptotic | Lead eigenvalue of Jacobian of plausible food web model | |
| van Altena et al. (2016) | Weighted C-Asymptotic | Lead eigenvalue of Jacobian obtained from real food webs | No relationship between unweighted C and stability |
| Allesina and Pascual (2008) and Allesina and Tang (2012) | S, Jacobian elements-Asymptotic | Lead eigenvalue of random, empirical, and model (cascade and niche) Jacobian of antagonistic interactions | Weak interactions are destabilizing |
| Borrvall et al. (2000) | S per functional group, interaction strength-Extinction cascades | Simulation of plausible generalized Lotka–Volterra food web model with three trophic groups | Higher risk of extinction if autotrophs (rather than top predators) are removed. Skewness towards weak interactions is destabilizing; Omnivory is stabilizing |
May’s (1972, 1973) stability criteria, they showed that the strength of predator–prey links increase the stability of small webs, but destabilize larger webs. They also revealed a new power law describing how food-web stability scales with the number of species. Pimm (1979, 1980b) showed that extinction cascades are more likely in model (generalized Lotka–Volterra) communities with larger total number of species, contrasted by Borrvall et al. (2000) that found the robustness (resistance) of the same model food web to increase with network redundancy (number of species per functional group). Considering the topology of realistic (Dunne et al. 2002a) and generated model (Dunne and Williams 2009) food webs, other authors found the same result, i.e., positive relationship between number of species and robustness, however ignoring strength of interactions and community dynamics. Therefore, such contrasts may result from dynamical properties of food webs.

Connectance

Exploring how the number of interactions varies with the number of species has been one of the most basic questions for ecologists trying to find universal patterns in the structure of ecological networks. Contradicting previous works which found that the number of interactions increases linearly with the number of species (Cohen and Briand 1984; Cohen and Newmann 1985), Martinez (1992) claimed the constant connectance hypothesis in food webs: trophic links increase approximately as the square of the number of species. However, with the improvement of methodological analysis and datasets, the constant connectance hypothesis has been called into question by later studies (Havens 1992; Dunne et al. 2002b; Banašek-Richter et al. 2009). One of the most generally accepted rule on food web connectance is that food webs display an average low connectance of about 0.11 (Havens 1992; Martinez 1992; Dunne et al. 2002b), which is however still relatively high compared to that of other real-world networks (Dunne et al. 2002b).

Since connectance has been used by May (1972, 1973) as a descriptor of network complexity, it has become central to early works on the complexity–stability debate (DeAngelis 1975; Pimm 1980b, 1984) and continues to be widely used as a descriptor for network structure (Havens 1992; Dunne et al. 2002a; Olesen and Jordano 2002; Tylianakis et al. 2010; Heleno et al. 2012; Poisot and Gravel 2014). Depending on the way stability is defined, the quality of empirical datasets, or the methods used to generate theoretical networks, contradiction has been observed in the relationship between network stability and connectance. While some studies reinforced May’s hypothesis of a negative relationship between connectance and stability (Pimm 1979, 1980b; Chen and Cohen 2001; Gross et al. 2009; Allesina and Tang 2012), others found that connectance enhances...
network stability (De Angelis 1975; Dunne et al. 2002a; Dunne and Williams 2009). For example, using extinction cascade as stability measure, Pimm (1979, 1980b) found that complex model food webs are more likely to lose additional species following the extinction of one species than simple food webs: complexity is negatively correlated with stability. By using different measurements of network stability (resilience and persistence), Thébault and Fontaine (2010) also confirmed the negative relationship between connectance and stability in food webs (however, the opposite holds for mutualistic networks, see next Section). Gross et al. (2009) also revealed a negative power law to describe how food-web stability scales with connectance.

The opposite view is sustained, among others, by De Angelis (1975): using plausible food web community matrix models, he showed that the probability of stability can increase with increasing connectance if the food web is characterized by a bias toward strong self-regulation (intraspecific competition) of higher trophic level species, low assimilation efficiencies, or a bias toward donor control. Also Haydon (1994), improving May’s assumptions but still relying on community matrices, found stability to increase with connectance. However, in contrast with De Angelis (1975), stability is found to be reduced by the prevalence of donor control interactions. Furthermore, robustness increases with connectance considering only the topology of real food webs (Dunne et al. 2002a; Dunne and Williams 2009).

Weighted connectance

Only a recent study by van Altena et al. (2016) started its use into the complexity–stability context, although they found that there is no relationship between food web stability and unweighted connectance and that a high level of weighted connectance stabilizes food webs. Following a different perspective, Haydon (2000) focused on communities constructed to be as stable as they could be, and show that communities built in this way require high levels of weighted connectance, in agreement with van Altena et al. (2016). According to these studies, high stability requires high connectance, especially between weakly and strongly self-regulated (intraspecific competition) elements of the community.

Degree distribution

Degree distribution in food webs differ from a Poisson distribution (typical of random networks). However, there is no universal shape that fits food webs degree distribution. Most of the webs display exponential degree distribution (Camacho et al. 2002; Dunne et al. 2002b) and those with high connectance show a uniform distribution. Power-law and truncated power-law with an exponential drop-off in the tail also fit few of food webs degree distribution (mostly those having very low connectance) (Dunne et al. 2002b; Montoya and Solé 2002).

The skewness of degree distribution, especially exponential-type degree distribution (Dunne and Williams 2009) makes food webs more robust to targeted removals (from the most generalists) (Solé and Montoya 2001; Dunne et al. 2002a). However, the hierarchical feeding feature due to size scaling laws imposes a cost to food web robustness (Dunne and Williams 2009). Allesina et al. (2015) showed that broad degree distributions tend to stabilize (in term of asymptotic stability of the community matrix) large size-structured food webs, obtained either empirically or with the cascade and niche models.

Strength of interactions

In contrast with May’s (1972, 1973) findings, Haydon (1994) found stability to increase with elements of the Jacobian. Yodzis (1981) also found that the networks were far more likely to be stable when such elements are chosen in accord with real food web patterns rather than strictly at random. Neutel et al. (2007) showed how non-random Jacobian elements patterns in naturally assembled communities explain stability. They used below-ground food webs, whose complexity increased along a succession gradient. The weight of the feedback loops of omnivorous species characterized stability (omnivory: feeding on more than one trophic level). Low predator–prey biomass ratios (biomass pyramid, a feature common to most ecosystems) in these omnivorous loops were shown to have a crucial role in preserving stability as complexity increased during succession. However, Allesina et al. (2015) showed that it is intervality, i.e., the propensity for each predator to feed upon all the species in a certain size interval, to be the driver of stability in large size-structured foodwebs.

Variability in link strengths have also been found to be related with stability, but only for relatively small webs, whereas larger webs are instead to be destabilized by link-strength variability (Gross et al. 2009). Stability is enhanced when species at a high trophic level feed on multiple prey species and when species at an intermediate trophic level are consumed by multiple predator species. Using an energetic approach, de Ruiter et al. (1995) and Rooney et al. (2006) found that different types of structural asymmetry in energy fluxes is key to stability of real food webs. In particular, de Ruiter et al. (1995) used empirically estimated community matrices of the generalized Lotka–Volterra model to show that simultaneous occurrence of strong top-down effects (consumer control) at lower trophic levels and strong bottom-up effects (donor control) at higher trophic levels in the patterns of Jacobian elements in real food webs is important.
to ecosystem stability. The pattern is a direct result of the energetic organization of the food web. Rooney et al. (2006) used empirical food web data into a nonlinear model with functional responses and predator adaptive switching behaviour to show that slow and fast energy fluxes coupled by top-predators in real food webs convey both local and non-local stability to food webs. In conclusion, even with very different approaches, complexity does not lead to instability.

A skewed distribution of interaction strength has been widely observed in food webs, i.e., there are many weak interactions and few strong ones (Paine 1992; Berlow 1999; Berlow et al. 2004; Wootton and Emmerson 2005). This skewness towards weak interactions has been related to stability. For example, McCann et al. (1998) found that weak links and intermediate strength of interaction (measured as the likelihood of one species to be consumed by another), taking into account nonlinear saturating consumption, non-equilibrium dynamics, and empirical strengths and patterns of interaction, reinforce the stability and the persistence of the community as they dampen the oscillation in predator–prey dynamics. Neutel et al. (2002) showed that weak interactions are more likely observed in long loops in real food webs. Specifically, Jacobian elements are organized in trophic loops in such a way that long loops contain relatively many weak links. They showed and explain mathematically that this patterning enhances stability, because it reduces the amount of intraspecific interaction needed for matrix stability. On the same line, Thébault and Fontaine (2010) showed that stability of trophic networks is enhanced in weakly connected architectures. van Altena et al. (2016) confirmed the role of weak interactions for stability of real food webs. However, given skewed distributions of Jacobian elements towards weak interactions, they found that stability was promoted by even distribution of fluxes over links, in contrast with de Ruiter et al. (1995) and Rooney et al. (2006) who emphasized the role of strong asymmetry. In a recent paper, Jacquet et al. (2016) disproved the association between Jacobian elements and (asymptotic) stability in empirical food webs, but showed that the correlation between the effects of predators on prey and those of prey on predators, combined with a high frequency of weak interactions, can stabilize food web dynamics. In agreement with Neutel et al. (2002) and Neutel et al. (2007), Emmerson and Yearsley (2004) showed that a skew towards weak interactions in feasible community matrices promotes local and global stability only when omnivory is present. A feedback is found between skewness toward weak interactions and omnivory, i.e., skewed Jacobian elements are an emergent property of stable omnivorous communities, and in turn this skew creates a dynamic constraint maintaining omnivory. Borrvall et al. (2000) however found that omnivory stabilizes food webs, but the skew towards weak interaction is destabilizing (they however use interaction strengths, not Jacobian elements). Omnivory appears to be common in food webs (Polis 1991; Sprules and Bowerman 1988). A previous theoretical work (Pimm and Lawton 1978) predicted that it should be extremely rare to find species that feed simultaneously both high and low in real-world food web, and also webs with a large number of omnivores should be rare in real world. However, the authors ignored feasibility of the community matrices they used to estimate resilience (asymptotic stability), possibly underestimating omnivorous interactions.

By contrast, Allesina and Pascual (2008) found that stability is highly robust to perturbations of Jacobian elements, but it is mainly a structural property driven by short and strong predator–prey loops, with the stability of these small modules cascading into that of the whole network. These considerations challenge the current view of weak interactions and long cycles as main drivers of stability in natural communities. In addition to that, Allesina et al. (2015) showed that average Jacobian element in large size-structured foodwebs have smaller influence on stability compared with variance and correlation. Also, Allesina and Tang (2012) showed that preponderance of weak interactions (measured by Jacobian elements) decreases the probability of food webs to be stable. In particular, trophic interactions are shown to be stabilizing (as opposed to mutualistic and competitive) but, counterintuitively, the probability of stability for predator–prey networks decreases when a realistic food web structure is imposed or if there is a large preponderance of weak interactions. However, stable predator–prey networks can be arbitrarily large and complex (positive complexity–stability relationship), provided that predator–prey pairs are tightly coupled (i.e., short loops and high Jacobian elements). Same negative relationship between stability and skewness of strength of interaction distribution has been found by Borrvall et al. (2000), although using different measures of strength (interaction strengths) and stability (extinction cascade).

Predator–prey body mass ratio, affecting the interaction strength distribution, contributes largely to food-web stability. Emmerson and Raffaelli (2004) empirically estimated Lotka–Volterra interaction strengths and equilibrium population densities and used such a community matrix to evaluate (asymptotic) stability, showing that using empirical scaling laws the resulting food webs are always stable in contrast with statistical expectations from random matrices (May 1972, 1973). Otto et al. (2007) used a bioenergetic model combining nonlinear functional responses and body mass ratios, showing that such scaling may promote the stability of complex food webs.

Network architecture

The effect of network architecture, in particular modular structures, has been observed in food webs and related to
their stability. Moore and Hunt (1988) showed that food webs may contain tightly coupled subunits whose numbers may increase with diversity. Communities may be arranged in resource compartments and within them species strength of interaction would decline as diversity increased. Same result has been found by Krause et al. (2003) and Thébault and Fontaine (2010), who showed that stability of trophic networks is enhanced in compartmented and weakly connected architectures. Also, Ives et al. (2000) showed that increasing the number of modular subcommunities in a stochastic discrete time generalized Lotka–Volterra foodweb model increases stability through different species reactions to environmental fluctuations (insurance hypothesis; Yachi and Loreau 1999). Similarly, Stouffer and Bascompte (2011) demonstrate that compartmentalization increases the persistence of food webs. Compartments buffer the propagation of extinctions through the community and increase long-term persistence. The latter contribution increases with the complexity of the food web, emphasizing a positive complexity–stability relationship. However, the recent study of Grilli et al. (2016) shows that the stabilizing effect of modularity is not as general as expected.

Nested diets have been observed in food webs: top predators are very generalists and prey upon all over species, while the next predator exploiting all but the top predators (in the niche model by Williams and Martinez 2000, and the nested-hierarchy model by; Cattin et al. 2004). Generalist top predators prey upon intermediate specialist predators also in the results of Neutel et al. (2002).

**Mutualistic communities**

As the interaction between a plant and its insect pollinator has often been used as a straightforward illustrative example of a reciprocal coevolution (Darwin 1862), early studies on mutualistic interactions were mainly dedicated to understanding coevolutionary processes (e.g., Ehrlich and Raven 1964; Brown et al. 1978; Wheelwright and Orians 1982; Herrera 1985). However, coevolution is often considered as a diffuse mechanism involving several species. Thus, ecologists started to study mutualism as a whole network of interactions for which tools provided by complex network theory can be used (Table 5).

**Species richness**

Network size or the total number of species in the network has been considered as an important determinant of mutualistic networks stability. By using a theoretical model with empirically informed parameters, Okuyama and Holland (2008) found a positive relationship between community size and community resilience. They mainly attributed this positive relationship to the use of a nonlinear functional response and its saturating positive feedback effect on population growth. Their finding was later supported by Thébault and Fontaine (2010) while they used a population dynamics model with a nonlinear Holling Type II functional response in which benefits gained from mutualism saturate with the effective densities of the interaction partners. They confirmed that a high number of species diversity promotes not only the resilience of mutualistic communities but also their persistence.

**Connectance and connectivity**

Contributing to their complexity, mutualistic networks have been observed to display non-random structural patterns. Motivated by the finding of scale invariance in food webs (Cohen and Briand 1984; Cohen and Newmann 1985), Jordano (1987) studied patterns of connectance and species dependences observed in a large dataset of pollination and seed-dispersal networks. He found that connectance decreases with species richness but the average number of links per species (or linkage density) stays invariant to changing network size. Using empirical mutualistic networks spanning different biogeographic regions (including those used in Jordano 1987), Olesen and Jordano (2002) observed that connectance indeed decreases exponentially with species richness. After controlling for species richness (network size), they also observed that connectance differed significantly between biogeographic regions. On average, mutualistic networks exhibit higher connectance than food webs and other real-world networks do. However, mutualistic networks still have low to moderate level of connectance (average of 0.11 in Olesen and Jordano 2002 and 0.18 in; Rezende et al. 2007).

The implication of connectance patterns to the stability of mutualistic networks has gained attention only recently. When extending the theoretical work of May (1972, 1973) so as to incorporate realistic network structures and to differentiate between different types of interactions (predator–prey, mutualistic or competitive), Allesina and Tang (2012) found that connectance negatively affects the local stability of mutualistic community networks. The analytical study by Suweis et al. (2015) is in agreement with this statement when they correlated connectance with the degree of localization (a system is defined to have a high degree of localization when perturbations cannot easily propagate through the network). They found that mutualistic networks are indeed localized and the degree of localization decreases with connectance. Moreover, Vieira and Almeida-Neto (2015) extended a previously existing model that explores patterns of species co-extinction (Solé and Montoya 2001; Dunne et al. 2002a; Memmott et al. 2004) to study the relationship between connectance and extinction cascades in mutualistic networks, emphasizing the role of the variation...
| References                  | Complexity–stability measures                                                                 | Methods and assumptions                                                                 | Additional results                                                                 |
|-----------------------------|------------------------------------------------------------------------------------------------|------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------|
| Negative complexity–stability relationship |                                                                                                |                                                                                          |                                                                                      |
| Vieira and Almeida-Neto (2015) | C-Extinction cascade                                                                         | Stochastic coextinction model applied to a set of empirical networks                      | Extinction cascades occur more likely in highly connected mutualistic communities    |
| Feng and Takemoto (2014)     | Heterogeneity of degree, species strength, and strength of interaction (visiting frequency adjusted for uneven species abundance) distributions-Asymptotic | Theoretical study based on the analytical expression of the dominant eigenvalue           | Heterogeneity of node degree and strength of interaction distribution primarily determine the local stability of mutualistic ecosystems; Nestedness additionally affects it |
| Suweis et al. (2015)         | C-Localization                                                                               | Evaluation of the components of the eigenvalues of a set of empirical networks            | Mutualistic communities are localized; Localization is negatively correlated with connectance |
| Allesina and Tang (2012)     | $S, C, \sigma, \text{nestedness-Asymptotic}$                                                  | Analytical analysis of artificial networks with realistic structure                        | Mutualistic interactions are destabilizing; Stability is negatively affected by nestedness |
| Campbell et al. (2012)       | Nestedness-Extinction cascade                                                                  | Dynamic binary network-based model of plant-pollinator community formation                | High nestedness may in extreme circumstances promote a critical over-reliance on individual species and enhances extinction cascade |
| Thébault and Fontaine (2010) | Modularity-Resilience, persistence                                                            | Simulation of model and real pollination networks                                         | A highly connected and nested architecture promotes community stability in mutualistic networks |
| Positive complexity–stability relationship |                                                                                                |                                                                                          |                                                                                      |
| Okuyama and Holland (2008)   | $S, L$, symmetry of strength of interaction (similarity of pairwise half-saturated constants), nestedness-Resilience | Theoretical analysis with empirically informed parameters; Non-linear functional response | Community resilience is enhanced by increasing community size and connectivity, and through strong, symmetric strength of interaction of highly nested networks |
| Thébault and Fontaine (2010) | $S, C$, nestedness-Resilience, persistence                                                    | Simulation of real pollination networks under a model using a nonlinear Holling type II functional response | A highly connected and nested architecture promotes community stability               |
| Memmott et al. (2004)        | Nestedness-Extinction cascade                                                                  | Topological coextinction model; Explored the effects on plant extinction of the preferential removal of the most linked pollinators | Plant species diversity declined most rapidly with removal of the most-linked pollinators; Declines were no worse than linear, because of the nested architecture |
| James et al. (2012)          | Species degree, $C$, nestedness-Persistence                                                    | Population dynamics model that incorporates both competition and mutualism                 | Species degree is a much better predictor of individual species survival and hence, community persistence; Nestedness is only of secondary importance to community persistence |
| Bascompte et al. (2006)      | Heterogeneity of species strength distribution, asymmetry of species dependences-Domain of coexistence | Population dynamics model (generalized Lotka–Volterra); Species dependences estimated from empirical quantitative networks | The asymmetry of plant-animal dependences enhance long-term coexistence and facilitate biodiversity maintenance |
| Suweis et al. (2015)         | $S$, heterogeneity of species strength distribution-Localization                              | Evaluation of components of the eigenvalues of empirical interaction matrices              | Mutualistic communities are localized; Localization is positively correlated with network size and the variance of the weighted degree distribution |
| Bastolla et al. (2009)       | Nestedness-Domain of coexistence                                                              | Theoretical model of population dynamics (interspecific competition among species in the same trophic level is also incorporated); Nestedness of simulated networks informed from empirical networks | Nestedness reduces effective interspecific competition and enhances the number of coexisting species |
of species dependences after each extinction event. They used a stochastic co-extinction model in which a species does not necessarily need the extinction of all its interaction partners to go itself extinct. The chance of a species to survive indeed depends on its level of dependence upon its interaction partners. Contradicting previous pattern observed in food webs (Dunne et al. 2002a), they found that extinction cascades were more likely to happen in highly connected communities. However, highly connected communities were also shown to be persistent (James et al. 2012) and resilient (Okuyama and Holland 2008), which was also confirmed by Thébault and Fontaine (2010).

**Degree distribution**

Although network size and connectance partially determine the complexity of the network, they discard important information regarding individual species connectivity as well as distribution of the overall connectivity among species (node degree distribution). Early studies on species connectivity in mutualistic networks mainly concentrated on how interactions are distributed among species. Attenditions were mainly focused on the prevalence of either generalists or specialists in mutualistic networks (Waser et al. 1996; Memmott 1999; Vázquez and Aizen 2003). Stimulated by these early studies, Jordano et al. (2003) found generalized patterns in the node degree distribution of a large number of plant-pollinator and plant-frugivore networks. Most of the networks showed a distribution of node degree that fits a truncated power-law regime, suggesting the prevalence of specialists and the rarity of super generalists. Few of the networks showed a power-law or an exponential distribution in their node degree. Moreover, gamma distribution was also found to best fit the distribution of node degree in mutualistic networks (Okuyama 2008). The heterogeneity of node degree distribution was found years later to be a primary factor affecting negatively the local stability of mutualistic networks (Feng and Takemoto 2014). However, when node degrees are considered individually for each species, they were shown to be a good predictor of species own survival and thus of the community persistence (James et al. 2012).

**Strength of interactions**

Instead of only considering qualitative interactions (presence or absence), quantitative measurement of strength of interaction also prevails in mutualistic network studies. In plant-pollinator as well as in plant-frugivory interactions, strength of interaction often refers to the relative number of visits of the animal to the plant. Jordano (1987) observed an extremely skewed distribution of species dependences in mutualistic communities: weak dependences greatly exceed in number strong ones. By including more datasets in their
study, Bascompte et al. (2006) confirmed Jordano’s (1987) finding of a skewed distribution of interaction dependences. Additionally, mutualistic networks were also found to be highly asymmetric in terms of species roles: while animals depend strongly on the plants, plants rely poorly on their animal pollinators or seed dispersers (Bascompte et al. 2006).

The maintenance of biodiversity was suggested to be facilitated by both the heterogeneity of species strength distribution and the asymmetry of species dependences (Bascompte et al. 2006). Localization, or the ability of the system to reduce the propagation of perturbations through the network, has also been shown to be enhanced by the heterogeneity of species strength distribution (Suweis et al. 2015). Notice that Suweis et al. (2015) defined the strength of a species as its weighted degree or the sum of interaction strengths in which the species is involved. Opposed to the finding of Bascompte et al. (2006) who used a linear functional response in their model, Okuyama and Holland (2008) argued that the asymmetry of species dependences, implying an asymmetry of strength of interaction between animals and plants (measured as similarity of the pairwise half-saturation constants), has a negative effect (although small) on the resilience of mutualistic communities when a nonlinear functional response is used. Feng and Takemoto (2014) also showed that the heterogeneity of the distribution of strength of interaction (estimated from visiting frequencies adjusted for uneven species abundances) indeed impacts negatively on the local stability of mutualistic communities. Moreover, by also using a saturating functional response, Rohr et al. (2014) demonstrated that regardless of the distribution of interaction strength, mutualistic communities that have on average a high level of interaction strength are more likely to be structurally stable (have a wider domain of feasible and stable coexistence).

**Network architecture**

Although modularity or compartmentalization is a feature commonly observed in food webs, mutualistic networks also exhibit a certain level of modularity. A test for modularity in a wide datasets allowed Olesen et al. (2007) to affirm that pollination networks with a relatively high number of species are indeed modular. Moreover, the observed level of modularity increases with network size. The number of modules and the level of modularity observed in pollination networks are found to be invariant to sampling efforts at different time (Dupont and Olesen 2012). Mello et al. (2011) also noticed a high level of modularity in seed-dispersal networks. Little is known about the implication of modular structure to mutualistic network stability. Thébault and Fontaine (2010) emphasized that structural patterns favouring stability fundamentally differ in food webs and mutualistic networks: while the modularity pattern enhances food web stability, it has a negative effect on the persistence and resilience of mutualistic networks.

A widely accepted topological feature proper to mutualistic networks is nestedness. Bascompte et al. (2003) started to explore this feature in a meta-analysis of empirical mutualistic communities and found that mutualistic networks are indeed highly nested. They also found that nestedness increases with network complexity expressed in terms of species richness and connectivity. Nestedness has always been believed to be the most important determinant of mutualistic network stability. For example, extinction cascades following the removal of the most generalist pollinator in a pollination community have been shown to happen only linearly because of the stabilizing effect of nestedness (Memmott et al. 2004). The nested structure of mutualistic networks also enhances the number of coexisting species by reducing effective interspecific competition (Bastolla et al. 2009). Nestedness also has a positive effect on the persistence and resilience of mutualistic communities (Okuyama and Holland 2008; Thébault and Fontaine 2010). Rohr et al. (2014) showed that the parameter domain leading to both dynamically stable and feasible equilibrium, i.e., the domain of stable coexistence of species (an extended measurement of the system’s structural stability) is maximized when artificial networks are assumed to have a high level of nestedness. However, some recent studies started to discard the importance of nestedness to network stability. James et al. (2012) indeed found that nestedness is, at best, a secondary covariate rather than a causative factor for species coexistence in mutualistic communities and has no significant effect on community persistence. By means of analytical analyses of artificial networks with realistic structure, Allesina and Tang (2012) affirmed that local stability is negatively affected by the nestedness of mutualistic community matrices. Campbell et al. (2012) also showed that extreme nestedness facilitates sequential species extinctions (extinction cascades).

**Competitive communities**

Competitive interactions have sometimes been considered together with trophic interactions in food webs models, and their contribution to stability assessed. There is common agreement that self-regulating interactions due to intraspecific competition (i.e., negative terms on the diagonal of the interaction or community matrix) increase stability. For example, De Angelis (1975), using plausible food web models, showed that the probability of stability increases if the food web is characterized by a bias toward strong self-regulation (intraspecific competition) of higher trophic level species. Haydon (1994) found a similar result, i.e., that considering intraspecific competition increases food web stability. Again, Haydon (2000) focused on communities constructed...
to be as stable as they could be, and show that communities
built in this way require high connectance between weakly
and strongly self-regulated (intra-specific competition) ele-
ments of the community. Neutel et al. (2002) showed and
explain mathematically that the patterning of real food web
Jacobian elements enhances stability because it reduces the
amount of intraspecific interaction needed for matrix sta-
bility. Yodzis (1981) also found that the presence of self-
regulatory terms (intraspecific competition) in some con-
sumer species stabilizes the network. However, the role of
interspecific competition is less clear. For example, Yodzis
(1981) showed that interspecific competition tends to be
destabilizing: assuming that interspecific competition only
happens among consumers sharing resources, he found that
the fraction of stable community matrices decreases with the
number of competitive pairs. By contrast, Allesina and Tang
(2012) showed that competitive interactions are destabiliz-
ing, in the sense that the number of species $S$ and the con-
nectance $C$ that result in an unstable equilibrium are lower
for competitive rather than trophic communities.

In the 1970s, it was believed that ecological communities
were structured by competitive interactions (e.g., MacArthur
1972). Theoretically speaking, purely competitive commu-
nities are simpler compared to food webs and mutualistic
networks because they are composed of only one trophic
level. Thus, the simplicity of competitive communities
makes them an ideal theoretical framework for studying the
relationship between community complexity and stability,
and studies relating biodiversity and ecosystem function
tended to focus on the diversity of primary producers (e.g.,
Hooper et al. 2005). For these reasons, extensive experi-
mental (Lawlor 1980; Tilman and Downing 1994; Tilman
1996; Lehman and Tilman 2000) and theoretical (Lawlor
1980; Tilman et al. 1997, 1998; Doak et al. 1998; Tilman
1999; Cottingham et al. 2001) studies have been done on the
relation between species richness of plants and community
stability (Table 6).

Species richness

Species richness has been reported to affect the stability
of competitive communities. Tilman and Downing (1994)
empirically showed that primary productivity in more
diverse plant communities is more resistant and recovers
fully after a major drought. Tilman et al. (1997) confirmed
such findings using theoretical competition models. Doak
et al. (1998) however showed that such result could be sta-
istically inevitable using the temporal variation in aggregate
community properties as indicators of stability (see also Til-
man et al. 1998 for a reply). Lehman and Tilman (2000)
analysed different models of multispecies competition and
empirical data (Tilman 1996), finding that greater diversity
increases the temporal stability of the entire community but
decreases the temporal stability of individual populations.
Specifically, temporal stability of the entire community
increases fairly linearly without saturation with increased
diversity. Species composition of each community was also
predicted to be as important as diversity in affecting com-
munity stability. The work by Tilman (1999) summarizes
the empirical and theoretical positive relationship between
species diversity and community stability, primary produc-
tivity, and invasibility in grassland competitive com-
munities (see, however, the critical review in Cottingham
et al. 2001). Lawlor (1980) compared observed communi-
ties (defined by symmetric interaction matrices where each
competition coefficient is given by a measure of overlap of
resource utilization) with analogous randomized versions of
them (note that he randomizes the resources utilization
spectra rather than the competition coefficients themselves):
he found that stability of observed communities decreases
with the number of species, however, observed communities
are generally more stable than randomly constructed com-
munities with the same number of species. The higher stabil-
ity of observed (compared to random) communities is due
to lower similarities among consumer species, suggesting
that interspecific competitive processes are very important
in shaping communities. Christianou and Kokkoris (2008)
reported that increasing the number of species in the com-
munity also decreases the probability of feasibility of the
system, however, species richness does not significantly
affect the probability (proportion of random communities)
of local stability and the resilience of feasible competitive
communities. By contrast, Fowler (2009) demonstrated that
increasing the number of species in a discrete-time competi-
tion model (both symmetric and asymmetric, with a skew
towards weak interactions) results in an increased probabil-
ity (species growth rate parameters region) of local stability
in competitive feasible communities: increasing the competi-
tive negative feedbacks adding more species or links in the
network dampens oscillatory dynamics and contributes to
equilibrium stability.

Connectance

Fowler (2009) also showed that an increase in network con-
nectance and in the number of competitive links (connectiv-
ity) reduces per-capita growth rates through an increase in
competitive feedback, thus stabilises oscillating dynamics.
Furthermore, he affirmed that these results stay robust to
changes in species interaction strengths.

Strength of interactions

Most studies on competitive communities focused on the
implication of competition coefficients, i.e., interactions
strengths, on community stability. However, different
| References                  | Complexity–stability measures | Methods and assumptions                                                                 | Additional results                                                                                     |
|-----------------------------|-------------------------------|--------------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------|
| **Negative complexity–stability relationship** |                               |                                                                                             |                                                                                                        |
| Lawlor (1980)               | $S$-Asymptotic stability     | Lead eigenvalue of random vs. observed symmetric interaction (overlap) matrices              | Observed communities are generally more stable than randomly constructed communities with the same number of species |
| Lehman and Tilman (2000)    | $S$-Asymptotic, temporal stability | Lead eigenvalue and simulations of three different models (mechanistic, phenomenological, statistical) and empirical time series | Greater diversity decreases the temporal stability of individual populations                           |
| Christianou and Kokkoris (2008) | $S$, interaction strength-Asymptotic, feasibility, persistence, structural stability | Model of competitive community                                                             | Asymptotic stability is not affected by the number of species $S$, but structural stability (domain of stable coexistence) decreases with species richness; Weak interaction strengths enhances structural stability |
| Kokkoris et al. (1999)      | Interaction strength-resistance to invasion | Community assembly model from a regional species pool                                        | Weak interaction strengths enhances resistance to invasion                                             |
| Kokkoris et al. (2002)      | Interaction strength-Asymptotic, feasibility, persistence, structural stability | Model of competitive community                                                             | Weak interaction strengths enhances species coexistence                                               |
| **Positive complexity–stability relationship** |                               |                                                                                             |                                                                                                        |
| Lehman and Tilman (2000)    | $S$-Asymptotic, temporal stability | Lead eigenvalue and simulations of three different models (mechanistic, phenomenological, statistical) and empirical time series | Greater diversity increases the temporal stability of the entire communities                          |
| Fowler (2009)               | $S$, C, connectivity-Asymptotic, structural stability | Lead eigenvalue and simulation of discrete-time model of competitive community              | Result robust to change in interaction strengths                                                      |
| Hughes and Roughgarden (1998) | Interaction strength-Temporal stability | Discrete-time two-species competition model                                                 | Stability independent on the magnitude but related to asymmetry of interaction strengths               |
| Allesina and Tang (2012)     | $S$, C, Jacobian elements-Asymptotic | Lead eigenvalue of random, empirical, and model Jacobian of competitive interactions      | Equilibrium becomes unstable for smaller $S$ and $C$ in competitive compared to trophic communities   |
measurements of stability have been used. For example, Hughes and Roughgarden (1998) studied temporal stability measured as the aggregate community biomass in a discrete time two-species competition model. They found that temporal stability is relatively independent of the magnitude of interaction strengths but the degree of asymmetry of interactions is the key to community stability. Quantifying the stability of the community by its invulnerability to invasion, Kokkoris et al. (1999) studied the distribution of interaction strengths (competition coefficients)—not Jacobian elements—during the assembly process of theoretical competitive communities. They found that the mean interaction strength drops as assembly progresses and most interactions that are formed are weak. It suggests that communities that are invulnerable to further invasion are those where interspecific interactions are weaker than the average interaction strength between competing species of a regional pool. In a later study (Kokkoris et al. 2002), the same authors explored how the number of coexisting species vary with the average interaction strength. Confirming their previous finding on the importance of weak interactions to community stability, they found that the preponderance of weak interactions indeed allow many species to coexist. Moreover, correlation in the interaction matrix, mainly a result of trade-offs between species characteristics, can increase the probability of species coexistence. Christianou and Kokkoris (2008) even deepened the study on the importance of weak interactions to stability by considering system feasibility of a competitive community. Consistent with previous findings, they showed that the probability of feasibility decreases with increasing interaction strength.

Recent developments

In this section we briefly introduce the most recent developments in the theory of the complexity–stability relationship. Including more details and making models more realistic seem to give more space for a positive complexity–stability relationship. These extensions include, but are not limited to, considering multilayer networks (accounting for different interaction types varying in space and interconnected communities, see Pilosof et al. 2017 for a recent review), or describing trait mediated interactions and adaptive networks. After a brief description of multilayer networks, specific focus will be given to the latter two extensions.

Considering multiple interaction types, i.e., trophic, mutualistic, and competitive in the same community, can alter ecological networks dynamics, complexity, and stability (see review by Fontaine et al. 2011). Melian et al. 2009 combined mutualistic and antagonistic (herbivorous) interactions in an empirically derived model of such ecological network, showing that species persistence is increased by the correlation between strong species dependences and the ratio of the total number of mutualistic to antagonistic interaction per species. Mougi and Kondoh (2012), using random, cascade, and bipartite (Thébault and Fontaine 2010) models, showed that a moderate mixture of antagonistic and mutualistic interactions can stabilize community dynamics, and increasing complexity (species richness and connectance) leads to increased (asymptotic) community-matrix stability. Mougi and Kondoh (2014) confirmed their previous results in an extended version of their model also considering competition, adding that the hierarchically structured antagonistic interaction network is important for the stabilizing effect of mixed interactions to emerge in complex communities. Mougi (2016a), using interaction strengths and (asymptotic) stability of community matrices, showed that overlooked unilateral interactions (where only one species affects the partner species, e.g., amensalism or commensalism) greatly enhance community stability. Such unilateral interactions are however more stabilizing than symmetric interactions (competition and mutualism) but less stabilizing than asymmetric interactions (antagonistic), confirming previous results in Mougi and Kondoh (2014).

The effect of spatial dynamics have been shown to be stabilizing in classical theoretical ecology. However, only few recent contributions considered space into the complexity–stability debate, describing meta-communities, i.e., networks of networks. Considering local food webs connected through dispersal, both Mougi and Kondoh (2016) and Gravel et al. (2016) showed that indeed intermediate dispersal and the number of local patches can increase the asymptotic stability of the meta-community matrix.

Trait-mediated interactions and adaptive networks: food webs

The discussion thus far has implicitly assumed that links among species remain unchanged over time. This is often a simplifying assumption, as adaptive foraging (see review in Valdivinos et al. 2010) or other forms of adaptive behaviour in response, e.g., to environmental changes (Stroma and Laferty 2016) can often cause links to form, change in strength, or disappear as time progresses. Adaptive networks has been shown to reproduce realistic food-web structures (Nuwagaba et al. 2015), to promote stability (Nuwagaba et al. 2017), and to allow for positive complexity–stability relationships. For example, Kondoh (2003) and Kondoh (2006) showed that foraging adaptation enhances stability of trophic communities. Without adaptation, complexity is destabilizing, while adaptive foragers help buffering environmental fluctuations resulting in a positive relationship between complexity and persistence. Visser et al. (2012) examined the effect of adaptive foraging behaviour within a tri-trophic food web and
demonstrated that adaptive behaviour will always promote stability of community dynamics. Predator–prey body mass ratio, affecting the interaction strength distribution, contributes largely to food-web stability (Emmerson and Raffaelli 2004; Brose et al. 2006; Otto et al. 2007). Heckmann et al. (2012) combined this allometric body-size structure and adaptive foraging behaviour in random and niche food web models with nonlinear functional responses, showing that both body-size structure and adaptation increase the number of persisting species through stabilising interaction strength distributions Moreover, adaptive foraging explains emergence of size-structured food webs (in which predators tend to focus on prey on lower trophic levels and with smaller body sizes) from random ones, linking these two stabilising mechanisms.

Trait adaptation can also be modelled and give rise to complex trophic interaction networks (Brännström et al. 2011, 2012; Landi et al. 2013, 2015; Hui et al. 2018), and their complexity–stability relationship assessed (Kondoh 2007; Ingram et al. 2009). In particular, Kondoh (2007) studied adaptation in predator-specific defence traits, reporting its unimodal effect on the complexity–stability (connectance-persistence and robustness) relationship, while species richness always has a negative impact on stability. Ingram et al. (2009) studied body size and niche width adaptation in different environmental conditions, emphasizing a positive correlation between omnivory with temporal variability and species turnover through extinctions and invasions–speciations.

**Trait-mediated interactions and adaptive networks: mutualistic communities**

Pioneering studies addressing the effect of mutualistic community structure to community stability often utilized dynamic models of changing population abundance such as those based on extensions of the Lotka–Volterra model for mutualism, with various types of functional response (e.g., Okuyama and Holland 2008; Bastolla et al. 2009; Thébault and Fontaine 2010 all used a nonlinear functional response). Although these models have expanded our knowledge about the structure and dynamics of complex mutualistic systems, they disregarded important biological processes associated with plant-animal interactions. One important biological process is adaptation. Recent studies incorporated adaptation into the foraging behaviour of animal pollinators and seed dispersers. One way to reflect adaptive foraging is through rewiring of interactions. In a study by Zhang et al. (2011), the emergence of nestedness pattern in pollination and frugivory networks has been well reproduced when species are allowed to switch their mutualistic partner for another one providing higher benefit, as a consequence of adaptive foraging strategy. Going beyond the importance of adaptive rewiring to the emergence of network structure, other studies even explored its implication to network stability. Ramos-Jiliberto et al. (2012) used a spatially explicit model in which species occupy an infinite number of patches as habitats, and showed that when animal pollinators have the ability to rewire their connections after depletion of host plant abundances, the resistance of the network against additional extinction induced by primary species removal (i.e., network robustness) is enhanced. Moreover, preferential attachment to host plants having higher abundance and few exploiters enhances network robustness more than other rewiring alternatives. Foraging effort of pollinators can also be incorporated directly as an evolving trait affecting pollinator’s growth rate. Indeed, Valdivinos et al. (2013) developed a population dynamics model based on pollinator’s adaptive foraging and projected the temporal dynamics of three empirical pollination networks. In their model, asymmetries between plants and animals were considered based on the fraction of visits that end in pollination events, the expected number of seeds produced by a pollination event, and the amount of floral resources that the animal extracts in each visit to a plant. They found that incorporation of adaptive foraging into the dynamics of a pollination network increases network persistence and diversity of its constituent species. Moreover, Song and Fledman (2014) constructed a mathematical model that integrates individual adaptive foraging behaviour and population dynamics of a community consisting of two plant species and a pollinator species. They found that adaptive foraging at the individual level, complementing adaptive foraging at the species level, can enhance the coexistence of plant species through niche partitioning between conspecific pollinators.

Adaptation in mutualistic networks has also been modelled through the evolution of functional traits determinant of the interactions. Such traits are often those that can impose important constraints on the interactions, such as the proboscis lengths of a pollinator and the flower tube length of a plant (Eklöf et al. 2013; Zhang et al. 2013; Hui et al. 2018). For instance, Olivier et al. (2009) showed that tolerance traits (those responsible for minimising fitness cost but not reducing encounter rate), as opposed to resistance traits (those acting to reduce encounter rate between the interacting partners) are an important factor promoting stability of mutualisms. Moreover, they argued that a tolerance trait such as the phenotypic plasticity in honeydew production can prevent escalation into an antagonistic arms race and led to mutualistic coevolution. Using a theoretical model based on the interplay between ecological and evolutionary processes, Minoarivelos and Hui (2016) studied the evolution of phenotypic traits in mutualistic networks. By assuming that interactions are mediated by the similarity of phenotypic traits between mutualistic partners, they generated certain realistic architectures of mutualistic networks. In particular,
they showed that a moderate accessibility to intra-trophic resources and cross-trophic mutualistic support can result in a highly nested web, while low tolerance to trait difference between interacting pairs leads to a high level of modularity. Moreover, the similarities between functional traits can be approximated by phylogenetic similarities, allowing the architecture of bipartite mutualistic networks to be shaped by the phylogenies (coevolutionary history) of resident species (Rezende et al. 2007; Minoarivelo et al. 2014).

More abstract traits have also been used in modelling mutualistic coevolution. For instance, Ferrière et al. (2002) defined a trait measured as the per capita rate of commodities trading which represents the probability per unit time that a partner individual receives benefit from a mutualistic interaction. They found that the existence of ‘cheaters’, or individuals that reap mutualistic benefits while providing fewer commodities to the partner species, can lead to the coexistence of mutualistic partners and thus is a key to the persistence of mutualism. In contrast to their study, West et al. (2002) showed that one of the factors that may stabilize mutualistic interactions is when individuals preferentially reward more mutualistic behaviour and punish less mutualistic (i.e., more parasitic) behaviour. The stability of the plant-legume mutualism was also explained by this cost/reward process. Plants that are selected to supply preferentially more resources to nodules that are fixing more N₂ can be crucial to the establishment of effective legume-rhizobium mutualisms during biological invasions (Le Roux et al. 2017).

Finally, Mougi (2016b) also considers adaptive behavioural network dynamics in a two-interaction (antagonistic and mutualistic) community. While adaptive partner switch is destabilizing single-interaction communities and does not reverse the negative complexity–stability relationship (contrary to Kondoh 2003), it stabilizes hybrid communities with multiple interaction types and reverts the complexity–stability relationship to positive (with complexity measured by number of species and connectance, while stability measured by species persistence).

Conclusions

More than 40 years after May’s (1972, 1973) pioneering work, there is still no complete agreement on the complexity–stability relationship in ecosystems. The main issues (or rather progress) could be related to the use of different definitions and measures for both complexity and stability, and the use of model vs. real ecosystem data. Moreover, the adaptation and evolution of resident species has only recently started being explored, and their contribution to the debate is no doubt important, as foreseeable in the rapid changes that are affecting our planetary ecosystems in which all ecological networks are embedded. Generic evolutionary models and models that implement adaptive processes thus serve as a promising tool for resolving the debate and, importantly, furthering our understanding and better management of biodiversity in the era of the Anthropocene.

Acknowledgements

Open access funding provided by International Institute for Applied Systems Analysis (IIASA). PL and CH acknowledge support from the National Research Foundation (NRF) of South Africa (Grant 89967). CH further acknowledges support from the NRF (Grant 109244) and the Australian Research Council (Discovery Project DP150103017). HOM acknowledges support from DST-NRF Centre of Excellence in Mathematical and Statistical Sciences (CoE-MaSS; Grant BA2017/136). The contribution of two anonymous reviewers greatly improved the quality of the manuscript. This review is based on Landi et al. (2018) published as a chapter in the book “Systems Analysis Approach for Complex Global Challenges” (Mensah et al. 2018).

Open Access

This article is distributed under the terms of the Creative Commons Attribution 4.0 International License (http://creativecommons.org/licenses/by/4.0/), which permits unrestricted use, distribution, and reproduction in any medium, provided you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons license, and indicate if changes were made.

References

Allesina S, Pascual M (2008) Network structure, predator-prey modules, and stability in large food webs. Theor Ecol 1:55–64
Allesina S, Tang S (2012) Stability criteria for complex ecosystems. Nature 483:205–208
Allesina S, Tang S (2015) The stability-complexity relationship at age 40: a random matrix perspective. Popul Ecol 57:63–75
Allesina S, Grilli J, Barabás G, Tang S, Aljadeff J, Maritan A (2015) Predicting the stability of large structured food webs. Nat Commun 6:7842
Almeida Neto M, Guimarães P, Guimarães PR Jr, Loyola RD, Ulrich W (2008) A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. Oikos 117:1227–1239
Atmar W, Patterson BD (1993) The measure of order and disorder in the distribution of species in fragmented habitat. Oecologia 96:373–382
Baird D, Luczkojich JJ, Christian RR (1998) Assessment of spatial and temporal variability in ecosystem attributes of the St. Marks National Wildlife Refuge, Apalachee Bay, Florida. Estuar Coast Shelf Sci 47:329–349
Banášek-Richter C, Bersier LF, Cattin MF, Baltensperger R, Gabriel JP, Merz Y, Ulanowicz RE, Tavares AF, Williams DD, de Ruiter PC, Winemiller KO, Naisbit RE (2009) Complexity in quantitative food webs. Ecology 90:1470–1477
Bascompte J, Jordano P, Melián CJ, Olesen JM (2003) The nested assembly of plant-animal mutualistic networks. Proc Natl Acad Sci USA 100:9383–9387
Bascompte J, Jordano P, Olesen JM (2006) Asymmetric coevolutionary networks facilitate biodiversity maintenance. Science 312:431–433
Bastolla U, Fortuna MA, Pascual-Garcia A, Ferrera A, Luque B, Bascompte J (2009) The architecture of mutualistic networks minimizes competition and increases biodiversity. Nature 458:1018–1021
Haydon D (1994) Pivotal assumptions determining the relationship between stability and complexity: an analytical synthesis of the stability-complexity debate. Am Nat 144:14–29

Haydon D (2000) Maximally stable model ecosystems can be highly connected. Ecology 81:2631–2636

Heckmann L, Drossel B, Brose U, Guili C (2012) Interactive effects of body-size structure and adaptive foraging on food-web stability. Ecol Lett 15:243–250

Heleno R, Devoto M, Pocock M (2012) Connectance of species interaction networks and conservation value: is it any good to be well connected? Ecol Indic 14:7–10

Herrera CM (1985) Determinants of plant-animal coevolution: the case of mutualistic dispersal of seeds by vertebrates. Oikos 44:132–141

Hooper DU, Chapin FS III, Ewel JJ, Hector A, Inchausti P, Lavorel S, Lawton JH, Lodge DM, Loreau M, Naeem S, Schmid B, Setala H, Symstad AJ, Vandermeer J, Wardle DA (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecol Monogr 75:3–35

Hughes JB, Roughgarden J (1998) Aggregate community properties and the strength of species’ interactions. Proc Natl Acad Sci USA 95:6837–6842

Hui C, Richardson DM (2017) Invasion dynamics. Oxford University Press, Oxford

Hui C, Richardson DM, Landi P, Minoarivelo HO, Garnas J, Roy HE (2016) Defining invasiveness and invasibility in ecological networks. Biol Invasions 18:971–983

Hui C, Minoarivelo HO, Landi P (2018) Modelling coevolution in ecological networks with adaptive dynamics. Math Methods Appl Sci. https://doi.org/10.1002/mma.4612

Ingram T, Harmon LJ, Shurin JB (2009) Niche evolution, trophic structure, and species turnover in model food webs. Am Nat 174:56–67

Ives AR, Carpenter SR (2007) Stability and diversity of ecosystems. Science 317:58–62

Ives AR, Klug JL, Gross K (2000) Stability and species richness in complex communities. Ecol Lett 3:399–411

Jacquet C, Moritz C, Morissette L, Lagagneux P, Massol F, Archambault P, Gravel D (2016) No complexity–stability relationship in empirical ecosystems. Nat Commun 7:12573

James A, Pitchford JW, Plank MJ (2012) Disentangling nestedness from models of ecological complexity. Nature 487:227–230

Johnson KH, Vogt KA, Clark HJ, Schmitz OJ, Vogt DJ (1996) Biodiversity and the productivity and stability of ecosystems. Trends Ecol Evol 11:372–377

Jordano P (1987) Patterns of mutualistic interactions in pollination and seed dispersal: connectance, dependence asymmetries, and coevolution. Am Nat 129:657–677

Jordano P, Bascompte J, Olesen JM (2003) Invariant properties in coevolutionary networks of plant animal interactions. Ecol Lett 6:69–81

Kokkoris GD, Troumbis AY, Lawton JH (1999) Patterns of species interaction strength in assembled theoretical competition communities. Ecol Lett 2:70–74

Kokkoris GD, Jansen VAA, Loreau M, Troumbis AY (2002) Variability in interaction strength and implications for biodiversity. J Anim Ecol 71:362–371

Kondoh M (2003) Foraging adaptation and the relationship between food-web complexity and stability. Science 299:1388–1391

Kondoh M (2005) Is biodiversity maintained by food-web complexity? The adaptive food-web hypothesis. In: Belgrano A, Scharler UM, Dunne JA, Ulanowicz RE (eds) Acquatic food webs: an ecosystem approach. Oxford University Press, Oxford, pp 130–142

Kondoh M (2006) Does foraging adaptation create the positive complexity–stability relationship in realistic food-web structure? J Theor Biol 238:646–651

Kondoh M (2007) Anti-predator defence and the complexity–stability relationship of food webs. Proc R Soc B Biol Sci 274:1617–1624

Krause AE, Frank KA, Mason DM, Ulanowicz RE, Taylor WW (2003) Compartments revealed in food-web structure. Nature 426:282–285

Landi P, Piccardi C (2014) Community analysis in directed networks: in-, out-, and pseudocommunities. Phys Rev E 89:012814

Landi P, Dercole F, Rinaldi S (2013) Branching scenarios in eco-evolutionary prey-predator models. SIAM J Appl Math 73:1634–1658

Landi P, Hui C, Dieckmann U (2015) Fisheries-induced disruptive selection. J Theor Biol 365:204–216

Landi P, Minoarivelo HO, Brännström A, Hui C, Dieckmann U (2018) Complexity and stability of adaptive ecological networks: a survey of the theory in community ecology. In: Men-sah P, Katerere D, Hachigonta S, Roodt A (eds) Systems analysis approach for complex global challenges. Springer, Cham, pp 209–248

Lawlor LR (1978) Comment on randomly constructed model ecosystems. Am Nat 111:445–447

Lawlor LR (1980) Structure and stability in natural and randomly constructed competitive communities. Am Nat 116:394–408

Le Roux JJ, Hui C, Keet J-H, Ellis AG (2017) Co-introduction vs ecological fitting as pathways to the establishment of effective mutualisms during biological invasions. New Phytol 215:1354–1360

Lehman CL, Tilman D (2000) Biodiversity, stability, and productivity in competitive communities. Am Nat 156:534–552

Logofet DO (2005) Stronger-than-Lyapunov notions of matrix stability, or how “flowers” help solve problems in mathematical ecology. Linear Algebra Appl 398:75–100

Loreau M, de Mazancourt C (2013) Biodiversity and ecosystem stability: a synthesis of underlying mechanisms. Ecol Lett 16:106–115

MacArthur RH (1955) Fluctuations of animal populations and a measure of community stability. Ecology 36:533–536

MacArthur RH (1972) Geographical ecology: patterns in the distribution of species. Harper&Row, New York

Martinez ND (1992) Constant connectance in community food webs. Am Nat 139:1208–1218

Martinez ND (1994) Scale-dependent constraints on food-web structure. Am Nat 144:935–953

May RM (1972) Will a large complex system be stable? Nature 238:413–414

May RM (1973) Stability and complexity in model ecosystems. Princeton University Press, Princeton

McCann KS, Hastings A, Huxel GR (1998) Weak trophic interactions and the balance of nature. Nature 395:794–798

Melian CJ, Bascompte J, Jordano P, Krivan V (2009) Diversity in a complex ecological network with two interaction types. Oikos 118:122–130

Mello MAR, Marquitti VMD, Guimarães PR Jr, Kalko EKV, Jordano P, de Aguiar MAM (2011) The modularity of seed dispersal: differences in structure and robustness between bat- and bird-fruit networks. Oecologia 167:131–140

Memmott J (1999) The structure of a plant-pollinator food web. Ecol Lett 2:276–280

Memmott J, Waser NM, Price MV (2004) Tolerance of pollination networks to species extinctions. Proc R Soc B Biol Sci 271:2605–2611

Mensah P, Katerere D, Hachigonta S, Roodt A (eds) (2018) Systems analysis approach for complex global challenges. Springer, Cham

Millennium Ecosystem Assessment (2005) Ecosystems and human well-being: synthesis. Island, Washington

Minoarivelo HO, Hui C (2016) Trait-mediated interaction leads to structural emergence in mutualistic networks. Evol Ecol 30:105–121
Tilman D, Lehman CL, Thomson KT (1997) Plant diversity and ecosystem productivity: theoretical considerations. Proc Natl Acad Sci USA 94:1857–1861
Tilman D, Lehman CL, Bristow CE (1998) Diversity-stability relationships: statistical inevitability or ecological consequence? Am Nat 151:277–282
Tylianakis JM, Tscharntke T, Lewis OT (2007) Habitat modification alters the structure of tropical host-parasitoid food webs. Nature 445:202–205
Tylianakis JM, Laliberte E, Nielsen A, Bascompte J (2010) Conservation of species interaction networks. Biol Conserv 143:2270–2279
Valdovinos FS, Ramos-Jiliberto R, Garay-Narvaez L, Urbani P, Dunne JA (2010) Consequences of adaptive behaviour for the structure and dynamics of food webs. Ecol Lett 13:1546–1559
Valdovinos FS, de Espanés PM, Flores JD, Ramos-Jiliberto R (2013) Adaptive foraging allows the maintenance of biodiversity of pollination networks. Oikos 122:907–917
van Altena C, Hemerik L, de Ruiter PC (2016) Food web stability and weighted connectance: the complexity stability debate revisited. Theor Ecol 9:49–58
Vázquez DP, Aizen MA (2003) Null model analyses of specialization in plant-pollinator interactions. Ecology 84:2493–2501
Vieira MC, Almeida-Neto M (2015) A simple stochastic model for complex coexistences in mutualistic networks: robustness decreases with connectance. Ecol Lett 18:144–152
Visser AW, Mariani P, Pigolotti S (2012) Adaptive behaviour, tri-trophic food-web stability and damping of chaos. J R Soc Interface 9:1373–1380
Waser NM, Chittka L, Price MV, Williams NM, Ollerton J (1996) Generalization in pollination systems, and why it matters. Ecology 77:1043–1060
West SA, Kiers ET, Pen I, Denison RF (2002) Sanctions and mutualism stability: when should less beneficial mutualists be tolerated? J Evol Biol 15:830–837
Wheelwright NT, Orians GH (1982) Seed dispersal by animals: contrasts with pollen dispersal, problems of terminology, and constraints on coevolution. Am Nat 119:402–413
Williams RJ, Martinez ND (2000) Simple rules yield complex food web. Nature 404:180–183
Wolanski E, McLusky D (eds) (2011) Treatise on estuarine and coastal science. Elsevier, Amsterdam
Wootton JT, Emmerson M (2005) Measurement of interaction strength in nature. Annu Rev Ecol Evol Syst 36:419–444
Worm B, Duffy JE (2003) Biodiversity, productivity and stability in real food webs. Trends Ecol Evol 18:628–632
Yachi S, Loreau M (1999) Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. Proc Natl Acad Sci USA 96:1463–1468
Yodzis P (1981) The stability of real ecosystems. Nature 289:674–676
Zhang F, Hui C, Terblanche JS (2011) An interaction switch predicts the nested architecture of mutualistic networks. Ecol Lett 14:797–803
Zhang F, Hui C, Pauw A (2013) Adaptive divergence in Darwin’s race: how coevolution can generate trait diversity in a pollination system. Evolution 67:548–560