




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

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## 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

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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).

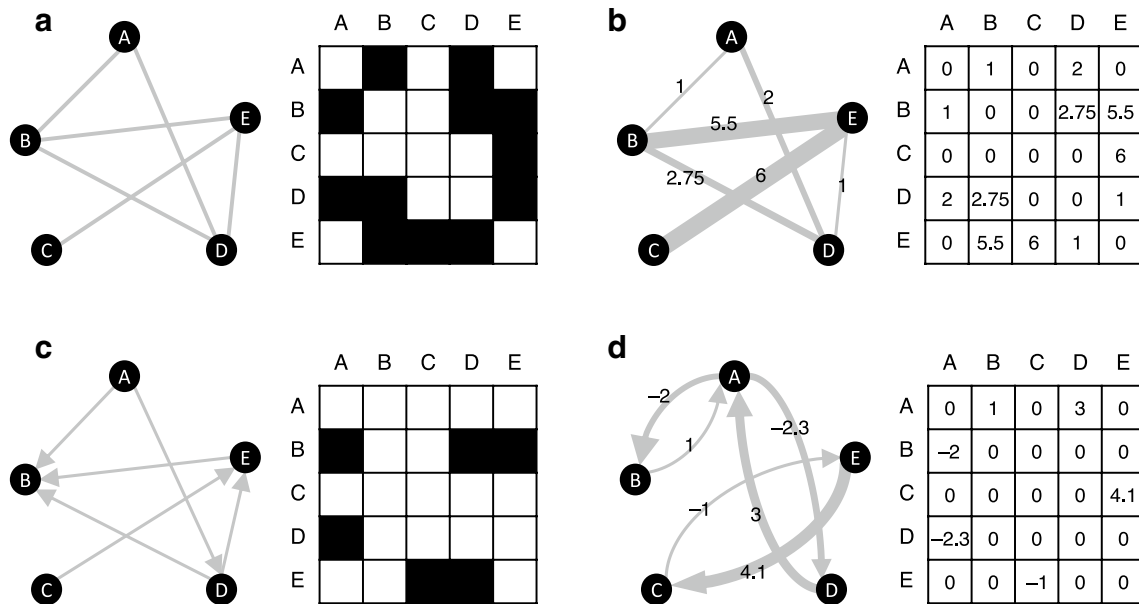
To appreciate the importance of this question, we first recollect and differentiate between the major different functions that ecosystems continuously provide. Natural ecosystems sustain life and provide services that can be divided into four areas (Millennium Ecosystem Assessment 2005): *provisioning*, 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  $\pm 1$  (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



**Fig. 1** Categorisation of ecological networks, according to link directionality and weight. Black (white) entries in matrices **a**, **c** represent presence (absence) of interaction. **a** Unweighted undirected; **b** weighted undirected; **c** unweighted directed; **d** weighted directed.

Note that links point to the affected species. For example, species A in **d** is positively affected by species B and D while negatively affecting species B and D

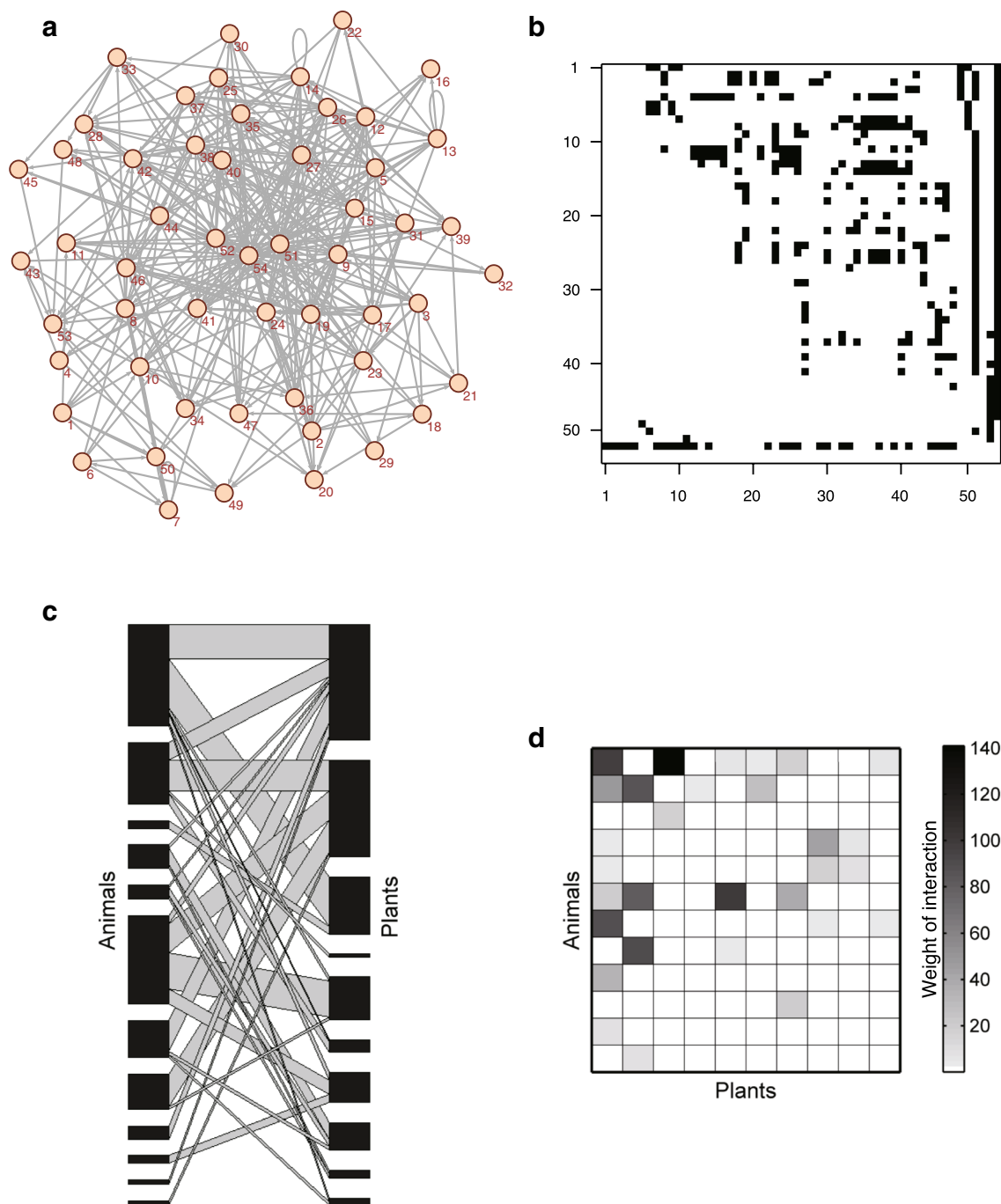
pollinators or antagonistic networks of host-parasite interactions, the matrix  $A = [a_{ij}]$  is a  $m \times n$  matrix (Fig. 2).

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



**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.

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

**Table 1** Measures of network complexity

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, $L/S^2$	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), Dunne and Williams (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, $L/S$	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>i</i> on species <i>j</i>	Number of visits between <i>i</i> and <i>j</i> divided by the total number of visits between species <i>i</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 connectance 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* (Borrvall 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, *invasibility* 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 invasibility).

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)



**Table 3** Measures of network stability

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 Yearsley (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), Christianou and Kokkoris (2008) and Fowler (2009)
Resilience	Return time to ecological regime after a small perturbation	Food webs: Thébault and Fontaine (2010) Mutualism: Okuyama and Holland (2008) Competition: Lawlor (1980) and Christianou and Kokkoris (2008)
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)	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 Fiedman (2014) Competition: Kokkoris et al. (2002) and Christianou and Kokkoris (2008)
Structural stability	Domain or probability of feasible existence of an ecological regime w.r.t. system perturbations	May (1972, 1973) Food webs: De Angelis (1975), Haydon (1994), Kondoh (2003, 2006, 2007) and Allesina and Tang (2012) Mutualism: Rohr et al. (2014) Competition: Christianou 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	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)
Robustness	Resistance of a system against additional extinction after species removal	Food webs: Dunne et al. (2002a) and Dunne and Williams (2009) Mutualism: Ramos-Jiliberto et al. (2012)
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 foodwebs 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

**Table 4** Complexity–stability relationship in food webs

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 antagonistic interactions model (cascade and niche) Jacobian of antagonistic interactions	
Krause et al. (2003) and Thébault and Fontaine (2010)	C, interaction strength-Resilience, persistence	Simulation 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 Yearsley (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 antagonistic interactions 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

Table 4 (continued)

References	Complexity–stability measures	Methods and assumptions	Additional results
Haydon (1994)	C, Jacobian elements-Asymptotic, feasibility	Lead eigenvalue of random and plausible model Jacobian at feasible equilibria	Stability is reduced by donor control interactions; Stability is increased by increased interaction strengths
Yodzis (1981)	Jacobian elements-Asymptotic	Lead eigenvalue of Jacobian of empirically inspired food webs	Intraspecific competition is stabilizing whereas interspecific competition tends to be destabilizing
de Ruiter et al. (1995)	Jacobian elements-Asymptotic	Model (generalized Lotka–Volterra) and time series of real and experimental food webs	Asymmetries in strength of interaction (i.e., strong consumer control interactions at lower trophic levels and strong donor control interactions at higher trophic levels) are stabilizing
Rooney et al. (2006)	Interaction strength-Asymptotic	Model (nonlinear functional response and predator adaptive behaviour) and time series of real and experimental food webs	Asymmetries in interaction strength (i.e., slow and fast energy fluxes coupled by top-predators) convey both local and non-local stability
Gross et al. (2009)	Jacobian elements-Asymptotic	Lead eigenvalue of Jacobian of realistic food web model (niche)	Increasing strength of interaction stabilizes small networks

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 (De Angelis 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

**Table 5** Complexity–stability relationship in mutualistic communities

References	Complexity–stability measures	Methods and assumptions	Additional results
<b>Negative complexity–stability relationship</b>			
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, $\sigma$ , 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
<b>Positive complexity–stability relationship</b>			
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



Table 5 (continued)

References	Complexity–stability measures	Methods and assumptions	Additional results
Rohr et al. (2014)	Species degree, interaction strength, nestedness-Structural stability	Population dynamics model; Explored the range of parameters necessary for stable coexistence	A maximal level of nestedness, a small trade-off between the number and intensity of interactions a species has, and a high level of mutualistic strength are factors that maximize stability

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. Attentions 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) elements 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 stability. Yodzis (1981) also found that the presence of self-regulatory terms (intraspecific competition) in some consumer 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 destabilizing, in the sense that the number of species  $S$  and the connectance  $C$  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 communities 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 experimental (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 statistically inevitable using the temporal variation in aggregate community properties as indicators of stability (see also Tilman 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 community stability. The work by Tilman (1999) summarizes the empirical and theoretical positive relationship between species diversity and community stability, primary productivity, and invasibility in grassland competitive communities (see, however, the critical review in Cottingham et al. 2001). Lawlor (1980) compared observed communities (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 communities with the same number of species. The higher stability 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 community 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 competition model (both symmetric and asymmetric, with a skew towards weak interactions) results in an increased probability (species growth rate parameters region) of local stability in competitive feasible communities: increasing the competitive 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 connectance and in the number of competitive links (connectivity) 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

**Table 6** Complexity–stability relationship in competitive communities

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 inter-specific 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 Piloşof 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 Valdovinos et al. 2010) or other forms of adaptive behaviour in response, e.g., to environmental changes (Strona and Lafferty 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, Valdovinos 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, Minoarivelo 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  $N_2$  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.

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