Ecological Networks: Information Theory Meets Darwin's Entangled Bank

Is it possible to untangle the 'entangled bank' — Darwin's metaphor for the complexity and connectedness of species in the natural world? Studies on webs of species interactions suggest so, but a major question remains unanswered: how specialized are different ecological networks? By considering how strongly species interact with each other, information theory may give the answer.

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Ecology has a very idiosyncratic problem: The scale of observation chosen to address a particular question may sometimes not be appropriate. Take for instance Darwin's 'entangled bank', in particular the fundamental question of how specialized the interactions between species are [1,2]. Observations made on one or a few plant or animal species cannot easily be extrapolated to the entire species assemblage. For instance, the extreme specialisation and tight coevolution reported for some taxonomic groups of pollinators and the flowers they visit might not be ubiquitous when the entire plant-pollinator network is analyzed [2]. The scale at which the question of specialization should be addressed is, therefore, the entire species assemblage, or network, not the species level. Recent studies on ecological networks have adopted this perspective, offering promising insights into old and fundamental questions within ecology and evolution. A novel study in this issue of *Current Biology* [3] together with earlier work form the same authors [4] represents a crucial advance to understanding how specialization varies within and across ecosystems.

The question of specialisation, i.e. the diversity of interspecific interactions associated with a given species, guild or network, is a fundamental one. Broadly speaking, specialization reflects the non-random self-organisation of ecological networks. Hutchinson [5] and MacArthur [6] were the first to introduce ideas of specialization, in particular how the niches of species contract as communities diversify. Thus, looking for patterns of specialization in ecosystems may give answers to longstanding questions in ecology concerning how species' ecological niches are organized. Research on specialization has focused on binary webs, where interactions between species (mutualistic or antagonistic) are either present or absent. Clear, though sometimes controversial, patterns emerge: Connectance, i.e. the proportion of realized links among the possible, decreases hyperbolically with the number of species present in the network [7,8]. In species-rich webs, the distribution of links per species is typically skewed: many species interact with only a few others, while a small number of species interact with many [9]. However, binary webs ignore link weights, that is how 'important' the connection is for the consumer and the resource, either in terms of biomass flux, per capita growth rate, or frequency of interaction [10]. To address specialization at the network and species level, one needs to account for link weight. In plant-animal mutualistic networks this can be measured by interaction frequency, e.g. the number of visits of a pollinator to a plant species. Blüthgen and colleagues [3] refine our understanding of specialisation by developing a quantitative index that captures the variability of link weight at both the species and network level (Figure 1). They do so using an old friend of ecology: information theory.

The authors [3,4] introduce two mathematically related indices derived from Shannon entropy. Generally, Shannon entropy measures how equally distributed a variable is among the constituents of a system. In ecology, it has been used widely to measure diversity, i.e. the way individuals within the ecosystem are distributed among species. Imagine two ecosystems with the same number of species: if individuals are more evenly distributed among species in the first one, then its Shannon diversity index will be larger than that of the second. Instead of using the number of individuals, the authors [3,4] use the frequency of interactions between plant and animal species in the network. The first of the two indices the authors derive describes the overall degree of specialization of the network, while the second characterizes the degree of

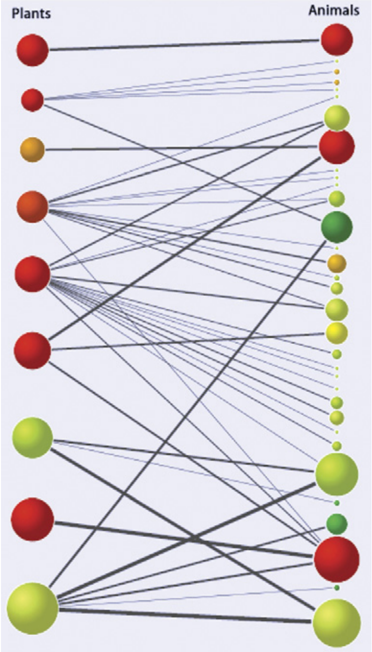

Figure 1. An example of a mutualistic network.

A plant–pollinator network is shown (after [3,20]). The circle radius represents species frequency and colour reflects the degree of species specialization using metrics derived from Shannon entropy [3], with red indicating high specialization and green low specialization. The width of the links corresponds to interaction strength, in this case the frequency of visits of an animal species on a plant species.

specialization at the species level. Both metrics define specialization as the deviation from an expected null probability distribution of interactions, overcoming the problems of using Shannon entropy in the context of diversity studies and network analyses. The Shannon diversity index is difficult to interpret when comparing communities that vary in both species richness and the evenness in the distribution of individuals among species. A similar problem is observed in a previous attempt to use the Shannon index to characterize the diversity of biomass fluxes in food webs [11]. Importantly, evaluation against a null model allows cross-comparisons among different webs that vary with regard to the number of species or the type of interaction. Blüthgen *et al.* [3] apply their index to one of the largest and most diverse datasets of plant-animal mutualistic networks, covering four types of mutualism — pollination, seed-dispersal, ant–myrmecophyte (obligate mutualisms) and ant–nectar plant associations.

Specialization Is Scale Invariant

Blüthgen *et al.* [3] found that the overall degree of specialization of each network is independent of its size, i.e. the total number of plant and animal species. In other words, more diverse communities are not more specialized than less diverse ones when link weight is accounted for. This poses a challenge to patterns of specialization observed in binary webs. Generally, in more diverse systems the mean number of links per species is lower than in less diverse ones. For instance, the diet breadth of consumers decreases towards the species-rich tropics [12], but see [13]. Within this variation, Blüthgen and colleagues [3], show that the frequency of different plant–animal associations is distributed within the network in a similar way, no matter how many species constitute the web. This scale invariance of specialization, therefore, emerges when details on how strong species interact are considered. As interaction strength determines the population dynamics of species, these results suggest that some type of dynamic constraint might be responsible for invariance of network specialization. One possibility is that the patterns of specialization observed in mutualistic networks may result in more stable or resilient communities [14], as it happens in food webs [15]. Further theoretical work is needed to explain why specialization seems scale invariant.

Different Mutualisms — Different Patterns?

Pollination systems are more specialized than seed-dispersal systems when binary webs are analyzed [16]. This result was confirmed when interaction frequencies were considered [3]. It is not only that pollinators are linked with fewer plants than seed-dispersers, but also that pollinators, within their niche breadth, interact much more frequently with some plant species than with others, while seed-dispersers tend to distribute their effort among the different plants more equitably. There is a type of mutualism that is even more specialized — the symbiotic associations between ant colonies that inhabit plants (myrmecophytes). This is expected given the particular nature of obligate myrmecophytic interactions: such associations often remain uninterrupted for several generations, such that tight, reciprocal specializations more commonly evolve.

A very interesting question is how the degree of specialization varies between guilds in the network — are consumers more specialized than their resources? In food webs depicting antagonistic interactions, predators may benefit from having different prey items, even if their preference (i.e. interaction strength) for each of them varies. Prey, on the contrary, will aim to have as few predators as possible, ideally interacting very weakly with them. These conflicting interests may tend towards specialization in prey species and generalism in their natural enemies, using the information theoretic index of Blüthgen *et al.* [4]. However, such clear conflicting interests do not operate in mutualistic interactions, where the degrees of specialization of the plant and animal guilds are highly correlated [3]. This pattern is constrained by the topology of the interaction network, in particular by the ratio of animal to plant species in the web. If animal species are more numerous than plants, the animal guild is less specialized than the plant guild — a result that presents two important challenges: First, it suggests competition for resources that may lead to resource partitioning may not be important in shaping mutualistic webs. If competition were important, then, as plant richness decreases, animals would tend to specialize by segregating their diet to avoid competition. Secondly, it illuminates the importance of understanding a fundamental determinant of ecosystem architecture, namely the mechanisms controlling the diversity within trophic levels (i.e. the ratio of animals to plants and vice versa).

Unexpected Patterns at the Species Level

Patterns become more complicated when one looks at how specialization varies between species [1,9]. Recent research highlights links between specialization and species traits generally applied in macroecology [17]. Many food web attributes are related to species body size [18]. Within a guild of aquatic invertebrates, for example, small animals are more specialized than large ones. In mutualistic webs, species abundance or frequency seems to play a more deterministic role. More abundant animals interact with more plant species than rare ones [19], and the same is observed for abundant and rare plants. But, as Blüthgen and collaborators show [3], intriguing patterns emerge when quantified links are considered. In pollination webs, frequent animals are more specialized than rare ones (Figure 1). Even if their diet is broader, abundant pollinators are more selective in their plant preferences. Pollinated plants show the opposite: those occurring at low densities are much more specialized than more frequent ones. These asymmetric patterns at the species level seem to be common to mutualistic networks [14], and more research is required to elucidate their evolutionary and ecological mechanisms.

The new work by Blüthgen [3] underscores the need to contemplate the architecture of the entire network of species interactions in order to understand how species' niches are organized. An understanding of specialisation is not only interesting in itself, but also essential to understand the persistence and vulnerability of species in a constantly changing world.

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Cytokinesis: LET-ting the Asters Signal

Cytokinesis is regulated by both astral microtubules and the midzone microtubules of the mitotic apparatus. A new study in *Caenorhabditis elegans* has identified the polarity factor LET-99 and its heterotrimeric G-protein regulators as components of the signaling pathway downstream of astral microtubules.

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Cytokinesis is the final act of cell division whereby the cytoplasm is separated by action of an actin and myosin II-based contractile ring. The problem of what controls the timing, placement and assembly of the contractile ring has been under study since the 19th century. Historically, the study of cytokinesis has led to polarizing views on the role of the mitotic apparatus in the signaling of cytokinesis. One argument concerns whether the asters of the mitotic apparatus induce the polar cortex to relax or whether the astral microtubules positively influence the equatorial cortex to assemble a contractile ring [1]. There have also been arguments over what part of the mitotic apparatus stimulates cytokinesis: the spindle midzone or the mitotic asters [2]. Studies in the past few years have suggested that cytokinesis is regulated by signals from both the midzone and the asters [3–5]. Two years ago, Bringmann and Hyman [6] reported evidence, based on laser ablation and RNA interference (RNAi) screening, supporting the existence of an astral signal for cytokinesis. The hunt has now focused on identifying the molecular nature of the astral signals. Now comes exciting work from the same group [7], published in *Current Biology*, which has cleverly identified molecules involved in astral signaling of cytokinesis in the nematode *Caenorhabditis elegans* [7].

It is well documented that the microtubules of the mitotic apparatus are essential for cytokinesis. The cell cortex responds to the signal, and the response involves a number molecules, including the small GTPase Rho, actin, myosin II, myosin light chain kinase, Rho kinase, myosin light chain, formin and may other actin binding and regulatory proteins, which make up the transient contractile ring [8]. Using an RNAi screen for embryos lacking the spindle midzone signal, Bringmann *et al.* [7] identified molecules involved in aster-positioned cytokinesis: LET-99, a DEP domain cortical protein known to play a role in anchoring microtubules and in spindle positioning, and heterotrimeric G proteins. By combining RNAi, genetics and live-cell imaging