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Editorial: Everything is connected: network thinking in entomology

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There have been significant advances in the theoretical understanding, construction, visualisation and analysis of complex species interactions networks in recent years (Ings et al., 2009; Fontaine et al., 2011; Kefi et al., 2012). Ecological networks describe the interactions among species, and a burgeoning number of metrics can be used to characterise their structure and complexity. Such networks provide a unique framework for understanding species' ecological roles, co-evolution and the mechanisms through which biodiversity influences ecosystem function (Thompson et al., 2012). Increasingly, they are used to quantify the effects of human activities (Tylianakis et al., 2008), with promising novel applications for nature conservation (Kaiser-Bunbury & Blüthgen, 2015) and restoration (Montoya et al., 2012).

Central to the development of network ecology has been the study of insects. To date, much attention has focused on bipartite mutualistic and antagonistic networks. Using plant–insect relationships as a study system, Memmott (1999) was one of the first to describe the structure of a quantitative plant–pollinator food-web, providing novel ways of studying the ‘robustness’ of mutualistic networks (plus other types) to simulated species loss, the effects of climate change and the impacts of non-native species. Likewise, guilds of hosts and parasitoids have also become a popular choice of assemblage for study by community ecologists (Hrček & Godfray, 2015), providing novel insights into how antagonistic networks are structured (Morris et al., 2014), and by what processes. Recent advances have attempted to merge these different types of species–interaction networks within a single conceptual framework (Fontaine et al., 2011). Pocock et al. (2012) created the first ‘network of ecological networks’ that included not only plant–pollinator and host–parasitoid interactions, but also bird seed–feeder and mammal–parasite food webs. This allowed a new way of identifying plants that were disproportionately important to network integrity, with implications for conservation and habitat restoration. It also provided a way of

examining the robustness of the networks to simulated habitat loss (Evans et al., 2013), a much-needed tool for examining the resilience of ecosystems to environmental change.

Creating highly-resolved quantitative networks is a daunting challenge and partly explains why most studies, to date, have focused on more simple bipartite interactions. These networks have mostly been created using 'traditional' construction approaches that rely on direct field observations or rearing specimens followed by morphological identification by taxonomists, which can lead to a number of biases (Evans et al., 2016). It has also been difficult to quantify the structure of many species-rich ecosystems owing to sampling, technical and logistical constraints (Gibson et al., 2011). Recent advances in DNA sequencing provide enormous potential to determine species interactions hitherto difficult to observe (Roslin & Majaneva, 2016). Combining DNA metabarcoding approaches with ecological network analysis presents important new opportunities for understanding large-scale ecological and evolutionary processes. It is clear that a huge amount of work is necessary to better understand the direct and indirect interactions between species through space and time, but molecular tools can aid in, for example, the rapid construction of trophic food webs from gut contents (Kitson et al., 2013) or the creation of highly-resolved plant–leaf miner networks even after the leaf miners have left the mine, leaving just fragments of DNA (Derocles et al., 2015). In this issue, Morales Hojas (2017) reviews how such advances in molecular ecology are providing a better understanding of the complex relationships between agricultural insect pests and their predators, with implications for global food production.

Beyond understanding species interactions across trophic levels, network analysis also has a long history in social biology with tremendous potential for the study of insect behaviour. For example, social insect colonies have been shown to have key network attributes, including nonrandom systems of connectivity and the self-organisation of group-level phenotypes (Fewell, 2003; Waters & Fewell, 2012). The ability to track individuals makes some insect groups much more accessible to experimental manipulation than many other complex systems (Mersch, 2016). Studies have shown that interactions between individuals generate a social environment at the population level which in turn selects for behavioural strategies at

the individual level (Dussutour & Simpson, 2009; Jeanson et al., 2012; Krause et al., 2015).

At the same time, we have an increasingly deterministic understanding of how individual behaviour can play out at the collective or network level (Petchey et al., 2008). As this understanding progresses, we can begin to ask bottom-up questions about how networks can be affected by perturbations – revealing several potentially important areas for future behavioural research. Two examples are explored in this issue. First, a predictive understanding of the effect of individual- and colony-level stressors upon collective behaviour may be an important area for the future study of pollination ecology (Gómez-Moracho et al., 2017). Pathogenic stressors are known to affect behaviour within social insect networks (Ugelvig & Cremer, 2007; Wilson-Rich et al., 2007; Bos et al., 2012; Quevillon et al., 2015), whereas inter-individual variation in foraging behaviour is critical for the structure and function of pollen transport networks (Tur et al., 2014). Second, mating systems, increasingly analysed as networks (e.g. Muniz et al., 2014), have traditionally been studied as isolated systems – whereas in fact, they play out in a complex world of interactions and interference, both con- and heterospecific, and are thus exposed to multiple perturbations (e.g. Vanbergen et al., 2013). Unravelling the nature of these disruptive interactions (see Shuker & Burdfield-Steel, 2017, this issue) may help us towards a predictive understanding of variation in sexual interaction networks as they play out on the ground.

It is becoming increasingly apparent that key network attributes, such as non-random structuring, appear consistently in complex biological systems, from molecules to ecosystems. In this Special Issue, arising from a Royal Entomological Society International Symposium & National Science Meeting at Newcastle University, the UK in September 2017, the theme ‘Entomological Networks: Ecology, Behaviour and Evolution’ is considered at all scales from the roles of genes in the evolution of complex social behaviour to the impacts of environmental change on species–interaction networks, along with broader interpretations of the ‘network’ theme. A total of six review and original research articles address this broad range of subjects, including DNA-sequencing methods to study agriculturally important insects (Morales Hojas, 2017); novel spatial movement networks to describe bee foraging decisions (Chittka et al., 2017); insect pathogen and immune dynamics (Miller & Cotter, 2017)

and decision making and motor control in predatory insects (Yamawaki, 2017). The issue also contains two reviews of behavioural phenomena that tend to disrupt the normal function of interaction networks: first, of key stressors affecting bee cognition (Gómez-Moracho et al., 2017), which impair the ability of bees to make the foraging decisions critical to the integrity of plant–pollinator networks; second, of reproductive interference (Shuker & Burdfield-Steel, 2017)-interactions between species resulting in the disruption of the normal function of one or both species' sexual interaction network, i.e. of their mating system.

Studying insects in a network context will help us to move towards a more holistic understanding of ecology and evolution. There is a huge amount of work to do not only to describe the complexity of insect (and other animal) interactions but also to understand the temporal and spatial dynamics of networks that incorporate insect behaviour. The genomics and bioinformatics revolution, combined with 'Big Data' and the rise of complexity science will provide unprecedented opportunities for more network thinking by entomologists.

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