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Molecular Ecology

DOI:

[10.1111/mec.14974](https://doi.org/10.1111/mec.14974)

[10.1111/mec.14974](https://doi.org/10.1111/mec.14974)

Published: 01/01/2019

Peer reviewed version

[Cyswllt i'r cyhoeddiad / Link to publication](#)

Dyfyniad o'r fersiwn a gyhoeddwyd / Citation for published version (APA):

Roslin, T., Traugott, M., Jonsson, M., Stone, G. N., Creer, S., & Symondson, W. O. C. (2019). Introduction: Special issue on species interactions, ecological networks and community dynamics – Untangling the entangled bank using molecular techniques. *Molecular Ecology*, 28(2), 157-164. <https://doi.org/10.1111/mec.14974>, <https://doi.org/10.1111/mec.14974>

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Article type : Special Issue

SPECIAL ISSUE: SPECIES INTERACTIONS, ECOLOGICAL NETWORKS AND COMMUNITY DYNAMICS

Introduction

Special issue on species interactions, ecological networks and community dynamics: untangling the entangled bank using molecular techniques

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This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1111/mec.14974

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“It is interesting to contemplate a tangled bank, clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth, and to reflect that these elaborately constructed forms, so different from each other, and dependent upon each other in so complex a manner, have all been produced by laws acting around us.” (Darwin, 1859)

In the last paragraph of the Origin of Species, Darwin (1859) marvels at the diversity of life forms, the complexity of links between them, and the forces creating this “tangled bank”. In this text, we may see the origins of community ecology – today defined as ‘the study of the interactions that determine the distribution and abundance of organisms’ (Krebs, 2009). To capture and quantify the key elements of this concept of community structure, we may conveniently describe communities as ecological networks (Hagen et al. 2012). In such networks, the nodes are formed by species (or other taxonomic units) and the links by their interactions (Gravel et al., 2018). Modern molecular methods offer unique opportunities for describing both elements of community structure (Roslin & Majaneva, 2016) and how they change in time and space (‘community dynamics’).

The last few years have seen a revolution in both sampling and sequencing technologies. For this reason, it is time to provide a sequel to the seminal Special Issue on the ‘Molecular Detection of Trophic Interactions’ edited five years ago by Symondson and Harwood (2014). Building on the previous Special Issue, the current one continues the quest of ‘Unpicking the Tangled Bank’ (Symondson & Harwood 2014). Yet, where the previous compilation focused on a specific type of ecological interactions (i.e. species feeding on each other), here we have endeavoured to provide a wider community and ecosystem relevant focus. Thus, the Special Issue of 2014 was prepared by attendees at a meeting on Molecular Detection of Trophic Interactions, but the current issue reflects the collaboration between this audience and ecologists with a wider interest in ecological networks – regardless of the tools applied. Hence, the current volume is the result of synergistic back-to-back

events organized at the Swedish University of Agricultural Sciences, Uppsala, in September 2017: the 3rd Symposium on Molecular Detection of Trophic Interactions and the 3rd Symposium on Ecological Networks, enhanced via further networking.

Many of the papers included in this volume were presented at one of these meetings, but others were added later to increase the scope and breadth of the Special Issue. The resulting issue offers a suite of studies applying molecular tools to resolving questions focused on ecological interaction networks and their dynamics. The papers included also comprise studies offering broad ranging technical solutions for dealing with large and diverse communities, as well as reviews and summaries identifying the limits and caveats associated with quantifying community and interaction structure by molecular means. When including research with a methodological focus, we have carefully looked for particularly important and impactful studies, where the results clearly transcend the specific system studied, i.e. where the methodological improvements achieved are likely to be useful for a wider range of future studies. In all other papers included in the Special Issue, the focus is on the ecology. In other words, these works deliver significant ecological findings obtained by molecular approaches.

By including a blend of papers studying multiple types of interactions, taxa and realms (both aquatic and terrestrial), we hope to provide, in a single issue of *Molecular Ecology*, a comprehensive glimpse of the state of the art in this rapidly developing field. In particular, we hope that this issue will serve as a stimulus and catalyst for ecologists contemplating the use of molecular tools for community dissection (see also Bohan et al., 2017). Individual papers reveal how molecular tools are being fruitfully applied to many types of nodes and links, and the many types of networks formed from such elements. As an arguably thought-provoking perspective, they also show molecular techniques can be applied to describe full communities rather than their parts simultaneously – i.e. to resolve multiple types of links among multiple kingdoms of taxa (Clare et al., XXXX), thus opening new vistas

on 'networks of networks'. Out of necessity, such initiatives so far have had to be built from multiple data sources (Pocock, Evans, & Memmott; 2012, Wirta et al., 2015).

A cornucopia of interaction types and taxa

In terms of the types of interactions addressed, this Special Issue shows how molecular techniques can be applied to resolving mutualistic interactions such as pollen transport (Bell et al., XXXX; Tiusanen et al., XXXX) and seed dispersal (Gonzalez-Varo et al., XXXX), antagonistic interactions including predator–prey interactions (Deagle et al., XXXX; Eitzinger et al., XXXX; Mata et al., XXXX; Sint, Kaufmann, Mayer, & Traugott, XXXX; Walters et al., XXXX), predator–prey-and-detritus interactions (Siegenthaler, Wangenstein, Benvenuto, Campos, & Mariani, XXXX), host–parasitoid interactions (Garipey et al., XXXX; Kitson et al., XXXX), host–symbiont interactions (Doña et al., XXXX; Doña, Serrano, Mironov, Montesinos-Navarro & Jovani, XXXX), plant–herbivore interactions (Bhattacharyya, Dawson, Hipperson, & Ishtiaq, XXXX), plant-fungus interactions (Schröter et al., XXXX; Sepp et al., XXXX) plant–prey interactions (Littlefair, Zander, de Sena Costa, & Clare, XXXX), fungus–fungivore interactions (Koskinen et al., XXXX) and multifaceted interactions (Clare et al., XXXX).

As a specific insight, the study by Doña et al. (XXXX) reveals how the application of molecular tools can even force us to re-evaluate previous concepts of the type of specific interactions. Using evidence from both light microscopy and metabarcoding, these authors show that vane-dwelling feather mites share a commensalistic–mutualistic association with their bird hosts, by feeding on fungi, microbes and detritus in the plumage. In fact, the authors find no evidence of feather mites feeding upon bird resources such as blood or skin. Consequently, the mites are recast as commensal organisms likely causing no harm but offering clear benefits to their hosts.

Emphasizing the message from previous reviews (from Symondson & Harwood 2014 to Roslin and Majaneva 2016), the featured case studies also reveal just how much power molecular tools add by resolving “hidden” and hard-to-observe ecological interactions (Wirta et al., 2014). By allowing us to pinpoint associations between organisms which liquefy their prey (Eitzinger et al., XXXX; Littlefair, Zander, de Sena Costa, & Clare, XXXX; Sint, Kaufmann, Mayer, & Traugott, XXXX), hide within their hosts (Gariepy et al., XXXX; Kitson et al., XXXX), lack all diagnostic characters as larvae (Gariepy et al., XXXX; Kitson et al., XXXX; Koskinen et al., XXXX), hunt at night (Mata et al., XXXX) or are simply too small and similar to describe by any other means (Walters et al., XXXX; Jones and Hallin XXXX), they reveal new aspects of community organization. Importantly, this is not a question of adding fine nuance to main color, but of repainting the whole picture. Since these types of interactions form the majority of *all* interactions on the globe, they will profoundly affect our understanding of not only specific communities (Wirta et al., 2014), but of how communities in general are assembled and work.

The findings regarding particular interactions range from insight into emergent features such as levels of specialization in ecological interaction networks (Doña et al., XXXX; Doña, Serrano, Mironov, Montesinos-Navarro & Jovani, XXXX; Koskinen et al., XXXX; Sepp et al., XXXX; Clare et al., XXXX) to the role of individual seed dispersers in seed dispersal networks. As a case in point, González-Varo, Arroyo, & Jordano (XXXX) are able to show how much of an ecological function (seed dispersal) is concentrated to particular species at particular points in time. Migratory bird species may only be passing through an area, but still be main agents of seed dispersal for particular plants. This emphasizes the need for resolving variation in network structure through time, for which molecular techniques are ideally placed (González-Varo, Arroyo, & Jordano, XXXX).

In a similar vein, molecular diet analysis sheds new light on the trophic position of individual species within larger communities and interaction networks. Siegenthaler, Wangenstein, Benvenuto, Campos, & Mariani (XXXX) use metabarcoding of gut contents to establish the diet of the brown shrimp, *Crangon crangon*, in six European estuaries. The species turns out to be an extreme generalist, feeding on hundreds of taxa, with its overall diet dominated by crustaceans, polychaetes and fish. Substantial variation in diet at both regional and local scales add to the impression of extreme flexibility in this common species (Siegenthaler, Wangenstein, Benvenuto, Campos, & Mariani, XXXX), but also reveal the potential for bottom-dwelling marine generalists to harvest the 'environmental DNA' (Bohmann et al., 2014; Deiner et al., 2017; Creer et al., 2016) signal of broader fish communities for biomonitoring purposes.

Where Siegenthaler, Wangenstein, Benvenuto, Campos, & Mariani (XXXX) use molecular techniques to identify what the shrimp feeds on, Tiusanen et al. (XXXX) apply them to the opposite task of identifying which arthropods visit the flowers of several arctic *Dryas* species (all known as mountain avens). Targeting multiple sites around the Arctic, they too find an astonishing taxonomic range and richness, in this case of literally thousands of arthropod species sharing this common floral resource. Resolving such taxonomic diversity across large scales would be next to impossible with morphology-based identification approaches.

Environmental imprints on ecological interactions

Much of community ecology to date has assumed that each particular interaction is a fixed feature: If two species interact at one point in space, then they are expected to do so wherever they meet.

However, recent research forces us to revisit this assumption, and add emphasis on just why interactions vary (Poisot, Stouffer, & Gravel, 2015; Pellissier et al., 2017; Gravel et al., 2018). Two papers in this issue show how molecular tools can reveal where, and under what circumstances, specific interactions occur.

Bhattacharyya, Dawson, Hipperson, & Ishtiaq (XXXX) analyze the plant contents of fecal pellets of Royle's pika (*Ochotona roylei*), a lagomorph endemic to the Himalayas. They show how the diet of the pika varies with elevation and with habitat structure, likely reflecting constraints and preferences during foraging (Bhattacharyya, Dawson, Hipperson, & Ishtiaq, XXXX).

Eitzinger et al. (XXXX) focus on a very different predator, the wolf spider *Pardosa glacialis* in the High Arctic. By describing the communities of both available and consumed prey along an elevational gradient, these authors demonstrate that spiders tend to prey on the same taxa – when available – regardless of their environment. However, the environment has a strong impact on available prey, and so the effect of current Arctic change will likely act indirectly, by changing what prey species are available, rather than directly modifying what is preferred (Eitzinger et al., XXXX).

Among predators of a different type, Littlefair, Zander, de Sena Costa, & Clare (XXXX) find an imprint of elevation on the prey community of carnivorous *Sarracenia* pitcher plants. Sites more different in elevation are also characterized by more different contents of the plants' pitchers. Since other studies have shown differences in free-living arthropod communities with elevation, this pattern may reflect differences in available prey rather than in realized interactions, but distinguishing between these is challenging – attesting to the need to resolve nodes and links separately in ecological interaction networks.

In further evidence of the power of molecular data in resolving spatiotemporal patterning in ecological interaction networks, Jones and Hallin (XXXX) target communities of microbes linked by ecological function. Where nitrification pathways tend to consist of separate steps in which bacterial or archaeal communities first oxidize ammonia to nitrite, and bacterial communities then further oxidize nitrite to nitrate, little is known about how these functionally-coupled organism groups co-occur in space. Here, Jones and Hallin (XXXX) are able to discern distinct modules of co-occurring

groups of microbes associated with the two steps: modules which occur in disparate areas are dominated by different lineages and are associated with different edaphic factors. Thus, this microbial ecology example reveals new dimensions in the structuring of ecological interaction networks: species groups can be linked by one group preparing the metabolic substrate for another, a concept perhaps less familiar to those of us working with macroscopic taxa.

Molecular insights into community assembly

The current issue shows how molecular data can reveal processes shaping communities. Tiusanen et al. (XXXX) study flower-visiting communities across the Arctic. By comparing patterns of phylogenetic diversity with those previously observed in plants, and by matching pairwise patterns of floristic and faunistic similarity across Arctic sites, they show that plants and arthropods have likely used similar expansion routes across the Arctic from shared refugia. This reveals a strong imprint of geological history on current patterns of community structure, beyond imprints of current climate such as precipitation and temperature (Tiusanen et al., XXXX)

Sint, Kaufmann, Mayer, & Traugott (XXXX) describe how arthropod communities assemble once soil is exposed in front of retreating glaciers. By revealing who feeds on what in replicate valleys of similar age, they are able to reconstruct how food webs are formed. Their findings suggest that the young food chains of glacier forelands are based on on-site processes rather than on resources blown in from other, more advanced communities.

Schröter et al. (XXXX) compare the composition of root-associated fungi across more than a hundred temperate forest sites, and find that the relative impact of different structuring forces differs across spatial scales. At local scales, forest management and tree selection have a clearer impact, but at larger scales, environmental cues and host resource traits are the most prevalent forces. From a net perspective, communities still end up very similar in terms of their trophic composition, with highly

similar proportions of symbiotrophic, ectomycorrhizal, saprotrophic, endotrophic, and pathotrophic fungi. Community assembly processes thus seem to secure functional resilience under the current range of climatic and edaphic conditions.

Sepp et al. (XXXX) examine how root-colonizing fungi forming arbuscular mycorrhiza (AM) are structured within a homogeneous plot of dry calcareous grassland. They find a significant imprint of host plant species, abundance and functional group on the richness and community composition of AM fungi with which they partner. Grasses host more fungal partners and appear more generalist in partner selection than do forbs. Moreover, plant species characterized by obligate rather than facultative mycorrhizal associations appear less specialized in terms of their fungal partners, as do locally more abundant plant species.

Doña, Serrano, Mironov, Montesinos-Navarro & Jovani (XXXX) take an evolutionary perspective by examining the evidence for host shifts among symbionts presumed to be highly host-specific. Building on extensive DNA metabarcoding, these authors study associations between nodes consisting of feather mite species and host bird species, finding much more variation in link structure than previously assumed. Yet, mites showed predictable fidelity in terms of host body size, and overall, the association network proved modular (i.e., some groups of bird and mite species tended to be more associated between them than with the other groups). Mites detected on unexpected hosts seemed to be there as more than just accidental tourists, with mite populations on rare hosts showing signs of both reproduction and some level of population differentiation. Overall, these patterns identify host-switching as a frequent phenomenon shaped by ecological filters such as host traits, painting a dynamic picture of the coevolution between symbionts and their hosts.

Overall, these insights regarding how communities form in space and time would be unachievable without the current molecular workflows, offering clues on both trophic position, taxonomic placement, and internal relatedness.

What community features can and cannot be quantified by sequence data

The Special Issue compiled five years ago (Symondson and Harwood 2014) featured several papers pondering whether sequence read numbers may or may not be used to quantify the relative abundance of community members; in that case focusing on communities of prey in samples of predator diet. The papers pointed out several biases, and also approaches that can adjust for them (e.g. Greenstone, Payton, Weber, & Simmons, 2014).

Contributions to the current Special Issue identify the issue of what we can and cannot quantify from sequence data as a still-vibrant and partly contentious field of research. Individual papers approach this from multiple perspectives.

Deagle et al. (XXXX) return to the issue at the heart of the previous Special Issue on dietary samples. Drawing on both critical literature analysis and simulations, Deagle et al. (XXXX) compare the approach of focusing on the frequency of occurrence of different food taxa across samples *versus* the use of relative number of sequence reads per sample. They stress that while the former approach is often advanced as more conservative than the latter, the latter may actually provide a more accurate view of population-level diet under many circumstances. Both approaches become less accurate with a higher diversity of food taxa in the samples.

Bell et al. (XXXX) turn to mixes of pollen grains, taking an empirical approach to examining the quantitative evidence provided by controlled blends of pollen from disparate taxonomic sources.

These authors demonstrate that metabarcoding is largely robust for determining pollen

presence/absence, but discourage the use of sequence reads to infer relative abundance of pollen grains.

Piñol, Senar, & Symondson (XXXX) approach related questions *in silico*, pointing to the fact that some experimental studies tend to report quantitative metabarcoding results whereas similar numbers fail to do so. Hence the question of *whether* metabarcoding is quantitative should actually be rephrased as *when, and under what circumstances*, the technique can be expected to be quantitative. They stress that “universal primers” will always come with more or fewer mismatches with heterogeneous sources of target template DNA, and thus focus on the number of primer–template mismatches as a metric of key interest. They show that quantitativity can be expected to vary with the primer pair used and on the characteristics of the mixture analyzed, but, inspiring hope, that quantification can oftentimes be reasonably good.

Lamb et al. (XXXX) present an empirical meta-analysis of studies published to date. Focusing on the extent to which proportions of sequence reads correspond to the original proportions of species in the community to be quantified, they find a weak quantitative relationship (slope = 0.52 ± 0.34). Yet, for a substantial fraction of studies, no quantitative relationship is detected, and neither sequencing platform type, the number of species used in a trial, or the source of DNA can account for the large variance between studies.

Together, these papers point to the issue of what can, versus cannot, be inferred from sequence data as a still-vibrant and partly contentious field of research. When combined, they draw a perhaps more optimistic picture of the information value included in the read counts than contributions to the Special Issue four years ago (cf. Bell et al., XXXX). Yet, each stress that for a balanced view, all sources of bias need to be considered and the methods used should be justified (Deagle et al., XXXX; Piñol, Senar, & Symondson, XXXX; Lamb et al., XXXX). Stronger biases at particular steps of sample

preparation, PCR and DNA sequencing will still blur correlations between original sample and relative sequence contents (Bell et al., XXXX; Lamb et al., XXXX).

Applied perspectives

Using molecular tools to spot interactions between species allows us to identify potential biological control agents against invasive species. Two papers use molecular tools to scout out potential and realized enemies of invasive species.

Targeting the invasive pentatomid bug *Halyomorpha halys*, Garipey et al. (XXXX) look for links between native bugs, their parasitoids and the newcomer. Molecular analysis of egg masses reveal high parasitism rates, but the invasive species was significantly less likely to be parasitized than native congeneric species. Some parasitoid species unable to develop on the eggs of the invasive species still try to exploit them under field conditions. How this translates into parasitism in the new range is now an active field of research.

Kitson et al. (XXXX) use nested-tagging DNA metabarcoding for exploring the parasitoid community of the oak processionary moth (*Thaumetopoea processionea*), an invasive species recently established in the UK. Overall, they are able to identify the main parasitoid of the late larval stages of *T. processionea* as *Carcelia iliaca* – at the same time creating the tools for describing all life stages of the oak processionary moth *and* the tag set needed to process massive ecological samples at the individual level.

However, applications clearly do not stop at identifying the enemies of economically important species. At the community level, Hooper et al. (XXXX) aim to identify quantitatively dominant species in the skin microbiome of the killer whale. By describing microbial communities associated with poor and better skin health, this research may lead us to novel insights into the determinants of skin

health among both larger and smaller species. All this they achieve by intensively and carefully re-analyzing shotgun sequence data from hard-to-come by samples of skin biopsies of killer whales, originally taken for population genomic studies. This shows the extreme potential for extracting more biodiversity information from extant samples of rare or elusive species, even at the community level.

Vistas

Community ecologists tend to deal with – or at least crave for – massive data featuring both nodes and links. Perhaps the most striking feature of the papers in this Special Issue are the large numbers involved. Here, we are not (only) referring to the high numbers of sequence reads. Sequencing power is currently increasing at a massive speed, and there is as yet no attenuation of that development in sight; quite the contrary (e.g. Loman et al., 2012). This development increases the information value generated from a single sequencing run, resulting in ever-improved resolution and precision in terms of tabulating the nodes present in the sample. Yet, equally importantly, we refer to the potential for handling and individual tagging (Kitson et al., XXXX) of large numbers of samples, allowing the simultaneous characterization of massive numbers of ecological samples and taxa.

In evidence of these claims, Doña et al. (XXXX) use high-throughput sequencing (HTS) and DNA metabarcoding to determine gut contents from 1,833 individual mites of 18 species inhabiting 18 bird species, whereas Doña, Serrano, Mironov, Montesinos-Navarro & Jovani (XXXX) report findings from 25,540 individual mites (representing 64 species) from 1,130 birds (representing 71 species). Tiusanen et al. (XXXX) sampled 31,345 arthropods, of which they individually sequenced 13,681 individuals, detecting 1,360 barcoding BINs in the process. Schröter et al. (XXXX) deal with root-associated mycobiomes encompassing a total of 5,955 different Operational Taxonomic Units across spatial scales of over 1,000 km in more than 100 temperate forest plots. Clare et al. (XXXX) tabulate

3304 interactions between 762 nodes of 8 trophic functions, thus encompassing parasitic, mutualistic, and predatory interactions. And the list goes on.

What these figures attest to is a quantum leap in community description. By building on the tools now available for community description, we can sample very many sites in a short time, thus bypassing phenological change and other types of shift in time complicating commensurability among samples when taken sequentially rather than simultaneously. They also circumvent the taxonomic impediment by automatic species delimitation and recognition. Overall, these numbers herald a new era in community ecology, allowing us to finally view the bigger ecological picture.

Together, the papers contributed to this Special Issue thus point to a fascinating development for all community ecologists: the scope for generating more relevant data in higher quantities on the key components of communities, i.e. the nodes and the links of which they are built. In terms of the links, molecular data offer unrivalled benefits. Where there are multiple modes of describing the species content of a community, direct data on link occurrence are often unachievable by other means (Roslin and Majaneva 2016). In particular, DNA metabarcoding based on nested tagging offers unique opportunities for constructing large, highly resolved species interaction networks (Kitson et al., XXXX). Generation of data on species associations without rearing the organisms involved to morphologically-identifiable stages bypasses both important biases and highly laborious stages of work (Kitson et al., XXXX; Koskinen et al., XXXX). These methods open new horizons for molecular analyses of both how communities are currently structured and how they change over time.

Clare et al. (XXXX) point to particularly fascinating perspectives – and to particularly strong challenges ahead. What this paper proposes is this: Given that we can now delimit both nodes and links by molecular data, may we not base our full description of communities and interaction

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networks on such data, thus curtailing the reliance on traditional approaches? And might not such approaches prove immediate, deep insights into systems where traditional data are limited or missing, such as many tropical and/or marine environments? This is a most stimulating perspective, but also one fraught with difficulties. A key step in making sense of communities is namely to connect lists of their members with what these members are: their life cycles, size, and other traits. Thus, naming a node connects it to everything that we know about what they are, what they do and how they live their lives. It is also the basis for grouping nodes into more and less similar blocks within webs, and for comparing the roles of such similar blocks among regions (e.g. “the role of blowflies in different ecosystems”). Mapping nodes (be they defined by any criteria, morphology or DNA) onto some concept of phylogeny will significantly increase our understanding of network/community structure (Tiusanen et al., XXXX), and mapping them onto known taxonomy (most papers in this Special Issue) is perhaps the easiest way to go. For each of these endeavors, we need to maintain a link between molecular barcoding, MOTUs and some aspects of traditional taxonomy (Hebert, Cywinska, & Ball, 2003; Hebert & Gregory 2005). Whether these taxa are then named by Latin binomials or some other designations (cf. Hebert et al., 2016; Ratnasingham & Hebert, 2013) is of secondary importance, as long as we know which particular node the name refers to, and this name stays constant across community networks. Only the latter criterion will allow us to compare the role of the same node across networks (Cirtwill et al., 2018).

To stress this point, we may consider contrasting scenarios. As a perhaps worst-case outcome of molecularly-based food web reconstruction, we may end up dealing with unnamed MOTUs of unknown life-cycle and unknown affinity to each other, with the numbers and connections between nodes varying with the similarity threshold that we use to define them *and* with the context of other species present in the community. Under such a scenario, molecular description of communities will contribute little insight into the “true” composition of the network or how it relates to other networks. But as a best case scenario, molecular characterization of communities allow us to rapidly

generate concepts of the nodes present, descriptions of who links to whom, with firm anchors in taxonomic position and what is known about the same or related species. If such approaches allow us to describe the structure of, say, a hundred replicate communities and to relate variation in their structure to e.g. variation in their functioning, then that is indeed a fantastic development. Where we are at present on the scale between these extremes is for anyone to judge, but where we should be aiming is well evident. We hope that this Special Issue showcases the true power of contemporary molecular approaches for determining ecological interactions and provides inspiration to the ecological community for the future investigation of biodiversity-ecosystem relationships.

Acknowledgements

The 3rd Symposium on Ecological Networks and 3rd Symposium on Molecular Detection of Trophic Interactions were generously supported by funds from the Swedish Research Council VR (Dnr 2016-06872) and the Swedish University of Agricultural Sciences, Centre for Biological Control. We would like to warmly thank Karen Chambers and Armando Moreno Geraldés for their extensive help with compiling this Special Issue for *Molecular Ecology*.

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