Restoring plant-pollinator communities: using a network approach to monitor pollination function

C.N. Kaiser-Bunbury[1,2]

[1]*Centre for Ecology and Conservation, Biosciences, University of Exeter, Penryn Campus, Penryn, Cornwall, TR10 9FE, UK.* [2]*Ecological Networks, Department of Biology, TU Darmstadt, 64287 Darmstadt, Germany.* *<C.Kaiser-Bunbury@exeter.ac.uk>.*

Abstract Ecological restoration is a common tool to mitigate the loss of species and habitats, ultimately aiming to restore ecosystem functioning. Large-scale experimental evidence is lacking, however, on whether standard management techniques, e.g. the removal of invasive alien plants, indeed restore ecosystem functions at the community level. One key ecosystem function is animal mediated pollination. Based on findings from an experimental network study on rocky outcrops (inselbergs) on the island of Mahé in the Seychelles, I present recommendations for conservation practitioners about how to incorporate a network approach into an evaluation of management effectiveness. Responses to restoration actions by plant-pollinator communities and pollination functions lead to several conclusions regarding the resilience of native fauna and flora and ecosystem functioning. Pollination network structure appears to be directly related to the quality and resilience of pollination services, which suggests that network analysis can be used to monitor management efficacy. I provide recommendations and advice to encourage the uptake of a network approach by conservation practitioners seeking to restore ecosystem functions.

Keywords: biomonitoring, management effectiveness, pollination networks, Seychelles, vegetation restoration

INTRODUCTION

Despite recent efforts to slow biodiversity decline worldwide, habitat degradation continues to degrade and simplify ecosystems, especially in the species-rich tropics (Butchart, et al., 2010). To mitigate the effects of habitat modification on ecosystems and assist species and ecosystem functions to adapt to changing environmental conditions, conservation practitioners employ a diverse set of management tools, including ecological restoration (Sodhi & Ehrlich, 2010). Such management tools often rely on a few well-studied target species to assess their outcomes, primarily because of limited time and resources. However, too little is known about the efficacy of restoration for achieving self-sustaining species communities and functioning ecosystems. Habitat restoration usually modifies ecosystems with the purpose of providing suitable habitat for target native species (Miller & Hobbs, 2007). Non-target species, however, can serve essential functional roles in the restored habitat and failure to recognise these species and the ecosystem-level interactions and processes that they are involved in may compromise restoration efforts and assessment (Ehrenfeld, 2000). Pollination is one such key ecosystem function; most tropical plants and crops heavily rely on pollination services for reproduction (Klein, et al., 2007; Ollerton, et al., 2011). Pollinators are rarely targets of habitat restoration (Williams, 2011), although this is slowly changing in agricultural areas where the benefits of wild bees in crop pollination have been considered (Kremen & M'Gonigle, 2015). Given that ecosystems are characterised by networks of interactions between organisms (McCann, 2007), the effect of habitat restoration on pollination interactions is often best studied with a network approach (Jordano, 1987; Proulx, et al., 2005). Thus, to assess the impact of habitat restoration on integrity of pollination services, an understanding of the implications of structural changes of pollination networks on functional performance is critical. Recent work proposed close links between network structure and ecosystem functioning (Coux, et al., 2016; Gómez, et al., 2011; Schleuning, et al., 2015), but field experiments at the community level are required to shed light on the relationships between habitat restoration, pollination network structure, the resilience of plant-pollinator communities, and the quality of pollination services.

Restoration practitioners worldwide place vegetation rehabilitation at the centre of habitat restoration, which often involves removal of exotic plants and assisted recovery of native plant communities (Clewell & Aronson, 2013). Assistance takes the form of fencing off native habitat against large herbivores or exotic seed predators (see e.g. Florens & Baider, 2013), or the reintroduction of large herbivores to replace now extinct seed dispersers (Hansen, 2015). These interventions enable native vegetation and their mutualists to establish and adapt to subtle changes in native and novel processes, which increase resilience against future disturbance. One important prerequisite for a self-sustaining restored plant community is a large and diverse native fruit crop, which is dependent to some degree on the quality and quantity of pollination services. To provide optimal functional performance, plant-pollinator communities mutually rely on diverse and reliable resources (pollen and nectar) and services (pollination). Weighted network metrics, which take into account the quantitative importance of species for their mutualistic partners, have been developed to assess the consequences of vegetation rehabilitation on pollination services by teasing apart changes in abundance, species diversity and the topology of species interactions, e.g. species generalisations (Banašek-Richter, et al., 2004; Blüthgen, et al., 2006; Tylianakis, et al., 2007).

RESTORING PLANT-POLLINATOR COMMUNITIES

In a recent study, Kaiser-Bunbury, et al. (2017) showed for the first time, with a large-scale field experiment, that not only were species communities fundamentally changed by restoration (the removal of invasive alien shrubs), but also plant-pollinator interactions became more resilient as a result of restoration. Restoration altered pollinator behaviour and increased pollinator species richness (Kaiser-Bunbury, et al., 2017). In this instance, the removal of invasive plants modified pollinator foraging patterns, which increased pollinator efficiency (i.e. more pollen delivered per visit) and frequency (i.e. higher visitation rate per flower) of native plants in the restored community (see Fig. 3 in Kaiser-Bunbury, et al., 2017). Simultaneously,

In: C.R. Veitch, M.N. Clout, A.R. Martin, J.C. Russell and C.J. West (eds.) (2019). Island invasives: scaling up to meet the challenge, pp. 568–570. Occasional Paper SSC no. 62. Gland, Switzerland: IUCN.

pollinator species became more generalised in restored communities, creating greater functional redundancy and lower mutual dependencies. These results appeared at first contradictory, as specialised pollinators tend to be more effective pollinators than generalists, due to lower interspecific pollen transfer (see Morales & Traveset, 2008 and references within). However, the data also suggested that while pollinator species became more generalised as a result of restoration, individual pollinators had increased floral constancy, providing high quality pollination services even at relatively low visitation frequencies (Kaiser-Bunbury, et al., 2017). Several plant species at the restored sites (nine species at restored vs. two species at unrestored sites) further benefitted from attracting more pollinator species – on average an increase in pollinator species richness by approximately 114% compared to the same plant species at the unrestored sites, thereby lowering their dependency on a few pollinator species for reproduction.

The effects of restoration on the plant-pollinator community and pollination services were reflected by changes in pollination network structure (Kaiser-Bunbury, et al., 2017). The findings on the connection between network structure and ecological processes are important for two reasons. Firstly, they corroborate previous theoretical and empirical, non-experimental work that suggested a direct relationship between network properties and ecosystem functioning (Gómez, et al., 2011; Schleuning, et al., 2015; Coux, et al., 2016). Secondly, network metrics, which are commonly used to characterise network properties, can now be employed to inform scientists and practitioners about the ecological and conservation status of communities and ecosystem functions when, for example, compared to baseline data. With future shifts in conservation approaches towards the protection of ecosystem services and functions (Harvey, et al., 2017), suitable tools and methods need to be developed that allow conservation biologists and practitioners to monitor and evaluate such processes. The Kaiser-Bunbury, et al. (2017) study provided an important cornerstone for interpreting processes in ecological communities by using a network approach.

Network ecologists have advocated for some time the potential of a network approach in applied ecology, based on advances in understanding the processes that shape community level interactions (e.g. Memmott, 2009; Kaiser-Bunbury, et al., 2010; Tylianakis, et al., 2010). More recently, a selection of network indicators, i.e. aggregate network metrics describing community properties, was proposed, which characterise the diversity and distribution of interactions at the species, guild (e.g. plants, pollinators) and network level (Kaiser-Bunbury & Blüthgen, 2015). These network indicators were selected because of ecological characteristics, sound empirical and theoretical support, conceptual similarities to well-established diversity indicators, and computational ease with which they can be generated (Kaiser-Bunbury & Blüthgen, 2015). The authors presented a conceptual framework on how to use network indicators to guide conservation decisions by evaluating management effectiveness, and proposed island ecosystems as suitable model system. Island biotas are not only in urgent need of extensive conservation action, but the simplicity of island ecosystems also facilitates comprehensive studies on interaction networks (Kaiser-Bunbury, et al., 2010). Thus, how can the insights gained from studies on network structure and ecosystem functioning (e.g., Kaiser-Bunbury, et al., 2017) be applied to biomonitoring and assessments of management effectiveness by island conservation practitioners?

IMPLICATIONS FOR ECOLOGICAL RESTORATION

Biotic interactions (here I refer to mutualistic interactions such as pollination and seed dispersal, but antagonistic i.e., trophic, interactions may equally be used) can be short-lived and highly variable across seasons, years or even longer time spans (Medan, et al., 2006; Olesen, et al., 2010; CaraDonna, et al., 2017). Network indicators that describe the ecological processes determining network structure may be most suitable to monitor ecologically meaningful changes in biotic interactions that reflect community-wide adaptations to specific restoration actions, for example, the removal of invasive species, reforestation with native plants, or landscape modifications. Methodological and ecological advances, however, are rarely used to their full potential for evaluating and monitoring conservation progress (Gardener, et al., 2010). To benefit from such advances, network indicators could be used to inform managers on whether conservation interventions actually restore or maintain ecosystem integrity (Noss, 2004). In the Seychelles, the positive effects of restoration on pollinator communities and native plant reproduction were reflected in corresponding changes in network indicators (Kaiser-Bunbury & Blüthgen, 2015). These included the total number of visits and interactions, interaction diversity and evenness, and the degree of network- (H_2') and species-level (d') specialisation (Kaiser-Bunbury, et al., 2017). Thus, recording community-wide biotic interactions and calculating network indicators for observed biotic interactions can provide restoration practitioners with a measure of effectiveness for achieving the overall goal of restoring ecosystem functioning.

A network approach may appear challenging, overly complicated and costly to most conservation practitioners. Instead of providing comprehensive instructions on how to apply a network approach in restoration, I aim to illustrate that using biotic interactions and network analyses are viable and effective tools to monitor conservation progress and adapt management approaches based on the outcome of the performance assessment. Below I outline four recommendations for consideration by practitioners who are interested in embracing a network approach in biodiversity conservation.

1) *Clearly define conservation goals that can be validated with network indicators*. Network indicators can only illustrate the properties of one specific ecosystem function at a time, for example, pollination, seed dispersal, or predation. It is therefore important to identify the ecosystem function to be targeted by the conservation intervention (Kaiser-Bunbury & Blüthgen, 2015). Decision-making tools that take into account multiple ecosystem functions may be required to prioritise conservation action (McCarthy & Possingham, 2007). Clear conservation objectives and outcomes will then provide the basis for selecting network indicators and setting threshold values of conservation targets (Kaiser-Bunbury & Blüthgen, 2015).

2) *Actively engage with applied network ecologists* who can assist with establishing data recording protocols and conducting network analysis, possibly via electronic data collection in the field and automated analysis (Kaiser-Bunbury & Blüthgen, 2015). At first, the network approach may appear dauntingly complex. However, the involvement of network ecologists in the planning phase of any conservation action will ensure that a suitable sampling protocol is developed, facilitating data analysis and interpretation to evaluate management effectiveness. Network ecologists are also more likely to follow advances in the field and can update protocols, sampling techniques and analyses based on the most up-to-date research. In return for the time invested, ecologists will have access to

empirical data for publications and contribute actively to maximising the impact of their research.

3) *Be realistic in sampling design.* Collecting data on biotic interactions involving all species in the community is often considered extremely time and labour intensive, and therefore costly. It is not necessary, however, to record 'every single interaction'. Interaction networks are inherently under-sampled (Vázquez, et al., 2009) but still provide meaningful insights into ecosystem complexity and functioning. It is more important to identify the most time and cost efficient sampling method (see e.g. Hegland, et al., 2010) and assess sampling completeness with appropriate extrapolation techniques (Colwell & Coddington, 1994). Depending on the conservation goals, sampling of subsets or at a lower frequency/density may suffice to reveal changes in network structure as a result of the restoration intervention.

4) *Select the most suitable sampling approach* for your habitat, available resources, and the accessibility of the management site. For example, pollination interactions can be observed using standardised transects, which is a time-efficient sampling method most suited to meadows, heathlands and other low-growing plant communities. Alternatively, by observing target plants for a set amount of time, pollination interactions can be recorded in a forest or shrubland habitat with a 3-dimensional structure and a patchy distribution of flowers (for a comparison of the methods see Gibson, et al., 2011).

Why should conservation practitioners and ecologists invest extra time and resources into monitoring processes? In short, moving conservation actions towards an ecosystem functions oriented approach (sensu Harvey, et al., 2017) will require tools that can monitor and evaluate the multi-facetted dimensions of biodiversity. The network approach can generate detailed insights into the functioning of ecological communities, is developing rapidly, and presents a promising and exciting method for improving biodiversity conservation in the 21st century.

ACKNOWLEDGEMENTS

I thank two reviewers for helpful comments on an earlier version of this manuscript. I acknowledge funding from the German Research Foundation (DFG; Heisenberg Fellowship KA 3349/3-1).

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