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Original Research Article

Flower-power: Flower diversity is a stronger predictor of network structure than insect diversity in an Arctic plant–pollinator network

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ABSTRACT

Both plant and insect communities undergo phenological changes across the season, leading to seasonal changes in species diversity and interactions. Network theory offers important tools for understanding how groups of flowering plants and insects interact. However, most studies of plant–pollinator networks aggregate samples over time, masking phenological changes in the network over the growing season. Furthermore, estimates of biodiversity are derived from network observations, meaning that the ecological community is not assessed independently from the structure of the network. Understanding how biodiversity influences network structure over time is important for predicting how global change will affect the ecological processes shaping networks. In this study, we sampled the flower community, insect community, and the pollination network of a high Arctic dwarf-shrub ecosystem over the course of an entire growing season. We found that the flower community was a stronger predictor of network complexity and interaction diversity than the insect community. We suggest that studying networks at scales relevant to both plants and pollinators can provide insight into the mechanisms underlying network formation. This improved knowledge could help to better understand and predict the ongoing phenological changes in Arctic and alpine ecosystems.

1. Introduction

Biotic interactions are important drivers of ecological communities (Waser and Ollerton, 2006), and vary widely over space and time (Bascompte and Jordano, 2014). Plant–pollinator interaction is a well-studied mutualism (Bronstein et al., 2006; Bronstein, 2009). Pollinators gain valuable nutrients from flowers, while their plant partners can achieve more efficient ovule fertilization and seed production. Many studies have examined individual behaviours of plants and their pollinators, but more recently, we have been able to study entire networks of plant–pollinator interactions (Olesen et al., 2006; Bascompte and Jordano, 2007, 2014). The network approach to plant–pollinator interactions has several advantages. First, it allows us to ask questions about degrees of specialization or generalization across entire communities (Waser and Ollerton, 2006). Second, we can compare overall properties of networks across space or time (Olesen and Jordano, 2002; Olesen et al., 2007; Dupont et al., 2009; Poisot et al., 2015). Finally, it allows us to consider conservation of network diversity, as well as conservation of species diversity, in our management of ecosystems (Burkle and Alarcón, 2011).

Pollinators are capable of dynamically responding to changes in flower abundance and diversity (Losapio et al., 2016), causing rewiring of plant–pollinator networks. Because of this, we might naïvely expect that changes in the pollinator community would most strongly control network structure. However, Burkle and Alarcón (2011) found that changes in network structure more closely mirrored week-to-week floral changes in a temperate plant community. This could operate differently in Arctic and alpine plant–pollinator networks, due to speed of species turnover, harshness of abiotic factors (e.g. low temperature), and low overall diversity. For example, Simanonok and Burkle (2014) found that week-to-week flower and pollinator turnover in an alpine pollinator network accounted for similar amounts of interaction turnover (41% and 36%, respectively).

Due to their sparse nature, describing networks requires large amounts of sampling (Olito and Fox, 2015), or aggregation of samples over large spatial or temporal scales (Burkle and Alarcón, 2011; Alarcón et al., 2008). However, aggregating samples can obscure spatial or temporal patterns of interest that occur at smaller scales, particularly in short-seasoned Arctic and alpine ecosystems. Furthermore, aggregated networks often have temporally- or spatially-forbidden links, which

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obscure the true nature of the interactions appearing at scales relevant to the network partners (e.g., hours, days) (Vázquez et al., 2009b). Viewing networks at scales relevant to their partners is crucial to our understanding of how these partners interact and how they will respond to changes in species composition.

Few studies of plant–pollinator networks independently measure all three components of community-level networks: 1) plant diversity, 2) insect diversity, and 3) the interaction network itself. All network studies sample the visitation network, and some have sampled the flowering plant community independently from the network (Alarcón et al., 2008; Olito and Fox, 2015; CaraDonna et al., 2017), but to our knowledge, none have sampled the insect community separately. This means that most studies have no independently-derived information about the abundance and diversity within the insect community, meaning that changes in the insect community are impossible to disentangle from changes in the network. Understanding how communities structure influences network structure over time is important for predicting how the effects of global change, such as shifting phenology or changing diversity, will affect ecological networks.

In this study, we present results from a day-to-day study of an Arctic pollination network, where we independently measured three aspects of the community-level network: insect diversity, flower diversity, and network structure, and relate them using path analysis. Given the mutualistic nature of pollination interactions (Vázquez et al., 2009a), we hypothesized that 1) insect and flower diversity would show coupled temporal dynamics, and that 2) network structure would change along with insect and flower phenology. We also expected that insect and plant diversity would influence network complexity with similar strength (Simanonok and Burkle, 2014).

2. Methods

2.1. Flower diversity

The study was conducted in a coastal lowland valley at Alexandra Fiord, Ellesmere Island, Nunavut, in the Canadian High Arctic (Fig. S1, detailed site description in Svoboda and Freedman, 1994; Jones et al., 1999). We studied the Xeric Shrub site, which is characterized by early snowmelt, peaty and sandy soils, and a relatively deep active layer (50–70 cm) (Muc et al., 1989; Jones et al., 1997, 1999). The dioecious deciduous dwarf-shrub *Salix arctica* is the dominant plant at the site, followed by graminoids such as *Poa arctica, Festuca brachyphylla* and *Luzula confusa*. The other flowering plants included *Dryas integrifolia, Stellaria longipes* and *Papaver radicatum*, with a few individuals of *Draba lactea, Saxifraga oppositifolia, Saxifraga cernua, Saxifraga tricuspidata, Cassiope tetragona*, and *Pedicularis capitata*.

To measure flower diversity, we monitored flowers in 14 1-m^2 random plots over the growing season, counting all open blossoms with anthers, stigmas and petals that had not yet begun to wither. Any receptive, open, non-graminoid flower was counted. Individual catkins of male and female *Salix arctica* were counted separately.

2.2. Insect diversity

To assess the structure of the overall flying insect community, we used the CANPOLIN (2009) bowl trap protocol using sets of white, yellow, and blue bowls, as well as targeted netting of visitors on plants. All forms of passive traps are known to be biased towards certain groups of flying insects (Geroff et al., 2014; Joshi et al., 2015), but our goal was to obtain an independent (i.e. not measured from the network), consistent measure of the flying insect community across the growing season. Five of each colour of bowl were randomly placed along a 140 m transect at the site, for a total of 15 bowl trap transects. The bowls were filled with unscented soapy water during the morning of the sampling days. The morning following the sampling day, the contents of the bowls were poured through a mesh strainer to catch arthropods present in the bowls. Non- flower-visiting arthropods, such as spiders, caterpillars, and aphids, were not considered in the study. We measured hourly air temperature at the site using a set of three HOBO® temperature loggers (*Onset Corporation*), mounted 15 cm above the ground and protected by a plastic radiation shield.

2.3. Plant–pollinator network

To sample the visitation network, we netted insects visiting flower over the course of the entire flowering season every second day, which in our Arctic site lasted from June 23 to August 6 2014. Near the end of the survey, insect activity was visibly decreased, and few receptive flowers were available. Field workers walked a patrol route across the site, capturing any visiting insects they saw on flowers, and recording the species of flower that the insect was visiting. The length of time during the patrol was recorded, and patrols were repeated over the course of the day. All insects were identified at the genus level, whenever possible. We recognize that increases in taxonomic resolution may change our results, given that the flower network was identified to the species level, but most family-level identified insects were rare in the network (see Table S1), and would not strongly change estimates of genus- or species-level diversity within the network if they were identified more precisely. Bowl trap diversity would increase overall if identified more precisely, but this would likely not change the direction of the overall diversity-time relationship.

2.4. Network analysis

Using the netted insects over each plant species, we created pollination networks for each day of sampling ($n = 20$). For each network, we calculated network complexity and interaction diversity. Network complexity was calculated computing the weighted linkage density (Eq. (1); Bersier et al., 2002) where the averages of the equivalent numbers of pollinators $m_{C,k}$ and plants $m_{R,k}$ is weighted by the relative abundance (i.e., row sums $a_{k\cdot}$ and column sums $a_{\cdot k}$ by total number of interactions $a_{\cdot\cdot}$) of each pollinator and plant species a. Network-level interaction diversity was calculated using the Shannon index (Eq. (2); Bersier et al., 2002). Finally, we calculated the (daily) Shannon diversity for both the independent samples of flower and insect communities.

$$LD_q = \sum_{k=1}^{C} \frac{a_{k\cdot}}{a_{\cdot\cdot}} m_{c,k} + \sum_{k=1}^{R} \frac{a_{\cdot k}}{a_{\cdot\cdot}} m_{R,k} \times \ 0.5 \tag{1}$$

$$H_2 = \sum_{i=1}^{i} \sum_{j=1}^{j} \left(\frac{a_{ij}}{m} \times ln \frac{a_{ij}}{m} \right) \tag{2}$$

To assess the effects of flower and insect diversity on network complexity and interaction diversity over the season we used path analysis via a piecewise Structural Equation Model (SEM) approach (Shipley, 2009; Grace et al., 2012). In our model, both flower diversity and insect diversity are controlled by their seasonal phenology, and the network properties are a function of the interaction between these separate communities. We modelled day-to-day temporal autocorrelation in the data using a continuous autocorrelation process of order 1 (`corCAR1` in `nlme`; Pinheiro et al., 2018). We also included daily average air temperature, as increases in temperature (especially in Arctic insects) could improve flight efficiency of foraging insects (Afik and Shafir, 2007), potentially resulting in higher network diversity and complexity, either directly or indirectly. To test whether this effect was direct or indirect, we fit two models, one with a direct effect of temperature on the network properties, and one with an indirect effect on the abundance of insects and flowers (Fig. S2). R^2 for each endogenous variable was calculated from the correlation coefficient of regressing predicted values onto measured values. We performed all network analysis in R 3.4.4 (R core team 2018), using the