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

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ARTICLE INFO

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-m² 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 $a_{k.}$ and column sums $a_{.k}$ by total number of interactions $a_{..}$) 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.

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

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

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
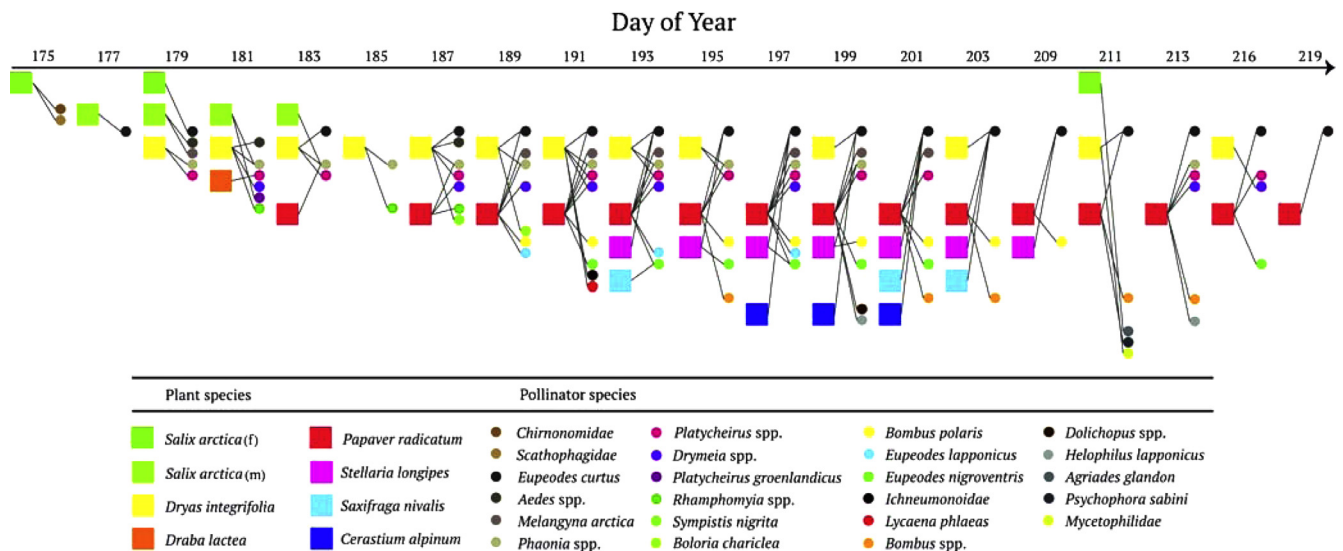
**Fig. 1.** Network structure across all 20 days of sampling. Flowering plants are displayed as boxes, visiting insects are displayed as circles, and individual interactions are displayed as lines.

`bipartite` (Dormann et al., 2009) and `vegan` (Oksanen et al., 2015) packages, and fit the path analysis models using the `piecewiseSEM` (Lefcheck, 2016) package. The R code and data used to perform the analysis can be found at https://github.com/samuelVJrobinson/AlexFiord-VisitNetwork.

## 3. Results

### 3.1. Plant-pollinator network over time

We observed a total of eight insect-visited flowering plant species at our study site (Fig. 1). However, the four dominant flowers were *Salix arctica, Dryas integrifolia, Stellaria longipes,* and *Papaver radicatum*. We netted a total of 408 flower-visiting insects over the entire growing season, yielding 23 individual insect morpho-species (Table S1). The coloured bowl traps caught a total of 2081 flower-visiting insects (3434 arthropods total). *Phaonia* spp. (Diptera: Muscidae) was by far the most common insect caught in coloured bowls (1019) and was very common on flowers (100). *Eupeodes curtus* (Diptera: Syrphidae) was the most common flower visitor (180) but was not well-represented in the coloured bowl traps (five individuals). The only recorded bee at the site, *Bombus polaris*, was not caught in any of the bowl traps, and only seven individuals were caught on flowers. Bowl-trap diversity increased throughout the season, while flower diversity peaked on July 9 (Day 191). The properties of the network also changed across the season (Figs. 1 and 2), with network complexity and interaction diversity exhibiting hump-shaped responses, peaking at roughly the same time as flower diversity. Air temperature varied strongly from day-to-day (Fig. 2), and we recorded the highest daily temperature of 17.7°C on July 9.

### 3.2. Changes in diversity over time

We found that the path analysis model with a direct effect of temperature on network structure and interaction diversity had the best fit with the data. The fitted model (Fig. 3) approximated the data covariance well ($\chi^2 = 4.69$, df = 4, $p = 0.32$, AIC = 30.7), and was better than the model with an effect of temperature on insect and flower abundance ($\chi^2 = 20.34$, df = 4, $p < 0.001$, AIC = 58.3). The fitted model explained a large proportion of variation network complexity ($R^2 = 0.70$) and interaction diversity ($R^2 = 0.65$). Neither flower diversity ($p = 0.19$) nor air temperature ($p = 0.54$) strongly influenced

insect diversity, indicating that the day-to-day estimates of insect diversity were likely not influenced by the surrounding diversity of flowers or air temperature. Flower diversity, insect diversity, and air temperature were all significant predictors of network complexity and interaction diversity (Table 1). However, flower diversity was a stronger predictor of network complexity and interaction diversity than insect diversity, as the path coefficients for flower diversity were 66% and 40% greater (0.63 & 0.38 for diversity, 0.64 & 0.46 for complexity, respectively). The coefficients for air temperature were roughly the same size as those for insect diversity, indicating that the effect of air temperature is approximately as strong as the effect of insect diversity (Fig. 3). Network complexity and interaction diversity were collinear ($r = 0.78$), and responded in similar ways to flower diversity, insect diversity, and air temperature.

## 4. Discussion

We found that pollination networks dramatically varied across the short Arctic growing season. Both insect diversity and flower diversity, as well as air temperature, were significant predictors of network complexity and diversity. However, the daily networks were more sensitive to flower variation than insect variation and air temperature, demonstrating the importance of bottom-up effects and phenological changes of plant communities in driving the structure and dynamic of ecological networks. Given that our study took place at a single location over a single season, we hesitate to make large-scale predictions about the nature of all plant-pollinator networks, as interactions vary from year-to-year as well as geographically (Poisot et al., 2015). However, we believe that the patterns we see could operate more generally, at least in Arctic and Alpine ecosystems, and we encourage others to consider independent measurements of insect and flower diversity when studying interaction networks in other environments.

Our study highlights the role of biodiversity in mediating the assembly of ecological networks over time. Indeed, network complexity and interaction diversity were both well-explained by flower diversity and secondarily by insect diversity and air temperature. This finding agrees with previous results (Alarcón et al., 2008; Burkle and Alarcón 2011; Losapio et al., 2016), where changes in the network closely mirrored changes in the overall plant community. Foraging insects require high body temperatures to fly efficiently (Heinrich, 1975a, 1975b), and small changes in air temperature or solar radiation can cause large changes in flower visitation (Bergman et al., 1996). Thus,
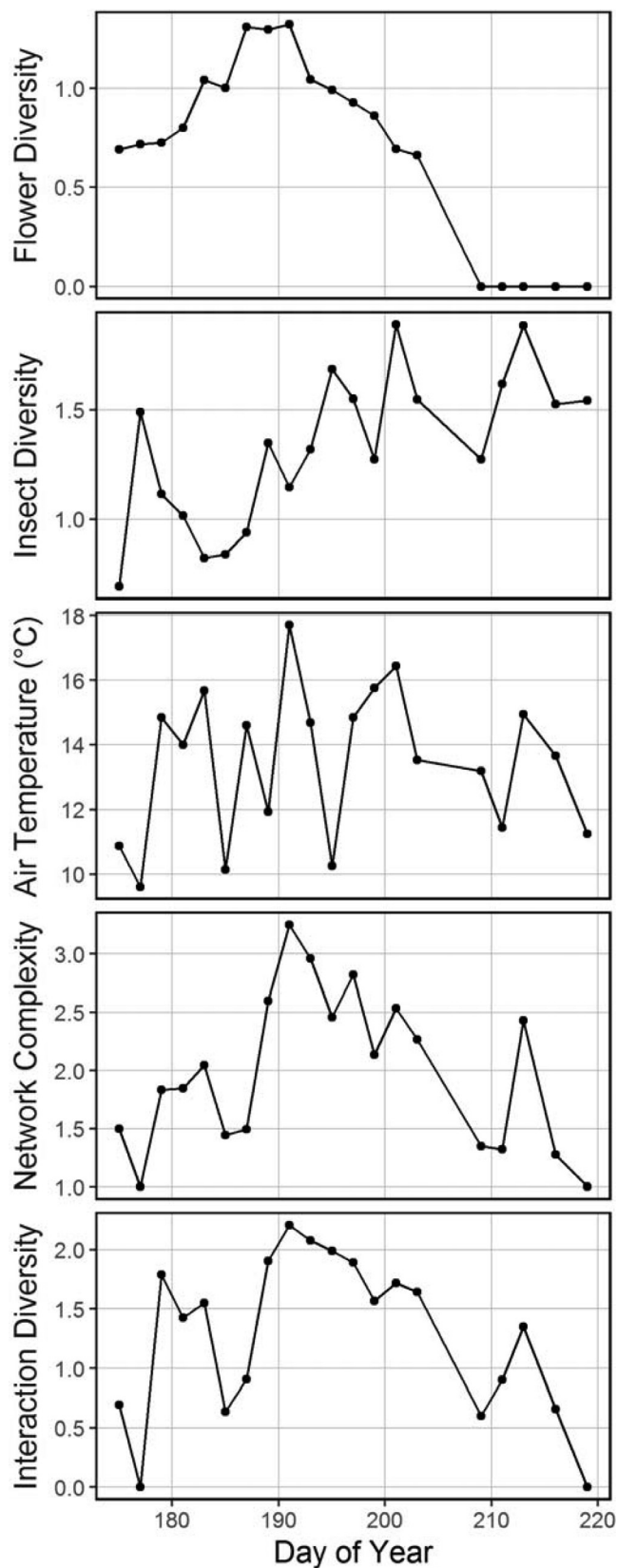
Fig. 2. Network properties across the flowering season, along with flower and insect diversity and air temperature. Flower diversity, insect diversity, and interaction diversity were calculated using the Shannon index, and network complexity was calculated as linkage density (Bersier et al., 2002; Oksanen et al., 2015).

abiotic processes influencing individual behaviours and activity of insect pollinators scale up to ecological interactions between insect and with their visited plant species (Vázquez et al., 2009a, b). Interestingly, we found that air temperature positively influenced network complexity and interaction diversity, but that phenological changes of plant and insect communities were stronger than that of air temperature *per se*. This indicates that biotic factors such as biodiversity can be as strong or stronger than abiotic factors for shaping the structure of ecological networks and how they change over time. Moreover, these findings suggest that global change could affect ecological networks directly by altering the physical environment, or indirectly by altering the diversity of species. Consequently, our study pinpoints that loss of biological diversity may exacerbate the impact of global change and highlights the need of understanding biological mechanisms underlying ecological networks at relevant temporal scales.

A large proportion of variance in the network remained unexplained by any of the factors we included in the model (31% for network complexity and 39% for interaction diversity). Much of this is likely due to stochasticity in plant–pollinator interactions and sample size limitations, but some of this may be attributable to other factors not contemplated in this study, such as trait matching (Vázquez et al., 2009a). However, CaraDonna et al. (2017) found that a simulation using plant–pollinator abundance and phenology (presence-absence) produced interaction turnover values that were consistent with observed turnover, and that species' traits produced only marginal improvements in model fit. Specialist plants and pollinators are rare in Arctic and alpine systems (Olesen and Jordano, 2002), and Olesen et al. (2008) found that most links in Arctic networks existed between a small group of generalists. Our observed networks were composed by a relatively small number of plant species (8), visited by relatively few insect species (23). This yields a small number of unique links in the network (39) but a relatively high level of overall connectance (21%). This high connectance is similar compared to other Arctic and alpine studies (Lundgren and Olesen, 2005). Moreover, we found that day-to-day connectance values were even higher (mean = 62%), likely because of the exclusion of forbidden links across the season. These results indicate that Arctic pollination networks are rather complex, despite the low species richness of these ecosystems. Future studies of how Arctic ecological networks will respond to global change will require a more detailed understanding of the underlying mechanisms, as well as the influence of environmental stochasticity. To our knowledge, this is the first study that measures biodiversity independently of the network across a growing season. Most studies use some proxy of insect abundance and diversity derived from the visitation network. While we recognize that all passive insect traps are biased in some way (Geroff et al., 2014; Joshi et al., 2015), our goal was to obtain a consistent measure of visiting insect diversity. In this way, we were able to show how insect diversity and flower diversity follow separate phenologies over the course of the season, and how they mediate network structure.

In summary, we have shown that independent measures of insect and plant communities from the observation of networks over time can provide useful insight into the study of ecological processes shaping the organization of biodiversity and natural ecosystems. However, the unexplained variance in network complexity and interaction diversity, as well as the null slope between flower diversity and insect diversity, suggest that pollinator dynamics were only partially related to plant community dynamics. A potential explanation could be that most of the pollinators were Dipterans, whose larval diet is often unrelated to flower availability. This finding differs from previous evidence that plant and pollinator phenology is typically tightly coupled, a phenomenon mainly seen in bee-dominated ecosystems (Bartomeus et al., 2011, 2013; Forrest, 2015), in which bees rely exclusively on flowers for their entire life cycle. Future work should focus on simulation of network dynamics as a function of abiotic factors and species-level interactions (e.g. CaraDonna et al., 2017). This requires a more detailed understanding of individual foraging behaviour and ecology, but will
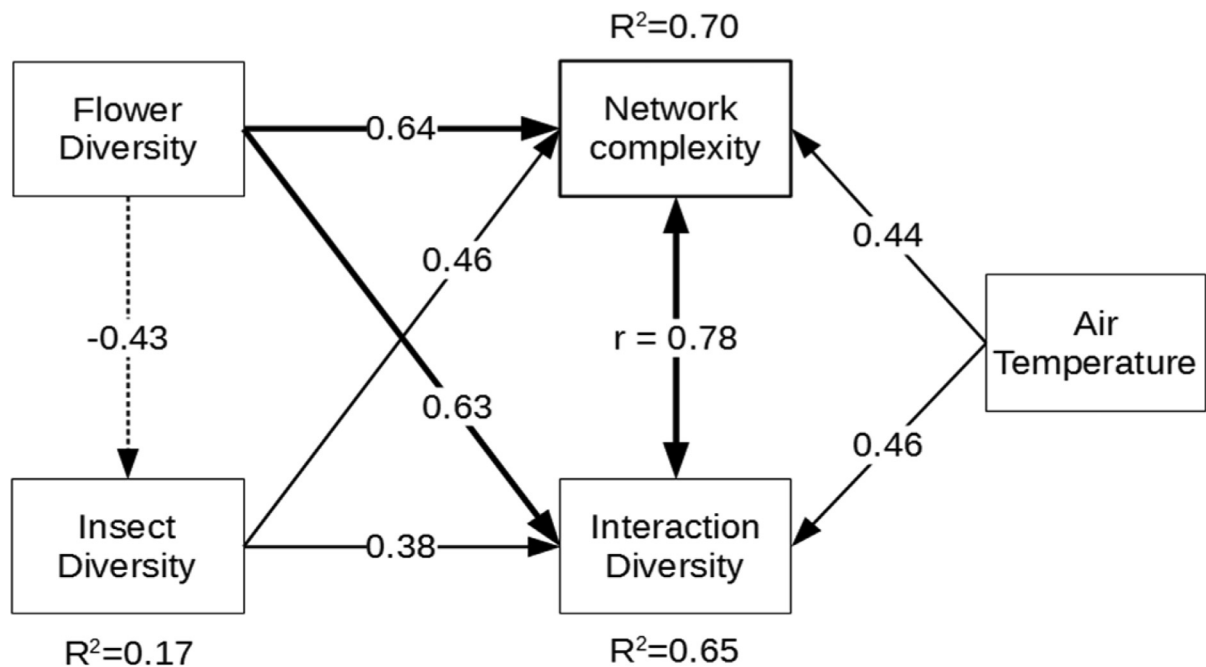
**Fig. 3.** Fitted path analysis ($\chi^2 = 4.69$, df = 4, $p = 0.32$) showing standardized effects (path coefficients) of flower and insect diversity contributing to network complexity and interaction diversity. Line thicknesses approximate the size of the path coefficients. Non-significant ($p > 0.05$) terms are indicated by dashed lines. $R^2$ values are displayed for endogenous variables.

**Table 1**
Regression coefficients for piecewise SEM (network complexity – interaction diversity is a correlation coefficient). Path coefficients are slope coefficients scaled by the standard deviation of the Predictor variable over the standard deviation of the Response variable.

| Response variable | Predictor variable | Slope coefficient | Standard error | *p*-value | Path coefficient |
| --- | --- | --- | --- | --- | --- |
| Insect diversity | Flower diversity | $-0.328$ | 0.245 | 0.196 | $-0.440$ |
| Interaction diversity | Flower diversity | 0.922 | 0.247 | 0.002 | 0.630 |
| | Insect diversity | 0.739 | 0.322 | 0.036 | 0.378 |
| | Air temperature | 0.135 | 0.044 | 0.007 | 0.459 |
| Network complexity | Flower diversity | 0.935 | 0.239 | 0.001 | 0.645 |
| | Insect diversity | 0.890 | 0.301 | 0.009 | 0.459 |
| | Air temperature | 0.128 | 0.039 | 0.005 | 0.437 |
| | Interaction diversity | 0.776 | NA | | |

yield a greater knowledge of how networks assemble and disassemble, with the potential to predict network properties in novel situations.

## Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ecocom.2018.04.005.

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