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Mutualistic networks and climate change: impacts on Arctic plant–pollinator interactions

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Table of Contents

Introduction

Network ecology is a fundamental tool that can be used to analyze information on the complexity of a given ecosystem, beyond the species that constitute it (Bascompte and Jordano, 2013). From our understanding of network structure, we can construct models that help our understanding of a system where no species functions independently from or outside of its environment. As its key contribution, network ecology makes the relationships between species explicit (Poisot et al., 2016), where the interactions involved are just as important to study as the species themselves. As a result, some theorists suggest that the concept of ecological networks brings a paradigm shift within ecology itself (Ings et al., 2009).

Networks can be defined as a collection of nodes (often represented by species), joined together by links (often represented by species interactions). In ecology, these are essentially probabilistic in nature – implying that when species meet, they will not always and unavoidably interact but do so with a given probability (Gravel et al., 2019). They can be modelled and constructed through a mixture of information such as species and individual abundance data or traits such as body size (Gravel et al., 2019). This information can then improve our understanding of, for example, the functional role of such species traits through highlighting links occurring between e.g. parasites and hosts, prey and predators, pollinators and plants, etc. (Delmas et al., 2019). Examining these interactions, such as those in mutualisms between plants and animals, not only adds weight to species identity but also allows us to see what can play a role for the relationship itself to function.

When the aforementioned information is applied in the construction of food webs, who eats whom is revealed (May 1973; Cohen 1978; Pimm 1982). The flow of energy down trophic levels can be used to understand the stability of species in communities and cascading effects through indirect interactions. Food webs include *host-parasitoid* and *mutualistic* interactions, two-mode networks depicting an arms race between species or an incorporation of beneficial interactions. As all life on earth is contained within food webs, linking species together in and across biological communities, these networks are the perfect tool to better understand trophic niches, community assembly, and species coexistence (Montoya and Sole 2003; Barberan et al., 2012; Allesina and Levine 2011; Ulrich et al., 2014). Thus, food webs can be useful not just for questions concerning conservation, habitat fragmentation, and climate change, but can also be used for applied biological questions regarding biological control, restoration ecology, ecosystem services, and urban ecology among others (Memmott, 2009).

Mutualistic relationships, where two or more species benefit from one another, can offer an exceptional window into network dynamics. These networks, including pollination and plant-animal seed-dispersal, are the supporting backbone of most ecosystems on earth (Bascompte and Jordano, 2013). Plant-pollinator networks are a web of interactions between plants (food source) and pollinators (animals consuming pollen or nectar) that prove mutually beneficial to both organisms. These interactions tend to be nested, modular, and robust in nature (Bascompte et al., 2003). Studying mutualistic networks can give us a better understanding of what could happen to the structure and resiliency of ecosystems if a disturbance such as rapid warming from climate change were to act upon such a network (Nagaishi and Takemoto, 2018).

One area where the alteration of mutualistic relationships is likely to be particularly important is the Arctic. Rapid changes in temperature, ice cover, snow, and availability of nutrients have altered trophic interactions in the Arctic faster than any other biome on earth (IPCC, 2014). Here, some areas have also experienced major shifts in large parts of the ecosystem, such as the advancement of flowering times (Cirtwill et al., 2018; Høye et al., 2007; Post et al., 2009; Schmidt et al., 2016). As a result, plant and pollinator phenologies are predicted to advance 1-3 weeks globally towards the end of the 21st century, with considerable variation between individual species (Memmott et al., 2007). This can strain plant-pollinator networks, where potential phenological mismatches can result in pollinators emerging with no food source, or plants blooming without a particular pollinator (Memmott et al., 2007; Renner and Zohner, 2018). Examining these relationships through the lens of climate change can provide valuable information on the dynamics of mutualistic networks and species interactions, not just for the Arctic but in other biomes as well.

Objectives:
In this essay, I will give a background to mutualistic networks and highlight the importance of studying Arctic plant-pollinator networks. I also aim to tackle the following questions:

1. Why are networks such a helpful and crucial tool in ecology?
2. Mutualistic networks drive ecosystem dynamics; how can plant-pollinator relationships and community modeling further illustrate this?
3. How can Arctic plant-pollinator networks provide valuable insight into the effects of climate change?
4. What are the current and future challenges in this field?

Ecological Interaction Networks

Under the vast umbrella that is network science, many types of interactions can be studied. For example, metabolic networks between metabolites and metabolic reactions (Noda-Garcia et al., 2018); neural networks composed of neurons and their synapses (Ma and Tang, 2017); social networks of people and their relationships (Urena et al., 2019)…so what exactly is network science in relation to ecology?

Like neurons are connected through their synapses, all species on earth are connected through some sort of interaction. For example, Williams et al. (2002) showed that 80% and 97% of species are respectively within two or three links from one another, in a study examining seven species-rich webs. Further, as the number of species in a network increases, so do the interactions in that network. At first look, networks can thus seem daunting; however, they depict community complexity and variation. Ultimately, ecological networks help to visualize and describe ecosystems by working towards answering one of the most fundamental questions in ecology: how can so many species coexist, and why (Poisot et al., 2016)? As no species exists in true isolation, often a large variety of factors play a role that influence each individual's behavior and traits. Studying species interactions is thus essential to understanding ecosystem function and we need a tool that can quantify this.

Network descriptions and descriptors

Networks can be defined through mathematics, where they are synonymously referred to as graphs. These can be quantified through the representation of nodes (species) and links (interactions) through matrices, best explained in Newman 2018 and adapted below. In **Figure 1A**, an adjacency matrix is defined by:

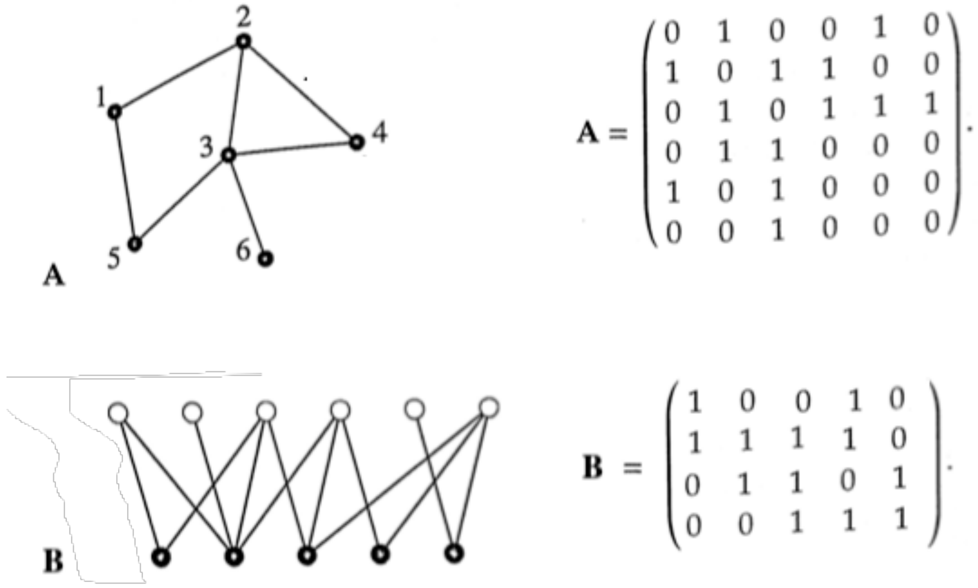
$\mathbf{A}_{ij}$ = {1 if a link exists between i and j nodes, 0 if there is no edge}

Here, *i* and *j* can represent a variety of elements, but for this example relating to ecology, they represent species and their interactions, respectively. This matrix will typically be symmetrical (except in the case of directed graphs, **Box 1**), because if there is an interaction between *i* and *j*, there will also exist an interaction between *j* and *i.* An adjacency matrix can then be graphed into a unipartite (one-mode) network, representing one type of node and its interactions (for example, plants or animals). To examine more than one node and its edges, such as the relationship between pollinators and the plants they visit, an incidence matrix is needed.

Incidence matrices depict a bipartite graph. These are two-node graphs, representing something like plants and animals with interactions between but not among each other (Bascompte and Jordano, 2013). If we have a 4 × 5 incidence matrix $a \times p$ (where a represents pollinating animals and p represents plants), defined by:

$\mathbf{B}_{ij}$ = {1 if *j* belongs to subset *i*, 0 if it does not)

We will get a matrix like the one in **Figure 1B**, which can be graphed into a bipartite graph that shows us the interactions of pollinators between their respective plants. Bipartite graphs are the essential embodiment in mutualistic network theory, as most mutualisms are composed of two distinct species types that do not overlap, with interactions only between different sets (pollinators cannot pollinate other pollinators, for example) (Newman, 2018).



$$\mathbf{A} = \begin{pmatrix} 0 & 1 & 0 & 0 & 1 & 0 \\ 1 & 0 & 1 & 1 & 0 & 0 \\ 0 & 1 & 0 & 1 & 1 & 1 \\ 0 & 1 & 1 & 0 & 0 & 0 \\ 1 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 \end{pmatrix}.$$

$$\mathbf{B} = \begin{pmatrix} 1 & 0 & 0 & 1 & 0 \\ 1 & 1 & 1 & 1 & 0 \\ 0 & 1 & 1 & 0 & 1 \\ 0 & 0 & 1 & 1 & 1 \end{pmatrix}.$$

Figure 1: A) Unipartite network graph showing interactions among one type of node, with adjacency matrix. **B)** Bipartite network including two distinct types of nodes interacting, with respective incidence matrix. Adapted from Newman 2018.

Both unipartite and bipartite graphs can be weighted, as a result of some nodes showing a higher value/strength (for example, 2 or 0.5 can replace 1 in the above matrix) or directed, where links show arrows instead of lines to depict directions of edges (represented by a 1 if there is an edge from *j* to *i*, and 0 if otherwise). Directed networks are especially helpful when studying food webs, as they can illustrate the energy flow from prey to predators. Both matrices can also be either quantitative where the results are weighted, or qualitative, consisting of presence or absence data.

However, in ecology it is useful to examine not just a system containing two-way interactions, but more specifically also a network with one type of node (unipartite). This may be the case, for example, if one wishes to examine only pollinators in a system to get a better idea of shared patterns. Bipartite networks can be transposed into a one-mode projection to do just this, as in the case with the plant-pollinator network in **Figure 2**. Here, two unipartite graphs, depicting shared partner patterns among animals and plants respectively, were constructed from data from a bipartite plant-animal mutualistic network (Bascompte and Jordano, 2013). In doing so, we can see how the plants are indirectly interacting through their shared pollinators (**B**), or how the pollinators are linked indirectly through their plant visits. This is particularly helpful and will be explained in further detail later on in the *Mutualistic networks* section. Like the previous graphs and matrices, these transpositions (elements therein) can also be weighted or directed.

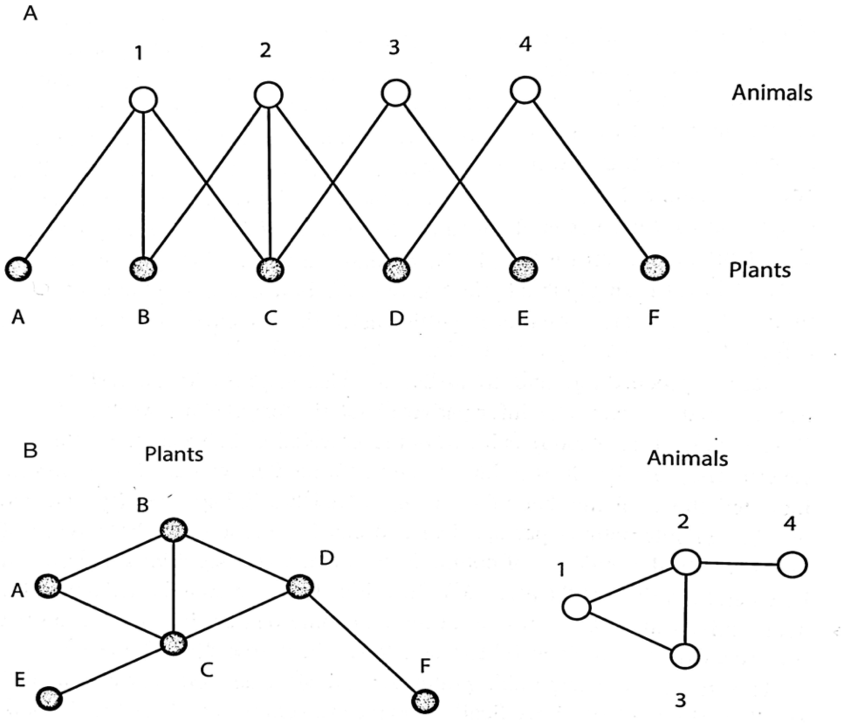


Figure 2: A) Bipartite plant-animal mutualistic network showing two sets of nodes: animals and plants, with between- but not within- interactions **B**) Two unipartite graphs constructed from **A,** showing shared partner pattern among species in each set. (Bascompte and Jordano 2013).

One of the most important components for networks is the degree distribution (**Box 1**). It provides information about a network through the frequency with which nodes of different degrees are represented (Newman, 2018). The degree of a node is the number of connections it has to other nodes, and this degree distribution (*P (k)*) represents the frequency distribution of these degrees across the whole network. An even clearer idea of network structure is obtained when the degree distribution is paired with additional data, such as network size or connectance. Connectivity, path-length, and strength distributions of the relationships can further expand the understanding of networks by showing the importance of various node interactions. While modularity and linkage density (see **Box 1** again for definitions) are commonly used in community structure, because they group the nodes together according to a function and then compare this function among all sets of nodes. Further, path-length can be used to explore the *small-world effect*, commonly experienced in many networks and described later on (**Box 1**). Thus, ecological networks are essentially a "toolbox" that utilizes each of the aforementioned components in a way to provide a visual and analytical description for species interactions.

Box 1: Definitions in network theory

Asymmetry: The strength of interactions among species in a network favoring one type of species over another. For example, specialist species interacting only with generalists, such that the effect of the specialists on the generalists is not reciprocal (becomes one-sided).

Bipartite network: A two-mode network, with connections occurring only between (not among) these two sets of nodes. Represented by an incidence matrix.

Mutualistic network: Ecological network of mutually beneficial interactions where one type of species (plants) is represented by one class of nodes, while another node class represents another species type (pollinators). Interactions (mutualistic actions such as pollination) are represented by links connecting these nodes.

Species richness (*S*): The total number of species in the network. E.g. in a plant-pollinator network, the total number of species $S= P+A$, where P is the total number of plants and A represents the total number of animals.

Connectance (*C*): The fraction of realized interactions. From the notation above for a plant-pollinator network: $C=L/(P*A)$. L (also understood as the links connecting species), represents the number of realized interactions.

Degree distribution: The frequency distribution of total number of interactions per species, based on a probability distribution describing the likelihood of interactions taking place. Represented by: $P(k) = n_k/n$, where n is the number of nodes and k is the degree.

Interaction strength: A quantitative measurement for the strength of the interaction. In plant pollinator networks, this can be the relative frequency a pollinator visits a plant.

Linkage density: The average number of links per species, also referred to as complexity of the network. The higher the linkage density, the more complex the network.

Path length: The distance between two nodes, measured as the number of links between them.

Nestedness: The predisposition of the most specialized species' interactions to be subsets of the most generalized species' interactions. Can also be interpreted as specialists (species with fewer interactions) tend to interact with the subsets of mutualistic partners of species that have more interactions, considered generalists.

Modularity: A measure of the compartmentalization of the network, or of the existence of "neighborhoods" (modules), within which species interact more frequently among themselves than with species outside of the module.

Resilience: After a perturbation, the rate of return to equilibrium in a community.

Robustness: The resistance to species loss of a network due to species extinctions.

Small-world property: The case where distances (path length) between pairs of nodes are short, so that no species is too far removed from another. Originally sourced from social networks, where one person is never far from another's mutual acquaintance.

Unipartite network: One-mode network, represented by an adjacency matrix.

Weightedness: Links that are measured are proportional in strength to their interaction. A weighted network shows the intensity of the interactions among nodes.

Box 1: Set of definitions in network theory adapted from (Bascompte and Jordano, 2013), (Newman 2018), and (Valdovinos, 2019).

Reconstructing networks

Given such complexity, how can we construct a model that accurately depicts an ecosystem? To understand species interactions, we can first observe realized interactions in the field and collect data on species traits, thereby aiming to resolve the impact of the latter on the former. Traits are characteristics of a given species that are well defined and can be identified down to an individual level (Pey et al., 2014; Violle et al., 2007). However, as there is no one particular trait that can be applied unanimously across all ecosystems to evaluate a particular function, it is important to determine which traits are functionally relevant for the studied system depending on the perspectives taken. Through this, biological traits and consumption of resources can then be used to construct models that predict the dynamic structure of networks and their responses to disturbances (Valdovinos, 2019). However, these models still come with a few pitfalls, particularly where accurate sampling is concerned.

In essence, networks can be seen as probabilistic, where data include random meetings that can produce different results (even under the same conditions), rather than deterministic (Gravel et al., 2019). This means that one will not always observe an interaction between two species even if they sometimes interact. The uncertainty with which one will observe an interaction can be split into three types of uncertainty: Could the species interact (what is the probability of them interacting and are there traits that prohibit this?), did they interact during the sampling (a meeting may not have occurred for a variety of reasons, even under ideal conditions), and was this interaction observed (measurement/human error is a common problem in science)? In the explicit context of those three types, finite sampling generates a variation in observed interactions, which can pose a problem to interactions that have not been observed and also creates difficulty ruling out that unobserved interactions have not actually occurred (Cirtwill et al., 2019). However, Cirtwill et al. propose a solution to this issue: through informative priors (such as knowledge regarding a system using a probability distribution via Bayesian statistics), uncertainty for more common interactions can be constrained, albeit not eliminated entirely due to the stochastic nature of networks.

Mutualistic networks

A short history of mutualistic networks

Until the 1970's, antagonistic interactions dominated the investigation of biological associations. This was largely due to models such as those introduced by Lotka and Volterra, with the specific aim of understanding antagonistic predator–prey relationships, where predation and competition were considered the most significant forces that drove community dynamics (Bascompte and Jordano, 2013). However, recent studies have found that current ecosystems would simply collapse without mutualistic relationships involving animal-mediated pollination and seed dispersal (Bascompte and Jordano, 2013). The fundamental understanding of ecological network structures can be further improved through examining the underlying mechanisms involving species interactions in ecology as well as the functional consequences and dynamics that mutualistic network theory can provide (Valdovinos, 2019).

So, what does this mean?

A mutualistic network can be defined as a network that is composed of interactions between species that are beneficial to each other; this mostly includes plant-animal seed dispersal, plant-animal pollination, and ant species that protect the plants they consume (Newman, 2018). Mutualistic networks differ in architecture and stability from antagonistic networks like trophic food webs, in that they tend to be more nested (see Box 1. For definition), while food webs are more modular, containing dense connections between nodes within their own module but few connections with nodes in neighboring modules. This means that community stability in mutualistic networks is promoted by a highly connected and nested architecture, whereas compartmented (modular) and weakly connected architectures stabilize trophic networks. **Figure 3** shows such an example: strong variations favoring stability can limit ecological networks and different architectures will result depending on the interaction type (mutualistic or trophic). Here, Thébault and Fontaine (2010) used a meta-analysis of 103 mutualistic and trophic networks from actual pollinator and herbivory data. They built a population dynamics model that could simulate species density changes with time in both types of networks and found strong architecture stability variations, depending on the type of interaction. This ultimately groomed ecological networks toward different architectures. These architectural patterns were based on species diversity, connectance, nestedness, and modularity.

The holy quinternity of networks: Nestedness, asymmetry, heterogeneity, small-world properties, and modularity

The structure of a “nested” network means that the diet of a highly specialized species becomes a subset of the diet of the next more common species, whose diet is then also a subset of the next more common species (and so on) (Bascompte et al., 2003). In plant-pollinator networks, this shows that specialist plant species with a few pollinator links will tend to interact with a portion of the many pollinator partners that any of the generalist plant species interact with. Thus, mutualistic networks become asymmetrical in nature: generalist plants tend to be pollinated by generalist and specialist pollinators alike, while specialist plants tend to be visited mainly by generalist pollinators; if a plant depends strongly on a pollinator species then the same pollinator depends weakly on the plant (Bascompte et al., 2006). These factors combine to reduce competition among pollinators and enhance ecosystem stability; they are the reason behind why mutualistic networks tend to be more stable than antagonistic feeding webs, which feature compartmentalized competition of resources.

Bascompte (2003) analyzed 52 mutualistic networks and found them to be highly nested, which suggests asymmetrical interactions among species were the core of interactions that organized the community. The results of this study show that these networks are not randomly assembled, but that they also are not sectioned off into parallel specialization; rather, nestedness increases with complexity and for each given number of species, the more interactions a community has the more nested it will be. It has been hypothesized that this sort of structure can promote greater species biodiversity through minimization of competition in a community among species (Bastolla et al., 2009). Indeed, within highly nested networks, species guilds sharing ecological niches typically contain both generalists and specialists; with generalists consisting of species that have many links and specialists consisting of species with few links (Jonhson et al., 2013). However, generalists also interact with generalists and in the case of mutualistic networks, pollinator specialists can interact with precise subsets of plant species that generalist pollinators also happen to interact with.

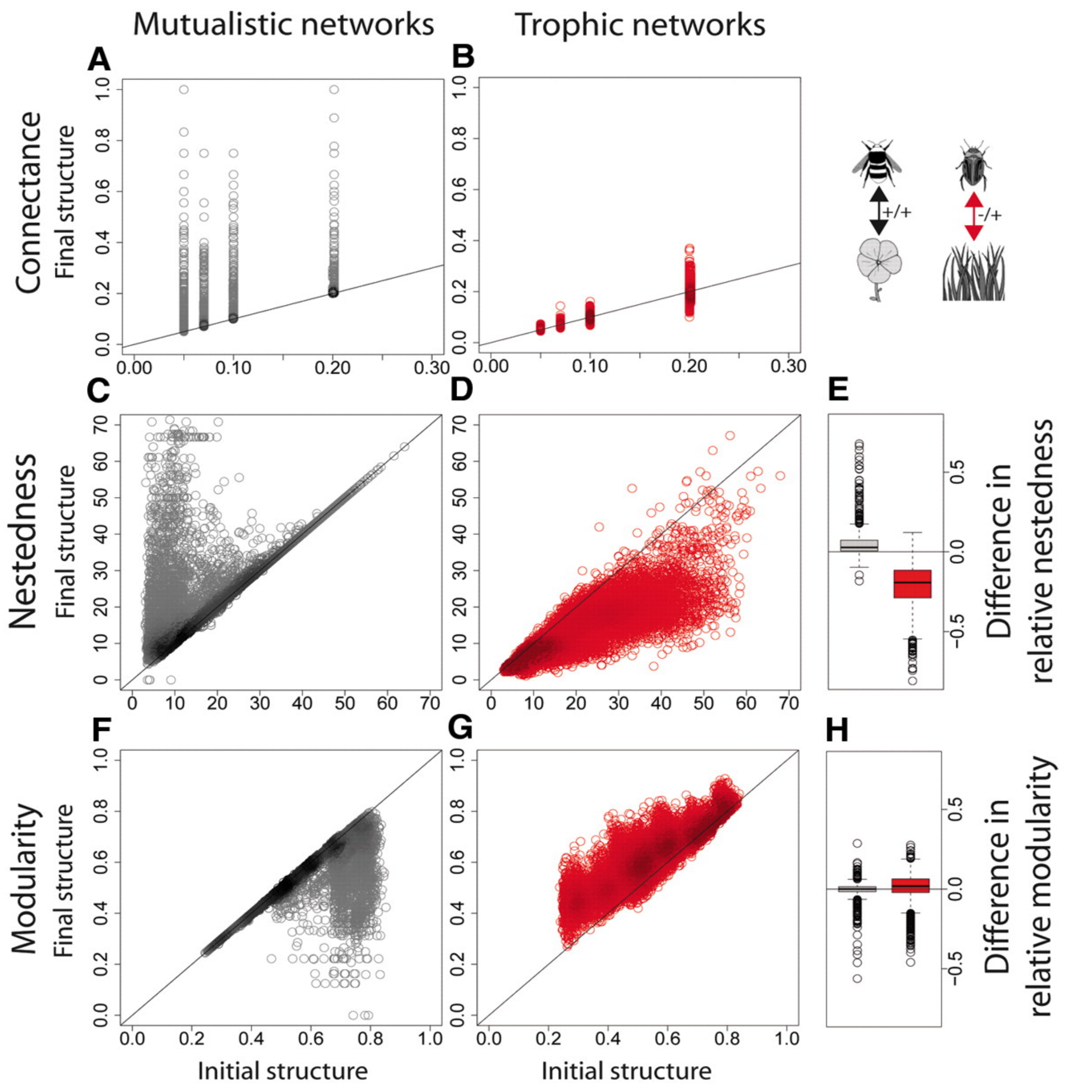


Figure 3: Simulations containing species density changes from a population dynamics model using actual interaction data of trophic and mutualistic networks, resulting in differences in architecture. Index values describe the number of species, how much sharing of interaction partners among species is happening, how many interactions are occurring relatively, and the compartmentalisation degree of networks. Mutualistic (gray) and trophic (red) networks are compared after reaching equilibrium, or relative stability, to show their initial structure vs. final structure in terms of connectance (**A** and **B**), nestedness (**C** and **D**), and modularity (**F** and **G**). Box plots of differences in the initial and final architectures are shown in (**H**) and (**E**), where relative nestedness and modularity can be seen for mutualistic (gray) and trophic (red) networks. Top and bottom limits are represented by lower and upper quartiles for each respective box; black horizontal bands show the median. (From *Thebault and Fontaine 2010*).

Thus, these networks end up forming asymmetrical interactions where the majority of species do not depend on the presence of one particular species, yet some are largely dependent on specific species and their absence can cause an ecosystem collapse. This has been observed in areas where habitat loss and hunting have driven generalist seed-dispersal species to near extinction – resulting in cascading effects on plant fitness and decreased species biodiversity due to the reduction in seed dispersal (Dirzo and Miranda 1990, Kearns et al. 1998, Wright 2003). **Figure 4** demonstrates an example, beginning with the removal of the most generalist plant species and ending with the removal of the most specialist plant species. In the example case, this causes a cascade of secondary extinctions throughout the network. However, this network depicts a fragile structure and would be more resilient if the first species to undergo extinction were specialists or lost at random (Bascompte and Jordano, 2007). Thus, nestedness can help to pinpoint species function and importance, as well as allow for different routes in system responses to disturbances, while weak and asymmetrical interactions provide the opportunity for events such as the persistence of rare species.

While mutualistic networks are complex, their repeated and universal structural patterns are independent of species size, composition, and ecology; showing a heterogenous structure where the majority of interacting species have only one or few interactions (Bascompte and Jordano, 2013). These interactions, however, can be traced down to the fact that all species are close to each other. These networks have the strongest "small-world" (**Box 1**) property of any network studied so far; meaning they contain a shorter on average path length and a highly clustered composition than other networks. A short path length (counted by the number of links to a particular node) means only a few steps are required for connecting any two species in a network, while a high clustering coefficient means that species interacting with a certain other species also have a higher tendency to interact among themselves (Olesen et al., 2006).

These interactions can also occur within neighborhoods, or "modules", which has additional impacts.

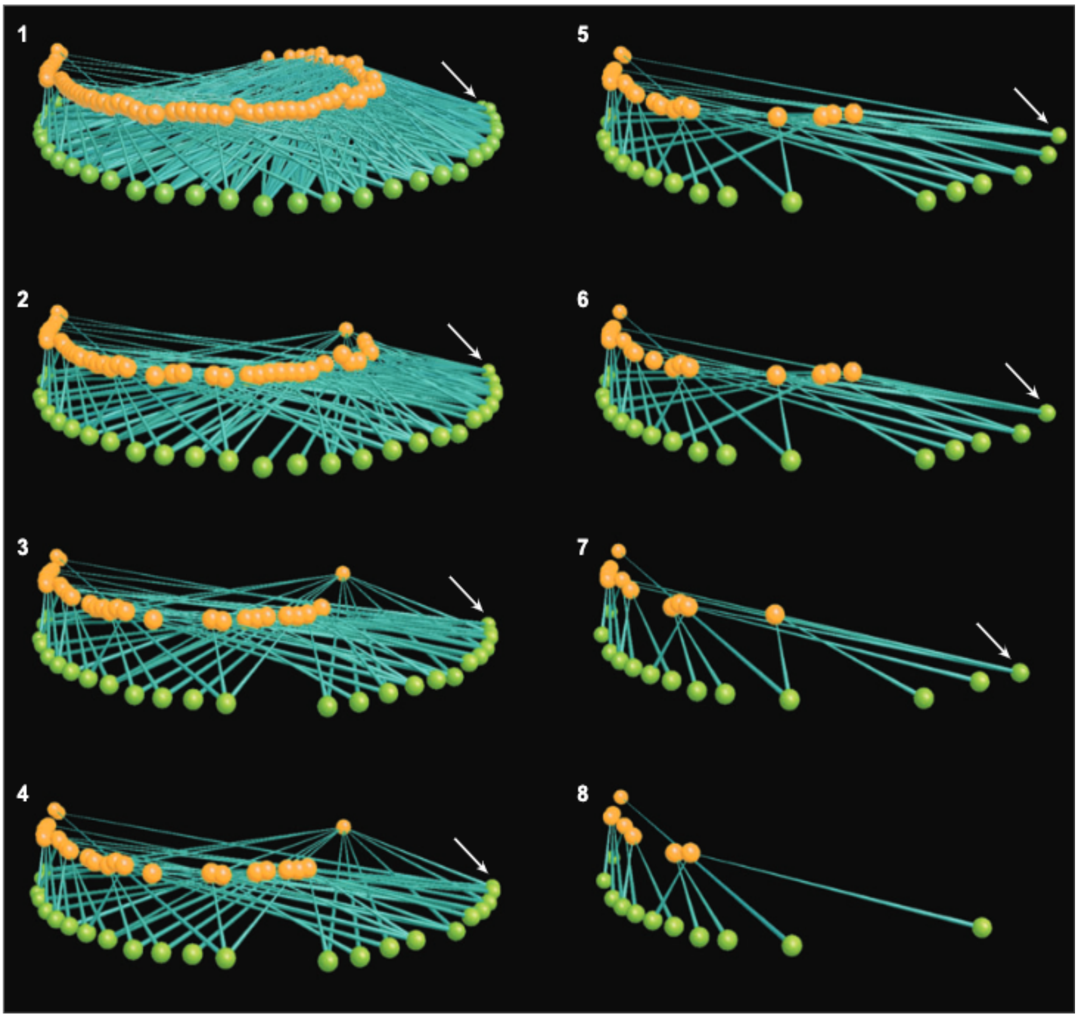


Figure 4: Results of species extinction in mutualistic networks, when a single plant species is removed at each step (1-8) starting from the most generalist and ending with the most specialist species. The key assumption in generating these graphs was that all species isolated as a result of other (primary) extinctions, will undergo coextinction. (from Bascompte and Jordano, 2007).

Mutualistic networks are modular (though not as dominant in this as food webs) in nature (**Box 1**), which can be thought of as neighborhoods in the community. Individual species can play a specific role in the network; a generalist can represent a central gathering point, or "hub", that connects other species through its interactions, within and outside its own module, while a specialist can be thought of as a "peripheral species" that only interacts within its own module (Olesen et al., 2007). To further examine this, Guimera and Amaral, 2005 proposed a method where one could find modules by classifying nodes according to two variables: 1. within-module degree, where species were ranked according to how well connected they are within their own module; and 2. participation coefficient, where connectivity of a node was measured from the point of view of the whole network, which measured how well spread the links of one node are compared to the rest of the modules. When applied to a pollination network, this study found that 11% of pollinating insects were connecting several modules together, and the role of each species could be identified as well as their species dependencies (Olesen et al., 2007). Further, it showed that the disappearance of these species could actually alter the entire network due to connectivity loss among modules.

Plant pollinator networks

Nestedness, modularity, robustness, oh my!

Plant-pollinator networks are a special type of mutualistic networks. They are typically represented as bi-partite networks, where plants and pollinators are represented by nodes, while the pollination interactions are links. Although both nested and modular in nature, they are most stable when highly nested and become more nested with increasing links, versus food webs which are most stable when highly modular (Thébault and Fontaine, 2010, **figure 3**). This means that while a specialist pollinator could be removed from the network due to generalist pollinators taking over their niche, if a generalist is removed it could result in a system-wide collapse because they make up the core of the network.

Thanks to generalists being more abundant than specialists in this system, plant-pollinator networks are among the most robust. This means that the number of floral visitors per plant becomes redundant since plants that are visited by a few specialized pollinators are also visited by more generalized ones (Memmott et al., 2004). This asymmetry contributes to the robustness of pollinator networks, which has been shown in predictive models where the last species to suffer extinction are the most generalized (Fortuna and Bascompte, 2006). Another factor contributing to robustness are "hubs": generalists in their own module that connect many different species from neighboring modules through their interactions (Olesen et al., 2007). Interestingly, these hubs tend to be plants, rather than pollinators. In a study of heathland sites in Denmark, plant communities were similar while the insect composition varied greatly, with an aggregation around one or two hub plant species. Identical such patterns were found across sites (Dupont and Olesen, 2009). This means that even when plant communities can differ, the interactions between them and their pollinators follow a general pattern: asymmetrical pollination networks dominated by generalist pollinators.

It's a small world

Pollination networks also have the strongest small-world properties of any networks studied. **Figure 2** (above) actually demonstrates a bipartite graph collected from 22 pollinator networks that has been transposed into two unipartite graphs showing respective plant and animal interactions (Olesen et al., 2006). Both the transformed plant and animal graphs behave similarly, as there is a strong correlation between their path length. However, there was no correlation between clustering coefficients (the probability that neighboring nodes of a given node are themselves also joined by a link) in comparison to the non-transposed network (A). This means that regardless of interaction, the nodes are tightly knit in groups which have a high density of connected links. As these links are not connected at random, pollination networks have strong small-world properties. However, this can also challenge the robustness of network structure, since it shows that each pair of species is quite close. This means a disturbance could quickly affect any other species in the entire network. Memmott et al (2004) performed such a simulation, where the secondary extinction of the plants was measured through the progressive extinction of pollinators involved in the mutualism (Jordano et al. 2006, Memmott et al. 2004, Morris 2003). This study found a relative tolerance to extinction among pollination networks, which differed significantly from trophic webs. A possible factor in this however, could be trophic rewiring, i.e., adaptive reconfiguration of ecological interactions as a response to a disturbance (Staniczeno et al. 2010). In many cases, this can reduce the effects of primary extinctions, when phylogenetically similar species take over where another is species is lacking (Reed-Tsochas, 2010). However, trophic rewiring could also compound extinctions, in cases where an overexploitation of resources exaggerates species loss on food webs (Gilljam et al., 2015).

In general, the small-world properties of pollination networks means that these species are much more compactly linked than species in traditional food webs, because they have a higher link density, a shorter distance between species, and are more clustered (Olesen et al., 2006). However, most of these network properties are scale-dependent, i.e. they are dependent upon network size; a larger network with more modules results from a higher species number. For example, the same study that found pollination networks modular in nature, also found that networks of less than 50 species were not modular at all (Olesen et al., 2007). This presents a potential pitfall when analyzing smaller networks in less biodiverse areas.

Arctic plants and pollinators

A decrease in biological diversity with increasing latitude represents an easily recognized and old pattern in ecology (Willig et al., 2003). In this context, the Arctic emerges as one of the least species rich regions in the world. In this essay, the Arctic ecosystem definition focuses on the High Arctic region (**Figure 5**). As there is a very large similarity for species composition across the region (for example, the Canadian High Arctic and Greenland) (Elberling and Olesen, 1999; Kevan, 1973), this essay will use references from different regions encompassing this area. The high Arctic landscape is characterized by a treeless zone, negative (°C) mean annual air temperature, short snow-free growing season, low atmospheric moisture and precipitation, as well as the existence of permanently frozen subsoil (permafrost) (Barry et al., 1981; Bliss, 1987; Hare, 1968). It is essentially a desert region, with frigid and cold temperatures cycling between 24-hours of daylight in peak summer and complete darkness in winter months. Most life forms in the area have become adapted to harsh conditions. Organisms migrated to the region following the last glacial epoch 8-10,000 years ago, however some species may have survived as refugia present through the glaciation (Alsos et al., 2007; Bennike, 1999; Funder, 1979). Plants here evolved to metabolize and grow in temperatures only slightly above freezing; their growth is determined by low air and soil temperatures, nutrient deficiencies, day-light hours, permafrost, and drought stress at higher elevations (Billings, 1987). Thus, their growth and reproduction are influenced not just by environmental factors, but also by the genetic structure of winter-adapted flora that results in constrained growth and relatively old plants.

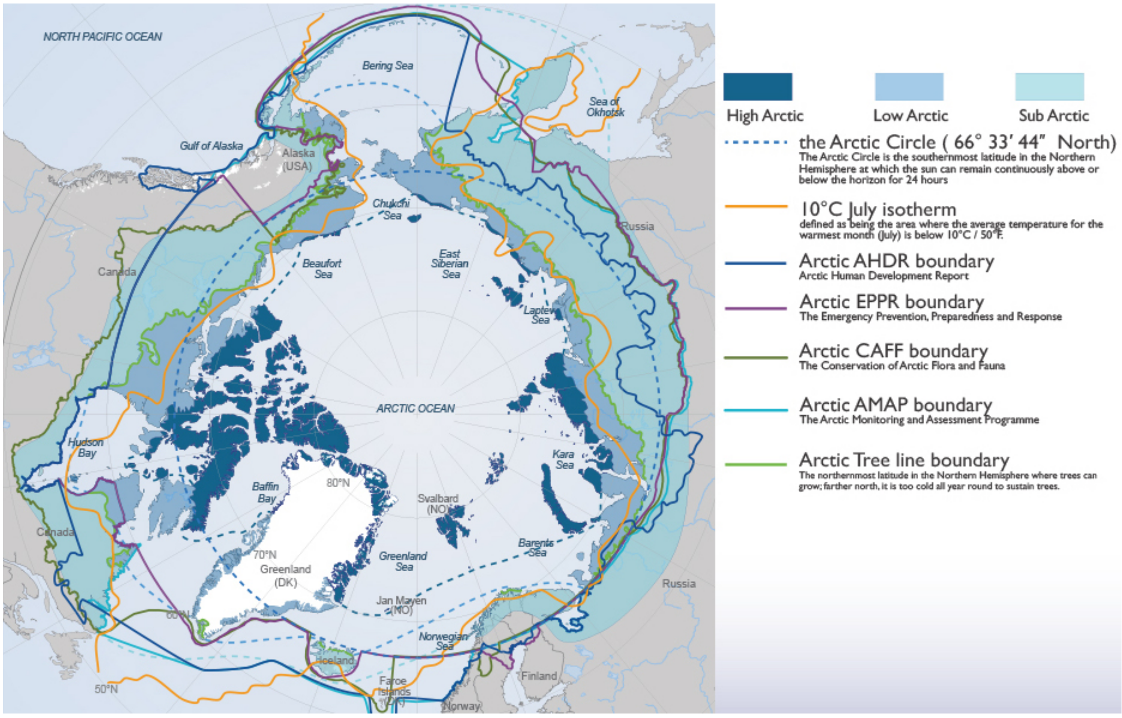


Figure 5: Map of the Arctic region, showing High Arctic, Low Arctic, and Sub Arctic zones. Boundaries are represented by lines; the Arctic tree line can be seen in a light green border**.** *Adapted from Arcticportal.org*

Pollinators here are also adapted to harsher conditions, with seasonal patterns such as temperature and snow melt determining species abundance (Höye et al., 2007; Kankaanpää et al., 2018; Totland, 1994). Muscid flies in the area dominate as pollinators, above all other insects (Elberling and Olesen, 1999; Kevan, 1972; McAlpine, 1965). The Arctic region is often thought of as a simple system where species interactions are easily understood, however recent studies have found great ecological interconnectedness (Callaghan and Johansson, 2009; Walker et al., 2008; Wirta et al., 2016, 2017, 2015).

So then, what happens in these networks?

Arctic biotic interaction networks are complex and largely dominated by arthropods; with their species dynamics influenced by environmental conditions (Schmidt et al., 2017). How these species respond differently to environmental change can decouple existing interactions, with cascading effects across all trophic levels. In the Zackenberg region of Greenland, Elberling and Olesen (1999) found that more than 76 species of insects were associated with pollination of flowering plants through their visits of 31 plant species. Here, plant species seemed to have a random relationship with the pollinators, while insects were more frequently associated with specific plant species, suggesting a highly nested nature of High Arctic plant and pollinator networks.

Olesen et al. (2008), in a study of temporal dynamics, found that new species who entered the network interacted most with well-connected existing species; a process commonly known as “preferential attachment”. This resulted from a higher abundance and longer phenophase (for plants: the timing of when the first individual flowers until the last individual no longer flowers. For insects: the timing of when the first pollinator visits a flower, until the last individual visits a flower) of these existing species. Thus, a heterogenous distribution of species interactions dependent on climatic conditions and temporal dynamics was observed and could be viewed as a defining characteristic of high Arctic biomes (Olesen et al., 2008). Temporal comparisons of pollination networks spanning large latitudinal gradients (Arctic and non-Arctic regions), have also found consistent numbers of pollinators and plants across all sites with time, but with high turnover (cycles of increased taxon additions or losses resulting in a change from the original community) for pollinators and their interactions (Dupont et al., 2009). However, shifts in the network can occur from a turnover in plant-pollinator community composition, which results in increased variation of species roles between plants and pollinating insects over time (Cirtwill et al., 2018).

While plant and pollinator networks are regarded as robust, current studies are signaling threats from climate change. Höye et al (2013) and Schmidt et al. (2016) point to a community-wide phenological clash between pollen transport and plant flowering, suggesting a functional disruption in pollination networks. Findings from this study are an indicator of changes in community functioning due to climate change. In addition, Tiusanen et al. (2016) found that flies in the family Muscidae were the most dominant pollinators of the key plant genus *Dryas* (through their reliability in seed set) despite a diverse pollinator species community visiting the plants. However, this is cause for concern and may show a vulnerability in the network; since the numbers of muscid flies have seen a significant decrease: 80% over the last two decades in some areas (Loboda et al., 2018). This supports the notion that pollinators are potentially at a greater risk of extinction than the plants they interact with (Memmott et al., 2004). Timing in local snow melt may therefore be a key indicator of community-level changes, because phenology affects pollinators through the offset of emerging plants, whose germination can be influenced by snowpack duration (Kankaanpää et al., 2018). These results all suggest that Arctic networks are dynamic and sensitive to change.

How exactly is climate change affecting these networks?

In the Arctic, warming is occurring at double the rate compared to other ecosystems, with potential consequences for many habitats and biomes in areas all around the world (IPCC, 2014, 2013). While the global mean surface temperature has increased by 0.4°C over the past 150 years, Arctic warming has been two to three times that amount (IPCC, 2014). One probable result of the rapid onset of climate change is an interruption of biotic interactions (Parmesan, 2006). Reproduction, seasonal growth and activity patterns, and dispersal of all organisms are changing in response to climate change (Kankaanpää et al., 2020a, 2020b, 2018; Tiusanen et al., 2019, 2016). For example, shifts in plant and herbivore interactions have led to unpredictable patterns of either increased synchrony (match-up of plant emergence and herbivore feedings) where herbivore populations increase, or decreased synchrony that results in a decline of herbivore populations (Tikkanen et al., 2000; Van Asch et al., 2013). This has also affected predator and prey interactions, where herbivores have declined due to phenologically mismatched food sources and subsequently caused predator decline as well (Evans et al., 2013). In addition, flowers may be blooming before pollinators are available in sufficient abundances (Schmidt et al., 2016). Inter-species interactions such as pollination and plant sexual reproduction and dispersal of propagules are essential mechanisms that support biodiversity in many biomes. However, in areas such as Greenland, the majority of flowering plants are insect pollinated and this pollination confined to a brief window of time. Thus, the impact of seasonal variation becomes disproportionately accentuated (Elberling and Olesen, 1999; Klein et al., 2008). There exists a strong domination of pollination services provided by a select few pollinators, and a recently observed decline in these species along with an increase in phenological mismatches between plants exacerbates competition of available resources (Tiusanen, 2018) .

Because visitations of plants by pollinators depend on phenology, climate change can result in a temporal mismatch. If an insect emerges too soon or if the desired plant blooms too early, then the original plant-pollinator interaction will no longer occur (Kharouba et al., 2018; Renner and Zohner, 2018; Visser and Both, 2005). **Figure 6** shows such an example from Morton and Rafferty (2017), where spatial and temporal transplants were used to monitor phenological shifts in plant-pollinator interactions. Using a baseline pre-climate change, they showed different scenarios of species response based on a temporal/phenological shift, a spatial and distributional shift, and both temporal/phenological and spatial/distributional shifts combined. In this example, some shifts are more extreme than others, where both historic and novel interactions are lost (**Figure 6, C**). This illustrates potential differences in the way species respond to disruptions to their original interactions, with possible repercussions to entire ecosystems.

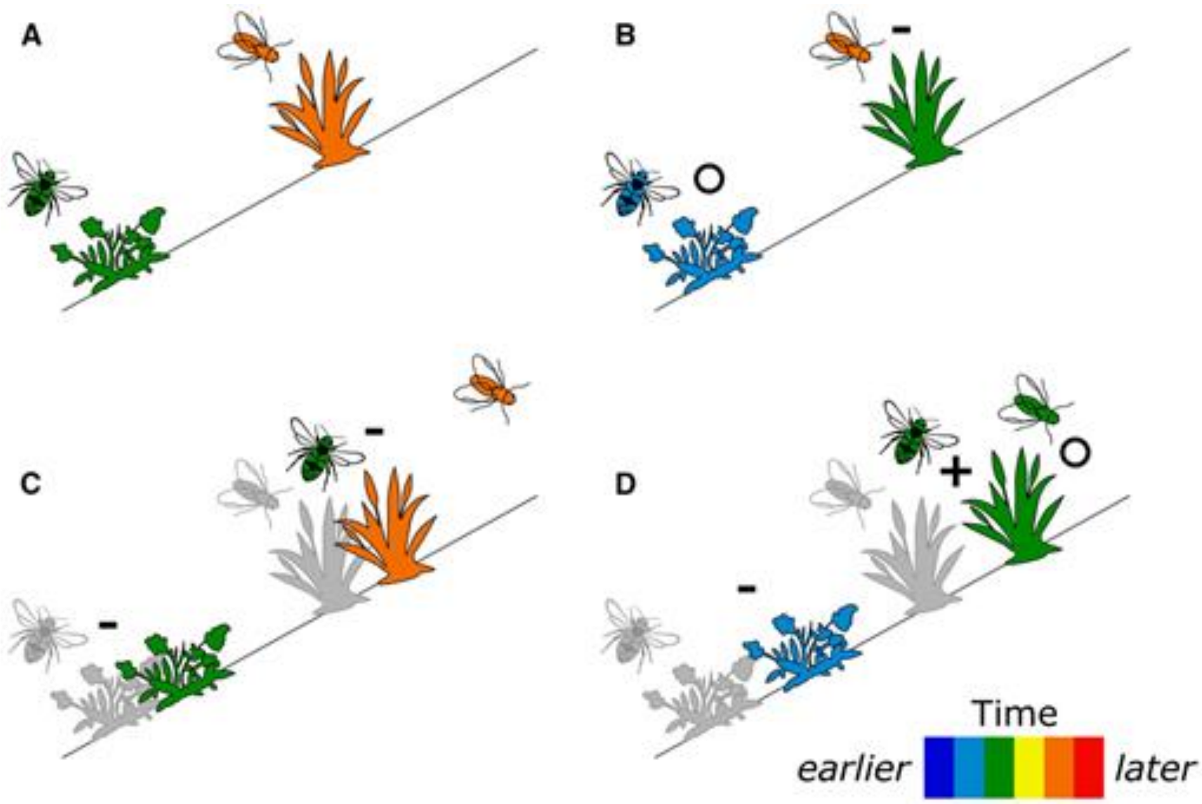


Figure 6: Illustration showing different scenarios of species interaction adaptations. Pre climate change distributions are in grey. (A) Organism positions of populations prior to climate change (historical baseline). (B) temporal/phenological shifts to species. (C) Spatial/distributional shifts to species. (D) Both temporal/phenological and Spatial/distributional shifts to species combined. Each example highlights direction of shifts: (i) historical interactions maintained and represented by O, (ii) historical interactions lost and represented by -, (iii) historical interactions altered by new interactions represented by +. (Morton and Rafferty, 2017)

Currently the Arctic has observed shifts in flowering times by several weeks (Høye et al., 2013), which has the potential to disrupt ecosystem functioning on multiple levels; impacting individual species to interactions between species (Post et al., 2009; Schmidt et al., 2017). While plants are flowering earlier on average, insects are not showing a corresponding change in when they emerge. When combined, this can cause temporal mismatches in terms of plant flowering versus pollen transport services (Schmidt et al., 2016). General simulations of plant-pollinator interactions have suggested that phenological shifts brought on by climate change can affect up to 50% of pollinator species within a network (Memmott et al., 2007).

The loss of a species results in a loss of interactions, which may lead to a loss of functions – a problematic issue in pollination ecology where mutualist partner interactions provide key ecosystem services (Tylianakis et al., 2010). In the Arctic, high-turnover rates in these relationships are expected due to stochasticity in annual temperature and precipitation patterns, where snowmelt and air temperature can offset phenology patterns of plants and insects (Hanssen-Bauer and Førland, 1998; Höye et al., 2013, 2007; Höye and Forchhammer, 2008; Kankaanpää et al., 2018), Cirtwill et al. 2018). Variable phenologies can impact which species co-occur during a given time and which are available to interact in a plant-pollinator network for each given year, thus further offsetting pollinator relationships long-term (Simanonok and Burkle, 2014). Other variables can further exacerbate the problem. For example, changes in the pollinator fauna may come with changes in the pollinators' trait distribution. As pollinator feeding parts may only fit specific plant species (causing "pollinator syndromes") this may cause a community-level functional mismatch (Miller-Struttmann et al., 2015).

Environmental variables also play a part in shifting plant phenologies. Water availability and soil moisture is and will continue to be a major constraint limiting plant growth in the high High Arctic (Klein et al., 2008). With the continuing shift in snowmelt, individual groups of organisms will differ phenologically in the way they adapt, partly due to variation in life history and diet. In one arctic landscape, snow-melt timing at early melting locations has been shown to advance more than at late-melting ones (Kankaanpää et al., 2018). At the same time, many areas are experiencing increased snowfall (Cohen et al. 2012), which makes the prediction of net changes in the timing of snowmelt difficult. Because of altered precipitation regimes, future snow cover under climate change is expected to become more variable in space and time (Wipf and Rixen 2010). In addition, warming could trigger a variety of plant responses. For example, increased temperatures could increase production in seeds by decreasing the maturation time for male and female reproductive structures (Wagner and Mitterhofer 1998), increase pollen tube growth or germination rates (Savithri et al. 1980; Dag et al. 2000; Boavida and McCormick 2007), or decrease the time it takes for fertilized ovules to ripen into seeds (Robinson and Henry, 2018). These factors all add to the unpredictability of anticipating important food sources for emerging pollinators.

Where is the research lacking, what remains?

Over the last decade, Arctic research has seen rapid progress in the general field of ecological networks. Once considered a simple system of species poor interactions (Legagneux et al. 2012), advances in this field have shown that the Arctic is actually full of complex interactions and interconnecting relationship, and highly sensitive to climatic changes such as increased temperatures or shift in precipitation (Schmidt et al., 2017; Wirta et al., 2016, 2015). Recent studies have demonstrated that phenological shifts are offsetting pollinator visitation patterns, as well as potential trait changes in plants. Unpredictable precipitation patterns are leading to increasing or decreasing snow fall, with snow cover (or lack thereof) and raised temperatures creating mismatches for plant and insect emergence for the warm season. This increased insight has also provided an urgency in understanding long-term consequences of Arctic environmental alteration and an exploration of how mutualistic networks will change in time and space.

These rapid changes to the network in the Arctic present a window to climate change and offer an early warning notion for what can be expected in ecosystems on a global scale, if the warming trend continues. However, the low number of studies in this field have severely hindered progress. For example, we are still ignorant with respect to what direction species composition will change in and which factors could shift due to indirect effects among multiple trophic levels. As such, this field could greatly benefit from disentangling the various types of interactions mentioned earlier. In reality, positive and negative interactions can have simultaneous effects on all species involved. This intertwining can make processes difficult to distinguish, as all species are part of the same network at some scale. Thus, an additional step that could shed light on Arctic ecological network interactions would be the joining together of different types of interactions into meta-webs that link various species interactions. For example, indirect effects of how below ground processes may alter nectar composition and pollinator visitations to Arctic plants. Still, conflicts in classification can arise when making generalizations based on positive and or/ negative interactions, such as cases where mutualistic pollinators rob plants of their nectar without transferring pollen (Hale et al., 2020). Such conflicts can be resolved by modeling mechanisms through which organisms interact and allow effects to emerge from the interactions instead of assuming these effects a priori. Thus, more studies focusing on individual species interactions in the Arctic are essential.

However, Virkkala et al., 2019 showed in an extensive review, that the Arctic region is still largely understudied in many topics when compared to other regions. Current studies are also unevenly distributed from a geographic perspective, with more research is needed in areas such as Greenland, the Canadian Arctic, eastern Siberia, and Alaska. Some scientists are citing cost as a reason for why the region remains understudied; with research in Arctic areas costing approximately eight times more than more southern locations (Mallory et al., 2018). Thus, perhaps more stipends and grants can be awarded to researchers to cover the extra transportation and shipping costs for Arctic studies. Numerous studies have shown that most community changes in the Arctic will consist of shifts in species abundances. Nevertheless, there are few studies actually documenting the causes, degree, and consequences of ecological responses to climate change in the Arctic (Post et al., 2009). For example, Arctic insects are severely understudied (Høye, 2020; Høye and Culler, 2018; Høye and Sikes, 2013). However, monitoring Arctic invertebrates directly could allow for an extensive ecosystem-based monitoring program when paired with detail-oriented research projects that target causal patterns such as insect links to herbivory, pollination, nutrient cycling in soils, and even as bird nutrition (Taylor et al., 2020). This would allow for deeper data sets that, when paired with longer time series analysis, could link the traits mentioned earlier with an updated and changing network structure. Thus, different types of interactions could come together through meta-webs and shed light on the complex relationships that are already shifting in the rapidly warming Arctic.

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