Mapping a Species-level Trophic and Non-trophic Multilayer Network of Known Interactions for Boreal Tetrapods of North America

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A thesis submitted in partial fulfillment of the requirements for the degree of

Master of Science

in

Wildlife Ecology and Management

Department of Renewable Resources

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Abstract

Mapping trophic and non-trophic species interactions and mapping ecosystem-wide ecological networks have become important research avenues in network ecology, but until recently these two avenues have been separate endeavors. Now, a framework exists to combine multiple interaction types into 'multilayer networks', which are mathematical graph objects that have distinct layers corresponding to different interaction types. Trophic interactions are feeding interactions that may, or may not, be lethal to one species involved. Non-trophic interactions comprise all of the ecological interactions that are not directly related to feeding, such as habitat provisioning and competition for space. This research describes the creation and analysis of the largest scale trophic and non-trophic ecological network, focusing on the structure and importance of interactions in North America's continental boreal forest. To date, no terrestrial ecosystem-wide network of this kind has been compiled at this scale. To do this, I compiled data of real trophic and non-trophic ecological interactions between species in the boreal forest and created a multiple interaction type (multilayer) ecological network partitioned by interaction type and season. Key characteristics of the boreal forest network are also described, including the varying levels of connectance and modularity in the boreal food web and non-trophic interaction networks. The most central, or topologically important, species were also identified. The dataset contains over 400 species, most of which are only active or present in the summer months, and over 4000 recorded species interactions. The majority of interactions are trophic interactions, likely because the network focuses on tetrapods. Generalist predators, such as the great horned owl (*Bubo virginianus*) were the most connected species. The plants included in the network were involved in many non-trophic interactions such as provisioning of nest materials for tetrapod species. Data on non-trophic interactions in the winter months were scarce, especially for negative non-trophic interactions. This was likely due to both the types of non-trophic interactions considered for this research, a paucity of winter ecological research on non-trophic interactions, and a reduction in plant-related interactions in winter months. The connectance, level of interconnection within a network, and modularity, a measure of how well a network can be divided into clusters, of the boreal forest multilayer network were examined. The network was found to have low connectance and relatively high modularity, which are both indicative of ecological stability. The species and interactions of the boreal forest will vary with time and disturbance and this dataset could be a future reference point against which observations of qualitative network structure can be compared, which would be especially interesting for the winter network that may change disproportionately due to climate change. This network can also be used to identify important boreal species whose interactions may be of management utility or concern.

Acknowledgements

I would like to thank the many people who shared their time, energy, and experience with me during the long journey towards finishing my thesis. Firstly, I have to thank my supervisor Carol Frost for her endless patience and enthusiasm. Without your support and expertise, I may have never made it to the point where I am today. Thank you also for listening and engaging with my many ideas for this project, some of which were definitely better than others. Thank you also for being an incredible mentor and role model to me and the rest of the Frost Lab group. I know that we are all better for having been part of this lab group and community. Thank you also to John Acorn, who along with the rest of the Frost Lab group, made me feel very welcome when I first moved to Edmonton. To John, I also want to thank you for providing me with crucial perspective and support throughout this project – your guidance has been truly invaluable. I would also like to thank all of the members of the Frost Lab group for their engagement and support at lab meetings and coffee breaks.

Finally, I would like to thank my friends and family who have been nothing but encouraging especially when I needed it most. Specifically, I would like to thank my parents and my closest friend Taylor Brock-Fisher. Thank you to my parents, Anna and Joe, for letting me move back home after I had to leave Edmonton at a moment’s notice because of the COVID-19 pandemic and for always being optimistic about my thesis pursuits. Thank you, Taylor, for never giving up on me and thank you also for all the time you made for me when I needed help with R or when I just wanted to talk through some part of my research.

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Introduction

Fundamentally, ecology seeks to understand the interactions between species and the world they inhabit. Until recently the focus on interspecies interactions in networks has been limited primarily to trophic interactions, which involve the feeding of one species on another, while non-trophic interactions have been largely overlooked. This focus on feeding includes predator-prey cycles such as the lynx and the hare in the boreal forest of Canada (Krebs et al. 2001) or more complex food webs. Despite this long-held focus, an ecosystem cannot be fully described, or understood, through trophic interactions alone, as species interact with each other in many ways beyond the classic trophic interactions of predator-prey, host-parasite, and plant-pollinator systems. For example, ecosystem engineers interact with other species through non-trophic interactions when they create habitat for other species and can affect the abundance and distributions of the species who benefit from their activity (Bartel, Haddad, and Wright 2010; Barbosa, Fernandes, and Morris 2019; Kämpfer and Fartmann 2019; van der Hoek et al. 2020; Kucheravy, Roth, and Markham 2021). Recent research also suggests that non-trophic and indirect ecological interactions are important co-drivers of detectable community dynamics that trophic interactions alone cannot explain (Kawatsu et al. 2021). However, data about the nature, abundance, distribution, and strength of organismal interactions in real ecosystems is lacking, and this is especially true for non-trophic interactions. Efforts must be made to address this so-called 'Eltonian shortfall' (Peterson et al. 2011) to increase our understanding of biodiversity and ecological systems (Hortal et al. 2015).

Non-trophic interactions have been defined as "a direct non-feeding effect of a species on another" (Kéfi et al. 2012) and alternatively as being "different from the trophic, or "who-eats-whom, interactions of food webs" (Ellison 2019). They are a diverse group, often connected by little other than the absence of feeding. For example, both seed dispersal via adhesion and competition for space could be classified as non-trophic interactions. Additionally, sometimes feeding interactions such as parasitism will be classified as non-trophic instead of trophic (Tiede et al. 2016).

To help make sense of this loosely connected group, non-trophic interactions are often classified by the sign of their effect on each participating species. Under this framework, there are three effect signs possible for each species: positive (+), neutral (0), and negative (-). Combining these effects into pairwise interactions gives six possible interaction types. These are mutualism (+/+), competition (-/-), antagonism (+/-), commensalism (+/0), amensalism (0/-), and neutralism (0/0). All of these interactions, with the exception of neutralism, have the potential to affect both survival and reproduction. This framework may also be applied to trophic interactions where predator-prey and host-parasite interactions are antagonistic interactions, while successful pollination events are mutualistic interactions. As with trophic interactions, non-trophic interactions may vary by strength and frequency with some being more important to the survival of a species than others. Non-trophic interactions may also be indirect, meaning that the interaction is mediated through an intermediary species or abiotic factor such as substrate availability (Kéfi et al. 2012).

Non-trophic interactions are harder to observe than trophic interactions, both directly and indirectly, but their importance should not be overlooked (Bartholomew, Diaz, and Cicchetti 2000; Devereux et al. 2008; Dutra et al. 2011). Non-trophic interactions between species can affect ecosystem and community structure and function, sometimes in counterintuitive ways (Goudard and Loreau 2008). For example, predators have an obvious role in trophic interaction networks, but in some ecosystems their effects are mediated more through non-trophic interactions than trophic ones. This is the case with predatory flatworms in soil whose primary effect on ecosystem function is the acceleration of decomposition by improving habitat availability, rather than their lesser effects of predation on decomposers (Majdi et al. 2014). Gross (2008) found that positive interactions between resource competitors, whose relationships are dominated by strong negative interactions, can increase species richness by making stable coexistence between competitors more common. While efforts have been made to record, categorize, and understand non-trophic interactions in ecological networks (Arditi, Michalski, and Hirzel 2005; Vasas and Jordán 2006; Goudard and Loreau 2008; Majdi et al. 2014; Hammill et al. 2015; Kéfi et al. 2015; Sander, Wooton, and Stefano 2016; Borst et al. 2018; Miele et al. 2019; Richter et al. 2019; Terry, Morris, and Bonsai 2019), much of this work focuses on small or theoretical networks. The difficulty in observing non-trophic interactions has left room for uncertainty regarding the importance, abundance, and diversity of non-trophic interactions in complex ecological systems that research has only recently begun to address with large, real-world ecological networks (Kéfi et al. 2012; Barner et al. 2018).

Few large-scale networks have sought to describe both trophic and non-trophic interactions, with the main exception being a well-resolved trophic and non-trophic multilayer network of an intertidal zone on the Chilean coast described by Kéfi et al. (2015). This work can add complexity and realism to our understanding of ecological systems, as well as answer different questions about community structure and dynamics (Pilosof et al. 2017) such as whether the conclusions of models of community dynamics change substantially when non-trophic interactions are included. An ambitious approach to network creation, this work addresses several of the most promising avenues for network ecology research, such as the construction of multilayer and individual-based networks for a whole ecosystem (Ings et al.

2009). In ecology, multilayer networks are those that map more than one interaction type, with each interaction type forming a distinct layer in the network (Pilosof et al. 2017). The focus of this research is to map the trophic and non-trophic network interactions of the boreal forest ecological network and to examine how the topology of the network layers vary.

Network ecology uses mathematical graphs to represent ecological communities. Graphs contain nodes that are connected by edges, which represent species and interactions between them for the purpose of this paper. The edges, or interactions, can be assigned a numeric weight (interaction strength) in quantified networks, but the network presented here is qualitative. This means that no interaction strength is assigned to the edges. These graphs can be analysed with a wide variety of metrics, but the analysis of the ecological network layers in this study comprises network connectance, modularity, degree distribution, and species centrality. The degree of a node is the sum of edges connected to the node. In a food web, the degree of a plant species would be the number of animal species that eat it while the degree of an herbivore would be the sum of its predator and prey species. The distribution of degree within ecological networks is thought to follow a power law distribution (Williams 2011, Delmas et al. 2019). A power law distribution is taken to mean that the network is structured by preferential attachment (Delmas et al. 2019), where species with a high number of interactions accumulate more interactions than species with a low number (simply, ‘the rich get richer’). Any deviation from this pattern suggests a different attachment mechanism that should be investigated for ecological meaning (Delmas et al. 2019).

There are many different metrics for species centrality, but the goal of all of them is to rank species by their level of connectedness (often referred to as their importance) in a network (Rodrigues 2019). Central nodes may have the highest degree or may be most commonly passed through on the path between any two given species, for example. Connectance describes the complexity of the network as the proportion of realised interactions of all possible interactions (Bersier, Banašek-Richter, and Cattin 2002). Networks with higher connectance are more complex and have been associated with reduced secondary species extinction following resource losses (Dunne, Williams, and Martinez 2002). Modularity describes how well a network can be divided into clusters of nodes with fewer connections to other nodes outside of their own cluster (Delmas et al. 2019). Modularity is an important ecological network characteristic because modules that are connected by few edges to the rest of the network risk isolation if connecting edges or nodes are lost, which could be a significant concern for nutrient flow clusters of species. Modularity is also thought to be able to quarantine perturbations and prevent them from spreading rapidly throughout the rest of the network. Additionally, increasing modularity has been found to theoretically stabilize trophic networks and to destabilize mutualistic networks (Thébault and Fontaine 2010). Comparing values of these descriptive metrics for networks of different interaction types can illuminate any differences in organization related to interaction type within this ecosystem.

It is critical to gain a more holistic understanding of ecological interactions, particularly in northern ecosystems, because as the northern realm begins to show evidence of rapid environmental change, northern ecological communities are expected to follow suit (Vincent et al. 2011). Additional threats from development, natural resource extraction, and industrial disturbance pose significant threat to northern ecosystems such as Canada's boreal forest (Wells 2011). The exact nature and extent of these changes are as yet unknown, but they are projected to affect species and community distributions, ecosystem structure and function, and biodiversity (Vincent et al. 2011; IPCC 2019). The ecological outcomes of these environmental changes and other disturbances are difficult to predict because of uncertainty regarding the changes themselves and lack of holistic understanding of ecosystems. This is the case in Canada where recent "ecological forestry" practices are being developed based on a continuously improved understanding of the boreal forest and its ecological complexity (Nocentini et al. 2021), but funding and disciplinary restraints have inhibited the creation of published ecological networks in the boreal forest that could add to our understanding and management of this highly complex system (Burton 2013).

In the context of this important gap, I have created the most complete database of trophic and non-trophic interactions for the tetrapods (herpetofauna, birds, and mammals) of North America’s boreal forest region. To date there has only been one attempt to catalogue interactions at a continental scale (Maiorano et al. 2020), but it has not included non-trophic interactions. The lack of large-scale ecological network data makes it difficult to develop theory within network ecology because hypotheses can only be tested at smaller scales. This large scale is relevant in natural resource policy. In Canada, the location of most of the study area, forest management is attempted at a landscape scale and is influenced by both provincial and federal acts and policies, the creation of which can benefit from a better understanding of ecosystems at large scales. The creation of multilayer networks of large regional scale has also been previously identified as an important avenue of network research on the path to better understanding not only the magnitude, but the configuration of complex ecosystems (Dunne 2006; Ings et al. 2009). I used this database to produce a seasonally-partitioned qualitative multilayer ecological network of the boreal forest region, which provides much needed ecosystem-wide network data for the limited pool of data on the distribution and relative abundance of trophic and non-trophic interactions amongst terrestrial species.

Methods

Species and interaction scope

All extant tetrapod species (mammals, reptiles, amphibians, and birds) that regularly live, breed, or migrate in some portion of the North American boreal forest were included in this dataset. Although much of the non-trophic interaction literature focuses on plants, they were not included at the species-level in this work because of research constraints. This may result in a network with a lower proportion of non-trophic interactions to trophic interactions than would result from better resolution of plant species. Wild non-native species known to occur in self-sustaining populations in the boreal forest (Langor et al. 2014) were included in the database, but agricultural and companion animals were not unless they exist in feral, self-sustaining populations such as feral horses (Leverkus et al. 2018). Not all are woodland species, as the boreal forest region encompasses wetlands, urban areas, meadows, and some agricultural matrix. Species inhabiting all of these habitat types were included if they existed within the geographical boreal forest region of North America. The forested area is subject to natural and anthropogenic disturbances and so it contains a mix of seral stages, which may attract different animal species. The boreal forest region is defined here as the nearly 600 million hectares of forest-dominated area that span from Newfoundland and Labrador to Alaska in continental North America's boreal zone (Brandt et al. 2013). Given the wide scope of possible non-trophic interactions and varying degrees of ecological importance, the non-trophic interaction search focused primarily on interactions that affected nesting/denning, feeding, and access to territory, because these non-trophic interactions can affect species distributions and individual survival in an obvious way. All feeding interactions were considered and recorded.

Data sources

Trophic and non-trophic interaction data came from a variety of sources. These were primarily reference texts such as edited books and taxonomic guides as well as journal articles. Reference texts were used to determine the number and life history of the species in and around the boreal forest, while journal articles were used to provide finer resolution detail to species interactions. At least one reference for each species classifies it as living in or around the North American boreal forest. The primary reference books for boreal birds were Boreal Birds of North America (Wells 2011) and the American Museum of Natural History Birds of North America (Hess and Bird 2016). The primary reference books used for the herpetofauna were The Amphibians and Reptiles of Alberta (Russell et al. 2000), Amphibians & Reptiles of British Columbia (Matsuda, Green, and Gregory 2006), and The ROM Field Guide to Amphibians and Reptiles of Ontario (MacCulloch 2002). General boreal forest reference books were also examined, such as Ecosystem Dynamics of the Boreal Forest (Krebs, Boutin, and Boonstra 2001) and The Boreal Ecosystem (Larsen 1980) as well as reference books from neighbouring and overlapping ecosystems including Mammal Community Dynamics (Zabel and Anthony 2009), Mammals of Colorado (Fitzgerald, Meaney, and Armstrong 1995), and Churchill Hudson Bay: A Guide to Natural and Cultural Heritage (Brandson 2012). Mammal species present in the boreal forest and their natural history were discussed widely in the general boreal forest reference books, but Mammals of Canada (Eder 2011) and The Mammals of Canada (Banfield 1974) were also consulted. In addition to the books consulted, over 100 journal articles were also referenced in the database. Only recorded ecological interactions were included in the database.

Data collection and network assembly

Trophic and non-trophic interactions were extracted from the literature and directly encoded in a standardized way in MS Excel spreadsheets. Each boreal species was recorded in a master species list along with its taxonomic class, common name, scientific name, reference(s) indicating that they are a boreal species. The seasonal behaviour of the species was also recorded here, indicating whether the species is a seasonal, migratory, or year-round resident. Interactions between species were recorded in spreadsheets separated by interaction type and the season during which the interaction takes place. Both species' scientific and common names as well as relevant references were recorded for each species interaction.

The interaction information in these spreadsheets could then be extracted to create adjacency matrices, in which species in column *j* have an effect on the species in row *i*. Within a matrix, each cell contained either a '0' indicating no interaction or a '1' indicating an effect of species *j* on *i*, with the interaction effect varying depending on what matrix was being encoded. This is a unidirectional interaction, meaning that the corresponding effect of species *i* on *j* were encoded in a different matrix (or a different cell of the same matrix if the interaction was mutualistic or if the species eat each other, for example in different life stages). A total of eight matrices were created which correspond to four network layers for each season (summer and winter). Together, these matrices can be imagined as a multilayer network, which is an ecological network that can be thought of as containing multiple layers corresponding to different kinds of ecological interactions. In this case, a multilayer network consists of three layers: a food web (FW) layer, positive non-trophic (PNT) interaction layer, and a negative non-trophic (NNT) interaction layer. These layers were analysed individually as well as collectively as in the inclusive-network (IN) layer. Competitive (-/-) were indirectly encoded through shared prey species, or other interaction partners, and so were usually not encoded as their own interaction type.

Interactions were recorded to the species level when possible. When a lower level of resolution was the best available in reference texts, such as only a genus or species group (e.g., passerine birds), this was recorded and then research articles were used to improve resolution when possible. When this was not possible, a placeholder such as ‘undefined bird species’ or ‘small mammals’ was used for data entry so that these entries could be returned to and be replaced with species-level data with future research or with metaweb methods, which document potential interactions instead of observed interactions (see Maiorano et al. 2020). Placeholders and their interactions were removed from the network prior to analysis, but non-tetrapod species groupings were retained. Non-tetrapod species were classified into rough groupings summarized in Table 1, similar to the method used in another large-scale tetrapod-focused network study (Maiorano et al. 2020). These rough groups were counted as species within the network that could be both the ‘giver’ or the ‘receiver’ of an interaction, as any other species in the network. These species groupings are distinct from the placeholders used in data collection as they are meant to be analysed as a coarse group, rather than being entries to return to in future work.

Network analysis

Several topological metrics were calculated for the networks (seasonal FW, PNT, NNT, and IN), including degree distribution, connectance, and modularity. Degree distribution is one of the main comparative metrics for network topology and it is the proportion of nodes with a given number of edges, ranging from one, up to the maximum number of edges a node could have (Dunne, Williams, and Martinez 2002). The distributions were fit with the fit_power_law function from igraph in R (Csardi and Nepusz 2006). In this case, the maximum number of edges could be equal to the total number of species minus one. A skewed degree distribution can indicate the relative proportion of generalist and specialist species (Williams 2011). Connectance is a measure of network complexity and the proportion of realised interactions of all possible interactions (Bersier, Banašek-Richter, and Cattin 2002). Connectance was calculated using the edge_density function in igraph (Csardi and Nepusz 2006). Modularity is a measure of how much a network can be divided into modules, which are clusters of nodes with few connections to other nodes outside of their own cluster (Delmas et al. 2019). Modularity was calculated using the cluster_walktrap and modularity functions in igraph (Csardi and Nepusz 2006).

Null model analysis was also performed to assess whether the network modularity differed from that expected by random chance. Specifically, this analysis asked if the same degree of modularity would occur if the same number of interactions between the species in these networks were randomly generated. To conduct the null model analysis, 1000 random networks with the same number of nodes (species) and edges (species interactions) with random edge distribution were generated with igraph (Csardi and Nepusz 2006). The null model is based on an Erdős-Rényi random graph (Erdős and Rényi 1959) because no model exists yet for generating random ecosystem models with multiple interaction types, unlike null food webs which can be generated using a niche model, for example (Williams and Martinez 2000). Modularity was calculated for the null networks and compared with the empirical network metrics using a z-test to assess if observed network structure significantly varied from the simulated null networks (Dormann et al. 2009). All metrics were calculated and null model analysis was performed using R package igraph (Csardi and Nepusz 2006) or base R (R Core Team 2013) functions.

Results

Data summary

This database comprises 412 species that live, breed, or migrate through at least part of the boreal region of North America (see Appendix for species list). This number represents real species and does not include the species groupings from Table 1. Almost 80 taxonomic families are represented, but the majority (approximately three fourths) of the species are birds. Of these 41 species, the majority are only present and active in the boreal region in the summer (Figure 1). Of the 133 year-round residents, almost 40 of them are inactive during the winter due to hibernation or similar processes.

The total number of interactions recorded was 4041. The majority of these interactions were trophic interactions (Figure 1). Of the roughly 1908 non-trophic interactions recorded, the vast majority could be described as commensal (0/+) or antagonistic (+/-) (Figure 2). In addition to there being more species in the summer season, there was also more activity in terms of ecological interactions (Figure 3). The winter non-trophic layers were notably sparse compared to all other layers (Figure 3).

Degree distribution and degree centrality

The degree distribution is the probability distribution of the number of connections between nodes. The summer and positive non-trophic network winter layers display a power law distribution for the summer (Figure 4). The other winter network layers appear to follow a Poisson distribution (except for the negative non-trophic layer, which is too sparse to be analysed) (Figure 4). The majority of the networks display a power law distribution for the summer (Figure 4) and winter seasons ($p < 0.05$), except for the winter negative non-trophic interactions network layer which was too sparse to be tested.

The majority of species have a low degree, which means that they interact with relatively few other species. Taking the food web as an example, most species eat or are eaten by 10 or fewer other species while a few grouped prey items (e.g. terrestrial invertebrates) are eaten by up to 300 species (Figure 4).

The species with the highest degree in the FW and IN layers were almost identical for both the winter and summer layers. All of the grouped species were highly central, along with super generalist carnivores and important prey species (e.g. snowshoe hare (*Lepus americanus*)). In both the PNT and NNT, species were primarily avian species in the summer months and mammals in the winter months.

Connectance

Connectance is the proportion of possible interactions that are present in the network. Connectance values were generally low, with the highest connectance found in the PNT winter network and the lowest in the NNT summer network (Table 2). Connectance was higher in the winter layers than in the summer layers.

Modularity

Network modularity is a measure of how well a network can be divided into smaller groupings, or modules. Modularity ranged from 0.17 in the winter NNT layer to 0.48 in the winter PNT layer. Other modularity values were mostly around 0.3. The null model analysis showed that the modularity differed significantly from that expected by random chance ($p<0.05$)

for all summer layers, indicating that these network layers have non-random structure. The modularity of the null networks was higher than observed for the non-trophic layers (PNT and NNT) and lower than observed in the food web (FW) and inclusive layers (IN). In the winter layers, modularity differed significantly from the random expectation for the food web layer (FW) only ($p<0.05$) and, like with the summer layer, the null model produced a lower modularity than observed. All of the other network layers (IN, PNT, and NNT) were not significantly different than the null expectation, however this can likely be explained by the small size of the non-trophic networks (PNT and NNT) networks. Modularity and connectance showed no indication of covariance (-0.0031) and were not correlated ($p > 0.1$).

Discussion

Seasonal interaction differences

Over half of the species present in the boreal forest are not present in the boreal winter ecological network layers because of migration and dormancy. This is a striking reduction in biodiversity that results in a reduction in activity, or the number of interactions taking place, within the ecosystem. If the network were better resolved for plants and invertebrates, this difference in interaction activity would likely be even more dramatic because many of these species would participate in only summer interactions layers. The types of interactions considered in this research may have reduced the number of winter non-trophic interactions as well. However, much of the ecological research on negative non-trophic interactions (such as allelopathy or interference competition, for example) has focused on plants rather than tetrapods.

The winter non-trophic interactions layers are notably sparse compared to their summer counterparts, even when taking into account the reduction of total active species. This is likely because a large proportion of both positive and negative non-trophic interactions in this network are related to nesting, which is a predominantly summertime activity. The inclusion of more kinds of non-trophic interactions could alter this dynamic, but it is likely that summer ecological networks would have a larger number of non-trophic ecological interactions than winter ecological networks even when accounting for changes in number of species. This is because there are more non-trophic interactions possible in summer months than winter months for regions like the boreal forest that experience harsh winters. Most non-trophic interactions that take place in the winter months, such as refuge provisioning, can also take place in the summer, whereas many non-trophic interactions like pollination can only take place in the summer. However, winter ecology has been traditionally understudied and as this begins to change (Studd et al. 2021) it may become apparent that there are more non-trophic interactions of importance taking place during these months than previously known.

Changing species importance

The similarity in central species between the IN and FW layers indicates the importance of the FW layer as a large component of the IN layer. Plants and invertebrate groups were the most central food items. Terrestrial invertebrates were the most central, but this was not reflected in the literature while I was compiling the database. Information on the identity of species was often lacking, which necessitated the very coarse groupings used in this study. However, the inclusion of invertebrate functional groups in this database could provide extremely important information for conservation and natural resource management in the boreal forest. This is because invertebrates are a food source for a large proportion of tetrapod species in this network, but most species specialize on a limited range of invertebrates. Better resolution of invertebrates would be useful for managers concerned with increasing food availability for the many insectivorous boreal species. Improved resolution of terrestrial invertebrates would also facilitate better inclusion and resolution of non-trophic invertebrate interactions in the network, such as pollination.

Aside from the grouped species, the most central nodes in the FW and IN layers were extreme generalist predators like the great-horned owl (*Bubo virginianus*) as well as small mammals like the snowshoe hare (*Lepus americanus*). Generalist species have high degree centrality because they interact with many other species; however, other forms of centrality can also be used to find keystone and connector species (Gonzalez, Dalsgaard, and Olesen 2010). Highly central species often have special conservation and management significance because of their importance in the structural controllability of networks from their high potential influence on other species (Cagua, Wootton, and Stouffer 2019). A network with high structural controllability is one that has a topology, or structure, that is arranged in such a way that inputs to the system are likely to have the desired effects. As species with high centrality can have an influence on many other species, they increase the structural controllability of a network and their populations can be manipulated to promote desired outcomes (Cagua, Wootton, and Stouffer 2019).

The centrality of vegetation in the PNT layers highlights the importance of plants in providing physical structure and material in forested ecosystems. This is similar to a finding of Kéfi et al. (2015), which demonstrated that basal species participated in a relatively large number of positive non-trophic interactions. Most of these non-trophic interactions were the provisioning of habitat or refuge. Further resolution of these plant groups, especially the ‘Deciduous trees’ and ‘Coniferous trees’ groups, would reveal the foundation species of the boreal forest. These species interact with others primarily through non-trophic interactions and are prevalent basal species in an ecosystem (Ellison 2019). In forests, foundation species tend to be trees and in the boreal forest, coniferous trees are the most likely candidate because of their high abundance. The most central animal species were those t involved in positive non-trophic interactions, and all facilitate others through unintentional food provisioning. The other exceptions here are several large woodpecker species such as the pileated woodpecker (*Dryocopus pileatus*) and the northern flicker (*Colaptes auratus*), which are central species because of their important role in creating nest cavities in tree trunks. The most central species in the NNT layers all compete for space, whether it be nesting sites in the summer layers or territory exclusion in the winter layers.

The dataset compiled in this study relies on natural history information as well as recently published literature and as such, it describes the boreal forest as it is now. However, the species and their interactions may change in the future and this dataset could be used as a reference point against which observations of qualitative network structure can be compared to see if and how species centrality changes. This would be especially interesting in the winter network layers because cold-climate winters are changing under climate change in ways that are often disproportionate to warmer months (Studd et al. 2021).

Multilayer network topology

Low connectance values are common in empirical food webs, but the connectances of the boreal food web layers fall below the typical empirical range of 0.05–0.3 (Poisot and Gravel 2014). Similarly, the boreal forest ecological network also has low connectance (Table 2) when compared to the only other large-scale entire ecosystem multilayer network. The Chilean coast ecological network layers described by Kéfi et al. (2015) had a connectance 5-14 times higher than the boreal forest network layers, depending on the season and layer considered. This means that species are connected by fewer interaction links in the boreal network. This may be due to differences in the scales at which empirical food webs are generally observed, with it requiring less research effort to capture all interactions at a smaller spatial scale. It is also likely due to the fact that the species of the basal trophic level are not considered at the species level in this particular network.

The large difference in connectance values may not be due to methodological differences alone, however. It is also possible that there are differences in community and interaction structure between aquatic and terrestrial ecosystems that lead to sparser networks on land. It is difficult to speculate on because of a dearth of ecological networks at a similar scale. Issues of ecological scale are not unique to network ecology (Chave 2013), but network ecology is younger than many other ecological subfields. Because of this, there might be less variety in spatial scale for the existent data. More large-scale ecological networks must be created, for both trophic and non-trophic interactions, to narrow down the effects of spatial scale on network properties.

Connectance has been linked to an ecosystem's sensitivity to perturbation (Delmas et al. 2019) such as its robustness to invasion (Romanuk et al. 2017) and extinctions (Gilbert 2009; Vieira and Almeida-Neto 2015). This is because perturbations in networks with higher connectance offer more paths through which a perturbation can spread. In all network layers, the winter networks had higher connectance (Table 2). This indicates that the winter networks may be more sensitive to ecological and environmental perturbations than the summer networks.

In contrast with the connectance findings, the boreal forest is more modular than the Chilean coast network (Kéfi et al. 2015). Highly modular networks have 'clumps', or modules, of species that interact with each other more than with species outside of their module. The boreal forest region comprises multiple ecosite types with habitats suitable for deep-forest,

forest-edge, and wetland species, and it is possible that the modularity in the boreal forest is in some part due to this habitat mosaic. Further investigation such as partitioning the boreal forest network into finer spatial or ecological units could help shed light on whether this finding is a property of the boreal forest or a result of differences in scale. Interestingly, the Chilean network had a modularity approximately 10 times higher in its food web layer than in the inclusive network, while the modularity of the boreal forest network layers differed by much less. The boreal forest multilayer network cannot be formally compared with the Chilean coast multilayer network because of differences in spatial scale, species resolution, and interaction inclusion criteria, but as these are the only large-scale networks of their kind, it is interesting to informally see how these networks differ in topology.

Ecological networks that have a modular structure have been associated with ecological stability. Specifically, modular networks are able to limit the spread of perturbations by trapping a perturbation within a module so that it does not spread to the rest of the network as easily (Stouffer and Bascompte 2011). This, taken with the increased stability conferred by low connectance, would indicate that the boreal network is fairly robust and resistant to perturbations. However, these theoretical studies are typically performed with single-interaction type networks rather than diverse interaction networks such as the one studied here. Quantification of non-trophic interactions and more information on their relative abundance and distribution in real ecosystems would improve theoretical models and likely make their conclusions more robust.

Connectance is known to covary with other network metrics including modularity, with which it has an inverse relationship in bipartite mutualistic networks (Delmas et al. 2019). Despite this, there is no indication of a relationship between modularity and connectance in the boreal forest network layers. This may be due to differences in interaction type or to sparsity of winter interaction data in the dataset compiled in this study. It is impossible to say whether there is a trend of covariance between connectance and modularity in multiple interaction networks without more published examples of inclusive networks, such as the one described by this research.

Conclusions

A large amount of work remains in the collection, quantification, and classification of non-trophic interactions in real ecosystems, but this is necessary to better understand these complex systems. This research represents the first attempt to organize existing knowledge of non-trophic interactions in the boreal forest and while it is not an exhaustive collection, it is a start. The topology of the boreal network is undeniably affected by the grouping of non-tetrapod species in this network. This database and network should be further resolved with particular emphasis on plants and invertebrates, as these species groups proved to be central 'species' that are worth better understanding. Additionally, more ecological networks, such as the boreal and Chilean multilayer networks, must be collected to build understanding of the significance of non-trophic interactions within the field of ecology and further holistic understanding of real ecosystems. This multilayer network of North America's boreal forest is the largest terrestrial ecosystem-wide network of its kind. Analysis of this network has revealed intriguing patterns about the distribution of diverse ecological interactions across the boreal summer and winter that can contribute to our understanding of its ecological stability and the importance of different species within this system.

Tables

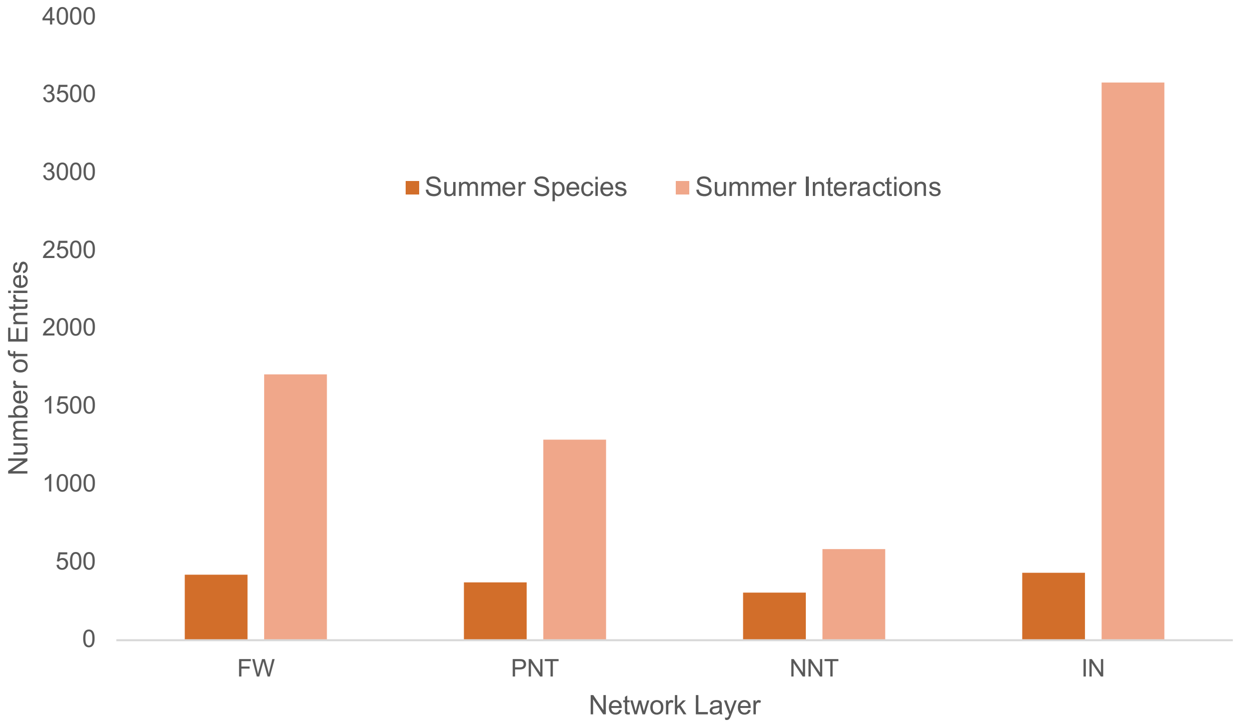
Table 1. Coarse species groupings and their description for the boreal forest multilayer network.

Coarse Group Name	**Boreal Forest Region Species Included**
Deciduous Trees	Deciduous trees
Coniferous Trees	Coniferous trees
Shrubs	Coniferous and deciduous shrubs
Forbs	Non-graminoid herbaceous flowering plants
Graminoids	Grasses, sedges, and rushes
Lichens	Lichens
Other ground vegetation	Mostly mosses, horsetails, and ferns, but any ground level vegetation that does not fit into any of the other categories
Aquatic vegetation	Algae, emergent, and submerged freshwater vegetation
Terrestrial invertebrates	All terrestrial invertebrates
Aquatic insects	Aquatic insects and aquatic larval forms of terrestrial insects
Other aquatic invertebrates	All non-insect aquatic invertebrates, mostly phylum Mollusca
Fish	All fish species

Table 2. Connectance and modularity for multilayer network layers of the boreal forest region ecological network.

Network Layer	**Season**	**Connectance**	**Modularity**
Food web	Summer	0.0093	0.34
(FW)	Winter	0.028	0.36
Positive non-trophic	Summer	0.0073	0.28
(PNT)	Winter	0.044	0.48
Negative non-trophic	Summer	0.0061	0.37
(NNT)	Winter	0.19	0.17
Inclusive	Summer	0.013	0.26
(IN)	Winter	0.027	0.30

Figures


4000
3500
3000
2500
2000
1500
1000
500
0
Number of Entries
Summer Species
Summer Interactions
FW
PNT
NNT
IN
Network Layer

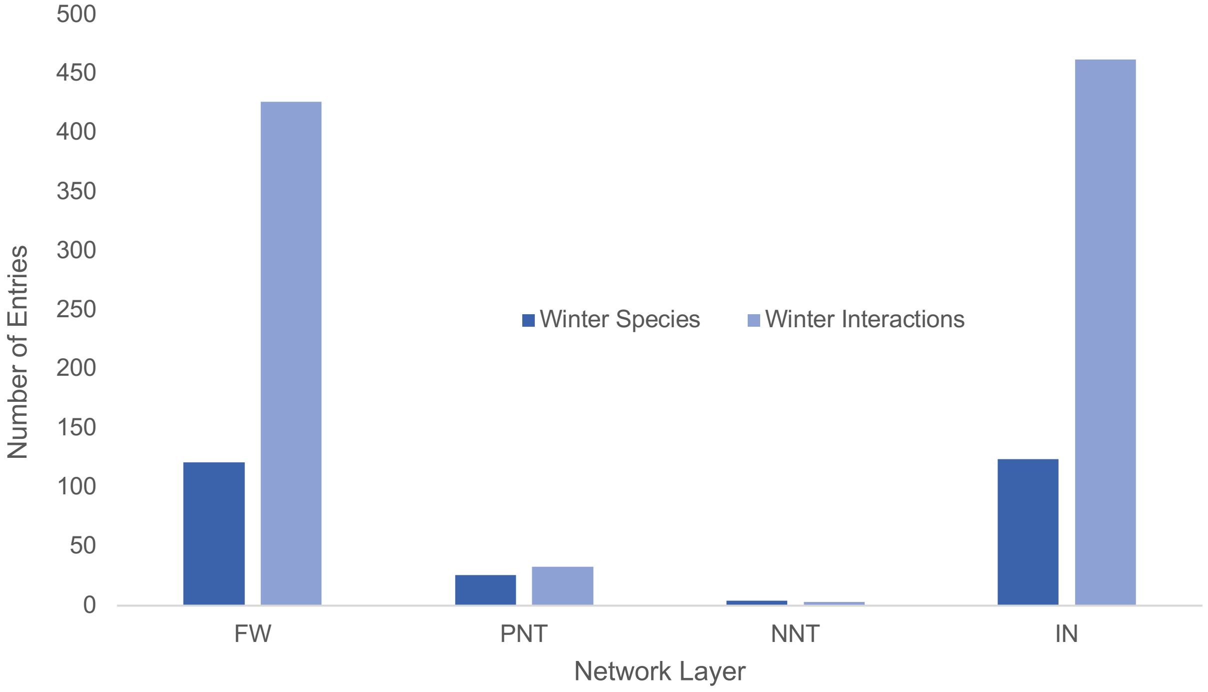

500
450
400
350
300
250
200
150
100
50
0
Number of Entries
Winter Species
Winter Interactions
FW
PNT
NNT
IN
Network Layer

Figure 1. Plots showing the number of species (nodes) and interactions (edges) for each network layer in the boreal forest ecological network partitioned by summer interactions (top) and winter interactions (bottom). Ecological layers are the food web (FW), positive and negative non-trophic (PNT and NNT), and inclusive network layers (IN).

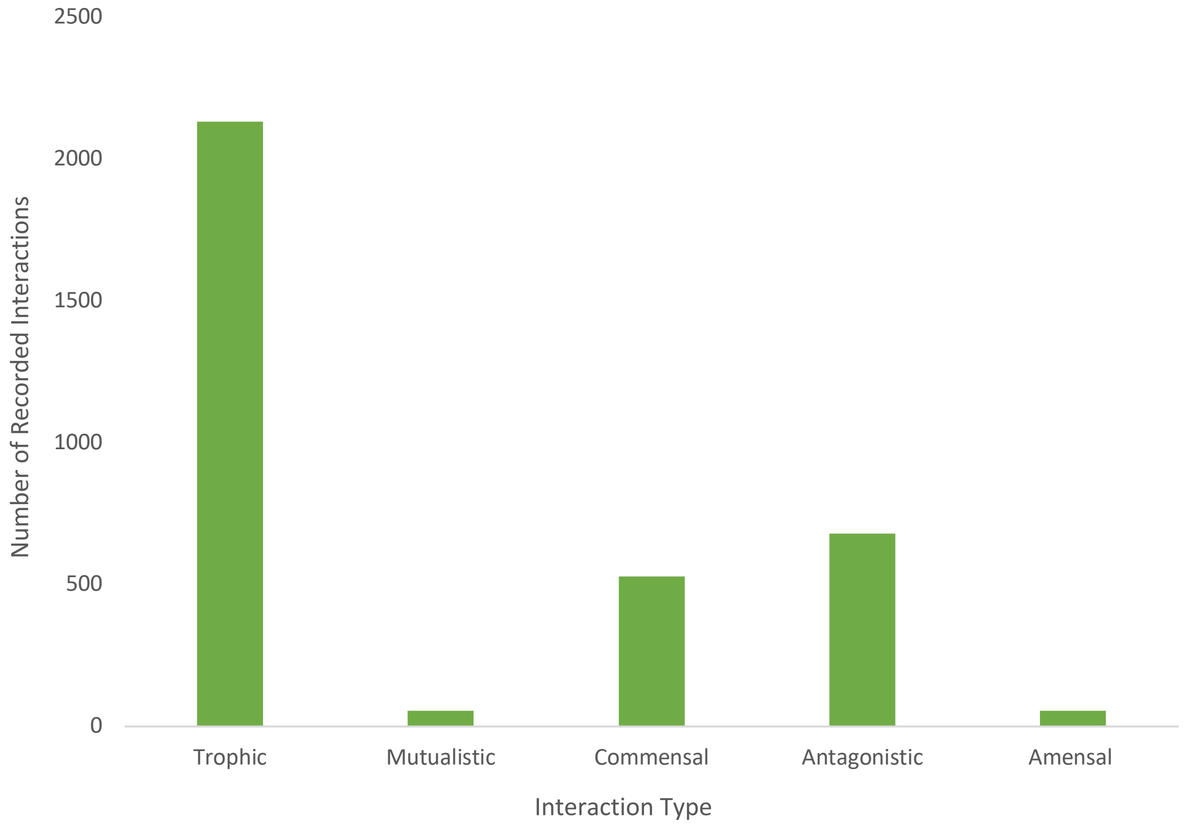


Figure 2. Number of trophic and non-trophic (mutualistic, commensal, antagonistic, and amensal) interactions in the boreal forest ecological network for both summer and winter.

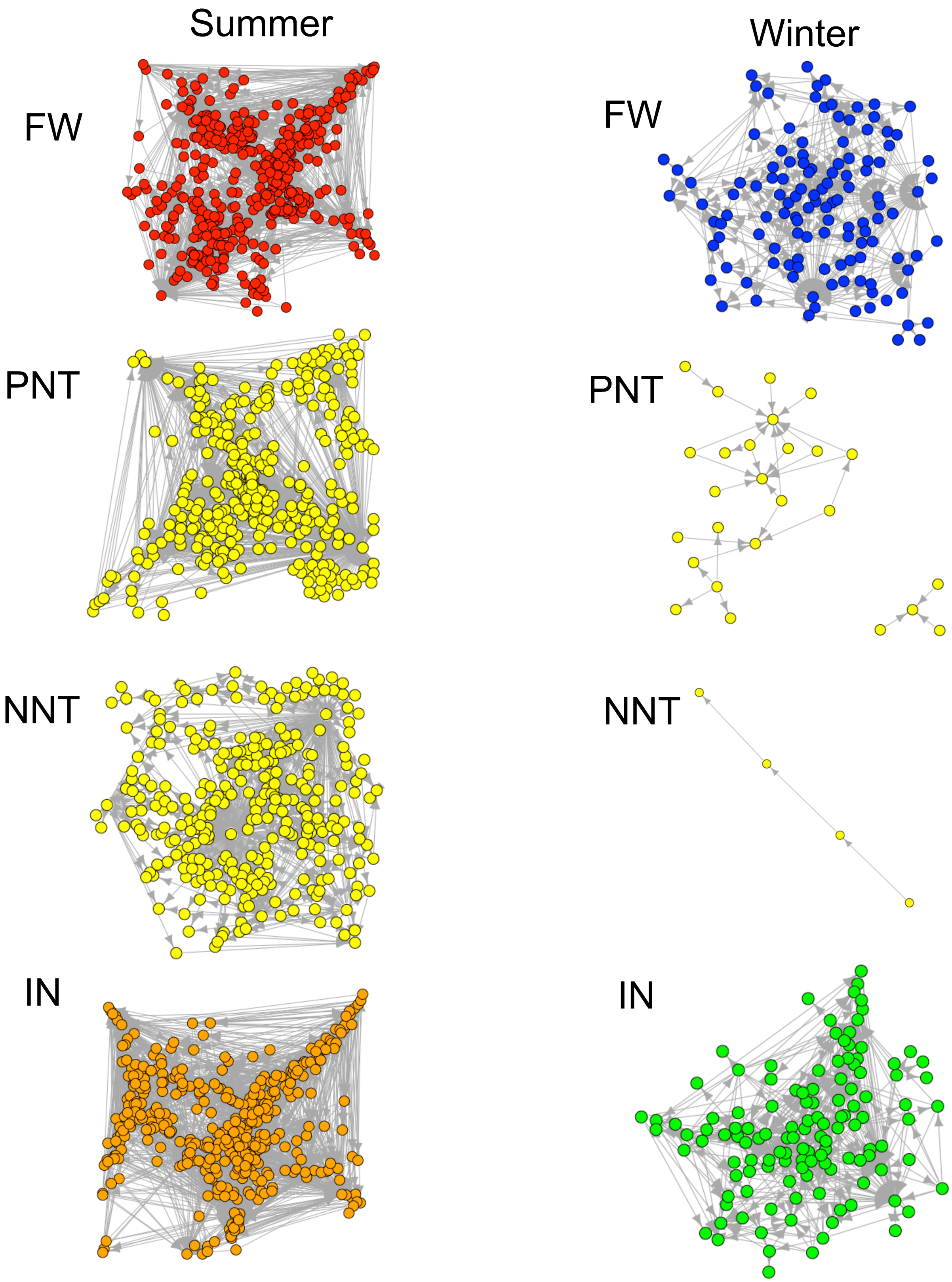


Figure 3. Graphs of the boreal forest multilayer network layers for summer (left) and winter (right), for food web (FW – top), non-trophic (PNT and NNT – middle), and inclusive network layers (IN – bottom). Graph layout was controlled by the Davidson-Harel simulated annealing algorithm. These presentations are included to demonstrate relative network size and complexity

only. Spatial position and clustering of points should not be used to compare network structure from these figures.

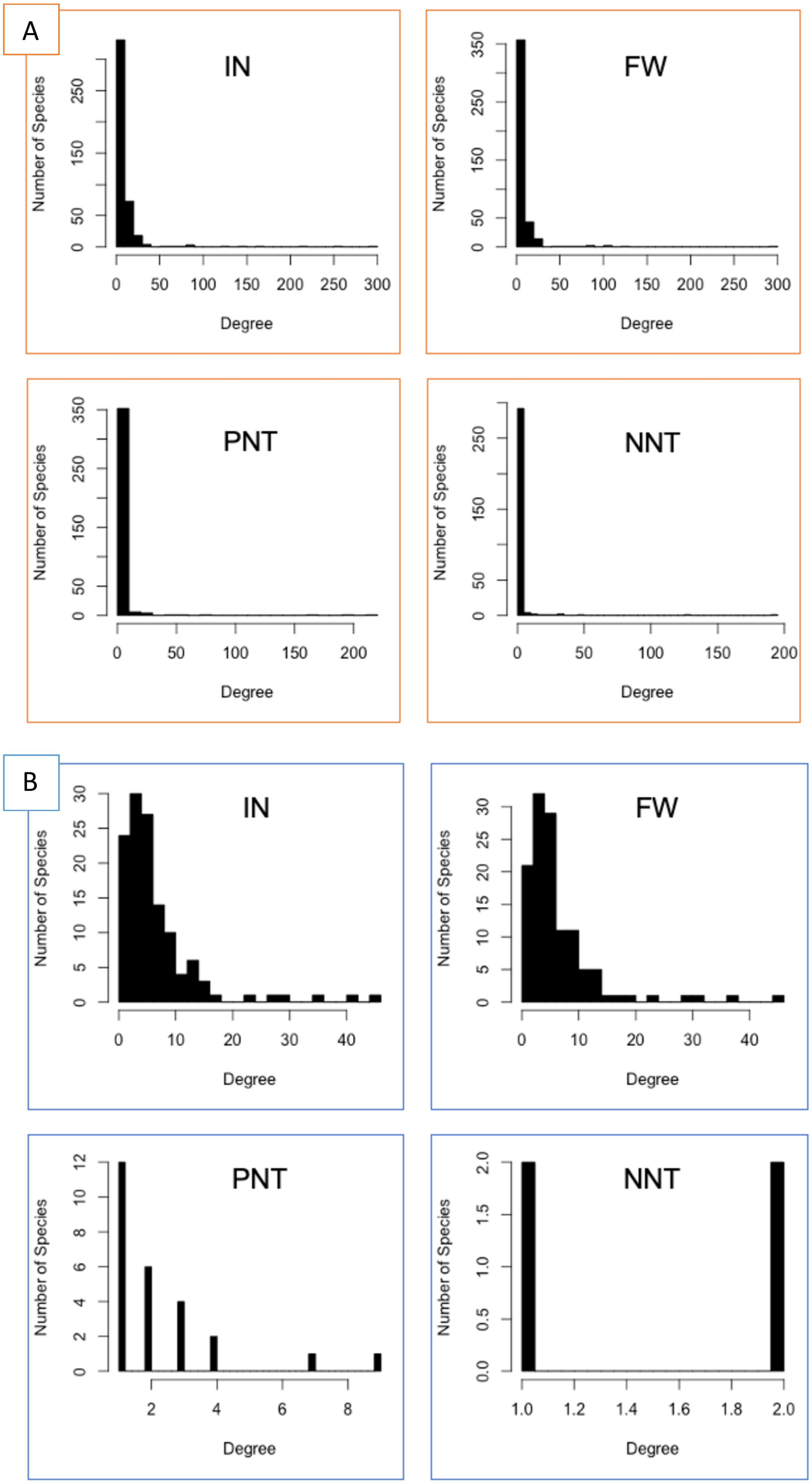

A
IN
Number of Species
0
50
150
250
0
50
100
150
200
250
300
Degree
FW
Number of Species
0
50
150
250
350
0
50
100
150
200
250
300
Degree
PNT
Number of Species
0
50
150
250
350
0
50
100
150
200
Degree
NNT
Number of Species
0
50
150
250
0
50
100
150
200
Degree
B
IN
Number of Species
0
5
10
15
20
25
30
0
10
20
30
40
Degree
FW
Number of Species
0
5
10
15
20
25
30
0
10
20
30
40
Degree
PNT
Number of Species
0
2
4
6
8
10
12
2
4
6
8
Degree
NNT
Number of Species
0.0
0.5
1.0
1.5
2.0
1.0
1.2
1.4
1.6
1.8
2.0
Degree

Figure 4. Degree distributions for the inclusive boreal forest network (IN), food web (FW), positive non-trophic network (PNT), and negative non-trophic network (NNT) for the summer season (A) and winter (B).

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Appendix

Table A.1. List of tetrapod species (and taxonomic classes) included in the boreal forest multilayer ecological network.

Class	Species
Amphibia	*Ambystoma laterale*
	Ambystoma macrodactylum
	Ambystoma maculatum
	Ambystoma tigrinum
	Anaxyrus boreas
	Bufo hemiophrys
	Desmognathus fuscus
	Eurycea bislineata
	Lithobates clamitans
	Lithobates pipiens
	Lithobates septentrionalis
	Necturus maculosus
	Notophthalmus virisdescens
	Plethodon cinereus
	Pseudacris crucifer
	Pseudacris maculata
	Rana luteiventris
	Rana sylvatica
Aves	*Acanthis flammea*
	Acanthis hornemanni
	Accipiter cooperii
	Accipiter gentilis
	Accipiter striatus
	Actitis macularius
	Aechmophorus occidentalis
	Aegolius acadicus
	Aegolius funereus
	Agelaius phoeniceus
	Aix sponsa
	Ammodramus leconteii
	Ammospiza nelsoni
	Anas acuta
	Anas americana
	Anas clypeata

Anas crecca
Anas discors
Anas platyrhynchos
Anas rubripes
Anas strepera
Anser albifrons
Anthus cervinus
Anthus rubescens
Anthus spragueii
Antrostomus vociferus
Aphriza virgata
Aquila chrysaetos
Archilochus colubris
Ardea herodias
Arenaria interpres
Arenaria melanocephala
Asio flammeus
Asio otus
Aythya affinis
Aythya americana
Aythya collaris
Aythya marila
Aythya valisineria
Bartramia longicauda
Bombycilla cedrorum
Bombycilla garrulus
Bonasa umbellus
Botaurus lentiginosus
Branta bernicla
Branta canadensis
Branta hutchinsii
Bubo scandiacus
Bubo virginianus
Bucephala albeola
Bucephala clangula
Bucephala islandica
Buteo jamaicensis
Buteo lagopus
Buteo lineatus
Buteo platypterus

Buteo swainsoni
Calcarius lapponicus
Calcarius pictus
Calidris alba
Calidris alpina
Calidris bairdii
Calidris canutus
Calidris fuscicollis
Calidris himantopus
Calidris maritima
Calidris mauri
Calidris melanotos
Calidris minutilla
Calidris ptilocnemis
Calidris pusilla
Carpodacus purpureus
Catharus bicknelli
Catharus fuscescens
Catharus guttatus
Catharus minimus
Catharus ustulatus
Centronyx bairdii
Certhia americana
Chaetura pelagica
Charadrius melodus
Charadrius morinellus
Charadrius semipalmatus
Charadrius vociferus
Chen caerulescens
Chen rossii
Chlidonias niger
Chordeiles minor
Chroicocephalus philadelphia
Chroicocephalus ridibundus
Cinclus mexicanus
Circus cyaneus
Cistothorus palustris
Cistothorus platensis
Clangula hyemalis
Coccothraustes vespertinus

Coccyzus erythropthalmus
Colaptes auratus
Columba livia
Contopus cooperi
Contopus sordidulus
Contopus virens
Corvus brachyrhynchos
Corvus corax
Coturnicops noveboracensis
Cyanocitta cristata
Cygnus buccinator
Cygnus columbianus
Dendragapus obscurus
Dendroica caerulescens
Dendroica castanea
Dendroica coronata
Dendroica fusca
Dendroica magnolia
Dendroica palmarum
Dendroica pensylvanica
Dendroica petechia
Dendroica striata
Dendroica tigrina
Dendroica townsendi
Dendroica virens
Dolichonyx oryzivorus
Dryocopus pileatus
Dumetella carolinensis
Empidonax alnorum
Empidonax difficilis
Empidonax flaviventris
Empidonax hammondii
Empidonax minimus
Empidonax oberholseri
Empidonax traillii
Eremophila alpestris
Euphagus carolinus
Euphagus cyanocephalus
Falcipennis canadensis
Falco columbarius

Falco mexicanus
Falco peregrinus
Falco rusticolus
Falco sparverius
Fulica americana
Gallinago delicata
Gavia adamsii
Gavia immer
Gavia pacifica
Gavia stellata
Geothlypis trichas
Glaucidium gnoma
Grus americana
Grus canadensis
Haliaeetus leucocephalus
Hirundo rustica
Histrionicus histrionicus
Hydrocoloeus minutus
Hydroprogne caspia
Hylocichla mustelina
Icterus galbula
Ixoreus naevius
Junco hyemalis
Lagopus lagopus
Lagopus leucura
Lagopus muta
Lanius excubitor
Lanius ludovicianus
Larus argentatus
Larus californicus
Larus canus
Larus delawarensis
Larus fuscus
Larus glaucescens
Larus glaucoides
Larus hyperboreus
Leucophaeus pipixcan
Leucosticte tephrocotis
Limnodromus griseus
Limnodromus scolopaceus

Limosa fedoa
Limosa haemastica
Limosa lapponica
Lophodytes cucullatus
Loxia curvirostra
Loxia leucoptera
Luscinia svecica
Megaceryle alcyon
Melanerpes erythrocephalus
Melanerpes lewis
Melanitta americana
Melanitta fusca
Melanitta perspicillata
Melospiza georgiana
Melospiza lincolnii
Melospiza melodia
Mergus merganser
Mergus serrator
Mniotilta varia
Molothrus ater
Myadestes townsendi
Myiarchus crinitus
Nucifraga columbiana
Numenius phaeopus
Numenius tahitiensis
Nycticorax nycticorax
Oenanthe oenanthe
Oporornis agilis
Oporornis philadelphia
Oporornis tolmiei
Oreothlypis celata
Oreothlypis peregrina
Oreothlypis ruficapilla
Oxyura jamaicensis
Pandion haliaetus
Parkesia noveboracensis
Parula americana
Passer domesticus
Passerculus sandwichensis
Passerella iliaca

Passerina cyanea
Pelecanus erythrorhynchos
Perdix perdix
Perisoreus canadensis
Petrochelidon pyrrhonota
Phalacrocorax auritus
Phalaropus fulicarius
Phalaropus lobatus
Phalaropus tricolor
Phasianus colchicus
Pheucticus ludovicianus
Phylloscopus borealis
Pica hudsonia
Picoides arcticus
Picoides dorsalis
Picoides pubescens
Picoides villosus
Pinicola enucleator
Pipilo erythrophthalmus
Pipilo maculatus
Piranga ludoviciana
Piranga olivacea
Plectrophenax nivalis
Pluvialis dominica
Pluvialis fulva
Pluvialis squatarola
Podiceps auritus
Podiceps grisegena
Podiceps nigricollis
Podilymbus podiceps
Poecile atricapillus
Poecile cinctus
Poecile gambeli
Poecile hudsonicus
Poecile rufescens
Pooecetes gramineus
Porzana carolina
Progne subis
Quiscalus quiscula
Rallus limicola

Recurvirostra americana
Regulus calendula
Regulus satrapa
Rhodostethia rosea
Riparia riparia
Sayornis phoebe
Sayornis saya
Scolopax minor
Seiurus aurocapilla
Selasphorus rufus
Setophaga pinus
Setophaga ruticilla
Sialia currucoides
Sialia sialis
Sitta canadensis
Sitta carolinensis
Somateria mollissima
Sphyrapicus nuchalis
Sphyrapicus ruber
Sphyrapicus varius
Spinus pinus
Spinus tristis
Spizella arborea
Spizella breweri
Spizella pallida
Spizella passerina
Stelgidopteryx serripennis
Stercorarius longicaudus
Stercorarius parasiticus
Stercorarius pomarinus
Sterna forsteri
Sterna hirundo
Sterna paradisaea
Strix nebulosa
Strix varia
Sturnella magna
Sturnella neglecta
Sturnus vulgaris
Surnia ulula
Tachycineta bicolor

	Tachycineta thalassina
	Toxostoma rufum
	Tringa flavipes
	Tringa incana
	Tringa melanoleuca
	Tringa semipalmata
	Tringa solitaria
	Troglodytes aedon
	Troglodytes hiemalis
	Tryngites subruficollis
	Turdus migratorius
	Tympanuchus phasianellus
	Tyrannus tyrannus
	Vireo cassinii
	Vireo flavifrons
	Vireo gilvus
	Vireo olivaceus
	Vireo philadelphicus
	Vireo solitarius
	Wilsonia canadensis
	Wilsonia pusilla
	Xanthocephalus xanthocephalus
	Xema sabini
	Zenaida macroura
	Zonotrichia albicollis
	Zonotrichia atricapilla
	Zonotrichia leucophrys
	Zonotrichia querula
Mammalia	*Alces alces*
	Bison bison
	Blarina brevicauda
	Canis lantrans
	Canis lupus
	Castor canadensis
	Cervus canadensis
	Condylura cristata
	Eptesicus fuscus
	Equus ferus caballus
	Erethizon dorsatum
	Felis concolor

Glaucomys sabrinus
Gulo gulo
Lasionycteris noctivagans
Lasiurus borealis
Lasiurus cinereus
Lepus americanus
Lontra canadensis
Lynx canadensis
Marmota caligata
Marmota monax
Martes americana
Martes pennanti
Mephitis mephitis
Microtus chrotorrhinus
Microtus longicaudus
Microtus miurus
Microtus oeconomus
Microtus pennsylvanicus
Microtus xanthognathus
Mus musculus
Mustela erminea
Mustela nivalis
Myodes rutilus
Myotis lucifugus
Napaeozapus insignis
Neotoma cinerea
Neovison vison
Ochotona collaris
Odocoileus hemionus
Odocoileus virginianus
Ondatra zibethicus
Oreamnos americanus
Ovis dalli
Peromyscus maniculatus
Phenacomys intermedius
Rangifer tarandus
Sorex arcticus
Sorex cinereus
Sorex fumeus
Sorex hoyi

	Sorex monticolus
	Sorex palustris
	Sorex tundrensis
	Spermophilus lateralis
	Spermophilus parryii
	Synaptomys borealis
	Tamias minimus
	Tamias striatus
	Tamiasciurus hudsonicus
	Ursus americanus
	Ursus arctos
	Vulpes lagopus
	Vulpes vulpes
	Zapus hudsonicus
	Zapus princeps
Reptilia	*Chelydra serpentina*
	Chrysemys picta
	Thamnophis sirtalis