

Scaling migrations to communities: an empirical case of migration network in the Arctic

1 **Louis Moisan^{1,2*}, Dominique Gravel², Pierre Legagneux^{3,4}, Gilles Gauthier⁵, Don-Jean Léandri-**
2 **Breton^{4,6}, Marius Somveille⁷, Jean-François Therrien⁸, Jean-François Lamarre⁹, Joël Bêty^{1*}**

3 ¹ Chaire de Recherche du Canada en Biodiversité Nordique, Centre d'Études Nordiques, Centre de la
4 science de la biodiversité du Québec, Département de biologie, chimie et géographie, Université du
5 Québec à Rimouski, Rimouski, QC, Canada

6 ² Chaire de Recherche du Canada en Écologie Intégrative, Centre d'Études Nordiques, Centre de la
7 science de la biodiversité du Québec, Département de Biologie, Université de Sherbrooke,
8 Sherbrooke, QC, Canada

9 ³ Chaire de Recherche Sentinelle Nord sur l'impact des migrations animales sur les écosystèmes
10 nordiques, Centre d'Études Nordiques, Centre de la science de la biodiversité du Québec,
11 Département de Biologie, Université Laval, Québec, QC, Canada

12 ⁴ Centre d'Études Biologiques de Chizé (CEBC-CNRS), Université de La Rochelle, France

13 ⁵ Centre d'études nordiques, Département de Biologie, Université Laval, Québec, QC, Canada

14 ⁶ Chaire de Recherche du Canada en Écologie Arctique, Centre de la science de la biodiversité du
15 Québec, Département des Sciences des Ressources Naturelles, Université McGill, Montréal, QC,
16 Canada

17 ⁷ Centre for Biodiversity and Environment Research, Department of Genetics, Evolution and
18 Environment, University College London, London, United Kingdom

19 ⁸ Acopian Center for Conservation Learning, Hawk Mountain Sanctuary, Orwigsburg, PA, USA

20 ⁹ Science and Technology Program, Polar Knowledge Canada, Cambridge Bay, NU, Chaire de
21 Recherche du Canada en Biodiversité Nordique, Centre d'Études Nordiques, Département de
22 biologie, chimie et géographie, Université du Québec à Rimouski, Rimouski, QC, Canada

23 *** Correspondence:**

24 Corresponding Author

25 Louis.Moisan@uqar.ca

26 joel_bety@uqar.ca

27 **Keywords: Seasonal migration, Meta-community, Meta-ecosystem, Migratory pathways,**
28 **Community migration network, Ecological network, Bipartite network, Arctic**

29 **Word count: 5115**

30 **Number of figures and tables: 7**

Abstract

Seasonal migrants transport energy, nutrients, contaminants, parasites and diseases, while also connecting distant food webs between communities and ecosystems, which contributes to structuring meta-communities and meta-ecosystems. However, we currently lack a framework to characterize the structure of the spatial connections maintained by all migratory species reproducing or wintering in a given community. Here, we present a framework to represent and characterize migratory pathways at the community level and provide an empirical description of this pattern from a High-Arctic terrestrial community. We define community migration networks as multipartite networks representing different biogeographic regions connected with a focal community through the seasonal movements of its migratory species. We focus on the Bylot Island High-Arctic terrestrial community, a summer breeding ground for several migratory species. We define the non-breeding range of each species using tracking devices, or range maps refined by flyways and habitat types. We show that the migratory species breeding on Bylot Island are found across hundreds of ecoregions on several continents during the non-breeding period and present a low spatial overlap. The migratory species are divided into groups associated with different sets of ecoregions. The non-random structure observed in our empirical community migration network suggests evolutionary and geographic constraints as well as ecological factors act to shape migrations at the community level. Overall, our study provides a simple and generalizable framework as a starting point to better integrate migrations at the community level. Our framework is a far-reaching tool that could be adapted to address the seasonal transport of energy, contaminants, parasites and diseases in ecosystems, as well as trophic interactions in communities with migratory species.

1. Introduction

Each year, billions of migratory organisms travel the world back and forth seasonally to complete their life cycle, which leads natural communities and ecosystems to shift their properties periodically (Holdo et al., 2011; Bauer and Hoyer, 2014; Furey et al., 2018). By moving from and to different natural systems, migratory species create ecological connections between remote communities and ecosystems, thus creating meta-communities and meta-ecosystems (Bauer and Hoyer, 2014; Gounand et al., 2018). Therefore, the effects of local environmental disturbances (**hereafter perturbation**) such as habitat loss, climate change, invasive species, disease outbreaks and subsidies of contaminants and nutrients can propagate between natural systems at the meta-level.

Local perturbations can modulate the effects of migratory species on communities and ecosystems that are located thousands of kilometers apart, leading to spatial cascades (Bauer and Hoyer, 2014). Spatial cascades are defined as the propagation of indirect effects between remote natural systems (García-Callejas et al., 2019). For instance, perturbations on the non-breeding ground of a migratory species can affect population size at a distant breeding ground through carry-over effects (Webster et al., 2002; Norris, 2005; Taylor and Norris, 2010; Wiederholt et al., 2018; Taylor, 2019). The resulting change in breeding population size can influence both the strength of trophic interactions in communities (Jefferies et al., 2004) and the flux of matter in ecosystems (Hessen et al., 2017; Springer et al., 2018) leading to local cascading effects. The effects of migratory species on communities and ecosystems are diverse, including positive, negative, direct and indirect trophic interactions, the dispersal of organisms and diseases and the exchange of energy, nutrients and contaminants (Holdo et al., 2011; Bauer and Hoyer, 2014; Viana et al., 2016). In a given community,

multiple migratory species maintain several spatial connections with other communities and ecosystems (**hereafter migratory pathways**) through which spatial cascades can occur. Although spatial cascades via migrations have been empirically described (Jefferies et al., 2004; Hessen et al., 2017; Springer et al., 2018), they have only been addressed theoretically based on dispersal and foraging movements (McCann et al., 2005; García-Callejas et al., 2019).

The seasonal discontinuity of migratory movements renders existing frameworks developed for dispersal and foraging movement inadequate for scaling migrations at the community level. The traditional meta-community framework represents dispersal and foraging movements as continuous links between communities, where at any time, some individuals relocate, and others forage in other communities. However, seasonal migration movements are often highly synchronous. All individuals leave one community and seasonally relocate to another within a short period of time, so it is more of a discontinuous on-and-off connection between communities than a continuous one. Moreover, migratory species must access distant communities at different seasons to complete their annual cycle. Therefore, they can only persist in a meta-community system, unlike resident species in the traditional meta-community framework.

The typical annual cycle of seasonal migratory species can be divided into periods of breeding, post-breeding migration, stationary non-breeding and pre-breeding migration. We define the breeding period as the length of time individuals are relatively stationary to breed and raise their young. We define the stationary non-breeding period (**hereafter non-breeding period**) as the portion of the time when individuals are located outside of their breeding ground and perform only local movements, which is often defined as wintering in the northern hemisphere. We define the migration periods as the relocation of individuals from breeding grounds to stationary non-breeding grounds and inversely. The presence of migratory species in a focal community is seasonal, and every individual of a migratory species will, for some time, be found outside the focal community (e.g., a breeding ground). Exceptionally, some individuals of partially migratory species are year-round residents. The effect of a local perturbation on migratory populations can then only propagate to another natural system during the following period of the annual cycle (e.g., from non-breeding to breeding).

Due to the characteristics of seasonal migrations, a novel framework is required to study migrations at the community and meta-community levels. Networks represent how information propagates through interconnected components (Newman, 2018) and are now widely used in ecology (Dale and Fortin, 2010). They are composed of nodes or vertices (circles) connected by edges (lines). They are represented by an adjacency matrix A where each element consists of pairs of nodes ij where 1 represents the presence and 0 the absence of an edge between node i and node j (Newman, 2018). Edges from node i to node j can be directed (unidirectional) or undirected (bidirectional) and unweighted (binary) or weighted (non-binary). In their simplest form, networks present a single type of node (unipartite), such as a food web, where the nodes illustrate the species of a community and the edges represent trophic interactions between those species (Dunne et al., 2002). Migratory pathways are commonly represented at the species level with unipartite migration networks, composed of geographic regions connected by the seasonal movements of individuals across the annual cycle, in order to better understand the demography of migratory species (Taylor and Norris, 2010; Iwamura et al., 2013; Knight et al., 2018; Lamb et al., 2019; Xu et al., 2019; Taylor, 2019). However, neither the food web nor the actual migration network frameworks can consider at the same time both community assemblage and seasonal migratory movements.

Through this paper, we aim to i) propose a framework to represent and characterize the migratory pathways maintained at the community level and ii) provide an empirical description of the structure

of migratory pathways at the community level from a case study. Terrestrial Arctic communities are relevant systems to scale migrations at the community level since they present a relatively low species richness with a high proportion of migratory species (Newton and Dale, 1996; Somveille et al., 2013). We propose the concept of community migration networks based on a simple network framework and traditional network metrics to characterize migratory pathways at the community level. We highlight the potential of the proposed framework by describing the community migration network of the Bylot Island tundra food web for which detailed ecological monitoring information is available over the last 30 years (Gauthier et al., 2011; Gauthier et al., 2013; **Figure 1**). Bylot Island hosts the largest greater snow goose (*Chen caerulescens atlantica*) colony, which represents the dominant herbivore of the system (Legagneux et al., 2012). Due to agricultural changes on the non-breeding and staging grounds, the snow goose population has increased dramatically at the study site (Gauthier et al., 2005). This increase led to important local changes in the community and ecosystem: a reduction in graminoid biomass through grazing (Gauthier et al., 1995), the exportation of nitrogen through young flying out of the island (Gauthier et al., 2011), and an increase in nest predation on other species through apparent competition (Lamarre et al., 2017; Duchesne et al., 2021; Clermont et al., 2021). Bylot Island has a relatively simple community for which we have long-term monitoring showing the local influence of migratory species on trophic interactions and the ecosystem dynamic, as well as their global migratory pathways (Therrien et al., 2012; Robillard et al., 2018; Léandri-Breton et al., 2019; Seyer et al., 2021; Lamarre et al., 2021; Legagneux et al., unpublished data).

2. Community Migration Networks

We propose the concept of community migration networks to scale migratory pathways at the community level. We consider community migration networks as multipartite networks representing the geographic regions connected with a focal community through the seasonal movements of its migratory species. In their simplest form, community migration networks are presented as bipartite with the species assemblage of a focal community and the migration destinations represented by geographic regions (either non-breeding, breeding or stopover grounds). For example, an arctic community where multiple migratory species come to breed (i.e., focal community) can be connected with different regions used as non-breeding grounds by the migratory species. Community migration networks can also be presented as tripartite with the species of the focal community and two types of migration destinations (e.g., non-breeding and staging regions). The focal community can be a breeding, a stopover or a non-breeding ground used by migratory species. However, the framework considers a single type of edge (migratory movements), currently preventing modeling trophic interactions within a given focal community.

The populations of migratory species are considered seasonal nodes in community migration networks (**Figure 2**). The species nodes are taxonomically defined as populations of the species in the focal community and spatiotemporally delimited by the arrival of the individuals in the focal community until their departure. Therefore, the temporal definition of the species nodes considers the populations of migratory species as seasonal (discontinuous) and populations of resident species as non-seasonal (continuous) since they stay in the community throughout the year. Populations of resident species are presented as unconnected nodes in the network. Partially migratory species with both resident and migratory individuals are represented by a seasonal and a non-seasonal species node, representing the proportion of migratory and resident individuals in the population respectively. The nodes representing the geographic regions are spatially defined by the boundaries of the regions and are considered temporally continuous since perturbation can happen in the regions

164 even when migratory species are absent (e.g., habitat loss or contaminant subsidies). The temporal
 165 definition of nodes and edges does not need to be considered explicitly to highlight the pattern of
 166 migrations at the community level, which is the scope of this paper. However, in a dynamic
 167 community migration network, the temporal definition of nodes would be essential.

168 The edges of community migration networks represent the seasonal movements of migratory species
 169 between geographical locations used at each period of their annual cycle. Edges can be either
 170 undirected or directed depending on whether the species use the same migratory pathways back and
 171 forth between nodes of different types (period of the annual cycle) or not. The edges can be weighted
 172 to represent the flux of individuals of each species between the focal community and the connected
 173 regions. Considering that edges are seasonal, it implies that a perturbation on a distant region would
 174 not propagate directly to the focal community but would reach the community in the next season,
 175 thus necessarily implying a delayed propagation of perturbations.

176 Community migration networks are unique relative to other types of networks because i) some nodes
 177 (migratory species) and all edges are seasonal, ii) during migration periods, all edges have the same
 178 direction, iii) some of the nodes (migratory species) depend on nodes of another type (distant
 179 regions), but not the opposite, and iv) the framework focuses on a local community at a global scale.
 180 The unique nature of community migration networks highlights a theoretical challenge in modeling
 181 dynamical community migration networks, but those characteristics are essential to represent the
 182 biology of migratory species.

183 Community migration networks can be described with multipartite network metrics at the node and
 184 network levels to highlight the structure of the migratory pathways at the species and community
 185 levels (**Figure 3**). At the node level, the *species degree* (number of regions connected with a species)
 186 reflects the population spread, defined as the mean distance in the location of individuals from the
 187 same population between different seasons (Finch et al., 2017). Highly spread populations will be
 188 found in more geographical regions. In a bipartite community migration network, the *region degree*
 189 represents the number of migratory species from the focal community hosted by a region in another
 190 annual cycle period (i.e., non-breeding region). The region degree could potentially be used to
 191 identify ecological hot spots thousands of kilometers away from a focal community.

192 At the network level, we suggest using *connectance*, *asymmetry*, *nestedness* and *modularity* to
 193 characterize community migration networks. *Connectance* represents the degree of spatial overlap
 194 between the species of a focal community during another period of the annual cycle. A high
 195 connectance would mean a large spatial overlap between the species of a focal community during
 196 another period of the annual cycle, suggesting perturbation of connected regions could potentially
 197 affect multiple species simultaneously. *Asymmetry* represents the proportion of species nodes versus
 198 region nodes in the network. It illustrates the relative concentration or spatial diffusion of species
 199 once they leave the focal community. A positive asymmetry value would represent more species than
 200 regions and a negative value would point toward the opposite. *Nestedness* assesses if small-range
 201 species are found inside the boundaries of broad-range species during another period of the annual
 202 cycle. If the network is nested, some regions host multiple species of different range sizes. A nested
 203 structure of migratory pathways would mean that if a perturbation happens on a species with a small
 204 non-breeding range, it also has a high chance of propagating to the community through species with
 205 larger non-breeding ranges. The *modules* represent groups of species that have more spatial overlap
 206 with each other on their range outside the focal community than with other species of the community.
 207 *Modularity* highlights the degree of overlap between the modules, with little overlap between
 208 modules showing high modularity. In this paper, we have decided to limit ourselves to a description

of the network and to propose interpretations for some traditional network metrics. Still, we will discuss the use of traditional network metrics in community migration networks.

3. Methods

3.1 Network definition

We studied the Bylot Island tundra community located at the northern tip of Baffin Island in Nunavut, Canada (73° N, 80° W). The study area of 425km² (Giroux et al., 2012) is located in the southern part of the island inside a mosaic of upland mesic tundra habitat interspersed with lowland wetlands (Gauthier et al., 2013). Based on a long-term community monitoring program, we identified 35 vertebrate species in the food web (5 mammals and 30 birds; see **Supplementary Material section 1.1** for details and **Table S1** for the species list and scientific names). Among the 35 vertebrate species, 28 are long-distance migrants, two are partial migrants (arctic fox and common raven), and five are residents (Gauthier et al., 2011). We define migrants as individuals performing seasonal and highly synchronous movements between a breeding and a non-breeding ground, residents as individuals performing movements within a community throughout the annual cycle, and partial migrants as the combination of resident and migratory and/or individuals performing long-distance foraging trips outside the community (Gauthier et al., 2011).

The non-breeding range of each migratory species was defined by the most representative range data available (**Supplementary Material section 1.2**). We used non-breeding range maps (BirdLife International and Handbook of the Birds of the World, 2019; Fink et al., 2020) along with global avian migration flyways (geographical grouping of annual ranges of avian migratory species; Wetlands International, 2022) when tracking data was unavailable for migratory species (22 of 28 species). The association of flyway(s) to each species was based on known migratory pathways by eastern Canadian arctic individuals. We retained only the portion of the non-breeding range within the boundaries of the flyway(s) assigned to each species, thereby removing portions of the non-breeding ranges where individuals from the focal community are absent. The seasonal migratory movement of long-tailed jaegers (Seyer et al., 2021), common-ringed plovers (Léandri-Breton et al., 2019), American golden-plovers (Lamarre et al., 2021), snowy owls (Therrien et al., 2012; Robillard et al., 2018) and snow geese (Legagneux et al., unpublished data) and the partial migratory movement of arctic fox (Lai et al., 2017) have been documented with tracking devices deployed from the study site. Migratory movements of king eiders were monitored from another breeding site in the eastern Canadian Arctic (Gilchrist et al., 2004). The non-breeding ranges of partially migratory species were defined with a buffer zone centered on the study site with a radius size corresponding to the maximum distance travelled during migratory or long-distance foraging movements observed in the literature.

We determined the biogeographic ecoregions associated with the defined non-breeding range of each species from the focal community (**Supplementary Material section 1.3**). Ecoregions represent relatively homogeneous species assemblages at the regional scale (Smith et al., 2018), and they consider ecological and geographical characteristics (e.g., Eastern Canadian forests), unlike biomes that focus only on ecological attributes (e.g., Boreal forests). We used worldwide classifications of terrestrial ecoregions from Olson et al. (2001) and marine ecoregions from Spalding et al. (2007). We derived a classification of coastal ecoregions based on Spalding et al. (2007). We extracted for each species a list of ecoregions overlapping the non-breeding range. We assigned main non-breeding

habitat type(s) (terrestrial, coastal and/or marine) to each species based on the available literature to filter ecoregions from the extracted list that would be marginally used by the species (**Supplementary Material section 1.4**). To validate our non-breeding ranges refinement and filtering methods, we performed a preliminary validation analysis based on the highly specific tracking programs available as reference ($n=6$; **Supplementary Material Section 1.5**). We used the ecoregions associated with each species to create an incidence matrix of $I \times J$ size, where I represents the total number of species in the focal community and J represents the total number of ecoregions connected with the community. Data manipulation and geoprocessing were done in R language and environment version 3.6.3 (R Core Team, 2020) with package *sf* (Pebesma, 2018) and *dplyr* (Wickham et al., 2021).

3.2 Network analysis

The community migration network was defined and analyzed as an unweighted and undirected bipartite network with species and biogeographic ecoregions. At the node level, we used the degree of each node (i.e., number of edges; Figure 3).

At the network level, we used *connectance*, *asymmetry*, *nestedness* (Dormann et al., 2009) and *modularity* (Farage et al., 2021). Connectance (C) is based on the proportion of realized edges in a network and is measured by $C = L \div (I \times J)$ in a bipartite network, where L represents the total number of edges. Network asymmetry (W) addresses the difference in the number of nodes of each type with respect to the total number of nodes, and it is measured by $W = (I - J) \div (I + J)$ with values ranging from -1 to 1. A network is considered nested when low degree nodes share a subset of the connections of high degree nodes. Nestedness (T) is comprised between 0 (perfectly nested structure) and 100 (random structure), and it is commonly used to describe bipartite ecological networks (e.g., plant-pollinators and host-parasites). We used the package *bipartite* (Dormann et al., 2008) to extract this network property. Finally, modularity (M) is a widely used network metric to assess the presence of sub-groups of nodes with more within-group edges than expected by random (Farage et al., 2021). The modularity analysis was performed with the package *infomap* based on network flow (Farage et al., 2021), representing the flow of migratory individuals between the focal community and non-breeding regions (**Supplementary Material section 2.1**). A modular community migration network would mean that the perturbation of an ecoregion or a set of close ecoregions would propagate to the focal community through a subgroup of species from the community. Modularity and nestedness were compared to 1 000 iterations of null models generated by the swap method in the package *vegan* (Oksanen et al., 2007).

4. Results

The species of Bylot Island are distributed latitudinally during the non-breeding period from the High-Arctic to the southern tip of South America and longitudinally from the Pacific Northeast to West Africa (**Figure 4**). Geese and swans, passerines, cranes and gulls are the only functional groups from Bylot strictly found in North America during the non-breeding period, whereas jaegers are strictly found outside of North America. Shorebirds, jaegers and raptors are the only functional groups associated with ecoregions outside North America. The community of Bylot Island is connected with 393 ecoregions through the distribution of its migratory species during the non-

breeding period (**Figure 5**). The peregrine falcon is the species with the highest degree in the network, associated with 257 ecoregions. On average, each migratory species potentially travels to 33 ± 46 ecoregions during the non-breeding season. The ecoregions are connected with one to 14 migratory species with a mean of 3.0 ± 2.4 . For both species and ecoregions, a small number of nodes are highly connected, and many are weakly connected, resulting in both left-skewed distributions of the number of edges per node (**Supplementary Material Figure S4**).

During the non-breeding period, the Bylot Island species are distributed in many ecoregions with a relatively low spatial overlap, which is further illustrated by the low connectance of the network ($C = 0.09$). The low asymmetry ($W = -0.84$) of the network is due to a large number of ecoregions (393) connected with the focal community compared to the number of vertebrate species present (35). The network presents a significantly lower nestedness than random networks ($T = 8.36$ $p < 0.001$).

The low spatial overlap among migratory species of Bylot Island during the non-breeding period is partly due to the presence of groups of species associated with common ecoregions (modules) during the non-breeding period ($M = 6.32$, $p < 0.001$; **Figure 6** and **Supplementary Material Table S4** for the list of ecoregions and their assigned module). The modularity analysis revealed nine modules consisting of one to 13 species and six to 126 ecoregions. Among those modules, four are composed of a single species located: in the marine Pacific Northeast (pacific loon), marine and coastal North Atlantic (king eider), coastal and terrestrial Northwest Africa (common-ringed plover) and throughout the Americas (peregrine falcon). Long-tailed jaeger and red phalarope are associated with marine ecoregions along West Africa and parasitic jaeger, ruddy turnstone, red knot and black-bellied plover are associated with coastal ecoregions from both Atlantic coasts. A group of five shorebird species is associated with terrestrial and coastal ecoregions of the southern part of South America. The partially migratory species (common raven and arctic fox) are identified as a distinct module. The module with the highest species and functional richness includes 13 migratory species associated with diverse environments (coastal, terrestrial and marine) across North America.

The modularity analysis performed with the Bylot Island community migration network allows us to complement existing food web models by linking migratory pathways with trophic interactions in the community (**Figure 7**). We illustrate that the shorebirds functional group composed of ten species in the Bylot Island food web is divided into four modules containing at least one species of shorebirds using distinct ecoregions during the non-breeding period. Therefore, the effect of high goose abundance driven by agricultural perturbations in temperate North America has the potential to propagate indirectly at the meta-community level to different sets of ecoregions through trophic interactions in the Arctic.

327

328 5. Discussion

We proposed a framework with simple network metrics to characterize the structure of migratory pathways maintained by species of a focal community and provided the first empirical description for a vertebrate community. We highlighted that through the annual movement of migratory species, terrestrial arctic communities could potentially be indirectly exposed to perturbations occurring in hundreds of ecoregions distributed across continents. The modular structure of migratory pathways observed at the community level suggests that distant perturbations could propagate to arctic communities through subgroups of migratory species. Community migration networks can be used as

336 a starting point to better study how distant perturbations can propagate at the community level
 337 through migratory species.

338 In our case study, the combination and centralization of migratory pathways knowledge in a
 339 community-based migration network allowed us to fill empirical gaps that could not previously be
 340 addressed on the spatial overlap of migratory species during the non-breeding period. The functional
 341 diversity observed in some of the species groups associated with distinct sets of ecoregions suggests
 342 that perturbations in certain regions of the globe are more likely to propagate to the focal community
 343 through multiple trophic levels. For example, a perturbation that would occur in a terrestrial
 344 ecoregion in temperate Northeastern America could simultaneously affect herbivorous, insectivorous
 345 and vertivorous species breeding on Bylot Island in the High Canadian Arctic. In contrast, a
 346 perturbation in a terrestrial ecoregion in northwest Africa could affect only one insectivore. On the
 347 other hand, spatial cascades that would spread through the community via migratory herbivores
 348 (geese and swans) could only originate from a single module composed of temperate ecoregions. As
 349 they are widely spread during the non-breeding period, the guild of avian predators would be
 350 expected to respond to perturbations occurring at a large (continental) scale. In some cases, species
 351 with similar trophic positions in the Bylot Island food web, like shorebirds, can face highly
 352 heterogeneous environmental conditions during the non-breeding period. Our results showed that
 353 high spatial overlap can occur for both functionally similar and functionally different species, but at
 354 the community level species have very little spatial overlap during the non-breeding period. The
 355 empirical advances made will help to assess better the vulnerability of the Bylot Island food web to
 356 global changes.

357 The modular (non-random) network structure observed in our case study suggests that evolutionary
 358 and geographic constraints as well as ecological factors potentially shape the structure of migratory
 359 pathways at the community level. The proportion of migratory species is strongly correlated with the
 360 magnitude of seasonality, at least for terrestrial bird communities (Hurlbert and Haskell, 2003;
 361 Somveille et al., 2013). Also, migratory birds tend to relocate from breeding to non-breeding grounds
 362 by minimizing migration distance to reach suitable grounds in terms of climate and resources, akin to
 363 a refuge from the harsher conditions of the breeding ground (Somveille et al., 2015; Somveille et al.,
 364 2019; Somveille et al., 2021, Bonnet-Lebrun et al., 2021). Unsurprisingly, most migratory species
 365 from Bylot Island reach non-breeding areas in temperate environments (intermediate migration
 366 distance from the focal community), suggesting an influence of community geographical location on
 367 the structure of migratory pathways. Somveille et al. (2019) also observed that trans-hemispheric
 368 migrants did not seem to respond to the same ecological drivers as migrants travelling within the
 369 same hemisphere. Interestingly, in the community migration network of Bylot Island, we observed a
 370 clear distinction between the functional groups performing trans-hemispheric migrations (shorebirds,
 371 jaegers and some raptors) and those who do not (geese and swans, passerines, cranes, gulls and ducks
 372 and loons and some raptors). The presence of modules composed of functionally similar species
 373 associated with common habitats (e.g., shorebirds in South American ecoregions) suggests that
 374 adaptive constraints on flight efficiency, environmental tolerance and diet may influence network
 375 structure by increasing the modularity. We could address the influence of phylogeny on migrations at
 376 the community level by linking phylogenetic distance, geographic distance and location of migratory
 377 destinations and species degree in the network. Within modules of functionally similar species,
 378 ecological factors such as interspecific interactions (mutualism or competition) could potentially
 379 increase or decrease the spatial overlap between species (Gotelli et al., 2010). Linking community
 380 and species traits, geography, phylogeny and species interactions with community migration network
 381 metrics will allow a better understanding of the factors and constraints shaping migratory patterns at
 382 the community level.

Ideally, community migration networks would be defined for focal communities with well-known geographic ranges and movements over their entire annual cycle for each migratory population. In our study, we estimated the non-breeding range of migratory species with the most accurate data available for our focal community. Despite the use of some rough non-breeding range maps, we still observed a highly structured network. We avoided interpretations at the node level (e.g., degree of ecoregions and species) because we used coarse spatial data for several species. Moreover, the proposed framework focuses on a single community, which prevents encompassing the complete spatial patterns at the species level. For instance, in our case study, we focused on a single breeding ground, which prevents the integration of population spread from non-breeding to breeding grounds. We did not include stopovers and staging grounds because data were too scarce, despite their recognized importance in migratory species demography (Newton, 2006; Iwamura et al., 2013). The ongoing refinement of range maps for migratory species with consideration of the spatiotemporal patterns of populations (Smith et al., 2022; Smithsonian Migratory Bird Center et al., 2022) will broaden opportunities to develop more accurate and precise community migration networks.

Community migration networks represent a simple conceptual framework that should be further developed by network ecologists to study migrations at the community level. The seasonal nature of migratory movements represents theoretical and methodological challenges to scale migrations at the community level. For instance, seasonal edges (temporally discontinuous) in a network of interacting local populations imply a time-delayed response of perturbations between nodes, which is often not considered in ecological models. As a result, we currently have limited knowledge of the effect of the ephemeral and predictable (seasonal) pulses of migratory organisms on community stability and resilience (Holdo et al., 2011; Jeltsch et al., 2013; Bauer et al., 2016; Furey et al., 2018). In our study system, it has been shown that the seasonal presence of migrants can substantially change the dynamic of the food web (Hutchison et al., 2020). It is important to note that the traditional network metrics we used have not been developed with networks comprising seasonal nodes and edges. We may have to develop specific metrics of community migration networks more relevant to the biology of migratory species. This could include centrality metrics that better represent the potential of species to spatially propagate perturbations and cause local cascading effects based on the population spread (species degree), the sensibility to perturbations, the degree of migratory connectivity between populations and the position in the food web.

We restricted our study to a descriptive case of a community migration network with a single breeding site. However, the approach could be replicated in other communities and the framework could be adapted and further developed to better address various ecological questions. Replicating our approach with several communities and comparing their metrics may reveal global biogeographic patterns of migratory pathways at the community level. Migratory pathways of avian species tend to converge towards the poles and migratory species tend to minimize migration distance (Somveille et al., 2015; Somveille et al., 2019; Somveille et al., 2021; Bonnet-Lebrun et al., 2021), so the structure of community migration networks could possibly vary with latitude. Quantifying the flow of migratory organisms in community migration networks would provide a better representation of energy and matter exchange at the meta-ecosystem level, offering a more direct way to link migrations and ecosystem processes. Since migratory species are important vectors of parasites and diseases (Tian et al., 2015; Viana et al., 2016; Varpe and Bauer, 2022), there may be interest in using community migration networks to address how these spread between distant regions of the globe through a common focal site used by multiple migratory species. Combining ecological (food webs, plant-pollinators and host-parasites) and migration networks within a single framework would allow a better representation of the net effects of perturbations in meta-communities maintained by migrations. Scaling migrations at the community level is a first step towards assessing community

430 vulnerability to changes occurring in distant locations connected through animal movement. The
 431 development of community migration networks should thus improve our ability to anticipate the
 432 effects of global changes on ecosystems.

433

434 **Figure captions**

435 **Figure 1.** Bylot Island tundra food web adapted from Gauthier et al., 2011. Labels represent the
 436 functional groups, and the groups composed of migratory species are colored (red= raptors, pink=
 437 gulls, purple= cranes, dark blue = jaegers, light blue= ducks and loons, orange= shorebirds, yellow=
 438 passerines, green= geese and swans). The species composition of vertebrate functional groups is
 439 represented by icons (e.g., four species of passerines). Arrows represent biomass flow between
 440 functional groups and the size of the arrows is relative to the proportion of the diet; gray arrows
 441 represent minor portions of the diet.

442 **Figure 2.** Schematic representation and definition of the seasonal nature of community migration
 443 networks through a fictive community representing a summer breeding ground used by multiple
 444 migratory species (white rectangle) and their migratory pathways (dotted lines) to non-breeding
 445 regions (colored circles). **(1) Summer:** populations of diverse migratory, partially migratory and
 446 resident species (black icons) co-exist at the same location, which defines the focal community
 447 (white rectangle) **(2) Fall:** the migratory and a part of the partially migratory populations leave the
 448 focal community through the migratory pathways (dotted lines) to reach non-breeding regions
 449 (colored circles) **(3) Winter:** the migratory and a part of partially migratory populations are
 450 distributed across diverse non-breeding regions, and the resident and a part of partially migratory
 451 populations stayed at the focal community location **(4) Spring:** the migratory and a part of the
 452 partially migratory populations from the focal community leave the non-breeding regions to reach the
 453 focal community location through the migratory pathways.

454 **Figure 3.** Schematic definitions and examples of low and high values of bipartite community
 455 migration network metrics. The white rectangle represents the focal community, and the colored
 456 circles represent the connected geographic regions through migrations. The dotted lines represent the
 457 movements of species between the focal community and the regions used during another period of
 458 their annual cycle. The movements of species between the focal community and the connected
 459 regions are presented as undirected to represent the use of the same pathways back and forth.
 460 Resident species are represented by the absence of edges.

461 **Figure 4.** Non-breeding range centroids of vertebrate species from Bylot Island. The migratory
 462 species are colored by functional groups (red= raptors, pink= gulls, purple= cranes, dark blue =
 463 jaegers, light blue= ducks and loons, orange= shorebirds, yellow= passerines, green= geese and
 464 swans). The non-breeding centroid of residents and partial migrants are not represented since they are
 465 centered on Bylot Island. The centroids of migratory species with a continuous non-breeding range
 466 are represented by a circle, and squares are used to represent the centroids of divided non-breeding
 467 ranges (i.e., jaegers travel to both Atlantic coasts). The location of some centroids was slightly
 468 adjusted to better represent the species non-breeding habitat type, for instance, moving the centroid
 469 of a coastal species falling inland to the closest coastline.

470 **Figure 5.** Community migration network of Bylot Island with the 35 species labeled in an
 471 anticlockwise way and the 393 biogeographic ecoregions colored by type (green= terrestrial, purple=

coastal and blue= marine). Migratory species were colored based on their functional groups (red= raptors, pink= gulls, purple= cranes, dark blue = jaegers, light blue= ducks and loons, orange= shorebirds, yellow= passerines, green= geese and swans). The chord diagram representation was done with the R package *circlize* (Gu et al., 2014).

Figure 6. Partition of the Bylot Island community migration network with the highest modularity based on the *infomap* algorithm ($M = 6.32$, $p < 0.001$), with nine modules of species and ecoregions sharing more edges between them than with other species and ecoregions of the network. Modules are represented by red boxes and can include multiple ecoregions and species. Interactions non-associated with a module are represented in light brown and are not included in boxes. Species and ecoregions are ordered by modules and species labels are colored by functional groups (red= raptors, pink= gulls, purple= cranes, dark blue = jaegers, light blue= ducks and loons, orange= shorebirds, yellow= passerines, green= geese and swans).

Figure 7. Snow geese and shorebirds breeding on Bylot Island share a predator (arctic fox), which may result in the spatial propagation of agricultural changes occurring in temperate ecoregions used by geese during the non-breeding period (green) to ecoregions used by shorebirds during the non-breeding period (orange). The functional group of shorebirds is divided into four circles representing the modules in the community migration network and the extent of their associated ecoregions is shown on the maps. Negative indirect effects of geese on shorebirds could also pass-through overgrazing on the breeding grounds, which reduces nest site quality or availability.

491

492 Conflict of Interest

493 *The authors declare that the research was conducted in the absence of any commercial or financial*
494 *relationships that could be construed as a potential conflict of interest.*

495

496 Author Contributions

497 JB, DG and LM designed the study. LM, JB and DG developed the conceptual approach. GG, JB and
498 PL secured the funding for the long-term monitoring program. J-FL, J-FT, D-JL-B, GG, JB and PL
499 collected the tracking data. J-FL, J-FT and D-JL-B process the raw tracking data. LM manipulated
500 the data. LM, DG and JB analyzed the data. LM, JB, DG and MS contributed to the interpretation of
501 the results. LM wrote the first draft of the manuscript with contributions from all authors. All authors
502 contributed and approved the submitted version.

503

504 Funding

505 This project was funded by (alphabetical order): Arctic Goose Joint Venture, Arctic Net, BIOS2
506 (NSERC CREATE Training Programs), Canadian Wildlife Service, EnviroNord (NSERC CREATE
507 Training Program in Northern Environmental Sciences), Fonds de recherche du Québec - Nature et
508 technologies (FRQNT), Indigenous and Northern Affairs Canada, Natural Resources Canada (PCSP),
509 Natural Science and Engineering Research Council of Canada (NSERC), Nunavut Wildlife

510 Management Board, Polar Knowledge Canada, Université Laval and Université du Québec à
511 Rimouski.

512

513 Acknowledgments

514 We are sincerely grateful for the data collected with a lot of effort from multiple researchers across
515 years of fieldwork at the Bylot Island research station that made this project possible, especially Y.
516 Seyer and A. Robillard that provided tracking data. We are thankful to eBird and BirdLife
517 International for providing us the access to those valuable datasets. We would also like to thank the
518 Center of Northern Studies for their research installations and the Polar Continental Shelf Program
519 and the Sirmilik National Park (Parks Canada) for the logistic help throughout this project. We would
520 also like to especially thank the Mittimatalik community and the Mittimatalik Hunters & Trappers
521 Organization for their long-term support of the Bylot Island ecological monitoring and for allowing
522 us to pursue research on their land. Finally, we thanked the reviewers for their constructive comments
523 that contributed to the quality of this manuscript.

524

525 Data Availability Statement

526 Publicly available datasets were analyzed in this study. This data can be found here:
527 eBird range maps: <https://ebird.org/science/status-and-trends>
528 Birdlife range maps: <http://datazone.birdlife.org/species/requestdis>
529 Long-tailed Jaegers: [https://www.movebank.org/cms/webapp?](https://www.movebank.org/cms/webapp?gwt_fragment=page=studies,path=study1978212368)
530 [gwt_fragment=page=studies,path=study1978212368](https://www.movebank.org/cms/webapp?gwt_fragment=page=studies,path=study1978212368)
531 Common-ringed plovers: [https://www.movebank.org/cms/webapp?](https://www.movebank.org/cms/webapp?gwt_fragment=page=studies,path=study849807214)
532 [gwt_fragment=page=studies,path=study849807214](https://www.movebank.org/cms/webapp?gwt_fragment=page=studies,path=study849807214) A
533 merican Golden-Plovers: [https://www.movebank.org/cms/webapp?](https://www.movebank.org/cms/webapp?gwt_fragment=page=studies,path=study565443493)
534 [gwt_fragment=page=studies,path=study565443493](https://www.movebank.org/cms/webapp?gwt_fragment=page=studies,path=study565443493)
535 Snowy owls: [https://www.movebank.org/cms/webapp?](https://www.movebank.org/cms/webapp?gwt_fragment=page=studies,path=study12112706)
536 [gwt_fragment=page=studies,path=study12112706](https://www.movebank.org/cms/webapp?gwt_fragment=page=studies,path=study12112706)
537 King eiders: [https://www.movebank.org/cms/webapp?](https://www.movebank.org/cms/webapp?gwt_fragment=page=studies,path=study43747715)
538 [gwt_fragment=page=studies,path=study43747715](https://www.movebank.org/cms/webapp?gwt_fragment=page=studies,path=study43747715)
539 Terrestrial Ecoregions of the World: [https://www.worldwildlife.org/publications/terrestrial-](https://www.worldwildlife.org/publications/terrestrial-ecoregions-of-the-world)
540 [ecoregions-of-the-world](https://www.worldwildlife.org/publications/terrestrial-ecoregions-of-the-world)
541 Freshwater Ecoregions of the World: <https://www.feow.org/download>
542 Marine and Coastal Ecoregions of the World: [https://www.worldwildlife.org/publications/marine-](https://www.worldwildlife.org/publications/marine-ecoregions-of-the-world-a-bioregionalization-of-coastal-and-shelf-areas)
543 [ecoregions-of-the-world-a-bioregionalization-of-coastal-and-shelf-areas](https://www.worldwildlife.org/publications/marine-ecoregions-of-the-world-a-bioregionalization-of-coastal-and-shelf-areas)
544 Major Flyways of the World: <https://wpp.wetlands.org/downloads/downloads>.

545 Scripts for data manipulation, analysis and visualization can be found at: [https://github.com/Louis-](https://github.com/Louis-Moisan/Community_Migration_Networks)
546 [Moisan/Community Migration Networks](https://github.com/Louis-Moisan/Community_Migration_Networks).

547 **References**

- 548 Bauer, S., and Hoyer, B. J. (2014). Migratory animals couple biodiversity and ecosystem functioning
549 worldwide. *Science* 344, 1242552. <https://doi.org/10.1126/science.1242552>
- 550 Bauer, S., Lisovski, S., and Hahn, S. (2016). Timing is crucial for consequences of migratory
551 connectivity. *Oikos* 125, 605-612. <https://doi.org/10.1111/oik.02706>
- 552 BirdLife International and Handbook of the Birds of the World. Data from: Bird species distribution
553 maps of the world Version 2019.1. (2019). Available at:
554 <http://datazone.birdlife.org/species/requestdis>
- 555 Bonnet-Lebrun, A. S., Somveille, M., Rodrigues, A. S., and Manica, A. (2021). Exploring
556 intraspecific variation in migratory destinations to investigate the drivers of migration. *Oikos* 130,
557 187-196. <https://doi.org/10.1111/oik.07689>
- 558 Clermont, J., Grenier-Potvin, A., Duchesne, É., Couchoux, C., Dulude-de Broin, F., Beardsell, A., et
559 al. (2021). The predator activity landscape predicts the anti-predator behavior and distribution of prey
560 in a tundra community. *Ecosphere* 12, e03858. <https://doi.org/10.1002/ecs2.3858>
- 561 Dale, M., and Fortin, M. J. (2010). From Graphs to Spatial Graphs. *Annu. Rev. Ecol. Evol. Syst.* 41,
562 21–38. <https://doi.org/10.1146/annurev-ecolsys-102209-144718>
- 563 Dormann, C. F., Gruber, B., and Fründ, J. (2008). Introducing the bipartite package: analysing
564 ecological networks. *R News* 8, 8-11.
- 565 Dormann, C. F., Fründ, J., Blüthgen, N., and Gruber, B. (2009). Indices, graphs and null models:
566 analyzing bipartite ecological networks. *Open Ecol. J.* 2, 7-24.
567 <http://dx.doi.org/10.2174/1874213000902010007>
- 568 Duchesne, É., Lamarre, J-F., Gauthier, G., Berteaux, D., Gravel, D., and Bêty, J. (2021). Variable
569 strength of predator-mediated effects on species occurrence in an arctic terrestrial vertebrate
570 community. *Ecography* 44, 1236-1248. <https://doi.org/10.1111/ecog.05760>
- 571 Dunne, J. A., Williams, R. J., and Martinez, N. D. (2002). Food-web structure and network theory:
572 the role of connectance and size. *Proc. Natl. Acad. Biol. Sci. U.S.A.* 99, 12917-12922.
573 <https://doi.org/10.1073/pnas.192407699>
- 574 Farage, C., Edler, D., Eklöf, A., Rosvall, M., and Pilosof, S. (2021). Identifying flow modules in
575 ecological networks using infomap. *Methods Ecol. Evol.* 12, 778–786. <https://doi.org/10.1111/2041-210X.13569>
- 577 Finch, T., Butler, S. J., Franco, A. M., and Cresswell, W. (2017). Low migratory connectivity is
578 common in long-distance migrant birds. *J. Anim. Ecol.* 86, 662-673. <https://doi.org/10.1111/1365-2656.12635>

- 580 Fink, D., Auer, T., Johnston, A., Strimas-Mackey, M., Robinson, O., Ligocki, S., et al. Data from:
 581 eBird Status and Trends, Data Version: 2019; Released: 2020. Cornell Lab of Ornithology, Ithaca,
 582 New York. (2020) <https://doi.org/10.2173/ebirdst.2020>
- 583 Furey, N. B., Armstrong, J. B., Beauchamp, D. A., and Hinch, S. G. (2018). Migratory coupling
 584 between predators and prey. *Nat. Ecol. Evol.* 2, 1846–1853. [http://dx.doi.org/10.1038/s41559-018-](http://dx.doi.org/10.1038/s41559-018-0711-3)
 585 [0711-3](http://dx.doi.org/10.1038/s41559-018-0711-3)
- 586 García-Callejas, D., Molowny-Horas, R., Araújo, M. B., and Gravel, D. (2019). Spatial trophic
 587 cascades in communities connected by dispersal and foraging. *Ecology* 100, e02820.
 588 <https://doi.org/10.1002/ecy.2820>
- 589 Gauthier, G., Hughes, R. J., Reed, A., Beaulieu, J., and Rochefort, L. (1995). Effect of grazing by
 590 greater snow geese on the production of graminoids at an arctic site (Bylot Island, NWT, Canada). *J.*
 591 *Ecol.* 83, 653-664. <https://doi.org/10.2307/2261633>
- 592 Gauthier, G., Giroux, J.-F., Reed, A., Béchet, A., and Bélanger, L. (2005). Interactions between land
 593 use, habitat use, and population increase in greater snow geese: what are the consequences for natural
 594 wetlands?. *Glob. Change Biol.* 11, 856-868. <https://doi.org/10.1111/j.1365-2486.2005.00944.x>
- 595 Gauthier, G., Berteaux, D., Bêty, J., Tarroux, A., Therrien, J.-F., McKinnon, L., et al. (2011). The
 596 tundra food web of bylot island in a changing climate and the role of exchanges between ecosystems.
 597 *Écoscience* 18, 223–235. <https://doi.org/10.2980/18-3-3453>
- 598 Gauthier, G., Bêty, J., Cadieux, M. C., Legagneux, P., Doiron, M., Chevallier, C., et al. (2013).
 599 Long-term monitoring at multiple trophic levels suggests heterogeneity in responses to climate
 600 change in the Canadian Arctic tundra. *Philos. Trans. R. Soc. B Biol. Sci.* 368, 20120482.
 601 <https://doi.org/10.1098/rstb.2012.0482>
- 602 Gilchrist, G., Mosbech, A., and Sonne, C. (2004). Data available on movebank.org, study name
 603 “Common/King Eiders; East Bay Island, Nunavut; Gilchrist/Mosbech/Sonne 2001 and 2003”, study
 604 ID 43747715).
- 605 Gilroy, J. J., Gill, J. A., Butchart, S. H., Jones, V. R., and Franco, A. M. (2016). Migratory diversity
 606 predicts population declines in birds. *Ecol. Lett.* 19, 308-317. <https://doi.org/10.1111/ele.12569>
- 607 Giroux, M.-A., Berteaux, D., Lecomte, N., Gauthier, G., Szor, G., and Bêty, J. (2012). Benefiting
 608 from a migratory prey: spatio-temporal patterns in allochthonous subsidization of an arctic predator.
 609 *J. Anim. Ecol.* 81, 533-542. <https://doi.org/10.1111/j.1365-2656.2011.01944.x>
- 610 Gotelli, N. J., Graves, G. R., and Rahbek, C. (2010). Macroecological signals of species interactions
 611 in the Danish avifauna. *Proc. Natl. Acad. Sci. U.S.A.* 107, 5030-5035.
 612 <https://doi.org/10.1073/pnas.0914089107>
- 613 Gounand, I., Harvey, E., Little, C. J., and Altermatt, F. (2018). Meta-ecosystems 2.0: rooting the
 614 theory into the field. *Trends Ecol. Evol.* 33, 36–46. <https://doi.org/10.1016/j.tree.2017.10.006>
- 615 Gu, Z., Gu, L., Eils, R., Schlesner, M., and Brors, B. (2014). circlize implements and enhances
 616 circular visualization in r. *Bioinformatics* 30, 2811–2812.
 617 <https://doi.org/10.1093/bioinformatics/btu393>

- 618 Hanski, I. (1998). Metapopulation dynamics. *Nature* 396, 41–49. <https://doi.org/10.1038/23876>
- 619 Hessen, D. O., Tombre, I. M., van Geest, G., and Alfsnes, K. (2017). Global change and ecosystem
620 connectivity: How geese link fields of central Europe to eutrophication of Arctic freshwaters. *Ambio*
621 46, 40–47. <https://doi.org/10.1007/s13280-016-0802-9>
- 622 Holdo, R. M., Holt, R. D., Sinclair, A. R., Godley, B. J., and Thirgood, S. (2011). " Migration
623 impacts on communities and ecosystems: empirical evidence and theoretical insights", in *Animal*
624 *migration: A synthesis*, ed. Milner-Gulland, E., Fryxell, J. M., and Sinclair, A. R. (Oxford University
625 Press), 131–143.
- 626 Hurlbert, A. H., and Haskell, J. P. (2003). The effect of energy and seasonality on avian species
627 richness and community composition. *Am. Nat.* 161, 83–97. <https://doi.org/10.1086/345459>
- 628 Hutchison, C., Guichard, F., Legagneux, P., Gauthier, G., Bêty, J., Berteaux, D., et al. (2020).
629 Seasonal food webs with migrations: multi-season models reveal indirect species interactions in the
630 Canadian Arctic tundra. *Philos. Trans. Royal Soc. A* 378, 20190354.
631 <https://doi.org/10.1098/rsta.2019.0354>
- 632 Iwamura, T., Possingham, H. P., Chadès, I., Minton, C., Murray, N. J., Rogers, D. I., et al. (2013).
633 Migratory connectivity magnifies the consequences of habitat loss from sea-level rise for shorebird
634 populations. *Philos. Trans. R. Soc. B Biol. Sci.* 280, 20130325.
635 <https://doi.org/10.1098/rspb.2013.0325>
- 636 Jefferies, R., Rockwell, R., and Abraham, K. (2004). Agricultural food subsidies, migratory
637 connectivity and large-scale disturbance in arctic coastal systems: a case study. *Integr. Comp. Biol.*
638 44, 130–139. <https://doi.org/10.1093/icb/44.2.130>
- 639 Jeltsch, F., Bonte, D., Pe'er, G., Reineking, B., Leimgruber, P., Balkenhol, N., et al. (2013).
640 Integrating movement ecology with biodiversity research-exploring new avenues to address
641 spatiotemporal biodiversity dynamics. *Mov. Ecol.* 1, 1–13. <https://doi.org/10.1186/2051-3933-1-6>
- 642 Knight, S. M., Bradley, D. W., Clark, R. G., Gow, E. A., Bélisle, M., Berzins, L. L., et al. (2018).
643 Constructing and evaluating a continent-wide migratory songbird network across the annual cycle.
644 *Ecol. Monogr.* 88, 445– 460. <https://doi.org/10.1002/ecm.1298>
- 645 Lai, S., Bêty, J., and Berteaux, D. (2017). Movement tactics of a mobile predator in a meta-
646 ecosystem with fluctuating resources: the arctic fox in the High Arctic. *Oikos* 126, 937–947.
647 <https://doi.org/10.1111/oik.03948>
- 648 Lamarre, J. F., Legagneux, P., Gauthier, G., Reed, E. T., and Bêty, J. (2017). Predator-mediated ne-
649 gative effects of overabundant snow geese on arctic-nesting shorebirds. *Ecosphere* 8, e01788.
650 <https://doi.org/10.1002/ecs2.1788>
- 651 Lamarre, J. F., Gauthier, G., Lanctot, R. B., Saalfeld, S. T., Love, O. P., Reed, E., et al. (2021).
652 Timing of Breeding Site Availability Across the North American Arctic Partly Determines Spring
653 Migration Schedule in a Long-Distance Neotropical Migrant. *Front. Ecol. Evol.* 9, 710007.
654 <https://doi.org/10.3389/fevo.2021.710007>

- 655 Lamb, J. S., Paton, P. W., Osenkowski, J. E., Badzinski, S. S., Berlin, A. M., Bowman, T., et al.
 656 (2019). Spatially explicit network analysis reveals multi-species annual cycle movement patterns of
 657 sea ducks. *Ecol. Appl.* 29, e01919. <https://doi.org/10.1002/eap.1919>
- 658 Léandri-Breton, D.-J., Lamarre, J.-F., and Bêty, J. (2019). Seasonal variation in migration strategies
 659 used to cross ecological barriers in a nearctic migrant wintering in Africa. *J. Avian Biol.* 50, e02101.
 660 <https://doi.org/10.1111/jav.02101>
- 661 Leibold, M. A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J. M., Hoopes, M. F., et al.
 662 (2004). The metacommunity concept: a framework for multi-scale community ecology. *Ecol. Lett.* 7,
 663 601–613. <https://doi.org/10.1111/j.1461-0248.2004.00608.x>
- 664 McCann, K. S., Rasmussen, J. B., and Ulanowicz, R. E. (2005). The dynamics of spatially coupled
 665 food webs. *Ecol. Lett.* 8, 513–523. <https://doi.org/10.1111/j.1461-0248.2005.00742.x>
- 666 Newman, M. E. J. (2018). *Networks*. New York: Oxford University Press.
- 667 Newton, I., and Dale, L. C. (1996). Bird migration at different latitudes in eastern North America.
 668 *Auk* 113, 626–635. <https://doi.org/10.2307/4088983>
- 669 Norris, D. R. (2005). Carry-over effects and habitat quality in migratory populations. *Oikos* 109, 178–
 670 186. <https://doi.org/10.1111/j.0030-1299.2005.13671.x>
- 671 Oksanen, J., Simpson, G., Blanchet, F., Kindt, R., Legendre, P., Minchin, P., et al. (2022). *vegan*:
 672 Community Ecology Package version 2.6-2. Available online at:
 673 <https://CRAN.R-project.org/package=vegan>
- 674 Olson, D. M., Dinerstein, E., Wikramanayake, E. D., Burgess, N. D., Powell, G. V., Underwood, E.
 675 C., et al. (2001) Terrestrial ecoregions of the world: A new map of life on earth: new global map of
 676 terrestrial ecoregions provides an innovative tool for conserving biodiversity. *BioScience* 51, 933–
 677 938. [https://doi.org/10.1641/0006-3568\(2001\)051\[0933:TEOTWA\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2)
- 678 Pebesma, E. (2018). Simple Features for R: Standardized Support for Spatial Vector Data. *R J.* 10,
 679 439–446. <https://doi.org/10.32614/RJ-2018-009>
- 680 R Core Team (2020). *R: A Language and Environment for Statistical Computing* version 4.2.1. R
 681 Foundation for Statistical Computing, Vienna, Austria. Available online at: [https://www.R-](https://www.R-project.org/)
 682 [project.org/](https://www.R-project.org/)
- 683 Robillard, A., Gauthier, G., Therrien, J.-F., and Bêty, J. (2018). Wintering space use and site fidelity
 684 in a nomadic species, the snowy owl. *J. Avian Biol.* 49, jav–01707. <https://doi.org/10.1111/jav.01707>
- 685 Seyer, Y., Gauthier, G., Bêty, J., Therrien, J.-F., and Lecomte, N. (2021). Seasonal variations in
 686 migration strategy of a long-distance Arctic-breeding seabird. *Mar. Ecol. Prog. Ser.* 677, 1–16.
 687 <https://doi.org/10.3354/meps13905>
- 688 Smith, J. R., Letten, A. D., Ke, P. J., Anderson, C. B., Hendershot, J. N., Dhami, M. K., et al. (2018).
 689 A global test of ecoregions. *Nat. Ecol. Evol.* 2, 1889–1896. [https://doi.org/10.1038/s41559-018-0709-](https://doi.org/10.1038/s41559-018-0709-x)
 690 [x](https://doi.org/10.1038/s41559-018-0709-x)

- 691 Smith, M. A., Mahoney, J., Knight, E. J., Taylor, L., Seavy, N. E., Bailey, O. H. et al. (2022). Bird
692 Migration Explorer. National Audubon Society. Birdmigrationexplorer.org [Accessed September 20,
693 2022]
- 694 Smithsonian Migratory Bird Center, Georgetown University, National Audubon Society and the
695 Cornell Lab of Ornithology (2022). The Migratory Connectivity Project - The Atlas of Migratory
696 Connectivity for the Birds of North America. [http://migratoryconnectivityproject.org/atlas-of-](http://migratoryconnectivityproject.org/atlas-of-migratory-connectivity/)
697 migratory-connectivity/ [Accessed August 29, 2022]
- 698 Somveille, M., Manica, A., Butchart, S. H. M., and Rodrigues, A. S. L. (2013) Mapping global
699 diversity patterns for migratory birds. *PLoS One* 8, e70907.
700 <https://doi.org/10.1371/journal.pone.0070907>
- 701 Somveille, M., Rodrigues, A. S. L., and Manica, A. (2015). Why do birds migrate? A
702 macroecological perspective. *Glob. Ecol. Biogeogr.* 24, 664-674. <https://doi.org/10.1111/geb.12298>
- 703 Somveille, M., Rodrigues, A. S. L., and Manica, A. (2018). Energy efficiency drives the global
704 seasonal distribution of birds. *Nat. Ecol. Evol.* 2, 962-969. [https://doi.org/10.1038/s41559-018-0556-](https://doi.org/10.1038/s41559-018-0556-9)
705 [9](https://doi.org/10.1038/s41559-018-0556-9)
- 706 Somveille, M., Manica, A., and Rodrigues, A. S. L. (2019). Where the wild birds go: explaining the
707 differences in migratory destinations across terrestrial bird species. *Ecography* 42, 225-236.
708 <https://doi.org/10.1111/ecog.03531>
- 709 Somveille, M., Bay, R. A., Smith, T. B., Marra, P. P., and Ruegg, K. C. (2021). A general theory of
710 avian migratory connectivity. *Ecol. Lett.* 24, 1848-1858. <https://doi.org/10.1111/ele.13817>
- 711 Spalding, M. D., Fox, H. E., Allen, G. R., Davidson, N., Ferdaña, Z. A., Finlayson, M., et al. (2007).
712 Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. *BioScience* 57, 573–
713 583. <https://doi.org/10.1641/B570707>
- 714 Springer, A. M., van Vliet, G. B., Bool, N., Crowley, M., Fullagar, P., Lea, M. A., et al. (2018).
715 Transhemispheric ecosystem disservices of pink salmon in a pacific ocean macrosystem. *Proc. Natl.*
716 *Acad. Sci. U.S.A.* 115, E5038–E5045. <https://doi.org/10.1073/pnas.1720577115>
- 717 Taylor, C. M., and Norris, D. R. (2010). Population dynamics in migratory networks. *Theor. Ecol.* 3,
718 65–73. <https://doi.org/10.1007/s12080-009-0054-4>
- 719 Taylor, C. M. (2019). Effects of natal dispersal and density-dependence on connectivity patterns and
720 population dynamics in a migratory network. *Front. in Ecol. Evol.* 7, 354.
721 <https://doi.org/10.3389/fevo.2019.00354>
- 722 Therrien, J.-F., Gauthier, G., and Bêty, J. (2012). Survival and reproduction of adult snowy owls
723 tracked by satellite. *J. Wildl. Manage.* 76, 1562-1567. <https://doi.org/10.1002/jwmg.414>
- 724 Tian, H., Zhou, S., Dong, L., Van Boeckel, T. P., Cui, Y., Newman, et al. (2015). Avian influenza
725 H5N1 viral and bird migration networks in Asia. *Proc. Natl. Acad. Biol. Sci. U.S.A.* 112, 172-177.
726 <https://doi.org/10.1073/pnas.1405216112>

- 727 Viana, D. S., Santamaría, L., and Figuerola, J. (2016). Migratory birds as global dispersal vectors.
 728 *Trends Ecol. Evol.* 31, 763–775. <https://doi.org/10.1016/j.tree.2016.07.005>
- 729 Varpe, Ø., and Bauer, S. (2022). " Seasonal Animal Migrations and the Arctic: Ecology, Diversity,
 730 and Spread of Infectious Agents ", in Arctic One Health, ed. Tryland, M. (Springer Cham), 47-76.
- 731 Webster, M. S., Marra, P. P., Haig, S. M., Bensch, S., and Holmes, R. T. (2002). Links between
 732 worlds: unraveling migratory connectivity. *Trends Ecol. Evol.* 17, 76-83.
 733 [https://doi.org/10.1016/S0169-5347\(01\)02380-1](https://doi.org/10.1016/S0169-5347(01)02380-1)
- 734 Wetlands International (2022). What are Flyways. <https://wpp.wetlands.org/background/WAF>
 735 [Accessed September 6, 2022]. Data available at: <https://wpp.wetlands.org/downloads/downloads>
- 736 Wickham, H., François, R., Henry, L., and Müller, K. (2021). dplyr: A Grammar of Data
 737 Manipulation version 1.0.9. Available online at: <https://CRAN.R-project.org/package=dplyr>
- 738 Wiederholt, R., Mattsson, B. J., Thogmartin, W. E., Runge, M. C., Diffendorfer, J. E., Erickson, R.,
 739 et al. (2018). Estimating the per-capita contribution of habitats and pathways in a migratory network:
 740 a modelling approach. *Ecography* 41, 815-824. <https://doi.org/10.1111/ecog.02718>
- 741 Xu, Y., Si, Y., Wang, Y., Zhang, Y., Prins, H. H., Cao, L. et al. (2019). Loss of functional
 742 connectivity in migration networks induces population decline in migratory birds. *Ecol. Appl.* 29,
 743 e01960. <https://doi.org/10.1002/eap.1960>
- 744 Zurell, D., Graham, C. H., Gallien, L., Thuiller, W., and Zimmermann, N. E. (2018). Long-distance
 745 migratory birds threatened by multiple independent risks from global change. *Nat. Clim. Change* 8,
 746 992-996. <https://doi.org/10.1038/s41558-018-0312-9>