Global Ecology and Biogeography

WILEY

Global Ecology and Biogeography A Journal of Macroecology

RESEARCH ARTICLE OPEN ACCESS

Arctic Migrations Shape Global Meta-Communities: Contrasting Insights From Species Occurrence, Abundance and Biomass

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Received: 17 January 2025 | **Revised:** 10 May 2025 | **Accepted:** 27 May 2025

Handling Editor: Kevin Healy

Funding: This project was funded by Canada First Research Excellence Fund (Sentinel North Program), Centre d'Études Nordiques, Centre de la Science de la Biodiversité du Québec, Environment and Climate Change Canada (Arctic Goose Joint Venture and Northern Ecosystem Initiative), Fonds Québécois de Recherche—Nature et Technologies, Garfield Weston Foundation, Indigenous and Northern Affairs Canada, International Polar Year programme of the Government of Canada (Arctic Research Infrastructure Fund), Natural Resources Canada (Polar Continental Shelf Program), Natural Sciences and Engineering Research Council of Canada (Northern Supplement, Research Tools and Instruments, Special programme of the International Polar Year, Discovery Frontiers (ADAPT), Canada Research Chairs, Collaborative Research and Training Experience program (CREATE) including BIOS2 training programme), Network of Centres of Excellence Canada (ArcticNet), Nunavut Wildlife Management Board, Parks Canada, Polar Knowledge Canada (Northern Scientific Training Program and Science and Technology Program), Université du Québec à Rimouski, Université Laval.

Keywords: animal migration | Arctic | ecoregions | meta-community | migration network | migratory link | modules | subsidies | tundra | vertebrate community

ABSTRACT

Aim: Seasonally migratory species generate large movements of organisms and biomass between distant breeding and non-breeding grounds. However, our understanding of how migratory species shape global networks of interconnected communities (meta-communities) remains limited. Migratory links between communities can be measured in different ways (e.g., species occurrence, abundance or biomass), each providing complementary information by modulating the relative importance of species in meta-communities. We aim at investigating to what extent measuring migratory links using species occurrence, abundance or biomass can reveal alternative structures (i.e., topology) in a meta-community linking an Arctic breeding ground to remote non-breeding grounds.

Location: We use as a study case the High-Arctic vertebrate community of Bylot Island (Nunavut, Canada), along with ecoregions of North and South America, Europe and Africa.

Time Period: Present.

Major Taxa Studied: Terrestrial Arctic birds (30 species) and mammals (5 species).

Methods: We first consider species occurrence at the non-breeding grounds to define migratory links within the meta-community. Secondly, we measure the number of individuals and the amount of biomass travelling along those links. Finally, we compare the meta-community structure under each scenario using a migration network representation.

Results: Patterns of species occurrence, abundance and biomass reveal that temperate ecoregions of South and especially North America maintain strong ecological connections with the vertebrate community of Bylot Island. However, the structural role of species within the network can vary substantially depending on how migratory links are measured (i.e., contrasting topological anomalies). Using abundance or biomass to measure migratory links results in a finer partitioning of the network into modules compared to using species occurrence alone.

Main Conclusions: We highlight that using different metrics of migratory links reveals unique, yet complementary structural features of meta-communities. These findings contribute to assessing the vulnerability of communities to perturbations occurring in distant but connected environments through migration.

1 | Introduction

The seasonal movements of migratory species couple distant communities and ecosystems of the globe (Polis et al. 1997; Jefferies et al. 2004; Bauer and Hoye 2014). We define seasonal migration (hereafter migration) as a regular, bidirectional and seasonally synchronised population-wide movement between breeding and non-breeding grounds (Webster et al. 2002; Mueller and Fagan 2008; Winger et al. 2019). As individuals move from one community to another, they impact both the food web they leave and the one they join, thus indirectly coupling the dynamics of distant food webs (McCann et al. 2005; García-Callejas et al. 2019). As a result, seasonal migration links sets of distant communities (creating a meta-community; Leibold et al. 2004), maintaining ecological dynamics over large spatial scales and spreading perturbations (Jefferies et al. 2004; Springer et al. 2018; García-Callejas et al. 2019).

Understanding the structure of migratory links between distant communities is essential to assess their vulnerability to environmental changes. Empirical evidence shows that the effects of local or regional environmental changes (hereafter perturbations) can propagate via migratory species and cause cascading effects in distant ecological systems (Jefferies et al. 2004; Hessen et al. 2017; Springer et al. 2018). However, attributing changes in a local ecological system to distant perturbations resulting from long-distance migration is difficult (Madigan et al. 2012; Springer et al. 2018). We thus need to position local communities within global migration networks to properly understand their structure and dynamics, and ultimately anticipate their vulnerability.

The spatial dimension intrinsically linked to migration is often overlooked in community ecology (Guzman et al. 2019; DeSimone et al. 2024). Much of the literature on migration ecology has focused on understanding the spatial and temporal patterns of migration at the individual, population or species level (Bowlin et al. 2010), or the impact of migratory subsidies in communities or ecosystems (Holdo et al. 2011; Bauer and Hoye 2014). However, migration has not yet been integrated into meta-ecological models (Gounand et al. 2018; Guzman et al. 2019). Theoretically, the meta-community and meta-ecosystem frameworks have been developed primarily with a focus on diffusive dispersal movements (Loreau et al. 2003; Leibold et al. 2004; Gounand et al. 2018), which happen constantly and move a small fraction of populations. However, migration and dispersal movements are fundamentally different, since migration is bidirectional, periodic, and synchronous unlike dispersal (Guzman et al. 2019).

The study of community migration networks, which represents the seasonal movements of all migratory species within a community as part of a meta-community, is still in its infancy and remains largely descriptive. We refer to community migration networks as a specific representation of meta-communities that considers only the movement of migratory organisms. Unlike dispersal movements, there is currently a lack of mathematical tools to understand the dynamic spread of perturbations through migration in a meta-community. Nevertheless, we have previously introduced a conceptual framework for examining migration network structure within communities (Moisan et al. 2023). We also empirically described the migration network of an Arctic vertebrate community based on species occurrences, which enabled us to identify the spatial pathways through which distant perturbations can propagate to the local community. However, species occurrence alone does not reflect the number of organisms or the amount of biomass that transit between distant communities. Just like for occurrence and abundance in the study of distributions (Boulangeat et al. 2012), it is well known that binary and quantitative links in ecological networks carry unique and complementary information that must be considered (Bersier et al. 2002; Delmas et al. 2019).

Measuring migratory links with species occurrence, abundance and biomass could offer complementary perspectives on the structure of meta-communities maintained by migration (Massol et al. 2011). Meta-community links defined by species occurrence and the traits they exhibit, such as the strength of their trophic interactions, their dispersal abilities, their role in pollination, and their potential to influence disease dynamics (epidemiological potential) can be used to represent the movement of individuals between communities (Massol et al. 2011). In some cases, species traits (e.g., dispersal abilities) are the determining factor of the meta-community dynamic, such as with the regional species coexistence in a patch dynamic (Massol et al. 2011; Calcagno et al. 2011). On the other hand, species abundance or biomass is often used in trophic meta-community models to describe the population dynamics of interacting species (Gross et al. 2020). Biomass is also widely used to model energy and nutrient fluxes within ecological networks (Subalusky et al. 2017; Barnes et al. 2018).

Here, we compare the structure of migratory links measured by species occurrence, relative and absolute abundance, and biomass within the migration network of an Arctic vertebrate community. This objective is addressed through a case study of the terrestrial community of Bylot Island (Nunavut, Canada), which is used annually as a breeding ground by 30 migratory species. This High Arctic site is well suited for such analysis, as both the non-breeding ranges of all migratory species (Moisan et al. 2023) and their local abundance and biomass (Moisan et al. 2025) have been previously established. We use migratory links between Bylot Island and distant ecoregions, defined by Moisan et al. (2023), with species occurrences as a baseline migration network. We then measure the number of individuals (i.e., abundance) and the amount of biomass migrating to each connected ecoregion and describe the resulting biogeographic patterns. To compare the migration network structure (i.e., topology) across scenarios, we examine the diversity of migratory link weights and the number and composition of modules. Finally, we assess the structural role of individual species and ecoregions by evaluating the number and strength of their links within the network.

2 | Methods

2.1 | Bylot Island Vertebrate Community

The case study is based on a 389 km^2 study area located on the south plain of Bylot Island in the Canadian High Arctic (73°N, 80°W; see Figure S1.1). This area is characterised by a relatively simple terrestrial vertebrate community (30 bird species and 5 mammal species, Moisan et al. 2025; see Table S1.1). For over 30 years, vertebrate monitoring has been carried out every year from May to August, covering the entire breeding season (Gauthier et al. 2013, 2024; Moisan et al. 2025). Most species in the community (28 species) migrate annually between their breeding grounds on Bylot Island and distant non-breeding grounds. We classify Arctic fox (*Vulpes lagopus*) and common raven (*Corvus corax*) as partially migratory species, as only some individuals leave the community temporarily during the non-breeding period to make short-distance migrations or extensive foraging trips in adjacent environments (Lai et al. 2017). Nearctic brown and collared lemmings (*Lemmus trimucronatus* and *Dicrostonyx groenlandicus*), American ermine (*Mustela richardsonii*), Arctic hare (*Lepus arcticus*) and rock ptarmigan (*Lagopus muta*) are the only residents (Gauthier et al. 2011).

The mean summer abundance and biomass of all vertebrate species in the Bylot Island community were estimated from the long-term ecological monitoring program (Gauthier et al. 2024; Moisan et al. 2025). We focus here on the mean abundance and biomass to highlight the long-term structure of migratory links between the focal community and distant ecoregions, thereby avoiding consideration of inter-annual variations. It is still worth noting that lemming populations exhibit large amplitude cycles at the study site, leading to significant inter-annual variations in the abundance of species that consume lemmings, such as ermines, snowy owls, long-tailed jaegers and rough-legged hawks (Legagneux et al. 2012). Species abundance and biomass estimates consider all individuals that settle in the study area during the breeding season but exclude individuals only passing through for a few days. We focus on adults for all species except lemmings, as we lack the necessary data to differentiate between adult and juvenile abundance for these two rodent species (Moisan et al. 2025).

For a stable population, the mean inflow and outflow of adults between the breeding and the non-breeding grounds should be similar, as losses due to migration and winter mortality are balanced by the return of juveniles as adults in subsequent springs. Many adult migratory birds exhibit strong fidelity to both breeding and non-breeding sites (Cresswell 2014; Winger et al. 2019). However, this does not preclude juvenile dispersal, as juveniles from Bylot Island may settle elsewhere and, conversely, individuals born at other sites may later breed on Bylot Island. The assumption therefore implies that juvenile breeding dispersal is relatively balanced, meaning that a comparable number of juveniles born on Bylot Island settle to breed elsewhere as juveniles from other sites settle to breed on Bylot Island. Under this assumption, migratory links between Bylot Island and distant ecoregions were considered bidirectional, reflecting the to-and-from migration of adults. This assumption is realistic as no temporal trend in abundance was observed in the vertebrate community of Bylot Island (Gauthier et al. 2013), with the notable exception of an increase in cackling geese (*Branta hutchinsii*, Moisan et al. 2025). We converted abundance into biomass using the mean body mass of adults, except for lemmings, where we used the mean body mass of all individuals captured in the study area (Moisan et al. 2025).

2.2 | Defining Migratory Links

We examined the structure of the Bylot Island meta-community using a community migration network representation (Moisan et al. 2023)—a specific meta-community representation that considers only migratory movements. A network is a system of nodes interconnected by edges (i.e., links), like species in a food web. Networks are well suited to study the emergent structure of interacting components, which would not be possible if we studied each component individually (Newman 2018). Here, we used two types of nodes: (i) *species nodes*, which represent the populations of various species within the focal community and (ii) *ecoregion nodes*, which depict the ecoregions of the globe connected to the focal community (here Bylot Island) through the migration ofdifferent species (Figure 1). Ecoregions are biogeographical units defined by the similarity of species assemblages (Olson et al. 2001; Spalding et al. 2007). Ecoregion boundaries effectively delineate transition zones in plant and vertebrate communities (Smith et al. 2018), representing broad communities on a global scale.

We defined a migratory link between a species and an ecoregion node whenever the non-breeding range of a species intersected with the boundaries of an ecoregion, irrespective of the extent of the overlap (Figure 1). The migratory links presented here are analogous to migratory connections defined in studies of migratory connectivity (Webster et al. 2002); however, by focusing on a single breeding site, we do not assess the degree of mixing among breeding populations. We here use the term *non-breeding* to denote the period during which individuals maintain a relatively stable home range outside of the breeding season, often referred to as the wintering period. We did not include staging and stopover sites due to insufficient data

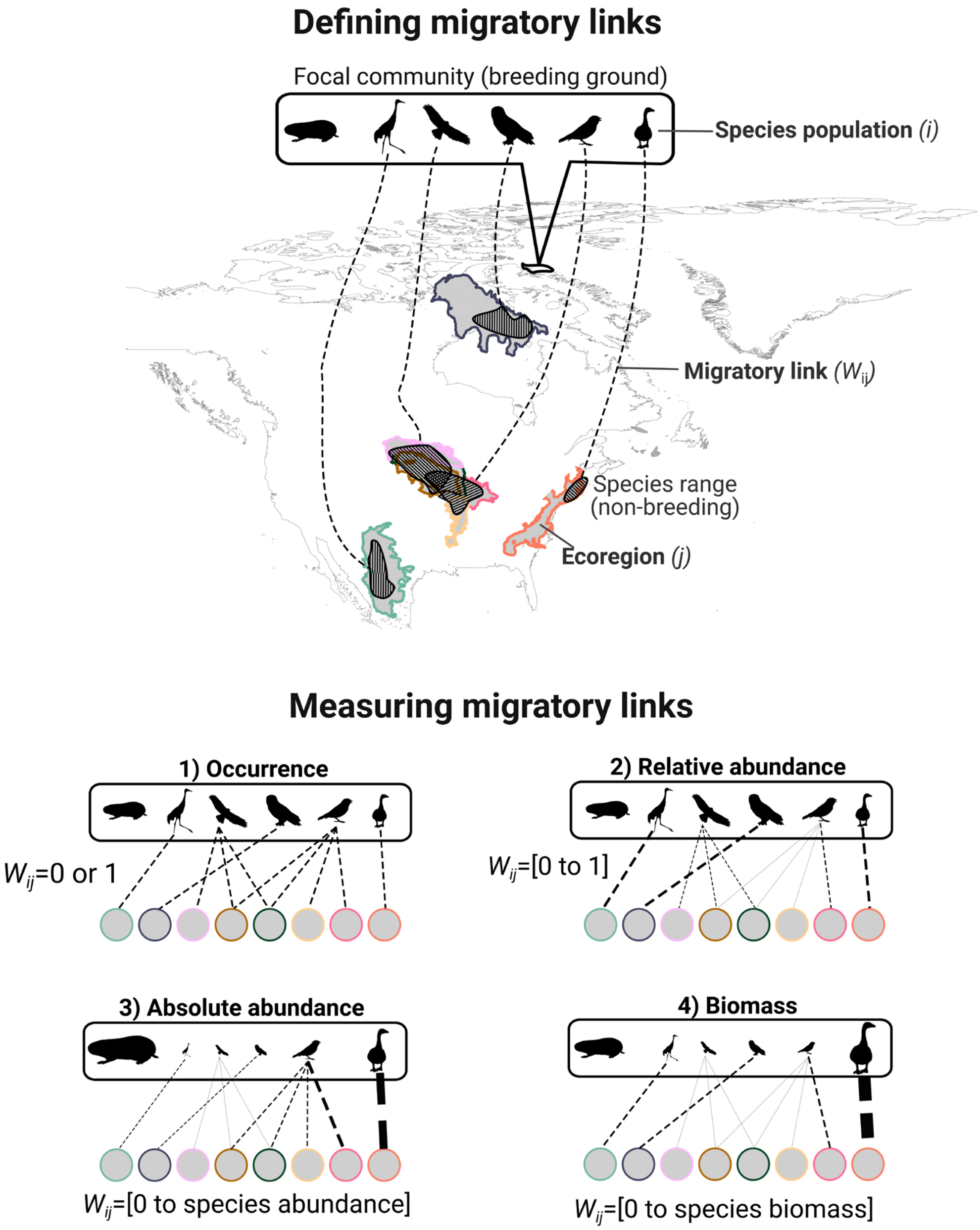

FIGURE 1 | **Top**: Schematic representation of a simplified and fictional community migration network, which encompasses all populations within the community (referred to as *species nodes*). These populations are linked to various ecoregions of the world (represented as *ecoregion nodes*) based on the delineation of their distribution ranges beyond the focal community. In this fictive case, the non-breeding range of the population of species *i* intersects with the boundaries of ecoregion *j*, thus a *migratory link* (W_{ij}) is drawn between species nodes *i* and ecoregion node *j* (each ecoregion is delimited by a different colour). **Bottom**: The measurement of migratory links (W_{ij}) can be approached in various ways. Here, we present schematically the four approaches employed in our study to measure migratory links: species occurrence, relative abundance, absolute abundance and biomass.

for most species. We used the previously defined non-breeding ranges of all migratory and partially migratory species of Bylot Island derived from tracking of individuals (6 species; Gilchrist et al. 2004; Therrien et al. 2012; Robillard et al. 2018; Léandri-Breton et al. 2019; LeTourneux et al. 2021; Seyer et al. 2021; Lamarre et al. 2021) and refined species range maps (BirdLife International and Handbook of the Birds of the World 2019; Fink et al. 2021; Moisan et al. 2023; see Appendix S2.1). We used the classifications of terrestrial (Olson et al. 2001), marine (Spalding et al. 2007) and freshwater ecoregions (only for large bodies of water; Abell et al. 2008). We defined coastal ecoregions as the portion of marine ecoregions located within a 3 km buffer along the coastline, excluding any areas extending further inland.

2.3 | Measuring Migratory Links

We measured and described the structure of the Bylot Island migration network under four different scenarios. First, we treated migratory links between nodes as binary (presence or absence) by using species occurrences, as presented in the migration network of Bylot Island by Moisan et al. (2023). In this scenario, migratory links represent pathways rather than quantities, because regardless of the number of individuals or biomass, all links are equivalent (Figure 1). However, species occurrence allows us to represent the presence and absence of species with specific traits in distant communities.

Secondly, we measured migratory links based on species relative abundance. Relative abundance is the proportion of total individuals present in each ecoregion of the non-breeding range. We began by mapping abundance indices of each population across their previously defined non-breeding range. Abundance indices in the non-breeding range were derived from tracking of individuals ($n = 6$ species) or abundance distribution models based on eBird observations ($n = 16$ species; Sullivan et al. 2009; Fink et al. 2021; see Appendix S2.2). Maps of abundance indices are unavailable for pelagic species (i.e., red phalarope, long-tailed duck, red-throated loon, Pacific loon, parasitic jaeger and glaucous gull, see Table S1.1 for scientific names) and Arctic partial migrants (i.e., common raven and Arctic fox). For these species, we assumed that the relative abundance is proportional to the overlapping area of the ecoregion within the defined species non-breeding range (see Appendix 2.2). In this scenario, migratory links present continuous values ranging from zero (absence of individuals of the species in a specific ecoregion) to one (all individuals of the species are found in the same ecoregion during the non-breeding period; see Figure 1).

Thirdly, we measured migratory links based on the number of individuals (i.e., absolute abundance of the species in the study area; Figure 1). To determine the number of individuals seasonally transiting between the focal community and a given ecoregion, we multiplied mean absolute abundance on Bylot Island (from Table S1.1) by the relative abundance found in the corresponding ecoregion for each species. In this scenario, values of migratory links range from zero (no individuals of a given species present in a specific ecoregion) to the species' mean abundance in the study area.

Fourthly, we quantified migratory links in terms of biomass (Figure 1). To estimate the amount of biomass moving between each ecoregion and the focal community, we multiplied the mean biomass of each species on Bylot Island (from Table S1.1) by the relative abundance found in the corresponding ecoregion. In this scenario, values of migratory links range from 0 to the species' mean biomass in the study area.

We performed a sensitivity analysis by considering an alternative assumption to estimate relative abundance: for all species, relative abundance in each ecoregion was assumed to be proportional to the area of overlap between the ecoregion and the species' defined non-breeding range. This alternative approach yields similar structural differences in the migration network across scenarios (see Appendix S2.3).

3 | Analysis

We used network metrics commonly used in community ecology (e.g., plant-pollinator, predator–prey, seed-dispersal and host-pathogen networks) to describe and compare the structure of the Bylot Island community migration network under the different scenarios. We only retained metrics applicable to both binary and quantitative networks, such as link diversity and the number and composition of modules. Link diversity simply represents the Shannon diversity index (H') of the weights of all migratory links in the network (see Appendix S3.1). It reaches its maximum when all links have the same weight, as with species occurrence. Modules (i.e., groups of nodes that are more strongly connected to each other than to other nodes in the network) are structural features of significant interest in ecological networks, since they can contain perturbations within clusters, thereby increasing the system stability (Stouffer and Bascompte 2011), especially in spatial networks (Gravel et al. 2016). In migration networks, modules represent groups of species and ecoregions interacting more closely together than with other nodes in the networks. We identified modules in the network using the *Infomap* algorithm, developed to describe flow modules in networks (Farage et al. 2021; see Appendix S3.2). As a sensitivity analysis, we also applied the *QuanBiMo* algorithm, developed to identify modules in weighted bipartite networks (Dormann and Strauss 2014). To compare the module partitions (i.e., a given classification of nodes into modules) between each scenario, we used the number and composition of modules.

To compare node composition within modules across scenarios, we used the Normalised Mutual Information (NMI) index (Danon et al. 2005; see Appendix S3.3) implemented in the *compare* function of the 'igraph' package (Csárdi et al. 2024). We compared the classification of nodes into modules separately for species and ecoregions. NMI quantifies the similarity between two network partitions (i.e., scenarios), providing values ranging from zero (completely different partitions) to one (the composition of a partition can be predicted perfectly from another one; Guimera et al. 2007; Thébault 2013; Beckett 2016). For example, an NMI value of one for species nodes between the occurrence and abundance scenarios indicates that species are assigned to identical modules in both cases.

The density of a given species, and consequently its abundance and biomass, can be influenced by how the study area is delineated, particularly when the species exhibits a highly aggregated spatial distribution. In our system, this is the case for snow geese because our study area is centred around a large breeding colony. As a result, snow geese represent a substantial proportion of the community's abundance and biomass. To avoid interpretations dominated solely by the study area delimitation, we also present analyses that exclude snow geese.

General data manipulation ('dplyr' 1.1.4: Wickham et al. 2023), spatial data processing ('sf' 1.0–16: Pebesma and Bivand 2023; 'raster' 3.6–26: Hijmans 2023), network analysis ('bipartite' 2.19: Dormann et al. 2008; 'Infomapecology' 2.0: Farage et al. 2021) and data visualisation ('ggplot2' 2_3.5.1: Wickham 2016) were conducted in R version 4.4.1 with x86_64 linux-gnu.

4 | Results

Species abundance decreases linearly with body mass on a log–log scale ($\beta = -0.71$; 95% CI [-1.16, -0.26]; $R^2 = 0.22$; Figure 2)

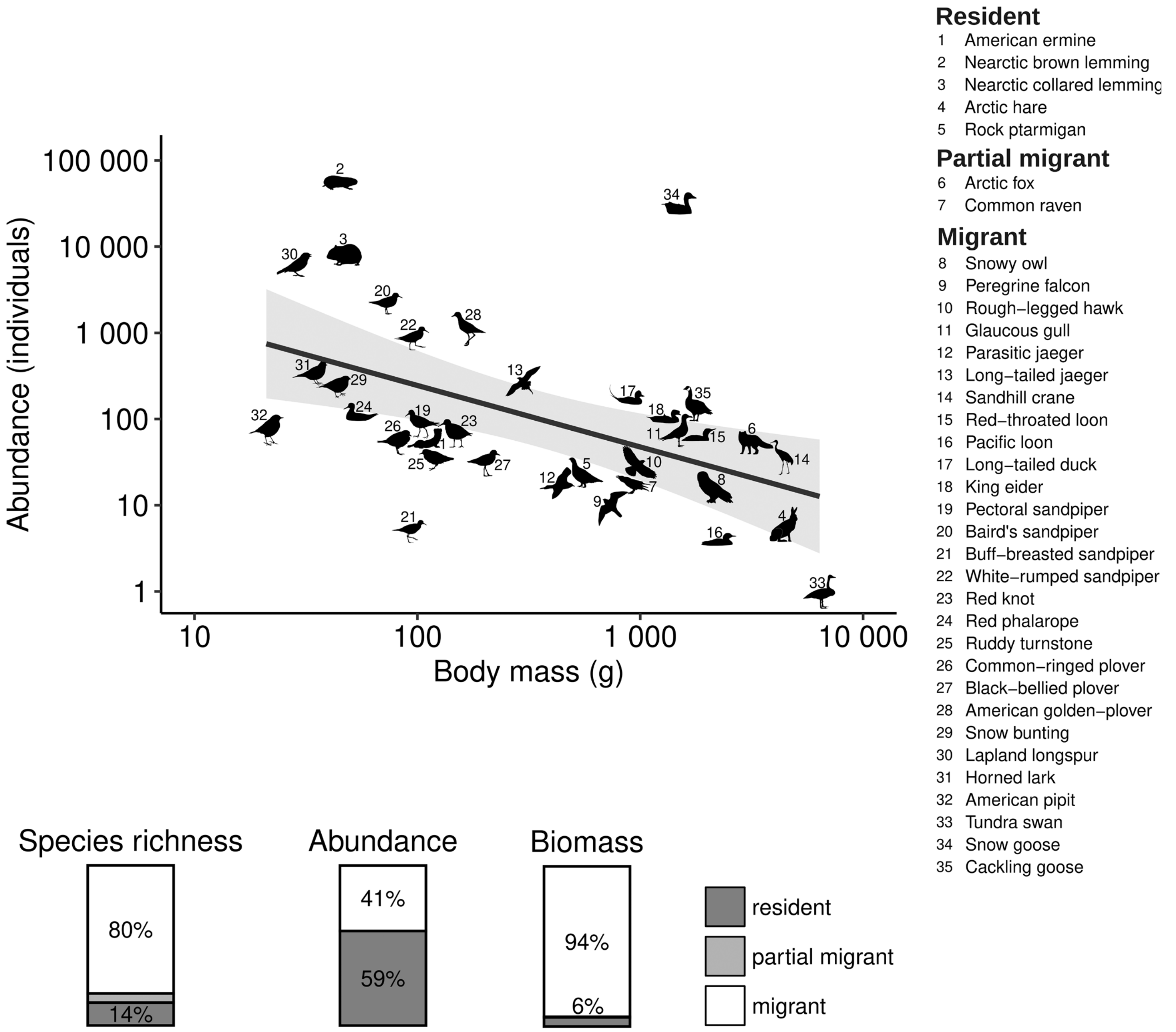

FIGURE 2 | **Top**: Relationship between mean species abundance and mean adult body mass in the Bylot Island vertebrate community during the breeding period (May–August). Juveniles are considered in the abundance and body mass of lemmings. Both variables are depicted on logarithmic scales, and each icon and label represents different species. **Bottom**: Proportion of species richness, mean abundance and mean biomass represented by migrants, partial migrants and resident species of the Bylot Island vertebrate community. Partial migrants represent 6% of the species richness, 0.07% of the abundance, and 0.4% of the biomass.

within the Bylot Island vertebrate community. Brown lemmings and snow geese are two outliers that present a much higher abundance than any other species of comparable body mass. In contrast, buff-breasted sandpipers and tundra swans present slightly lower abundances than expected based on their body mass. Migratory species, excluding partial migrants, account on average for 80% of the species richness, 41% of the total abundance and 94% of the biomass of the vertebrate community (Figure 2). When snow geese are excluded, migratory species represent 16% of the total abundance and 39% of the biomass (see Figure S4.1). A linear relationship is also observed between log species abundance and log biomass ($\beta = 0.66$; 95% CI [0.45, 0.88]; $R^2 = 0.55$; Figure S1.2). The Shannon diversity index is 1.37 when migratory links are calculated using species abundance and 0.51 when using species biomass.

Migratory species breeding on Bylot Island migrate across a broad latitudinal and longitudinal range, but most individuals are found in relatively restricted areas (Figure 3). Migratory individuals, primarily composed of snow geese (30,771 individuals) and Lapland longspurs (6080 individuals), are mostly found in the northeastern and central regions of North America. Beyond North America, shorebirds migrating to the southern part of South America also represent a substantial number of individuals (4226 individuals from five different species).

Ecoregions in temperate North and South America host the highest species richness and biomass of migratory vertebrates originating from Bylot Island (Figure 4). These ecoregions, spanning latitudes 30° to 55° in both hemispheres, support 38% of the total abundance and 93% of the biomass of the vertebrate community

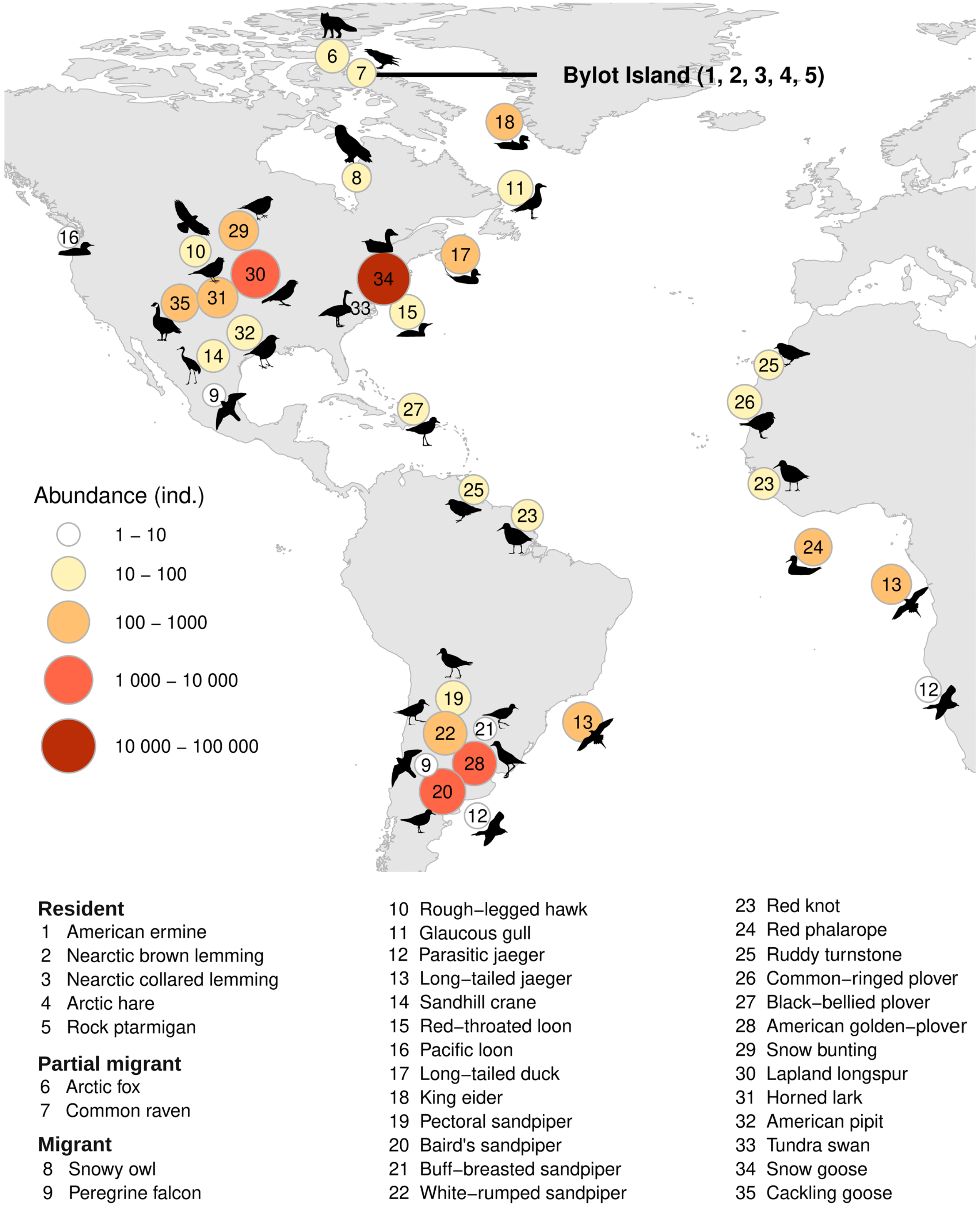

FIGURE 3 | Distribution of the non-breeding range centroids of migratory and partially migratory species from the vertebrate community of Bylot Island. Circle size is proportional to the mean flow of adults maintained between Bylot Island and each species' non-breeding range, while colours represent logarithmic abundance classes. The labels and icons represent the different species; some species are represented by two centroids, indicating that their non-breeding range is divided into distinct areas (e.g., 9: Peregrine falcon, 12: Parasitic jaeger, 13: Long-tailed jaeger, 23: Red knot and 25: Ruddy turnstone).

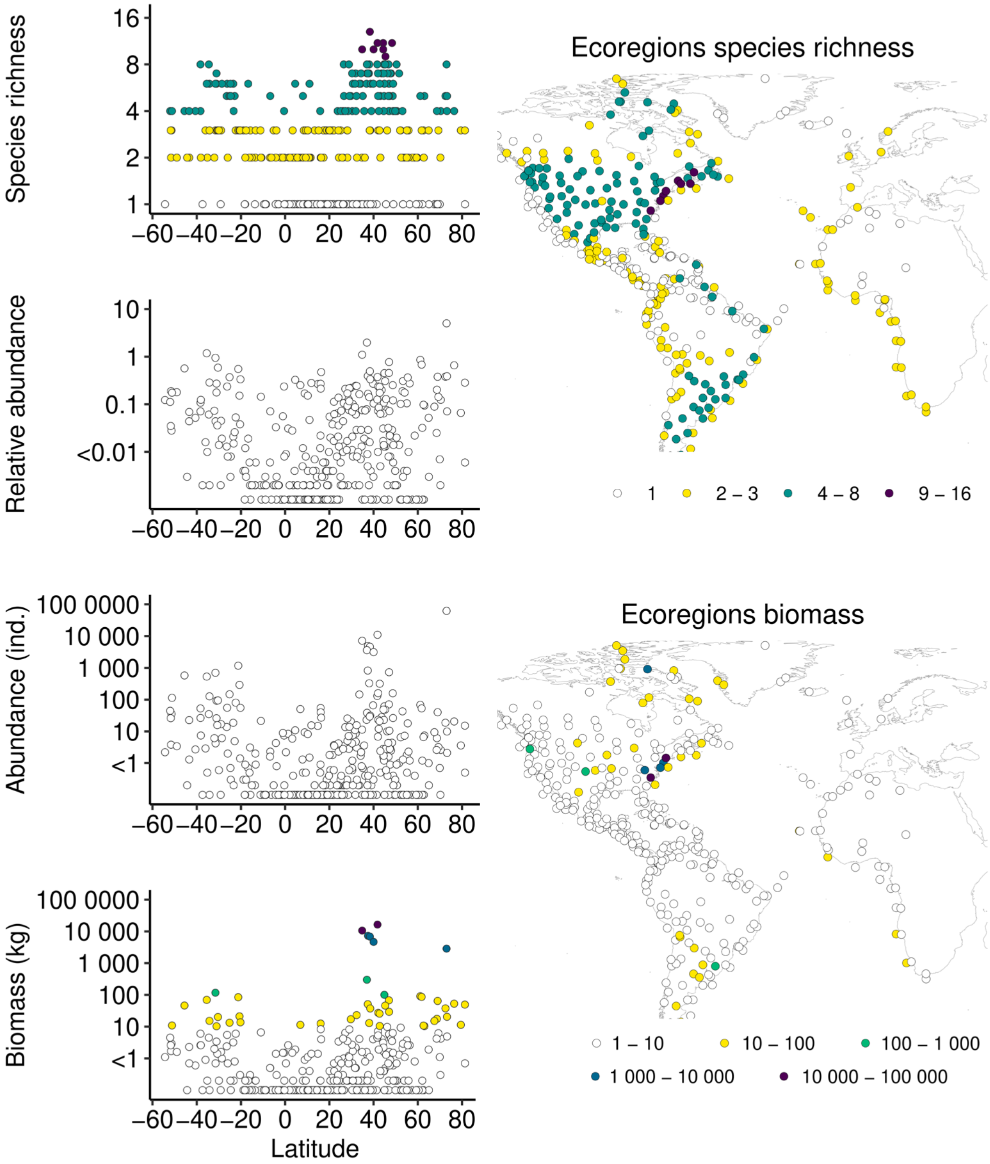

FIGURE 4 | **Left** (from top to bottom): Latitudinal distribution of species richness, cumulative relative abundance, absolute abundance and biomass of vertebrate species from Bylot Island in ecoregions during the non-breeding period. Each point represents a distinct ecoregion, with the latitude taken from its centroid. All *y*-axes are presented on a logarithmic scale. Negative latitude values represent the Southern Hemisphere, positive values the Northern Hemisphere. We use colours to visualise logarithmic classes of species richness and biomass, enabling clear cartographic visualisation on the right panel. **Right**: Cartographic representation of the species richness (top) and biomass (bottom) of Bylot Island-related species in ecoregions during the non-breeding period. The coordinates of ecoregion represent the ecoregion centroid.

during the non-breeding period. Some temperate ecoregions in eastern North America exhibit higher species richness and biomass of Bylot Island-associated species than Bylot Island itself during this period. Polar ecoregions (above 55° of latitude North or below 55° of latitude South), including Bylot Island, support most of the individuals (59% of the total abundance), but a relatively low portion of the biomass (7%), primarily due to the high abundance of small-bodied species such as lemmings. Tropical and subtropical ecoregions account only for 2% of the total abundance and 1% of the biomass. Excluding snow geese, temperate ecoregions of North and South America still show peak values in species richness, abundance, and biomass of migratory species in the temperate ecoregions of North and South America (see Figure S4.2). However, these peaks are less pronounced and have lower abundance and biomass compared to the resident community of Bylot Island. Despite the broad geographic distribution of migratory and partially migratory species during the non-breeding season, a large portion of the abundance and biomass remains in temperate environments of South and especially North America.

Using the case of the snowy owl and the snow goose, we illustrate how measuring migratory links with occurrence, abundance, or biomass can reveal species with contrasting structural influences in the network (i.e., topological anomalies; Figure 5). When using species occurrence, snowy owls maintain links with six times more ecoregions than snow geese. On the contrary, when using abundance, snow geese maintain a flux of individuals nearly 2000 times higher than snowy owls. This example emphasises the complementary information provided by the different measurements of migratory links. Globally, there is no relationship between log species occurrence in ecoregions and log local abundance ($\beta = -0.08$; 95% CI [−0.28, 0.12]; $R^2 = 0.01$) or log biomass ($\beta = -0.17$; 95% CI [−0.38, 0.05]; $R^2 = 0.04$) for species of the Bylot Island vertebrate community.

We observe some differences in the structure of the Bylot Island migration network depending on how migratory links are measured (Table 1). Link diversity is highest when migratory links are measured with species occurrence, intermediate with relative abundance, and lowest with absolute abundance and biomass. The number of modules is lowest when migratory links are measured with species occurrence (9 modules) but is similar when using relative abundance (16 modules), absolute abundance (17 modules) or biomass (15 modules). When applying the *QuanBiMo* algorithm, we observed fewer modules overall compared to our main analysis using the *Infomap* algorithm. Nevertheless, the *QuanBiMo* algorithm also identified the lowest number of modules in the occurrence scenario (three modules) and higher numbers in the relative abundance (four modules), absolute abundance (six modules) and biomass (five modules) scenarios. Excluding snow geese from the network has only a minor effect on module delimitation (see Table S4.1). The composition of modules based on species occurrence shows the greatest contrast of all pairwise comparisons among scenarios (Table 1, Figure S5.1).

Measuring migratory flows using different approaches yields different assemblages of species and ecoregions modules. For instance, in the network based on species occurrence, two modules composed of 9 and 7 species span most of North America (Figure 6). When distributing migratory flow proportionally to relative abundance, we observe a division of these modules into more geographically constrained modules (Figure 6).

5 | Discussion

Understanding the structure of migratory links within metacommunities is crucial for assessing the vulnerability of local communities to distant perturbations. Our results show that measuring migratory links using species occurrence, abundance

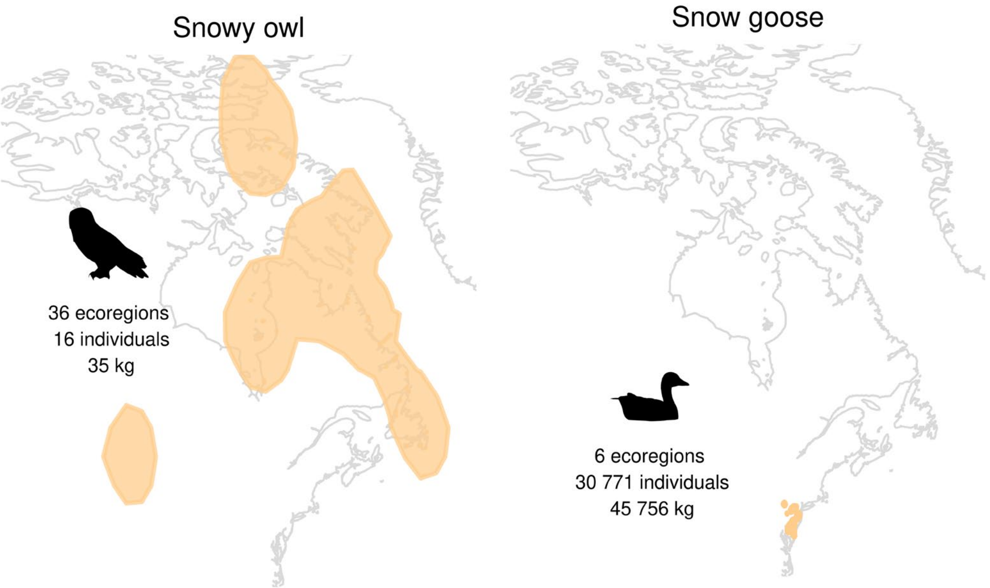

FIGURE 5 | Cartographic representation of the non-breeding range of the snowy owl (left) and the snow goose (right) from Bylot Island. These two species are presented as showcase examples due to their contrasting occurrences and abundances. We present the number of ecoregions within the non-breeding range of each species along with total abundance and biomass.

TABLE 1 | Emerging structural properties of the Bylot Island migration networks when migratory flows are measured with species occurrence, relative or absolute abundance, and biomass. The similarity in modules composition is assessed with the Normalised Mutual Information (NMI) index, with the partition based on species occurrence as a reference. Values range from zero (completely different partitions) to one (the composition of a partition can be predicted perfectly from another one).

Scenario of migratory link	Link diversity	Number of modules	Similarity module composition (species)	Similarity module composition (ecoregions)
Occurrence	7.04	9	1	1
Relative abundance	5.24	16	0.83	0.67
Absolute abundance	2.00	17	0.85	0.70
Biomass	1.96	15	0.88	0.69

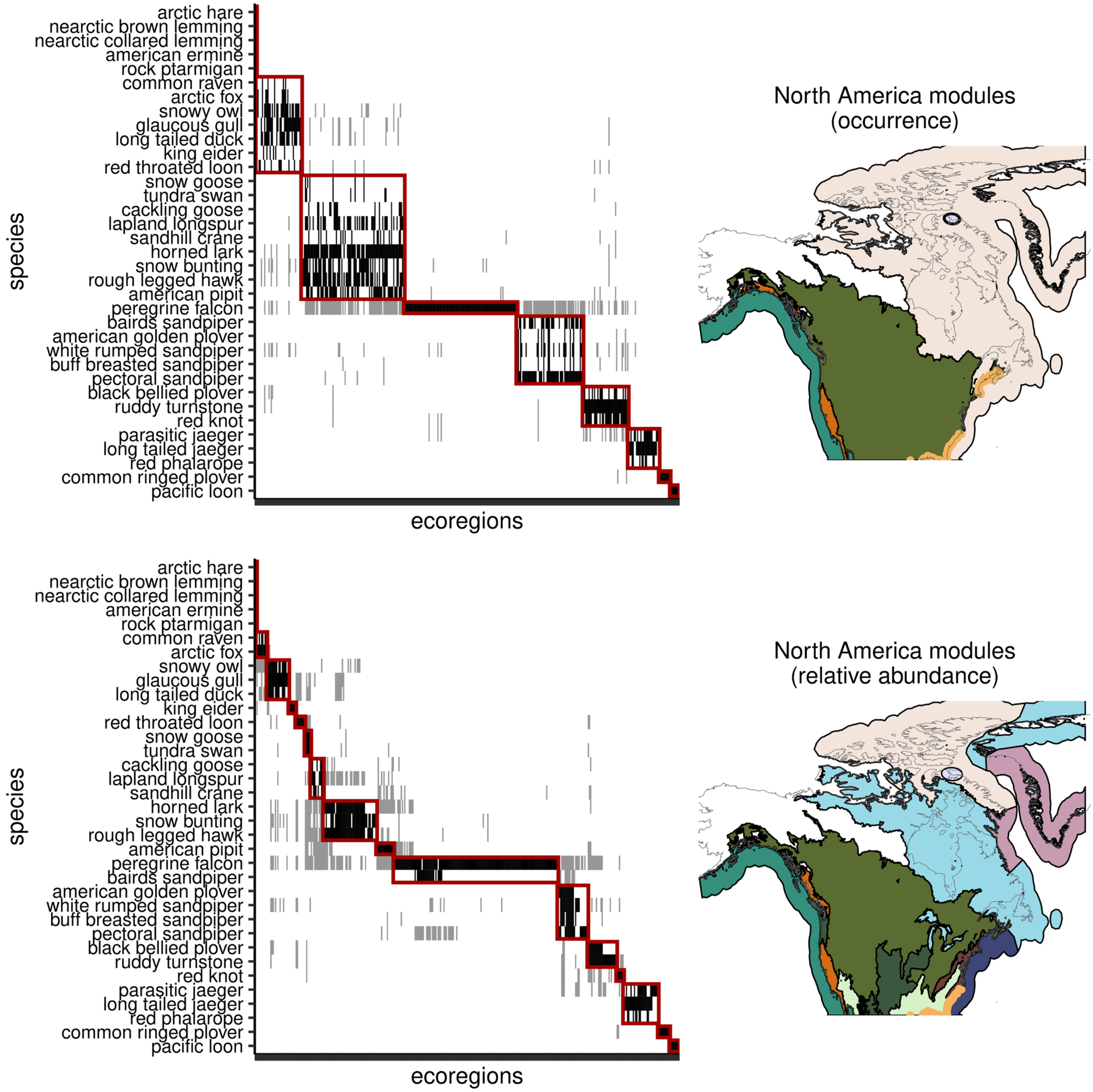

FIGURE 6 | **Left**: Matrix representation of the modules of species and ecoregions within the Bylot Island migration network when migratory flows are measured with species occurrence (top) and species relative abundance (bottom). In each matrix, species and ecoregions are ordered by modules (red boxes), causing the ecoregion order to vary between matrices. Migratory links, defined as connections between species and ecoregions, are represented by black lines when both the species and ecoregion belong to the same module (i.e., within-module connections). Grey line segments indicate connections between species and ecoregions that belong to different modules (i.e., between-module connections). **Right**: Cartographic representation of the North American modules (represented by colours) within the Bylot Island migration network when migratory flows are measured with species occurrence (top) and species relative abundance (bottom). Only modules in North America are shown to simplify cartographic visualisation.

and biomass reveals contrasting structural roles of individual species in the migration network (e.g., snow geese and snowy owls), but tend to highlight similar structural roles for individual ecoregions (e.g., temperate ecoregions). Integrating these three metrics allows us to identify 'key' ecoregions that host both a high diversity, number of individuals and biomass from the focal community during the non-breeding period. These ecoregions, thus, emerge as pivotal areas for the potential propagation of perturbations to the Bylot Island community. In terms of structural characteristics at the network level, we observe that when migratory links are weighted by species relative abundance, large groups of species associated with a common set of ecoregions (i.e., modules) divide into smaller ones. Given the substantial heterogeneity in the occurrence, abundance and biomass of migratory species, using multiple metrics to quantify migratory links provides complementary insights into the structure of global meta-communities.

Measuring migratory links with different metrics allows us to better understand how perturbations occurring in different regions of the globe could propagate to a distant community. For instance, we highlight the importance of temperate ecoregions of North and South America in the migration network of Bylot Island. However, considering the traits of species in those ecoregions, we propose that perturbations occurring in temperate terrestrial or coastal ecoregions of North America rather than in South America present a higher potential of generating cascading effects in the focal community. Temperate ecoregions of North America host a higher functional diversity (i.e., geese, swans, passerines, raptors, cranes, ducks and loons) than temperate ecoregions of South America (i.e., falcons and shorebirds). Perturbations occurring in temperate North America could then have a higher chance of causing additive, antagonistic or synergistic responses at the community level by affecting simultaneously species of different trophic levels (Beauchesne et al. 2021). Ecoregions of northeastern North America are particularly concerning due to intense anthropogenic pressures, including high human population density, extensive fertiliser and pesticide use, habitat fragmentation, and cropland expansion (Bowler et al. 2020).

Our case study enhances our understanding of how individual species within the Bylot Island community could contribute to the propagation of perturbations originating from distant ecoregions. Migratory species with restrained non-breeding ranges, such as the snow goose, are often less resilient to some perturbations (Gilroy et al. 2016), suggesting that the large flow of snow geese may be particularly susceptible to perturbations in their non-breeding range. Any alteration in the flow of snow geese could trigger cascading effects throughout the meta-community. For instance, snow geese influence the functional and numerical responses of the Arctic fox, the main predator in the focal community (Giroux et al. 2012), with cascading impacts on the occurrence and abundance of other species (Duchesne et al. 2021; Beardsell et al. 2023; Dulude-de Broin et al. 2023). Furthermore, waterfowl, including snow geese, are important vectors of pathogens such as avian influenza viruses (McDuie et al. 2024). On the other hand, the Lapland longspur, the second most abundant migratory species in the focal community, has a small body mass relative to snow geese. As a result, it contributes only a small portion to predator diets within the food web (Legagneux et al. 2012). Besides abundant species, low-abundance species could also play critical roles in the spread of epidemiological perturbations. For instance, species with unique migratory links (e.g., the common-ringed plover or the Pacific loon) can act as 'gateways' for the spread of novel pathogen strains within the community (Lam et al. 2012; Varpe and Bauer 2022). Therefore, we argue that the potential of migratory species to propagate perturbations likely depends on a combination of factors, including migratory destinations (i.e., occurrence), abundance, biomass, sensitivity and resilience to perturbations and traits.

Modules within multi-species migration networks represent co-migrations, shaped by diverse ecological, evolutionary, and geographical factors (Cohen and Satterfield 2020; DeSimone et al. 2024) and could potentially influence the vulnerability of a community to distant perturbations. The number and composition of modules in a network can have a major influence on its dynamics since modules can contain perturbations within clusters and increase the stability of the system (Stouffer and Bascompte 2011), in particular spatial ones, such as meta-community (Gravel et al. 2016). However, this observation has yet to be tested in migration networks. Our findings suggest that the distribution of abundance and biomass captures more effectively the climatic and habitat preferences of species compared to occurrence. Indeed, when migratory links are weighted proportionally to relative abundance, distinct modules emerge that seem to correspond to High-Arctic, Low-Arctic, temperate and subtropical regions. In contrast, these distinctions are far less clear when migratory links are measured using species occurrence. Similarly, species abundance and biomass reveal clearer habitat differentiation between modules (terrestrial, coastal and marine). These findings emphasise the value of considering abundance and biomass for a better understanding of ecological factors shaping migration patterns at the community level.

Despite intensive efforts to estimate species abundance and biomass on Bylot Island (Gauthier et al. 2024; Moisan et al. 2025) and to define the non-breeding ranges of its migratory species (Moisan et al. 2023), empirical limitations remain. For instance, we were unable to account for stopover or staging grounds due to the uncertainty surrounding their spatial delineation. Ideally, juvenile abundance and biomass would also have been included. However, doing so would have required assigning asymmetric weights to outgoing (post-breeding) and incoming (pre-breeding) migratory links based on season-specific survival rates, which are currently unavailable. We acknowledge that our data contain variable levels of uncertainty among species, which have not been quantified yet, and therefore make it difficult to determine confidence intervals on network metrics. In addition, as previously noted, the choice of algorithm can influence both the number and composition of modules (Beckett 2016). However, in our context, the *Infomap* algorithm (Farage et al. 2021) appears better suited, as it identified modules that were more geographically and ecologically coherent compared to those identified by the *QuanBiMo* algorithm (Dormann and Strauss 2014), which in some cases grouped species with highly distinct non-breeding grounds. Given the complexities associated with assessing uncertainty in community migration networks, we propose that it should represent a subject of in-depth analysis of its own, which is beyond the scope of this paper.

Community migration networks explicitly capture the seasonality of spatial connections between distant localities (i.e., between breeding and non-breeding grounds), providing valuable empirical information for meta-community and meta-ecosystem studies. In most meta-community and meta-ecosystem theories, populations are typically resident, with only a small fraction of individuals moving continuously to distant communities or ecosystems for dispersal or foraging (Gounand et al. 2018; Guzman et al. 2019). However, the periodic and recurrent movement of entire populations happening during migration is quite distinct. Novel theories, tools and data are thus essential for accurately representing seasonal migrations in future meta-ecological models (Moisan et al. 2023). The observations documented in this study make a first step towards that direction, but we still lack an integration of seasonal interactions among species and with abiotic components, limiting their applicability to investigate trophic meta-community or meta-ecosystem problems. Hybrid dynamical models, which capture the dynamics of systems with distinct states and shifting structures (e.g., changes in network topology), have recently been used to model food web dynamics in seasonal environments (Saavedra et al. 2016; Hutchison et al. 2020). Their study documented fundamentally different dynamics, conditions for coexistence and stability. Informing these models with spatially explicit information from migration networks may prove highly valuable to answer previous calls for spatially realistic meta-ecosystem models (Harvey et al. 2020). Here we documented the spatial movement of migratory organisms; the next step will be to use them to investigate spatial subsidies of energy and abiotic matter driven by migration (Subalusky et al. 2017; Subalusky and Post 2019; Bustnes et al. 2025) and investigate spatio-temporal cascades emerging from these movements (García-Callejas et al. 2019).

The biogeographical patterns of migratory species occurrence, abundance and biomass described in our case study can help inform future conservation efforts and research priorities. By identifying pivotal ecoregions in the migration network of Bylot Island, it could guide conservation efforts needed outside the Arctic to preserve the ecological integrity of this protected area. Furthermore, the distribution of species richness, abundance, and biomass observed in our study suggests that temperate environments may have the greatest potential to propagate perturbations to High-Arctic ecosystems through avian migration, while tropical environments are likely to have little to no influence. At the global scale, the distribution of avian migratory species during the non-breeding period is mainly explained by a trade-off between the avoidance of severe climates, food availability and the migration distance (Somveille et al. 2015), which might explain the strong connection observed between our focal High-Arctic tundra community and the temperate ecoregions of North America. Describing the structure of migratory links in different communities worldwide can enhance our understanding of how environmental changes in one ecosystem may propagate globally.

Author Contributions

Louis Moisan: conceptualisation, methodology, data curation, formal analysis, visualisation, writing – original draft, writing – review and editing. Dominique Gravel: conceptualisation, methodology, funding acquisition, writing – review and editing, supervision and mentoring. Gilles Gauthier: writing – review and editing, funding acquisition. Pierre Legagneux: writing – review and editing, funding acquisition. Joël Bêty: conceptualisation, methodology, writing – review and editing, funding acquisition, supervision and mentoring.

Acknowledgements

We are sincerely grateful for the dedicated students and researchers who have contributed to fieldwork at the Bylot Island research station, recording the data necessary for this project during decades. We wish to highlight the essential role of Marie-Christine Cadieux, Marie-Jeanne Rioux and Éliane Duchesne in coordinating and supporting field campaigns on Bylot Island. We also extend our gratitude to the Centre for Northern Studies, Natural Resources Canada (Polar Continental Shelf Program) and Sirmilik National Park (Parks Canada) for their ongoing logistic assistance. This research was made possible through the financial support of the Natural Sciences and Engineering Research Council of Canada (NSERC), Fonds de recherche du Québec—Nature et technologies (FRQNT), ArcticNet (a Network of Centres of Excellence of Canada) and Polar Knowledge Canada. Finally, we wish to express our deep appreciation to the Mittimatalik community and the Mittimatalik Hunters and Trappers Organization for their continued collaboration and for granting us the privilege to conduct research on their land.

Ethics Statement

Data collected on vertebrates on Bylot Island has been approved by ethical committees of Université du Québec à Rimouski and Université Laval according to the Canadian Council on Animal Care (CCAC) guidelines.

Conflicts of Interest

The authors declare no conflicts of interest.

Data and Code Availability Statement

All data used in this study are publicly available. The primary dataset is archived in Dryad at https://doi.org/10.5061/dryad.1vhhmgr4m, and the complete R project, including all data and code necessary to reproduce the analyses, is available on Zenodo at https://doi.org/10.5281/zenodo.14605503.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.