Université du Québec
à Rimouski

RÉSEAU DE MIGRATION ET EXPOSITION AUX PERTURBATIONS ENVIRONNEMENTALES D'UNE COMMUNAUTÉ DE VERTÉBRÉS ARCTIQUES

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RÉSUMÉ

Au cours de leur cycle annuel, les espèces migratrices saisonnières transportent de l'énergie et de la matière entre les écosystèmes qu'elles visitent, et interagissent avec les espèces des réseaux trophiques locaux. En reliant des écosystèmes et des communautés éloignés, les espèces migratrices génèrent des dynamiques écologiques sur de grandes échelles spatiales. Des perturbations environnementales peuvent alors se propager à travers ces réseaux d'écosystèmes interconnectés par la migration et ultimement influencer la structure et la dynamique de systèmes naturels éloignés, mais connectés par la migration. Ainsi, les communautés comprenant des espèces migratrices peuvent subir l'influence de perturbations environnementales distantes, se produisant parfois à des milliers de kilomètres. Cependant, la structure des connexions écologiques établies par les espèces migratrices n'a jamais été caractérisée pour l'ensemble des espèces d'une communauté.

Les objectifs de cette thèse sont de : i) développer un cadre permettant de représenter et de caractériser la structure des connexions migratoires maintenues entre une communauté focale et des communautés distantes, et ii) fournir une description empirique de la structure de ces connexions, ainsi que de l'exposition des espèces aux perturbations environnementales, en se basant sur une communauté de vertébrés arctiques. Nous nous concentrons sur la communauté de vertébrés de la plaine sud de l'île Bylot (~400 km^2 ; Nunavut, Canada). Les communautés arctiques constituent un excellent modèle pour étudier la migration, en raison de leur faible richesse spécifique, forte proportion d'espèces migratrices et diversité relativement élevée de stratégies migratoires.

Nous avons adapté la représentation des réseaux de migration, habituellement appliquée à l'échelle des espèces, pour caractériser les connexions migratoires entre une communauté focale et des écorégions distantes. Les « *réseaux de migration des communautés* » offrent un cadre pour caractériser la structure des connexions migratoires en utilisant des métriques traditionnellement utilisées dans les réseaux écologiques. L'approche conceptuelle proposée est facilement transférable à divers types d'écosystèmes à travers le globe.

En caractérisant les connexions migratoires entre la communauté de vertébrés de l'île Bylot et diverses écorégions à l'échelle mondiale, nous avons montré que les communautés arctiques peuvent faire partie intégrante de vastes réseaux de migration incluant des centaines d'écorégions. Bien que le chevauchement spatial des espèces de vertébrés de l'île Bylot soit faible pendant la non-reproduction, leur organisation est modulaire, avec des groupes d'espèces partageant des régions communes. Nous avons montré que le recours à l'occurrence, à l'abondance ou à la biomasse des espèces pour pondérer les connexions migratoires apporte des informations complémentaires sur la structure d'un réseau de migration. Certaines espèces présentent une large répartition, mais une faible abondance et biomasse, et inversement ; selon la métrique choisie, le rôle structurel des espèces peut donc varier au sein d'un réseau de migration. L'utilisation de l'abondance ou de la biomasse pour pondérer les connexions migratoires met en évidence une subdivision plus fine du réseau en modules comparativement à l'emploi de l'occurrence.

Par ailleurs, l'estimation de l'abondance et de la biomasse des espèces de vertébrés de l'île Bylot a permis de constituer un jeu de données unique et rare qui permettra d'évaluer les changements de biodiversité et modéliser la dynamique trophique au sein d'une communauté terrestre arctique.

Dans un dernier temps, nous avons quantifié l'exposition des espèces de vertébrés de l'île Bylot aux perturbations environnementales durant la période de non-reproduction. Nous avons observé que les espèces migratrices d'une communauté de la toundra sont exposées à diverses perturbations environnementales hors de la période de reproduction, mais surtout au réchauffement du climat et aux activités agricoles. Nous avons également observé que les espèces migratrices partageant un habitat et une diète similaires pendant la période de reproduction ont tendance à migrer vers des lieux distincts pendant la période de non-reproduction, tout en étant exposées à des perturbations environnementales similaires.

La caractérisation des connexions migratoires générées par les espèces migratrices de l'île Bylot contribue à une meilleure compréhension de la vulnérabilité de cette communauté face à des perturbations environnementales distantes. Globalement, cette thèse représente un premier pas dans l'étude des patrons migratoires à l'échelle des communautés et contribue à l'émergence d'un nouveau champ de recherche en écologie.

Mots clés : Migration saisonnière, Communauté de vertébrés, Métacommunauté, Réseau de migration, Perturbations environnementales, Arctique, île Bylot

ABSTRACT

Over their annual cycle, seasonally migratory species transport energy and matter between the ecosystems they visit, and interact with species in local food webs. By linking distant ecosystems and communities, migratory species generate large-scale ecological dynamics. Environmental perturbations can then spread through these networks of ecosystems interconnected by migration and ultimately influence the structure and dynamics of natural systems that are geographically distant yet connected through migration. Thus, communities that include migratory species may be affected by environmental perturbations occurring thousands of kilometers away. However, the structure of the ecological connections established by migratory species has never been characterized for all species within a community.

The objectives of this thesis are i) to develop a framework for representing and characterizing the structure of migratory connections maintained with a focal community, and (ii) to empirically describe both the structure of these connections and the exposure of species to environmental perturbations, using an Arctic vertebrate community as a case study. We focus on the vertebrate community of the south plain of Bylot Island (~400 km^2 ; Nunavut, Canada). Arctic communities represent an excellent model for studying migration due to their low species richness, high proportion of migratory species, and relatively diverse migratory strategies.

We adapted the representation of migration networks, typically applied at the species level, to study migratory connections between a focal community and distant ecoregions. Community migration networks provide a framework for characterizing the structure of migratory connections using metrics traditionally employed in ecological networks. The proposed conceptual approach is easily transferable to diverse ecosystems around the globe.

By characterizing migratory connections between the Bylot Island vertebrate community and various ecoregions worldwide, we showed that Arctic communities can be integral parts of extensive migration networks involving hundreds of ecoregions. Although spatial overlap among Bylot Island vertebrates is low during the non-breeding period, their organization is modular, with groups of species occupying common regions. We found that using species occurrence, abundance, or biomass to weight migratory connections provides complementary information on the structure of a migration network. Some species exhibit large distributions but represent a low abundance and biomass, and vice versa Thus, depending on the selected metric, the structural role of a species can vary within a migration network. Weighting migratory connections by abundance or biomass highlights a finer subdivision of the network into modules compared to using occurrence.

Furthermore, estimating the abundance and biomass of Bylot Island vertebrates produced a unique and rare dataset, useful for assessing biodiversity changes and modeling trophic dynamics within an Arctic terrestrial community.

Finally, we quantified the exposure of Bylot Island vertebrates to environmental perturbations during the non-breeding period. We observed that migratory species in a tundra community are exposed to various environmental perturbations outside the breeding period, primarily warming and agricultural activities. We also found that migratory species sharing a similar habitat and diet during the breeding season tend to migrate to distinct non-breeding sites, while being exposed to similar environmental perturbations.

Characterizing the migratory connections generated by migratory species of Bylot Island contributes to a better understanding of the vulnerability of this community to distant environmental perturbations. Overall, this thesis represents a first step in the study of community-level migration patterns and contributes to the emergence of a new field of research in ecology.

Keywords : Seasonal migration, Vertebrate community, Meta-community, Migration network, Environmental perturbations, Arctic, Bylot Island

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INTRODUCTION GÉNÉRALE

0.1 La migration saisonnière

Au fil des saisons, des milliards d'organismes migrateurs parcourent le globe afin de compléter leur cycle annuel (Varpe et al., 2005; Hu et al., 2016; Rosenberg et al., 2019) influençant ainsi la structure et le fonctionnement des écosystèmes (Holdo et al., 2011; Bauer and Hoye, 2014). Dans cette thèse, les termes **migration saisonnière** et **migration** seront utilisés de manière interchangeable pour désigner les mouvements bidirectionnels et saisonniers effectués par des individus entre une aire de reproduction et une ou des aires de non-reproduction (Webster et al., 2002; Mueller and Fagan, 2008; Winger et al., 2019). À noter que le terme « *migration* » est couramment employé en écologie pour désigner d'autres phénomènes distincts de la migration saisonnière, tels que les « *migrations humaines* », le « *taux de migration des gènes* », ou encore la « *migration de l'aire de répartition d'une espèce* » (Dingle and Drake, 2007). Le manque de cohérence dans la définition de la migration animale nuit à l'extraction de généralités et à une compréhension intégrée de la migration saisonnière à travers les différentes échelles écologiques, notamment en ce qui concerne les liens entre les processus agissant à l'échelle individuelle et les patrons observés à l'échelle des populations (Dingle and Drake, 2007). La définition retenue exclut ainsi les migrations s'étendant sur plusieurs générations, comme celle typiquement illustrée par les papillons monarques (*Danaus plexippus*), ainsi que les migrations à plus petite échelle temporelle, telles que les migrations verticales quotidiennes du plancton (Chapman et al., 2014). Dans certaines populations, on observe parfois la coexistence d'individus résidents et de migrateurs saisonniers, un phénomène désigné sous le terme de **migration partielle** (Chapman et al., 2011).

0.1.1 Évolution de la migration saisonnière

La migration saisonnière a évolué de manière indépendante chez plusieurs taxons, permettant aux organismes de réduire le risque de prédation (McKinnon et al., 2010; Skov et al., 2013), d'éviter des conditions environnementales défavorables (Boyle et al., 2010; Shaw, 2016) et de bénéficier d'un meilleur accès aux ressources (Somveille et al., 2015; Thorup et al., 2017). De manière générale, la forte fidélité des espèces migratrices à leurs sites de reproduction suggère que la migration pourrait avoir évolué comme une stratégie permettant de conserver cette fidélité tout en évitant les saisons associées à des conditions environnementales défavorables (Winger et al., 2019). La migration saisonnière représenterait ainsi une stratégie adaptative avantageuse pour faire face aux variations saisonnières des conditions environnementales, particulièrement chez les organismes dotés d'une grande capacité de déplacement.

Des cas de migration saisonnière ont été documentés chez une grande diversité de taxons, incluant les insectes, crustacés, mollusques, poissons, amphibiens, reptiles, mammifères terrestres et marins, ainsi que, bien entendu, chez les oiseaux (Shaw, 2016). Les oiseaux constituent sans doute le groupe chez lequel la migration saisonnière a été le plus étudiée (Chapman et al., 2014), notamment parce que 19 % des quelque 10 000 espèces d'oiseaux sont migratrices (Kirby et al., 2008) et que l'observation d'oiseaux migrateurs est relativement accessible comparée à celle d'autres taxons, tels que les organismes de petite taille (insectes) ou aquatiques (crustacés et poissons). En conséquence, de nombreuses avancées empiriques, conceptuelles et théoriques liées à la migration saisonnière proviennent de l'ornithologie (Newton, 2023).

0.1.2 Patrons de distribution des espèces migratrices aviaires

À l'échelle mondiale, les régions subtropicales et tempérées de l'hémisphère nord présentent la plus grande richesse spécifique d'espèces migratrices aviaires (**Figure 0.1**). Toutefois, la proportion d'espèces migratrices dans les communautés locales augmente avec la latitude, atteignant son maximum dans le Haut-Arctique, où environ 90 % des espèces aviaires sont migratrices (Newton and Dale, 1996; Somveille et al., 2013). La migration saisonnière est donc un phénomène plus accentué dans l'hémisphère nord, possiblement en raison d'un climat plus fortement saisonnier, lui-même lié à la forme plus étendue des continents dans cet hémisphère (Somveille et al., 2013). En plus du gradient latitudinal marqué de la richesse et de la proportion d'espèces migratrices, on observe également un gradient latitudinal fonctionnel au sein des oiseaux migrateurs (Newton and Dale, 1996). La proportion d'oiseaux aquatiques et côtiers augmente des régions subtropicales vers les régions nordiques. En revanche, la proportion d'oiseaux migrateurs terrestres croît des régions subtropicales jusqu'aux régions boréales, puis diminue graduellement à travers l'Arctique. En bref, la migration saisonnière est un phénomène écologique particulièrement associé aux régions soumises à de fortes variations saisonnières des conditions environnementales (Hurlbert and Haskell, 2003; Dalby et al., 2014; Somveille et al., 2015), en particulier dans les régions subtropicales, tempérées et nordiques de l'hémisphère nord.

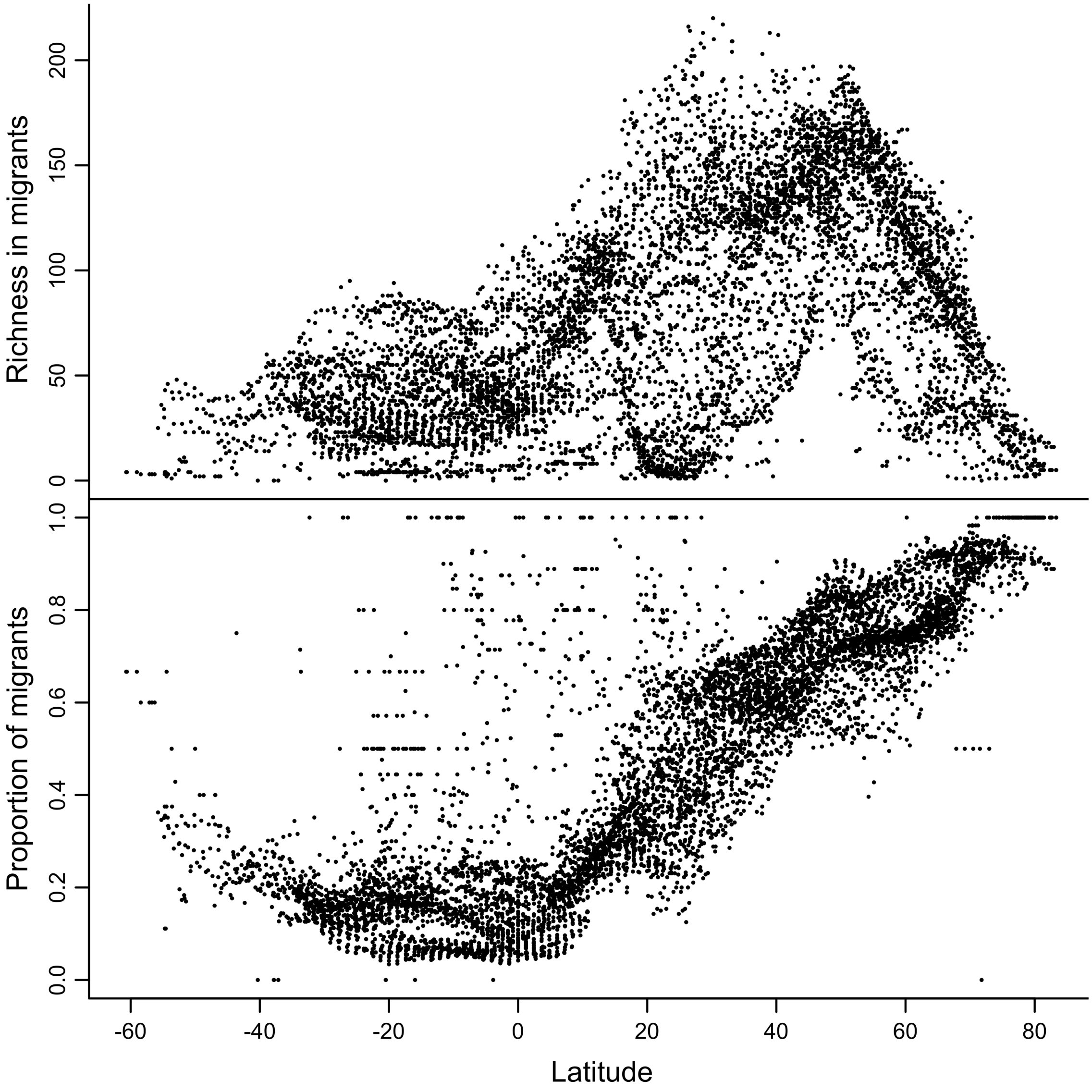

FIGURE 0.1 – Figure extraite de Somveille et al. (2013) illustrant, à l'échelle globale, la richesse et la proportion d'espèces aviaires migratrices (non permanentes) en fonction de la latitude. Chaque point représente une cellule d'environ 23 000 km^2, dans laquelle la proportion d'espèces d'oiseaux migrateurs a été calculée à partir des cartes de distribution des espèces à l'échelle mondiale.

Des barrières écologiques majeures (p. ex. chaînes de montagnes, déserts, océans, golfes et calottes polaires) façonnent les patrons migratoires des espèces aviaires à l'échelle globale et génèrent une convergence des migrations le long de corridors communs (**Figure 0.2**). Le concept de corridors de migration a longtemps été utilisé pour la gestion des populations de sauvagine en Amérique du Nord et plusieurs observations récentes supportent ce concept (Lam et al., 2012; Fourment et al., 2017; Roberts et al., 2023).

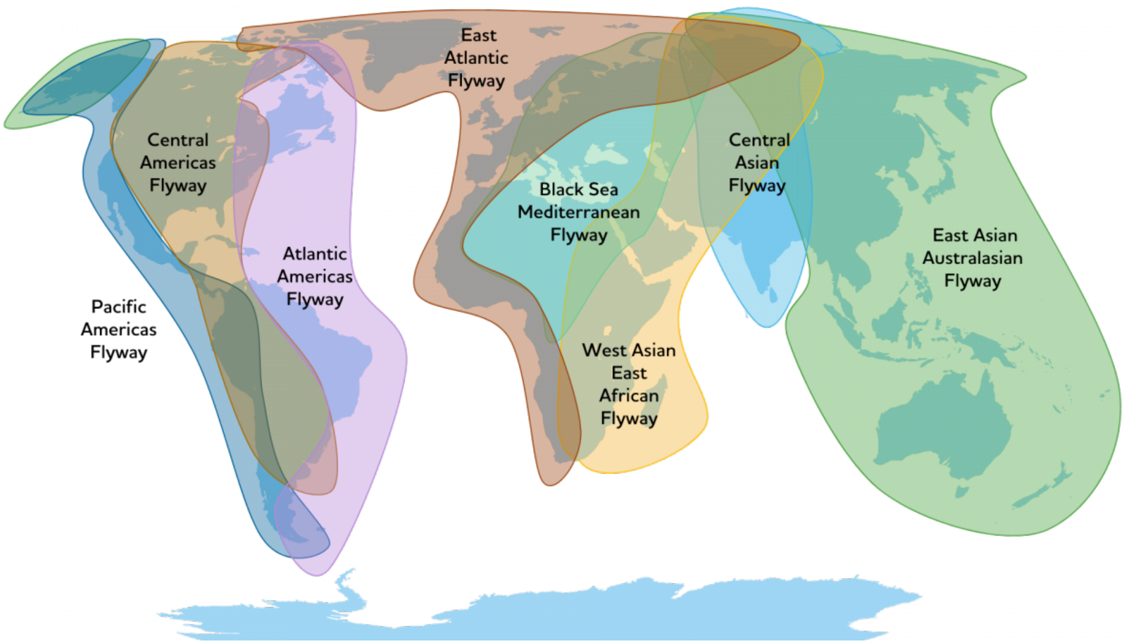

FIGURE 0.2 – Carte des huit principaux corridors migratoires globaux des oiseaux migrateurs. La figure a été extraite de `https://flyway.waddensea-worldheritage.org/flyway-conservation`.

0.1.3 Vulnérabilité des espèces migratrices aviaires

Les espèces migratrices saisonnières dépendent de plusieurs écosystèmes distants et peuvent ainsi être exposées à de multiples menaces tout au long de leur cycle annuel

(Vickery et al., 2014). Les perturbations environnementales sur les aires de reproduction peuvent affecter à la fois la survie et la fécondité des individus, tandis que celles sur les aires de non-reproduction n'agissent que directement sur la survie. Toutefois, les conditions environnementales rencontrées par les individus durant une saison peuvent également générer des effets reportés (« *carry-over effects* ») et influencer leur reproduction et leur survie lors d'une saison ultérieure (Norris, 2005; Norris and Taylor, 2006), un phénomène fréquemment observé chez les espèces migratrices (Harrison et al., 2011).

Les espèces migratrices semblent montrer une grande capacité d'adaptation, avec une flexibilité importante des traits migratoires (distance de migration, orientation et phénologie), résultant à la fois de l'évolution et de la plasticité phénotypique (Sutherland, 1998; Teitelbaum et al., 2016; Ozsanlav-Harris et al., 2023). Dans certains cas, des espèces ont transitionné de migratrices à résidentes, et inversement (Able and Belthoff, 1998; Pulido and Berthold, 2010). Par exemple, des roselins familiers (*Carpodacus mexicanus*) issus d'une population presque exclusivement résidente (2 à 3 % de migrateurs) en Californie ont été introduits à New York, où, en l'espace de seulement 20 ans, la proportion de migrateurs dans la population introduite a augmenté pour atteindre environ 30 % (Able and Belthoff, 1998). À l'opposé, une réduction marquée de l'activité migratoire a été observée sur une période de 14 ans dans une population de fauvette à tête noire (*Sylvia atricapilla*), probablement associée aux changements climatiques (Pulido and Berthold, 2010). Toutefois, certaines espèces migratrices montrent une forte fidélité des adultes à des sites qui semblent suboptimaux, ce qui peut réduire leur capacité d'adaptation (Ganter and Cooke, 1998). Par exemple, les petites oie des neiges (*Chen caerulescens caerulescens*) adultes ont montré une forte fidélité à leur site de reproduction malgré une dégradation continue de l'habitat (Ganter and Cooke, 1998). De manière générale, à l'échelle mondiale, les espèces migratrices de longue distance déclinent plus rapidement que les espèces résidentes ou migratrices de courte distance (Robbins et al., 1989; Wilcove and Wikelski, 2008; Vickery et al., 2014; Rosenberg et al., 2019). Cependant, au sein des groupes d'oiseaux migrateurs, on observe des tendances de populations contrastées (Rosenberg et al., 2019). Par exemple, entre 1970 et 2018, les populations de rapaces et de sauvagine en Amérique du Nord ont augmenté de 50 à 200 %, tandis que la majorité des passereaux et des limicoles ont diminué de 10 à 75 %, entraînant une perte nette d'environ trois milliards d'individus (Rosenberg et al., 2019). Le déclin a été particulièrement marqué sur la côte est de l'Amérique du Nord (Rosenberg et al., 2019).

0.2 Rôle des espèces migratrices au sein des communautés et des écosystèmes

Par leurs passages saisonniers, les espèces migratrices interagissent avec d'autres espèces et transportent énergie, matière et organismes tels que parasites et pathogènes, influençant ainsi périodiquement la structure et la dynamique des communautés et des écosystèmes à l'échelle du globe (Polis et al., 1997; Holdo et al., 2011; Bauer and Hoye, 2014).

0.2.1 Effets trophiques

Les espèces migratrices occupent diverses positions dans les réseaux trophiques, allant des herbivores, comme les oies, les gnous et les caribous, jusqu'aux grands prédateurs, tels que les rapaces, certains requins et mammifères marins (Bauer and Hoye, 2014; Holdo et al., 2011). L'impact du broutement des espèces migratrices compte parmi les exemples les plus iconiques de leur influence au sein des communautés (Jefferies, 2004; Fryxell and Sinclair, 1988). Malgré leur présence temporaire au sein des communautés, les herbivores migrateurs peuvent influencer drastiquement la biomasse, la productivité et la diversité des communautés végétales, avec des conséquences en cascade sur les propriétés du sol, les cycles des biogéochimiques, ainsi que les régimes de feux ou d'inondations (Holdo et al., 2011; Bauer and Hoye, 2014). Par exemple, l'augmentation exponentielle de la population de la petite oie des neiges (*Chen caerulescens caerulescens*) entre 1960 et 1990 en Amérique du Nord a entraîné une intensification du broutement sur les sites de reproduction dans les milieux arctiques (Jefferies, 2004). Ce broutement intensif a entraîné une augmentation de l'évaporation et une hypersalinisation des sols, conduisant à un changement drastique de la composition et de la productivité des communautés végétales (Jefferies, 2004).

L'arrivée massive et relativement synchronisée de proies migratrices dans un réseau trophique peut fortement influencer la réponse numérique et fonctionnelle des prédateurs (Holdo et al., 2011; Bauer and Hoye, 2014; Furey et al., 2018). Par exemple, dans le Haut-Arctique canadien, les renards arctiques (*Vulpes lagopus*) dont la tanière est située à l'intérieur ou à proximité d'une colonie d'oies migratrices ont une probabilité accrue de se reproduire (Giroux et al., 2012). L'arrivée massive de proies migratrices peut également entraîner un changement dans la diète des prédateurs, relâchant ainsi temporairement la pression de prédation sur les proies résidentes (Darimont et al., 2008; Furey et al., 2018). Inversement, la présence de proies migratrices peut entraîner une agrégation des prédateurs et accroître la pression de prédation sur les proies résidentes (Duchesne et al., 2021; Beardsell et al., 2023; Dulude-de Broin et al., 2023). Par ailleurs, les prédateurs migrateurs peuvent accroître le risque de prédation sur les proies résidentes, entraînant des effets en cascade sur l'ensemble du réseau trophique (Bauer and Hoye, 2014; Furey et al., 2018). Théoriquement, le couplage entre réseaux trophiques par l'intermédiaire de prédateurs favorise la stabilité des systèmes (McCann et al., 2005). Toutefois, cette question n'a jamais été testée dans un contexte de mouvements migratoires saisonniers. L'influence des proies et prédateurs migrateurs sur la stabilité et la résilience des réseaux trophiques reste encore peu documentée sur le plan théorique (Bauer and Hoye, 2014; Guzman et al., 2019). Le rôle des espèces migratrices au sein des communautés pourrait également varier au cours du cycle annuel, en raison de stades du cycle de vie ou de besoins physiologiques variables. Par exemple, la production de jeunes par les espèces migratrices pendant la saison de reproduction peut constituer une source importante d'énergie pour les prédateurs locaux (Giroux et al., 2012), ce qui n'est pas le cas lorsque les espèces migratrices visitent les écosystèmes en dehors de cette période.

0.2.2 Effets de transport

En visitant différents écosystèmes au cours de leur cycle annuel, les espèces migratrices génèrent des échanges d'énergie, de nutriments et de contaminantssur des distances pouvant atteindre plusieurs milliers de kilomètres (Holdo et al., 2011; Bauer and Hoye, 2014). Par exemple, à la suite de l'accident nucléaire de Fukushima au Japon, des thons rouges du Pacifique (*Thunnus orientalis*) ont transporté des éléments radioactifs des côtes japonaises jusqu'au large de la Californie (Madigan et al., 2012). En ce qui concerne l'énergie et les nutriments, certaines espèces migratrices peuvent générer des transferts de matière et d'énergie substantiels. Par exemple, la reproduction du hareng (*Clupea harengus*) dans les zones côtières entraîne un dépôt estimé à 1 300 000 tonnes d'œufs et de laitance (Varpe et al., 2005), tandis que les montaisons de saumons du Pacifique peuvent fournir chaque année environ 9 000 tonnes d'azote et 1 100 tonnes de phosphore sur les sites de reproduction sur le long de la côte ouest de l'Amérique du Nord (Brandt et al., 2024). Les transferts substantiels d'énergie et de nutriments effectués par les espèces migratrices peuvent ainsi fortement influencer les cycles biogéochimiques et la structure des écosystèmes (Subalusky and Post, 2019). Par exemple, lors de la traversée de rivières au cours de leur migration, des milliers de gnous se noient, et la décomposition de leurs carcasses dans les rivières entraîne, au cours du mois suivant, une augmentation substantielle des concentrations d'azote (entre 6 et 78 %), de phosphore (31-451 %) et de carbone organique dissous (18-191 % ; Subalusky et al. 2017).

De plus, les espèces migratrices peuvent transporter des pathogènes, des parasites, d'autres micro-organismes ainsi que des propagules entre différents écosystèmes (Altizer et al., 2011; Bauer and Hoye, 2014; Viana et al., 2016). Les oiseaux migrateurs jouent un rôle majeur dans la dynamique épidémiologique de pathogènes tels que la grippe aviaire et le virus du Nil occidental (Altizer et al., 2011; Lam et al., 2012; Hill et al., 2016; Swetnam et al., 2018), et, dans certains cas, des épidémies peuvent affecter sévèrement la dynamique des populations migratrices (Descamps et al., 2012). En transportant des propagules telles que des graines, des œufs ou des micro-organismes, les espèces migratrices peuvent également faciliter la dispersion d'organismes à faible capacité de déplacement, favorisant ainsi l'expansion de leur aire de répartition et leur adaptation au changement climatique (Viana et al., 2016). Toutefois, par ce même processus, les espèces migratrices peuvent favoriser l'introduction et la dispersion d'espèces exotiques (Green, 2016).

0.2.3 Influence de la migration sur la vulnérabilité des communautés et des écosystèmes

Les populations migratrices dépendent des conditions environnementales de plusieurs écosystèmes éloignés, si bien qu'un changement dans l'un d'eux peut modifier le rôle que jouent ces espèces dans un autre écosystème (Jefferies, 2000; Madigan et al., 2012; Hessen et al., 2017). Par exemple, des changements dans les pratiques agricoles dans les environnements tempérés ont contribué à l'augmentation de populations d'oies à travers l'Arctique (Ganter et al., 2013), causant des changements dans les communautés végétales via l'herbivorie (Jefferies, 2004) et des changements dans les communautés de vertébrés via des effets trophiques indirects (Duchesne et al., 2021), la modification de la structure d'habitat (Flemming et al., 2019), ainsi que des changements des propriétés physico-chimiques du sol (Jefferies, 2004) et des plans d'eau (Hessen et al. 2017 ; **Figure 0.3**). Les espèces migratrices peuvent ainsi propager spatialement les effets de perturbations environnementales locales ou régionales à l'échelle globale, en connectant la dynamique écologique d'écosystèmes distants. La structure et la dynamique des communautés ou des écosystèmes comprenant des espèces migratrices peuvent ainsi être influencées par des changements environnementaux survenant dans des environnements éloignés, mais connectés par la migration animale (Bauer and Hoye, 2014).

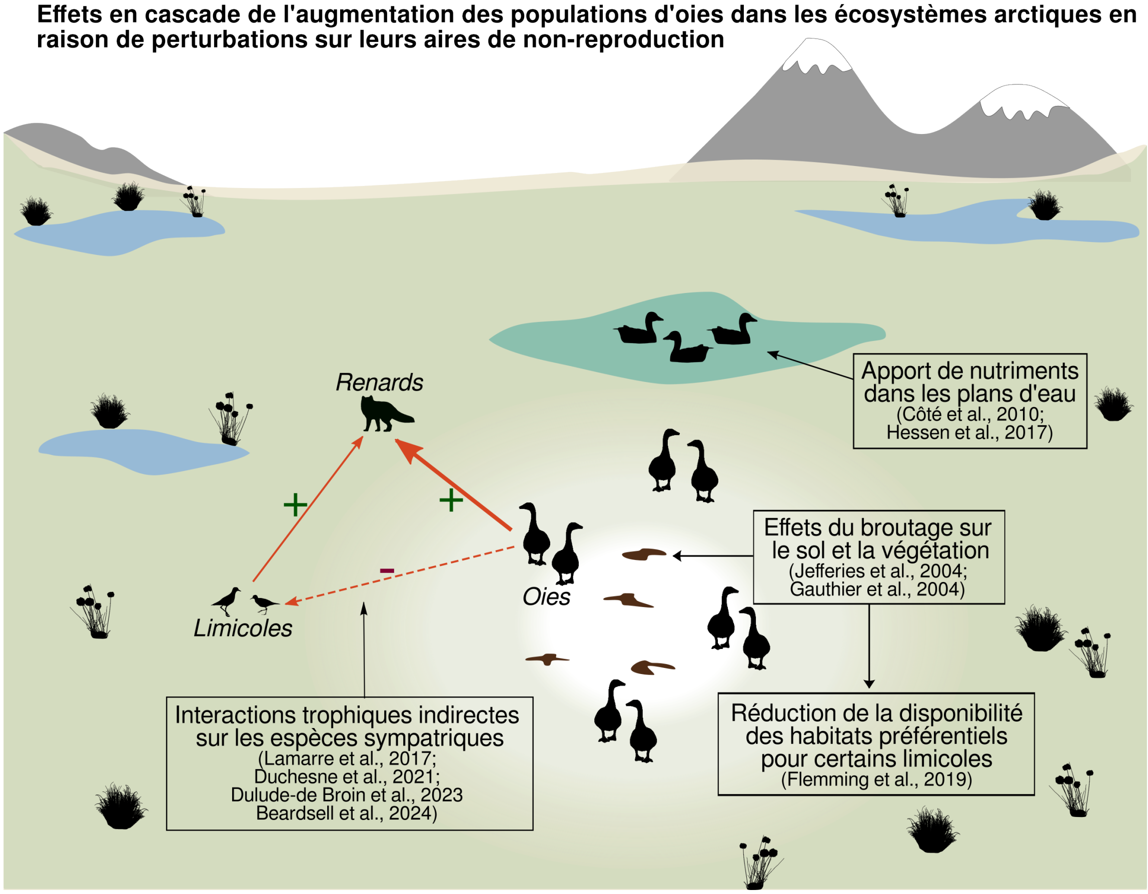

Figure 0.3 – Schématisation des effets en cascades engendrés par l'augmentation des populations d'oies à travers l'Arctique causé entre autres par des changements environnementaux dans les écosystèmes tempérés. Les références représentent différentes espèces d'oies et sites à travers l'Arctique.

À l'échelle d'une communauté, selon les stratégies migratoires des espèces, plusieurs espèces migratrices peuvent être influencées simultanément par une perturbation environnementale se produisant à l'extérieur de la communauté (**Figure 0.4**). Considérant la position des espèces impactées dans le réseau trophique, l'effet de la perturbation peut être cumulatif, antagoniste ou synergique (Beauchesne et al., 2021). Dans ce cas, une perturbation pourrait influencer simultanément l'ensemble des espèces d'un groupe fonctionnel d'une communauté et générer potentiellement un effet additif dans le réseau trophique. Au sein des groupes fonctionnels d'une communauté, les espèces migratrices peuvent occuper des aires de non-reproduction communes ou distinctes, et être ainsi exposées à des perturbations environnementales similaires ou contrastées (**Figure 0.5**). Il est donc essentiel de considérer les destinations migratoires de l'ensemble des espèces au sein d'une communauté, mais également leur position trophique pour évaluer exhaustivement la vulnérabilité d'une communauté face à des perturbations distantes. Toutefois, notre compréhension, tant empirique que théorique, de l'influence de la migration animale sur la vulnérabilité des communautés et des écosystèmes demeure très limitée. Considérant l'omniprésence des migrations animales (Somveille et al., 2013; Chapman et al., 2014) et la distribution hétérogène des changements environnementaux à l'échelle globale (Bowler et al., 2020), il est essentiel de mieux comprendre la connectivité écologique assurée par les espèces migratrices, ainsi que son rôle dans la vulnérabilité des communautés et des écosystèmes face aux changements globaux.

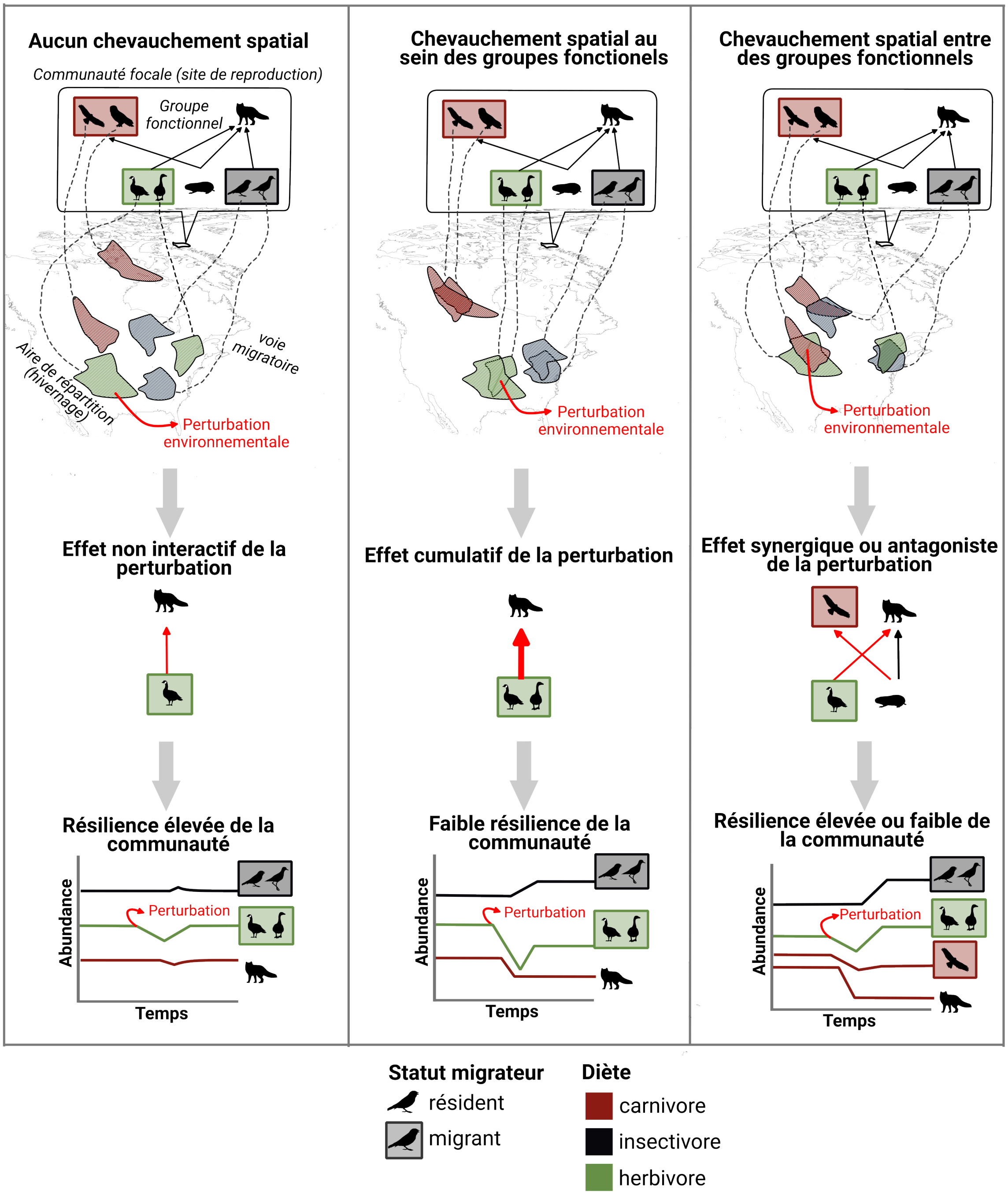

FIGURE 0.4 – Représentations schématiques et fictives de différents cas de patrons migratoires à l'échelle d'une communauté, mettant en évidence leurs effets potentiels sur la propagation des perturbations au sein des réseaux trophiques, ainsi que sur la résilience de la communauté face aux perturbations environnementales distantes.

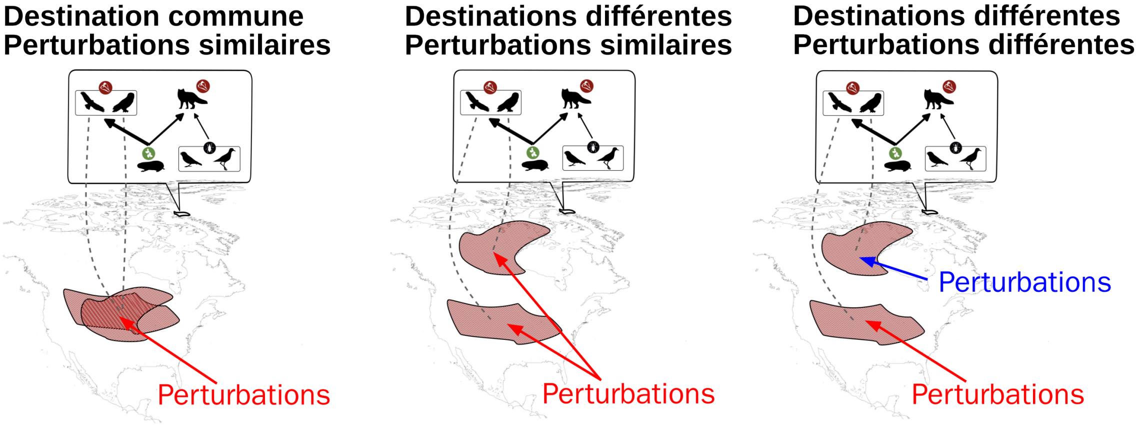

Figure 0.5 – Représentations schématiques de différents cas de figure illustrant les destinations migratoires des espèces migratrices appartenant à un même groupe fonctionnel d'une communauté au cours d'une saison donnée, ainsi que leur exposition à des régimes de perturbations similaires ou contrastés (représentés ici par différentes couleurs). La communauté focale est représentée par un encadré noir, au sein duquel figurent plusieurs groupes fonctionnels caractérisés par différents statuts migratoires (migrateurs : contour plein ; résidents : absence de contour) et régimes alimentaires (herbivores : icône verte ; insectivores : icône noire ; carnivores : icône rouge). Les cas de figure présentés sont illustrés uniquement pour le groupe fonctionnel des carnivores migrateurs afin de simplifier la figure.

0.3 Intégration théorique de la migration saisonnière en écologie

La migration saisonnière a été fortement étudiée à l'échelle des individus, des populations et des espèces, ce qui a permis d'importantes avancées théoriques. Toutefois, son intégration au niveau des communautés et des écosystèmes demeure encore très limitée.

0.3.1 La migration saisonnière, un mouvement distinct

Les caractéristiques des mouvements migratoires saisonniers se distinguent fondamentalement des autres types de mouvements (Mueller and Fagan, 2008; Chapman et al., 2014; Gounand et al., 2018; Guzman et al., 2019), ce qui pose un défi majeur pour leur intégration aux théories écologiques existantes. Premièrement, contrairement aux mouvements de dispersion ou d'alimentation, les mouvements migratoires sont liés à des phases spécifiques du cycle de vie. Ainsi, la reproduction et la non-reproduction des espèces migratrices se déroulent nécessairement dans des écosystèmes distincts (Gounand et al. 2018 ; **Figure 0.6**). Deuxièmement, les mouvements migratoires sont bidirectionnels, ce qui implique qu'un même individu effectue le parcours en aller-retour (Guzman et al., 2019; Gounand et al., 2018). Troisièmement, les mouvements migratoires sont saisonniers et donc relativement synchronisés, contrairement aux mouvements de dispersion qui sont généralement modélisés en écologie des communautés comme une diffusion continue d'individus d'un lieu à un autre tout au long de l'année (García-Callejas et al., 2019). Quatrièmement, les mouvements migratoires se déroulent souvent sur de plus grandes échelles spatiales et ne montrent pas une diminution graduelle du flux d'individus avec la distance (**Figure 0.6**). Globalement, dans les cas de dispersion, une population pourrait potentiellement se maintenir dans le temps même en absence de connexion avec des populations distantes ou à la suite de la dégradation d'écosystèmes distants. En revanche, dans le contexte des migrations saisonnières, une population ne peut pas persister en absence de connexion entre différents écosystèmes, et peut être affectée directement par des perturbations qui surviennent dans des écosystèmes distants. Les caractéristiques uniques des mouvements migratoires ont ainsi mené à l'élaboration de concepts théoriques spécifiques à la migration en écologie.

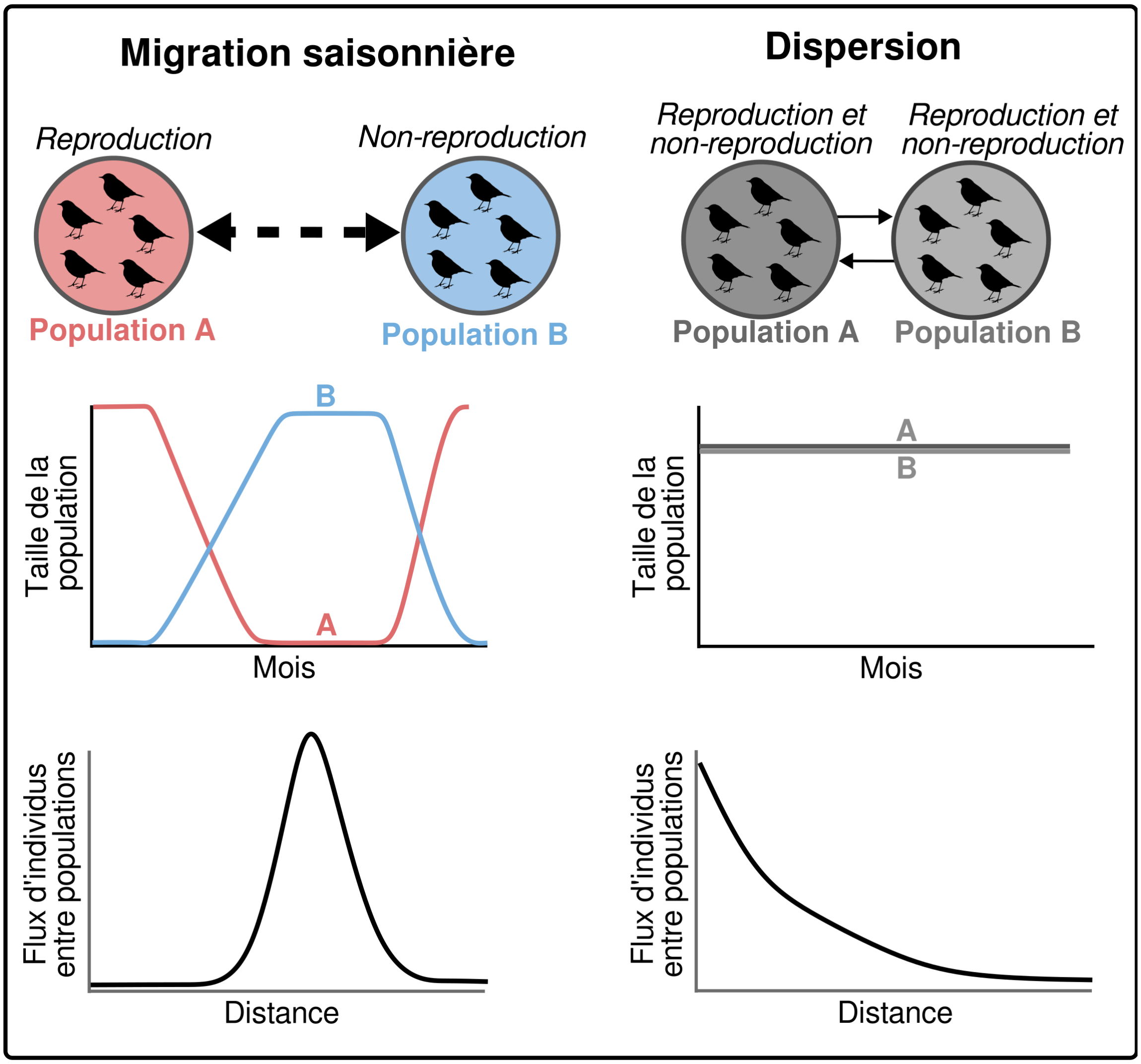

Figure 0.6 – Schématisation des différences majeures entre les mouvements migratoires saisonniers et des mouvements de dispersion. La flèche pointillée représente un mouvement saisonnier, synchronisé et bidirectionnel effectué par l'ensemble des individus d'une population. Les flèches pleines représentent des mouvements continus et unidirectionnels effectués par une faible proportion d'individus d'une population à une autre.

Populations et espèces

À l'échelle des populations, les caractéristiques uniques des mouvements migratoires ont donné naissance au concept de connectivité migratoire (Webster et al., 2002), un concept essentiel pour modéliser la dynamique démographique des espèces migratrices (Taylor and Norris, 2010; Taylor, 2019). La connectivité migratoire consiste à évaluer la force des liens entre différentes populations de reproduction et d'hivernage (Webster et al., 2002). Elle comprend deux composantes, soit la répartition des individus « *population spread* » qui représente à quel point les individus d'une population se répartissent sur une grande superficie ou se concentre en un endroit au cours d'une autre saison, et le niveau de mélange entre populations « *inter-population mixing* » qui indique le degré de mélange des individus issus de populations distinctes au cours d'une autre saison (Finch et al., 2017; Gao et al., 2020). Par exemple, si les individus de deux populations de reproduction distinctes se retrouvent chacun dans une population d'hivernage distincte, sans mélange des individus, on qualifie alors le patron de forte connectivité migratoire. En revanche, si les individus des populations de reproduction se distribuent uniformément dans plusieurs populations en période d'hivernage, avec un fort degré de mélange entre les individus issus des différentes populations de reproduction, on qualifiera le patron de faible connectivité migratoire. La connectivité migratoire est essentielle afin d'évaluer comment une perturbation dans un site de non-reproduction peut affecter les populations sur les sites de reproduction et inversement (Taylor and Norris, 2010; Iwamura et al., 2013; Betini et al., 2015). Sous une forte connectivité migratoire, une perturbation des conditions environnementales sur un site de non-reproduction devrait avoir un impact prononcé sur la population de reproduction qui lui est étroitement liée (Sutherland and Dolman, 1994; Taylor and Norris, 2010). À l'opposé, sous une faible connectivité, une telle perturbation pourrait exercer un impact moindre, mais réparti sur plusieurs populations de reproduction. De plus, une perturbation au sein d'une population de non-reproduction peut entraîner une variation de la taille d'une population de reproduction qui n'y est pas directement connectée, mais qui est reliée par l'intermédiaire d'autres populations (Taylor and Norris, 2010; Betini et al., 2015).

Communautés et écosystèmes

À l'échelle des communautés et des écosystèmes, les théories des métacommunautés (Leibold et al., 2004) et des métaécosystèmes (Loreau et al., 2003) ont été élaborées en se basant sur les caractéristiques des mouvements de dispersion. Ainsi, les approches actuelles ne représentent pas adéquatement la nature particulière des mouvements migratoires (Gounand et al. 2018; Guzman et al. 2019 ; **Figure 0.6**). Les **métacommunautés** et **métaécosystèmes** sont définis comme un ensemble de communautés ou d'écosystèmes connectés par le mouvement d'organismes, ainsi que par le transfert de matière ou d'énergie dans le cas des métaécosystèmes (Loreau et al., 2003; Leibold et al., 2004). Même si plusieurs cas empiriques soulignent la présence de réseaux de communautés et d'écosystèmes interconnectés par la migration (Polis et al., 1997; Jefferies, 2000; Madigan et al., 2012; Hessen et al., 2017; Springer et al., 2018; Brandt et al., 2024; Bustnes et al., 2025), l'intégration des mouvements migratoires dans la théorie des métacommunautés et des métaécosystèmes demeure encore à un stade préliminaire (Guzman et al., 2019; Gounand et al., 2018). La nature des mouvements influence la dynamique des métacommunautés (García-Callejas et al., 2019). Il est donc fort probable que les mouvements migratoires jouent un rôle distinct de la dispersion et des mouvements d'alimentation au sein des communautés et écosystèmes (García-Callejas et al., 2019; Subalusky and Post, 2019).

0.3.2 Les réseaux de migration, une avenue prometteuse pour étudier la migration dans les communautés

L'approche par réseau est couramment utilisée en écologie pour analyser la structure et la dynamique de composantes en interaction (Ings et al., 2009; Pilosof et al., 2017; Newman, 2018). Elle constitue ainsi un outil efficace pour représenter les connexions écologiques engendrées par le mouvement des organismes entre des parcelles d'habitat ou des écosystèmes distants (Dale and Fortin, 2010; Jacoby and Freeman, 2016). L'approche par réseaux permet d'évaluer des propriétés structurelles émergentes des systèmes, c'est-à-dire des caractéristiques qui ne sont observables qu'en prenant en compte les liens entre les composantes (Newman, 2018). Les réseaux sont représentés par des nœuds « *node* » et des arêtes « *edges* », dont la définition varie selon le contexte. Par exemple, dans un réseau trophique, les noeuds correspondent généralement à des espèces, tandis que les arêtes représentent les interactions trophiques entre espèces. Dans un contexte de réseau de migration, les nœuds représentent typiquement des sites ou des régions et les arêtes représentent des mouvements migratoires entre des sites (**Figure 0.7** ; Taylor and Norris 2010; Iwamura et al. 2013; Xu et al. 2020).

Les réseaux de migration à l'échelle des espèces ont été utilisés pour quantifier la connectivité migratoire (Taylor and Norris, 2010; Knight et al., 2018), identifier des corridors de migration (Buhnerkempe et al., 2016; Knight et al., 2018) ou des sites à haute valeur de conservation (Lamb et al., 2019; Xu et al., 2020), et pour modéliser les effets de la perte d'habitat sur la dynamique des populations migratrices (Taylor and Norris, 2010; Iwamura et al., 2013). Toutefois, dans les représentations actuelles des réseaux de migration, les arêtes sont généralement définies par la présence ou le nombre d'individus migrateurs, ce qui ne permet pas de distinguer les mouvements migratoires de plusieurs espèces simultanément. La représentation actuelle des réseaux de migration ne permet pas d'étudier les connexions générées par l'ensemble des espèces migratrices d'une communauté ou d'un écosystème. Il est fort probable que des contraintes empiriques, liées à l'identification des destinations migratoires de l'ensemble des espèces d'une communauté, aient freiné l'extension du concept de réseaux de migration à l'échelle des communautés. Il est donc nécessaire de développer de nouvelles approches pour analyser les patrons migratoires à l'échelle des métacommunautés et des métaécosystèmes.

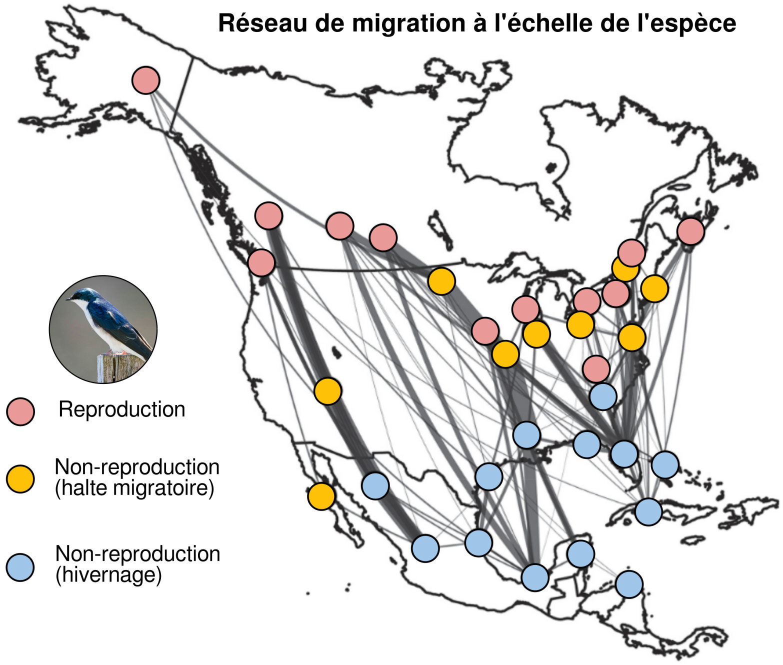

FIGURE 0.7 – Exemple empirique de réseau de migration pour l'hirondelle bicolore (*Tachycineta bicolor*) en Amérique du Nord. La figure a été extraite et adaptée de Knight et al. (2018). Crédit photo : Jack Bulmer (Unsplash).

0.4 Les milieux arctiques comme modèle pour l'étude de la migration saisonnière

Les écosystèmes terrestres arctiques représentent des modèles particulièrement pertinents pour étudier la migration saisonnière à l'échelle des communautés et des écosystèmes, en raison de leur richesse spécifique relativement faible, d'une forte proportion d'espèces migratrices (Gauthier et al., 2011; Somveille et al., 2013; Ganter et al., 2013) et d'une grande diversité de stratégies migratoires (**Figure 0.8** ; Johnson and Herter 1990; Ganter et al. 2013). Les écosystèmes terrestres arctiques se distinguent par leur forte saisonnalité et leur relativement faible productivité primaire due aux basses températures, aux faibles précipitations et à de courtes saisons de croissance engendrant une production secondaire et une diversité biologique restreinte (Ims et al., 2013). Toutefois, en période estivale, une grande diversité d'oiseaux migrateurs vient profiter du risque de prédation réduit (McKinnon et al., 2010) et d'une abondance relativement élevée de nourriture pour s'y reproduire (Ganter et al., 2013). Ainsi, une forte proportion des espèces de vertébrés arctiques passe en réalité la majeure partie de l'année à l'extérieur de l'Arctique (Ganter et al., 2013).

Les nombreuses espèces migratrices se reproduisant en Arctique utilisent des haltes migratoires et des aires d'hivernage réparties sur plusieurs continents (**Figure 0.8** ; Gauthier et al. 2005; Krapu et al. 2014; Lanctot et al. 2016; Robillard et al. 2018; Léandri-Breton et al. 2019; Seyer et al. 2021; Baak et al. 2021). Néanmoins, la connectivité globale maintenue par les espèces migratrices d'une communauté arctique n'a jamais été décrite. Considérant la distribution hétérogène des changements environnementaux et des pressions anthropiques à travers le globe (Bowler et al., 2020), les communautés de vertébrés arctiques pourraient ainsi être influencées par des changements environnementaux se produisant dans des écosystèmes distants, mais connectés par la migration animale. Il est donc essentiel de documenter les destinations des espèces migratrices d'une communauté au cours de leur cycle annuel, afin de caractériser à quels types de changements environnementaux elles sont exposées et, éventuellement, anticiper les conséquences de perturbations survenant dans des environnements éloignés sur les communautés et écosystèmes arctiques. Une meilleure compréhension de ces effets en cascade entre communautés ou écosystèmes permettrait d'améliorer notre capacité à préserver l'intégrité des environnements arctiques.

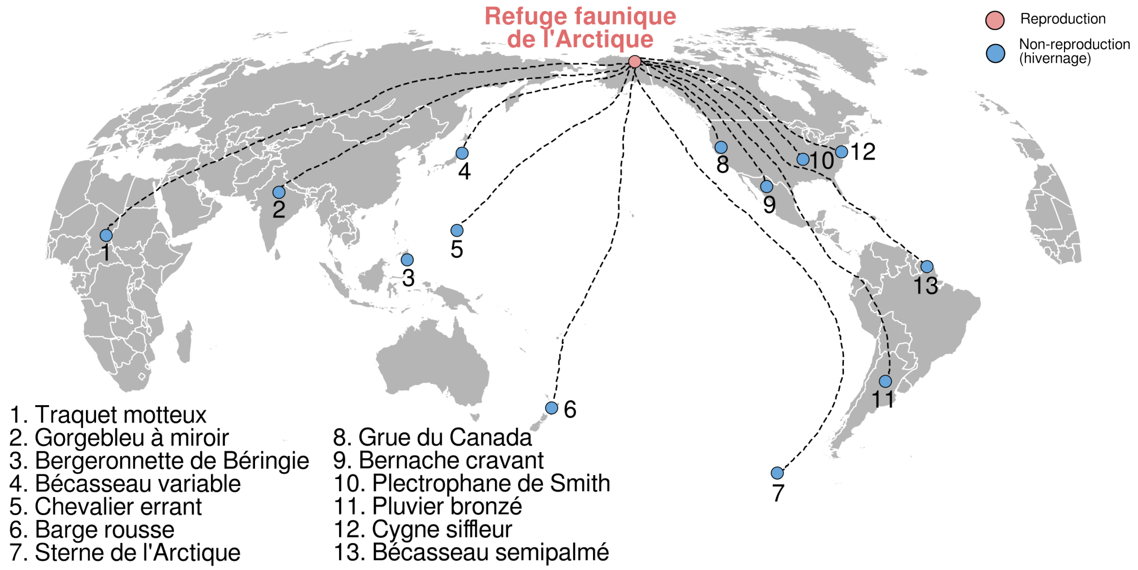

Figure 0.8 – Destination migratoire de non-reproduction de 13 espèces d'oiseaux se reproduisant dans un Refuge faunique de l'Arctique « *Arctic Wildlife Refuge* ». Figure adaptée de *US Fish and Wildlife Service.*

0.5 Objectifs

0.5.1 Résumé de la problématique

Les espèces migratrices saisonnières génèrent des dynamiques écologiques sur de grandes échelles spatiales en reliant entre elles des communautés et des écosystèmes géographiquement distants (Bauer and Hoye, 2014). Des changements environnementaux se produisant à un endroit peuvent ainsi se propager via ces connexions migratoires et causer des effets en cascades dans des environnements éloignés (Jefferies, 2000; Madigan et al., 2012; Springer et al., 2018). Il est donc crucial d'identifier les destinations des espèces migratrices d'une communauté lorsqu'elles la quittent au cours de leur cycle annuel, ainsi que de caractériser les types de changements environnementaux auxquels elles sont exposées durant cette période. Toutefois, les représentations et théories actuelles en écologie de la migration et des communautés ne permettent pas d'étudier simultanément les connexions migratoires saisonnières établies par l'ensemble des espèces migratrices d'une communauté (**Figure 0.9**). La structure des connexions migratoires maintenues par les espèces migratrices entre une communauté donnée et des écosystèmes distants n'a donc jamais été décrite jusqu'à présent. Étant donné le caractère encore préliminaire de l'étude des patrons migratoires à l'échelle des communautés, cette thèse adopte avant tout une approche descriptive, ouvrant la voie à de futures études hypothético-déductives.

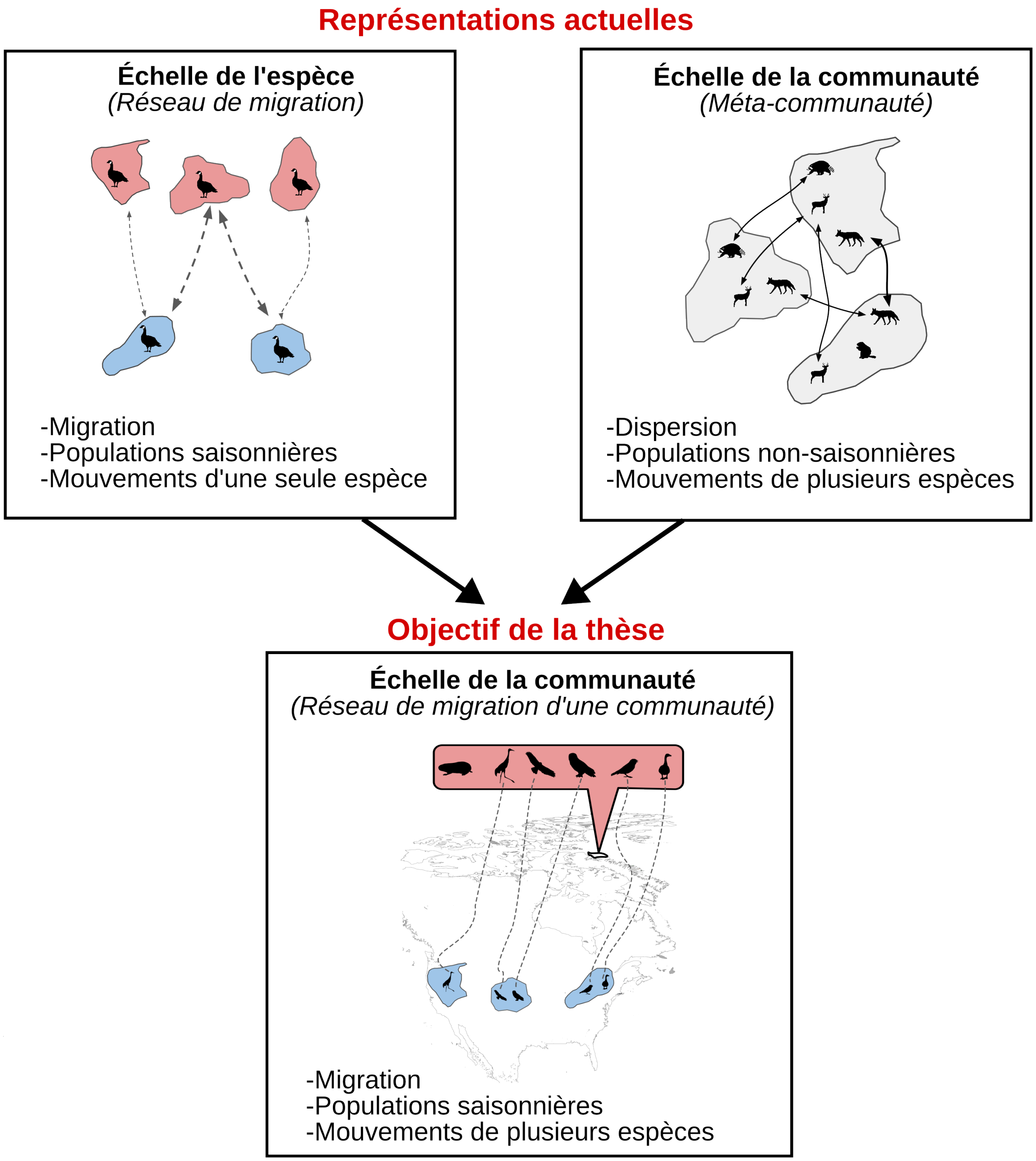

Figure 0.9 – Représentation schématique d'un des objectifs de la thèse, qui consiste à développer un cadre conceptuel intégrant les connexions migratoires saisonnières de l'ensemble des espèces migratrices d'une communauté. Le cadre conceptuel proposé s'inscrit à l'interface de l'écologie de la migration, incluant notamment les réseaux migratoires (Webster et al., 2002), la théorie des métacommunautés (Leibold et al., 2004) et des métaécosystèmes (Loreau et al., 2003).

0.5.2 Objectifs

La présente thèse s'inscrit dans un objectif à long terme visant à évaluer la vulnérabilité des écosystèmes arctiques aux changements globaux, en tenant compte de la distribution annuelle des espèces migratrices. Les objectifs principaux de cette thèse sont de i) développer un cadre permettant de représenter et de caractériser la structure des connexions migratoires maintenue avec une communauté focale, et ii) fournir une description empirique de la structure de ces connexions ainsi que de l'exposition des espèces aux perturbations environnementales, en se basant sur une communauté de vertébrés arctiques. Le **premier chapitre** a pour objectifs de proposer un cadre permettant de représenter et de caractériser les voies migratoires maintenues à l'échelle d'une communauté, et de fournir une description empirique de la structure de ces voies migratoires à partir d'une étude de cas. Le **deuxième chapitre** vise à décrire la structure d'une communauté de vertébrés arctique, en estimant l'abondance et la biomasse, tant annuelles que moyennes, de l'ensemble des espèces de vertébrés. Cette description servira ensuite à comparer, dans le cadre du **troisième chapitre**, la structure des connexions migratoires à l'échelle d'une communauté en fonction de l'occurrence des espèces, de leur abondance relative et absolue, ainsi que de leur biomasse. Enfin, le **quatrième chapitre** vise à caractériser l'exposition aux perturbations environnementales durant l'hiver boréal pour l'ensemble des espèces de vertébrés d'un réseau trophique arctique comprenant une forte proportion d'espèces migratrices. On pourrait s'attendre à ce que, au sein des groupes fonctionnels du réseau trophique, les espèces migratrices se retrouvent dans des aires de non-reproduction communes et soient ainsi exposées à des perturbations environnementales similaires, en raison de préférences alimentaires et d'habitat similaires. Le deuxième objectif de ce chapitre est alors d'évaluer si, au sein des groupes fonctionnels, les espèces migratrices sont exposées à des régimes de perturbations environnementales similaires ou contrastés selon leurs destinations de migration.

0.6 Système d'étude

0.6.1 Aire d'études

Les cas d'étude décrits dans cette thèse reposent sur la communauté de vertébrés terrestres de la plaine Sud de l'île Bylot (~400 km^2), située dans le Haut-Arctique canadien, au Nunavut (73°N, 80°W). Grâce à son exposition sud et à la protection contre les vents du nord assurée par la cordillère Arctique, le climat de la plaine Sud de l'île Bylot est relativement doux pour cette latitude (Gauthier et al., 2024*b*). La zone d'étude reste généralement dégagée de neige de la mi-juin à la fin septembre (Gauthier et al., 2013). L'aire d'étude est dominée par une toundra mésique, composée d'arbustes rampants, de plantes herbacées, de graminées et de mousses, qui couvrent principalement les collines et les pentes douces (Gauthier et al., 2013). Ces milieux sont entrecoupés de zones humides de basse altitude, où dominent les mousses, les graminées et les carex. La très faible densité, voire l'absence, de grands herbivores, tels que le caribou (*Rangifer tarandus*) et le boeuf musqué (*Ovibos moschatus*), ainsi que la présence d'une importante colonie d'oies des neiges (*Anser caerulescens atlanticus*) distinguent principalement la communauté de vertébrés de l'île Bylot de celles de latitudes similaires (Legagneux et al., 2014). Les populations de lemmings présentent des variations cycliques d'abondance de grande amplitude influençant également l'occurrence et la reproduction de plusieurs espèces au sein de la communauté (Legagneux et al., 2012; Therrien et al., 2014). On retrouve au sein de la communauté de vertébrés de l'île Bylot une grande diversité fonctionnelle d'espèces migratrices avec des plongeons, des oies, des cygnes, des canards, des rapaces, des grues, des limicoles, des goélands, des labbes et des passereaux (**Figure 0.10** ; Gauthier et al. 2011, 2024*b*).

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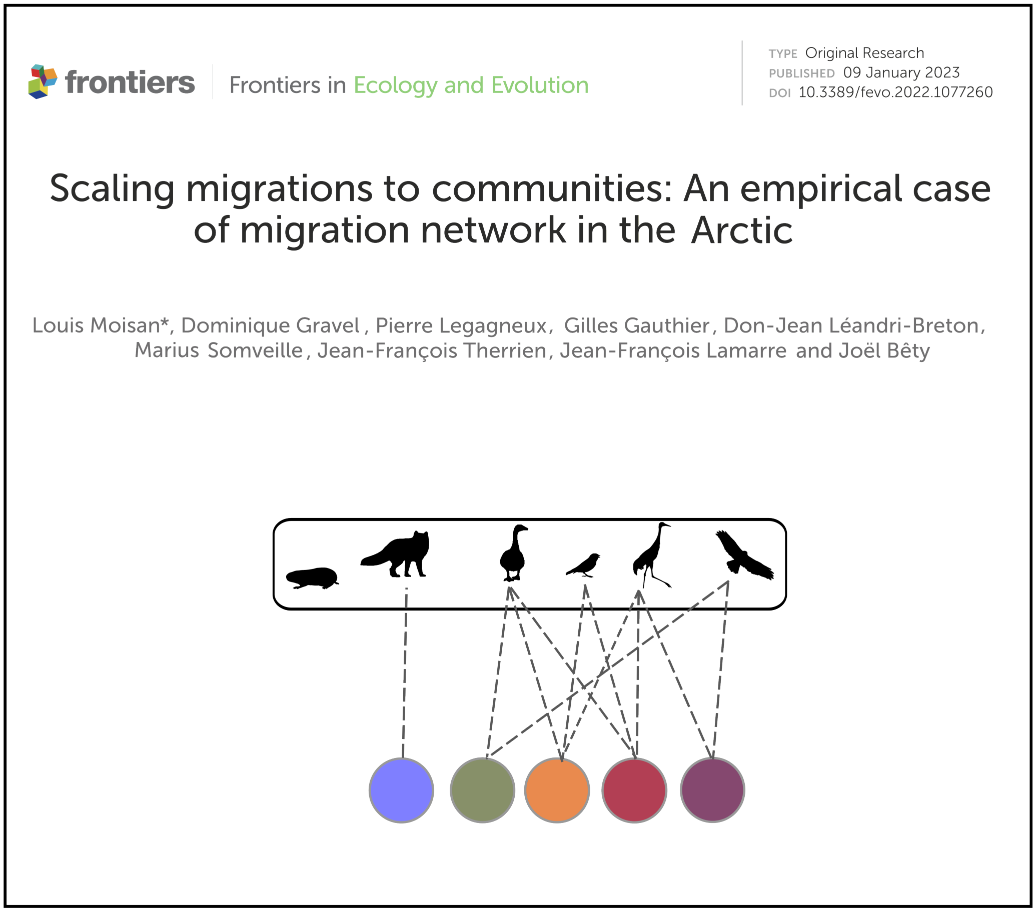
Figure 0.10 – Photos illustrant une sélection d'espèces résidentes, migratrices et partiellement migratrices de la communauté de vertébrés terrestres de la plaine Sud de l'île Bylot.

ARTICLE 1

ÉTENDRE LES MIGRATIONS À L'ÉCHELLE DES COMMUNAUTÉS: UN CAS EMPIRIQUE DE RÉSEAU DE MIGRATION EN ARCTIQUE



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

Louis Moisan*, Dominique Gravel , Pierre Legagneux , Gilles Gauthier, Don-Jean Léandri-Breton, Marius Somveille, Jean-François Therrien, Jean-François Lamarre and Joël Bêty

1.1 Contexte et publication associée

L’article « *Scaling migrations to communities: An empirical case of migration network in the Arctic* » a été publié en janvier 2023 dans la revue *Frontiers in Ecology and Evolution*, dans le cadre d’une édition spéciale consacrée aux patrons et processus spatiaux au sein des réseaux écologiques. L’éditrice associée de l’article était Dr Marie-Josée Fortin, et l’évaluation a été réalisée par trois réviseurs: Dr Nigel Yoccoz, Dr Marie Auger-Méthé et Dr Courtney R. Shuert. Cet article propose un cadre original pour étudier les patrons spatiaux de migration à l’échelle d’une communauté, en s’appuyant sur une nouvelle représentation par réseau qui permet de considérer simultanément les destinations migratoires de plusieurs espèces au sein d’un même réseau de migration. De plus, à notre connaissance, il s’agit du premier cas empirique documentant des patrons migratoires à l’échelle d’une communauté de vertébrés. Cet article a été réalisé dans le cadre d’un passage accéléré au doctorat. La représentation par réseau et l’interprétation des métriques ont été élaborées conjointement au cours de discussions entre Joël Bêty, Dominique Gravel et moi-même, de même que la méthode de délimitation des aires de non-reproduction des espèces de l’île Bylot. En tant que premier auteur, j’ai rédigé la première version complète du manuscrit et développé l’ensemble des codes nécessaires à la préparation des données, aux analyses et à la visualisation des résultats. Joël Bêty, Pierre Legagneux, Gilles Gauthier et Jean-François Therrien ont assuré la continuité à long terme du suivi sur l’île Bylot et la réalisation d’études sur la migration de plusieurs espèces. Don-Jean Léandri-Breton, Jean-François Lamarre et Jean-François Therrien ont collecté et analysé des données de suivi de migration intégrées à cette étude, et ont révisé les aires de non-reproduction définies pour l’ensemble des espèces de l’île Bylot. Marius Somveille a contribué à l’interprétation des résultats. Dominique et Joël ont commenté et révisé le manuscrit, puis l'ensemble des auteurs l'ont également relu et révisé avant publication. J'ai échangé avec Joël Bêty tout au long de la réalisation de cet article. Le contenu de l'article a été présenté au 5e Symposium sur les Réseaux écologiques (EcoNet), tenu en novembre 2021 en Espagne, sous la forme d'une présentation orale et d'une communication par affiche.

1.2 Résumé de l'article en français

Les migrateurs saisonniers transportent de l'énergie, des nutriments, des contaminants, des parasites et des maladies, tout en connectant des réseaux trophiques distants entre les communautés et les écosystèmes, ce qui contribue à structurer des métacommunautés et des métaécosystèmes. Cependant, nous manquons actuellement d'un cadre permettant de caractériser la structure des connexions spatiales maintenues par toutes les espèces migratrices se reproduisant ou hivernant dans une communauté donnée. Nous utilisons ici une approche par réseau pour représenter et caractériser les voies migratoires au niveau d'une communauté et fournissons une description empirique pour une communauté terrestre du Haut-Arctique. Nous définissons les *réseaux de migration des communautés* comme des réseaux multipartites présentant différentes régions biogéographiques reliées à une communauté focale par les mouvements saisonniers de ses espèces migratrices. Nous nous concentrons sur la communauté terrestre du Haut-Arctique de l'île Bylot, un site de reproduction estivale pour plusieurs espèces migratrices. Nous définissons l'aire de non-reproduction de chaque espèce à l'aide de dispositifs de suivi, ou de cartes de répartition raffinées selon les corridors migratoires et les types d'habitats utilisés par les espèces. Nous montrons que les espèces migratrices se reproduisant sur l'île Bylot se répartissent dans des centaines d'écorégions à travers plusieurs continents durant la période de non-reproduction, et présentent un faible chevauchement spatial. Les espèces migratrices sont réparties en groupes associés à différents ensembles d'écorégions communes. La structure non aléatoire observée dans le réseau de migration de l'île Bylot suggère que des contraintes évolutives et géographiques, ainsi que des facteurs écologiques, agissent pour façonner les patrons de migrations au niveau de la communauté. Dans l'ensemble, notre étude fournit un cadre simple et généralisable, constituant un point de départ pour mieux intégrer les migrations à l'échelle des communautés. Ce cadre est adaptable afin d'étudier le transport saisonnier d'énergie, de contaminants, de parasites et de maladies entre écosystèmes, ainsi que les interactions trophiques dans les communautés comprenant des espèces migratrices.

Les sections suivantes sont celles de l'article **publié**.

1.3 Title

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

1.4 Authors

Louis Moisan, Dominique Gravel, Pierre Legagneux, Gilles Gauthier, Don-Jean Léandri-Breton, Marius Somveille, Jean-François Therrien, Jean, François Lamarre and Joël Bêty

1.5 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 use a network approach 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.

1.6 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 Hoye, 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 Hoye, 2014; Gounand et al., 2018). Therefore, the effects of environmental disturbances in a given ecosystem (**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.

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 Hoye, 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, 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 Hoye, 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, 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).

Meta-community frameworks have been defined for dispersal and foraging movements, but have never been adapted to migratory movements. The traditional meta-community framework defines dispersal and foraging movements as continuous links between communities, where at any time, some individuals relocate, and others forage in other communities. However, seasonal migratory 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. Unlike resident species, if the movement of migratory species between communities is prevented, the species become extinct. Migratory species can only persist in a meta-community system, unlike resident species in the traditional meta-community framework. Therefore, the way in which dispersal and foraging movements are incorporated into traditional meta-community frameworks does not fit the characteristics of migratory movements.

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 (Rubenstein and Hobson, 2004; Mueller and Fagan, 2008). 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. Because of their seasonal movements, migratory individuals are present for only part of their annual cycle in the visited communities and ecosystems. Therefore, a perturbation occurring on a non-breeding ground may only spread to a breeding ground in subsequent seasons, and vice versa, generating a seasonal delay in the spatial spread of perturbations.

Due to the characteristics of seasonal migrations, we need to adapt existing frameworks in community ecology to study migrations at the community level. 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). 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). Networks are represented by an adjacency matrix A where each element consists of pairs of nodes ij (e.g., species i and species j) where 1 represents the presence and 0 the absence of an edge (e.g., trophic interaction) 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; e.g., diet matrix). Networks have been used to study ecological interactions within communities (Dunne et al., 2002; Fortuna et al., 2010), migratory pathways at the species level (Iwamura et al., 2013; Knight et al., 2018; Taylor, 2019) and dispersal or foraging movements between set of communities (García-Callejas et al., 2019). However, we still lack a network approach that can highlight the meta-ecosystem and meta-community connections maintained by the migratory species from a focal community, while taking into account the seasonality of migrations.

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 approach commonly used in community ecology, but which will be adapted here to the context of community-level migrations. We propose a novel network definition and thus novel interpretations of traditional network metrics, but do not make any mathematical advances. 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, 2013; **Figure 1.1**). For the purpose of the study, all species from the community are considered here (5 mammals and 30 birds). 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 dynamics, as well as their global migratory pathways (Therrien et al., 2012; Robillard et al., 2018; Léandri-Breton et al., 2019; Lamarre et al., 2021; Seyer et al., 2021, Legagneux et al., unpublished data). Bylot Island hosts the largest greater snow goose (*Chen caerulescens atlantica*) colony, which represents the dominant herbivore of the system (Legagneux et al., 2012). We use this species whose migratory pathways and trophic effects have been well documented at our study site to show how our framework can be used to complement existing food web models by illustrating the spread of perturbations at the meta-community level. 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; Clermont et al., 2021; Duchesne et al., 2021).

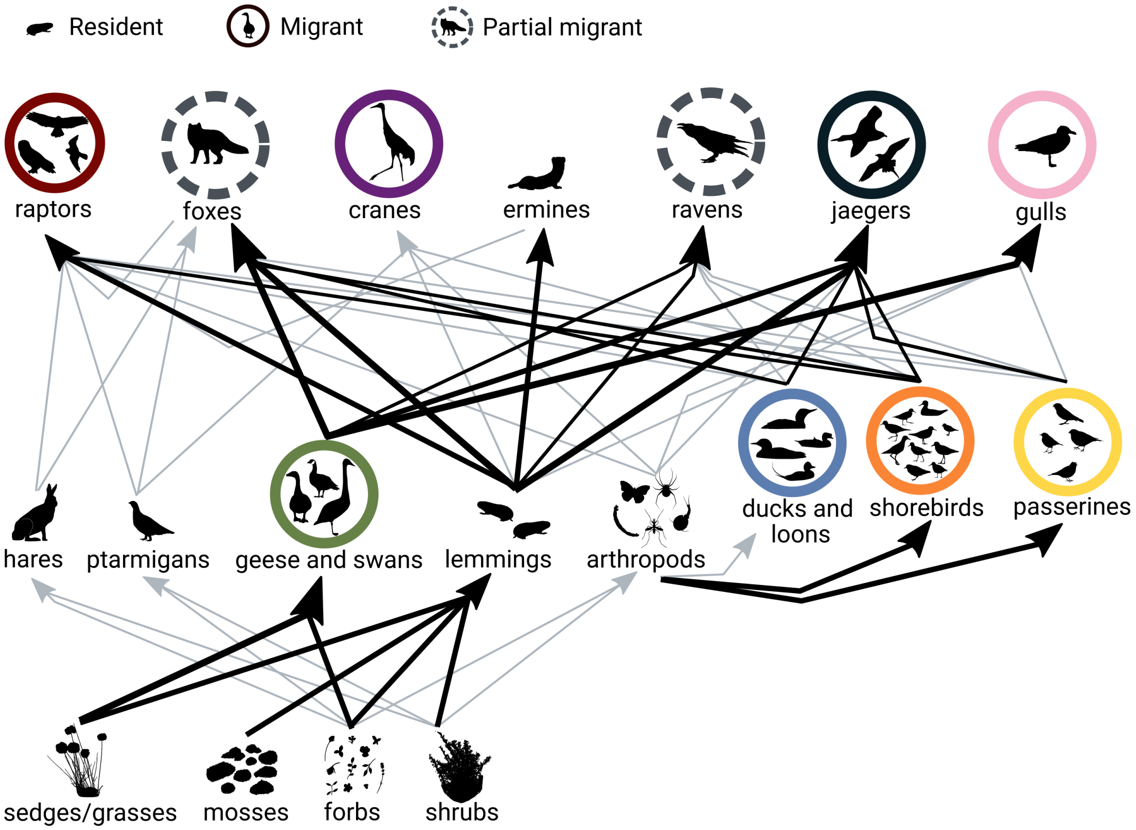

Figure 1.1 – Bylot Island terrestrial tundra food web adapted from Gauthier et al. (2011). Labels represent the functional groups, and the groups composed of migratory species are colored (red =raptors, pink=gulls, purple=cranes, dark blue=jaegers, light blue=ducks and loons, orange=shorebirds, yellow=passerines, green =geese and swans). The species composition of vertebrate functional groups is represented by icons (e.g., four species of passerines). Arrows represent biomass flow between functional groups and the size of the arrows is relative to the proportion of the diet; gray arrows represent minor portions of the diet.

1.7 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 (i.e., different types of nodes) representing the geographic regions connected with a focal community through the seasonal movements of its migratory species. Although multipartite networks have been widely used in community ecology (host–parasite, plant-pollinator, seed-disperser; Fortuna et al., 2010), they have never been adapted to study the spatial connections made by animal movement at the community level. Community migration networks, in their simplest form 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 1.2**). 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 (Chapman et al., 2011) 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 even when migratory species are absent (e.g., habitat loss or contaminant subsidies). The temporal definition of nodes and edges does not need to be considered explicitly to highlight the pattern of migrations at the community level, which is the scope of this paper. However, in a dynamic community migration network, the temporal definition of nodes would be essential.

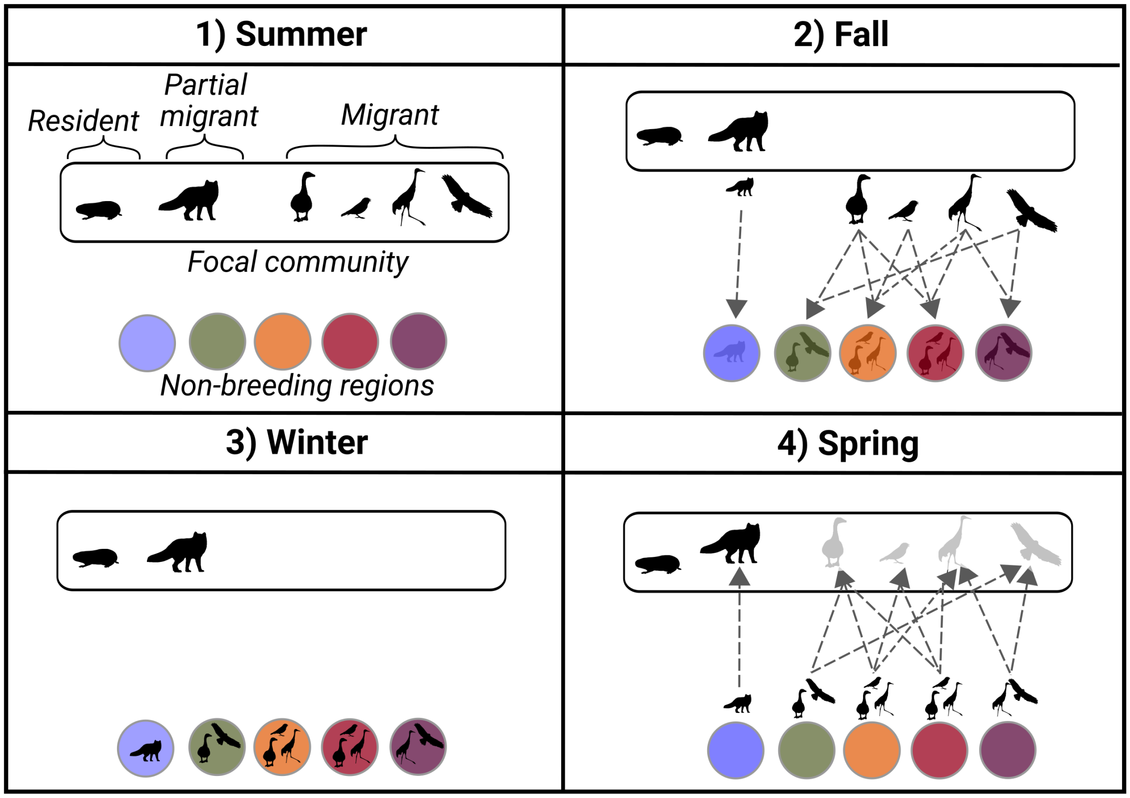

Figure 1.2 – Schematic representation and definition of the seasonal nature of community migration networks through a fictive community representing a summer breeding ground used by multiple migratory species (white rectangle) and their migratory pathways (dotted lines) to non-breeding regions (colored circles). (1) Summer: populations of diverse migratory, partially migratory and resident species (black icons) co-exist at the same location, which defines the focal community (white rectangle) (2) Fall: the migratory and a part of the partially migratory populations leave the focal community through the migratory pathways (dotted lines) to reach non-breeding regions (colored circles) (3) Winter: the migratory and a part of partially migratory populations are distributed across diverse non-breeding regions, and the resident and a part of partially migratory populations stayed at the focal community location (4) Spring: the migratory and a part of the partially migratory populations from the focal community leave the non-breeding regions to reach the focal community location through the migratory pathways.

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

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

Community migration networks can be described with multipartite network metrics at the node and network levels to highlight the structure of the migratory pathways at the species and community levels (**Figure 1.3**). At the node level, the *species degree* (number of regions connected with a species) reflects the population spread, defined as the mean distance in the location of individuals from the same population between different seasons (Finch et al., 2017). Highly spread populations will be found in more geographical regions. In a bipartite community migration network, the *region degree* represents the number of migratory species from the focal community hosted by a region in another annual cycle period (i.e., non-breeding region). The region degree could potentially be used to identify ecological hot spots thousands of kilometers away from a focal community.

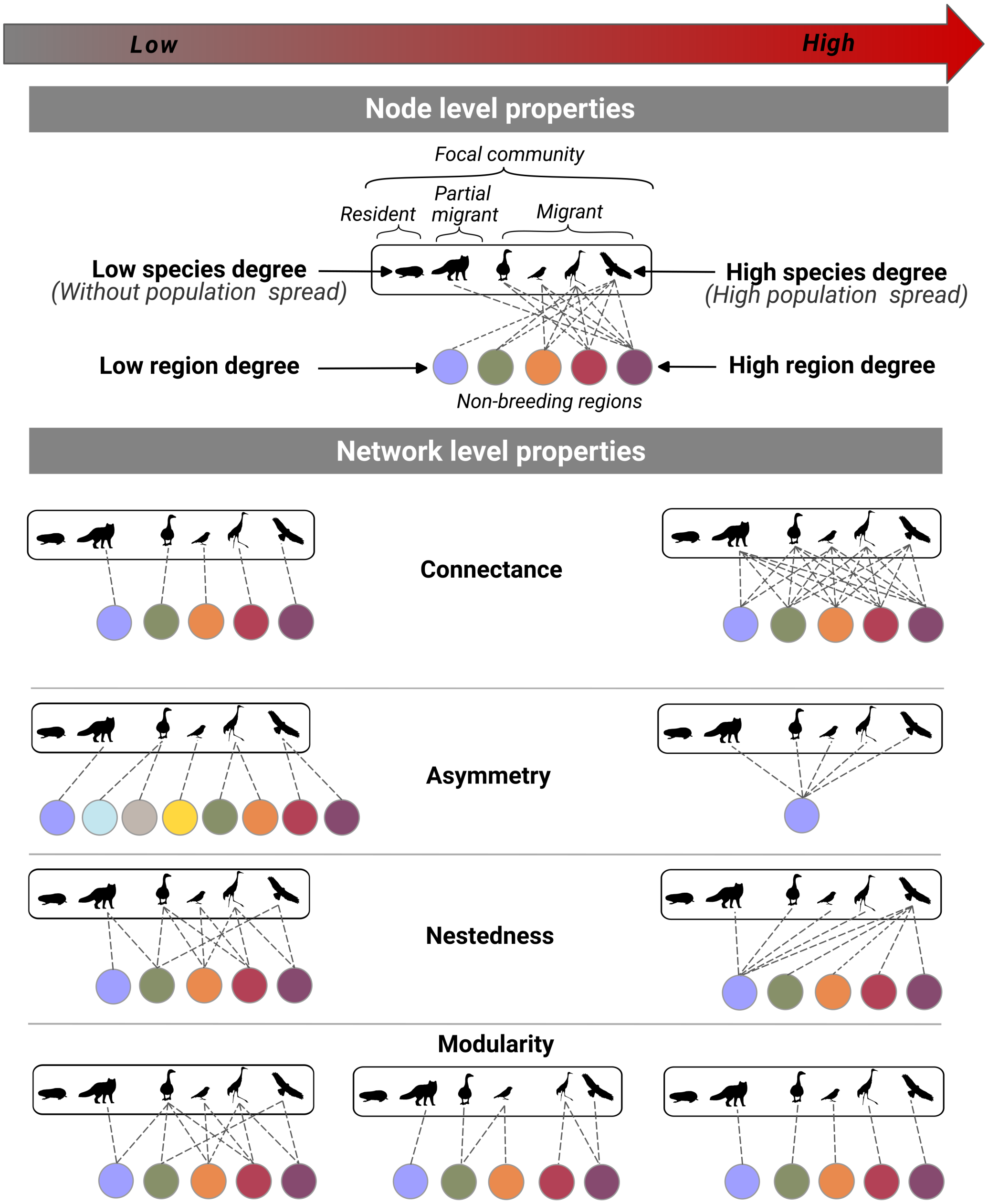

Figure 1.3 – Schematic definitions and examples of low and high values of bipartite community migration network metrics. The white rectangle represents the focal community, and the colored circles represent the connected geographic regions through migrations. The dotted lines represent the movements of species between the focal community and the regions used during another period of their annual cycle. The movements of species between the focal community and the connected regions are presented as undirected to represent the use of the same pathways back and forth. Resident species are represented by the absence of edges.

At the network level, we suggest using *connectance*, *asymmetry*, *nestedness* and *modularity* to characterize community migration networks. *Connectance* represents the degree of spatial overlap between the species of a focal community during another period of the annual cycle. A high connectance would mean a large spatial overlap between the species of a focal community during another period of the annual cycle, suggesting perturbation of connected regions could potentially affect multiple species simultaneously. *Asymmetry* represents the proportion of species nodes versus region nodes in the network. It illustrates the relative concentration or spatial diffusion of species once they leave the focal community. A positive asymmetry value would represent more species than regions and a negative value would point toward the opposite. An extremely high asymmetry would represent the concentration of the species in a small number of regions and suggest that the focal community is exposed to highly localized perturbations occurring in distant but connected regions. *Nestedness* assesses if small-range species are found inside the boundaries of broad-range species during another period of the annual cycle. If the network is nested, some regions host multiple species of different range sizes. A nested structure of migratory pathways would mean that if a perturbation happens on a species with a small non-breeding range, it also has a high chance of propagating to the community through species with larger non-breeding ranges. The modules represent groups of species that have more spatial overlap with each other on their range outside the focal community than with other species of the community. *Modularity* highlights the degree of overlap between the modules, with little overlap between modules showing high modularity. A modular community migration network would mean that perturbations occurring on distant but connected regions would propagate to the focal community through subgroups of species. 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.

1.8 Materials and methods

1.8.1 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 425km^2 (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 *Vertebrate community definition* for details and **Table 1.1** 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 (Rubenstein and Hobson, 2004; Mueller and Fagan, 2008), 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 (Chapman et al., 2011; Gauthier et al., 2011).

The non-breeding range of each migratory species was defined by the most representative range data available (Supplementary Material *Non-breeding range delimitation*). We used non-breeding range maps (BirdLife International and Handbook of the Birds of the World, 2019; Fink et al., 2020*b*) along with global avian migration flyways (geographical grouping of annual ranges of avian migratory species; Wetlands International 2022) when tracking data was unavailable for long-distance 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 partially migratory species in the community (Arctic fox and common raven) perform short-distance movements within the Arctic. They are thus considered circumpolar residents at the species level, and it was not possible to use species non-breeding range maps for these species as we did for long-distance migrants. 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 (see Supplementary Material *Association between species non-breeding range and biogeographic ecoregions*). 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 *Filtering selected ecoregions based on species' non-breeding habitats*). On average, the non-breeding range of each species was associated with 33 ± 46 ecoregions, including no connections for resident species. To validate our non-breeding ranges refinement and filtering methods, we performed a preliminary validation analysis based on the specific tracking programs available as reference (n = 6 species; American golden-plover, common-ringed plover, snowy owl, long-tailed jaeger, snow goose and king eider; Supplementary material section 1.5). Our method of refining and filtering non-breeding ranges removed a considerable number of irrelevant ecoregions associations. However, the use of refined species range maps still tend to overestimate the number of connected ecoregions in comparison with specific tracking data. We used the ecoregions associated with each species to create an incidence matrix of I × 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., 2022).

1.8.2 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 1.3**).

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, host-parasites, island biogeography; see Rodríguez-Gironés and Santamaría, 2006 for more details on the algorithm and the equation). 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 (see Farage et al., 2021 for more details on the algorithm and the equation). The modularity analysis was performed with the package *infomapecology* 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). The modularity and nestedness values are influenced by other structural properties of the network (Fortuna et al., 2010). Therefore, we needed to compare the observed values with networks with the same degree distribution and connectance, but with randomly assigned edges. We used the *quasi-swap* algorithm (detailed in Miklós and Podani, 2004) from the package *vegan* (Oksanen et al., 2022) to simulate 1,000 null models. More specifically, the algorithm maintains the row and column sums of the original matrix (i.e., same degree distribution and connectance) and repeatedly shuffles the edges in 2×2 subsets of the original matrix (Miklós and Podani, 2004).

1.9 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 1.4**). 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 1.5**). The peregrine falcon is the species with the highest degree in the network, associated with 257 ecoregions. On average, the non-breeding range of each species overlapped the boundaries of 33 ± 46 ecoregions, including no connections for resident species. 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 1.12**).

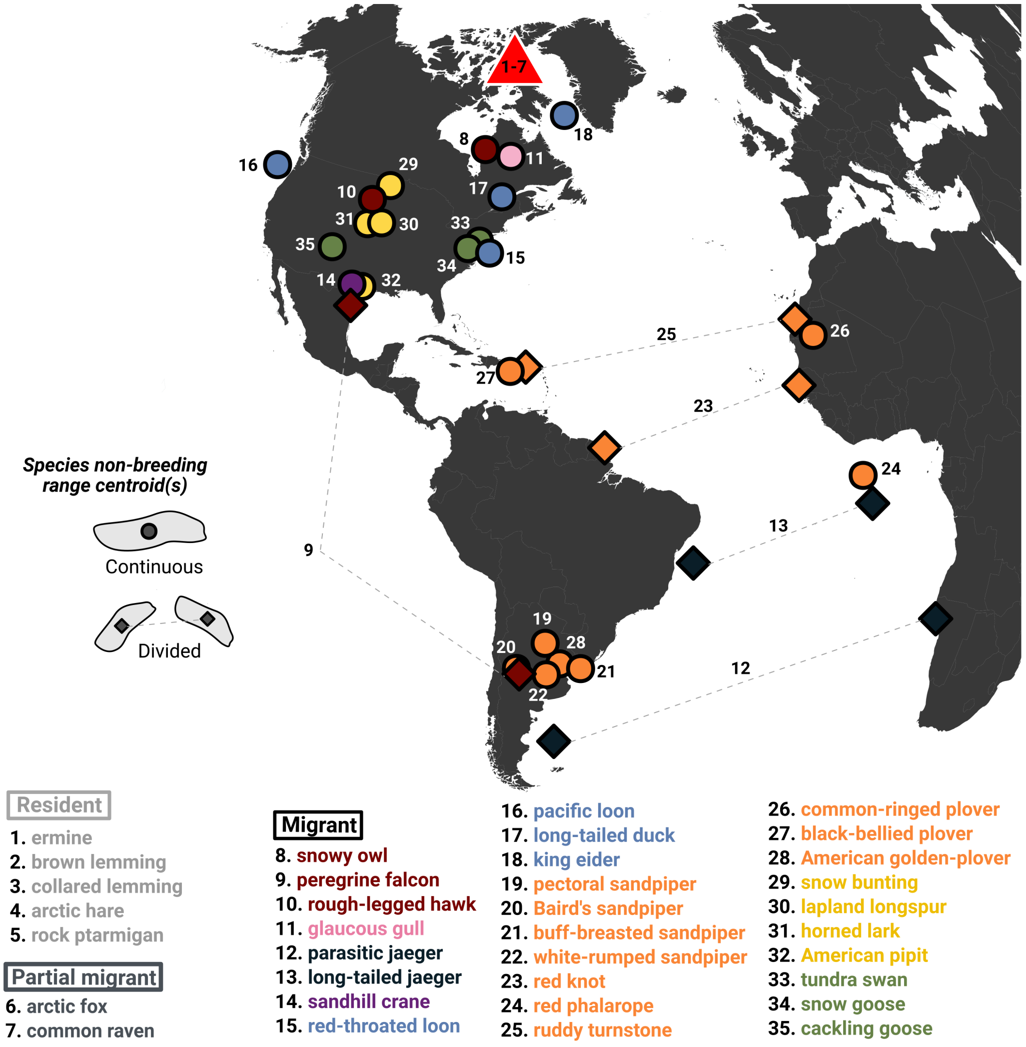

Figure 1.4 – Non-breeding range centroids of vertebrate species from Bylot Island. The migratory species are colored by functional groups (red=raptors, pink= gulls, purple=cranes, dark blue =jaegers, light blue=ducks and loons, orange=shorebirds, yellow=passerines, green= geese and swans). The non-breeding centroid of residents and partial migrants are not represented since they are centered on Bylot Island. The centroids of migratory species with a continuous non-breeding range are represented by a circle, and squares are used to represent the centroids of divided non-breeding ranges (i.e., jaegers travel to both Atlantic coasts). The location of some centroids was slightly adjusted to better represent the species non-breeding habitat type, for instance, moving the centroid of a coastal species falling inland to the closest coastline.

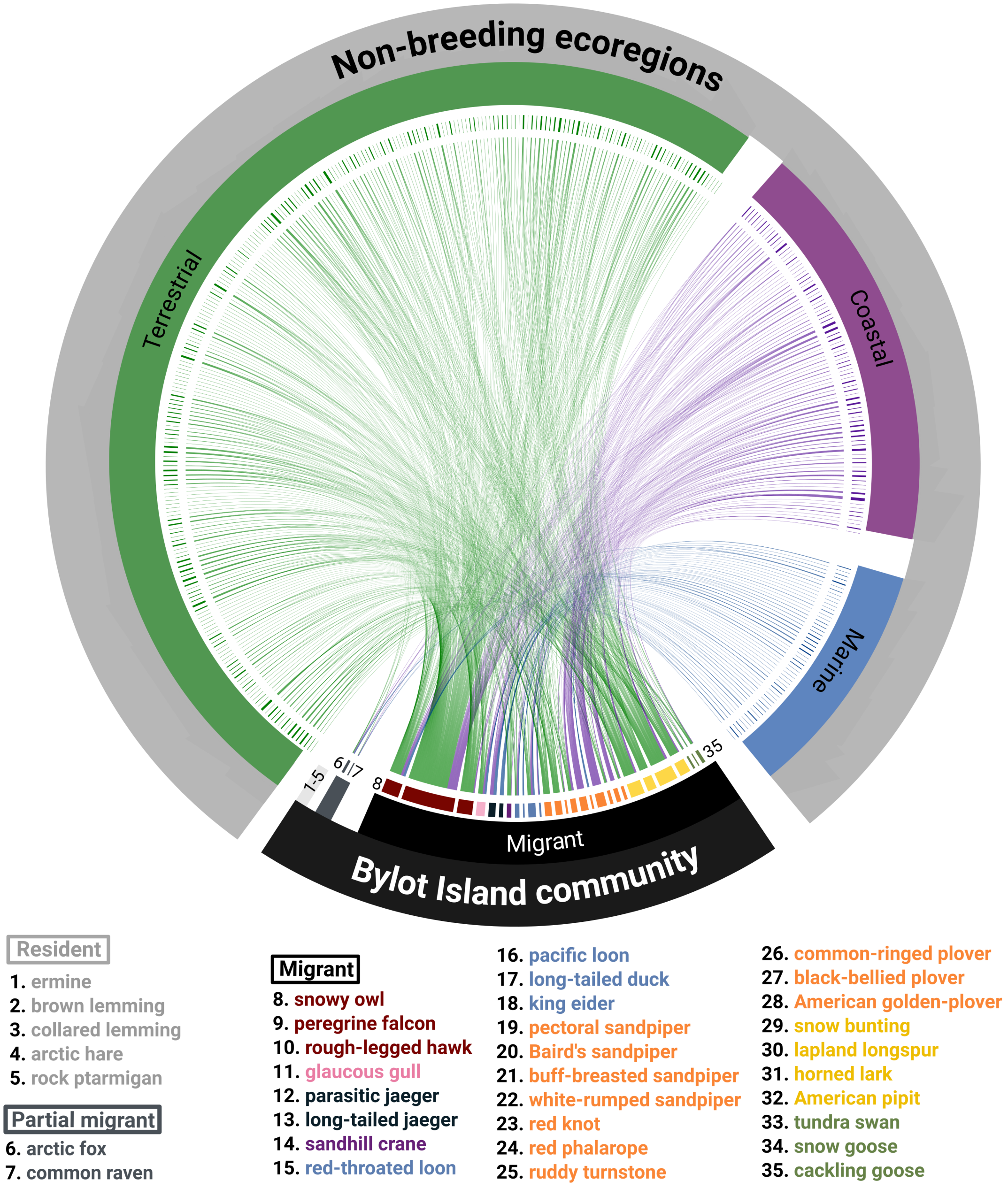

Figure 1.5 – Community migration network of Bylot Island with the 35 species labeled in an anticlockwise way and the 393 biogeographic ecoregions colored by type (green=terrestrial, purple=coastal and blue=marine). Migratory species were colored based on their functional groups (red=raptors, pink= gulls, 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).

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 1.6** and see **Table S4** in the online supplementary material for the complete list of ecoregions and their assigned modules.). 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.

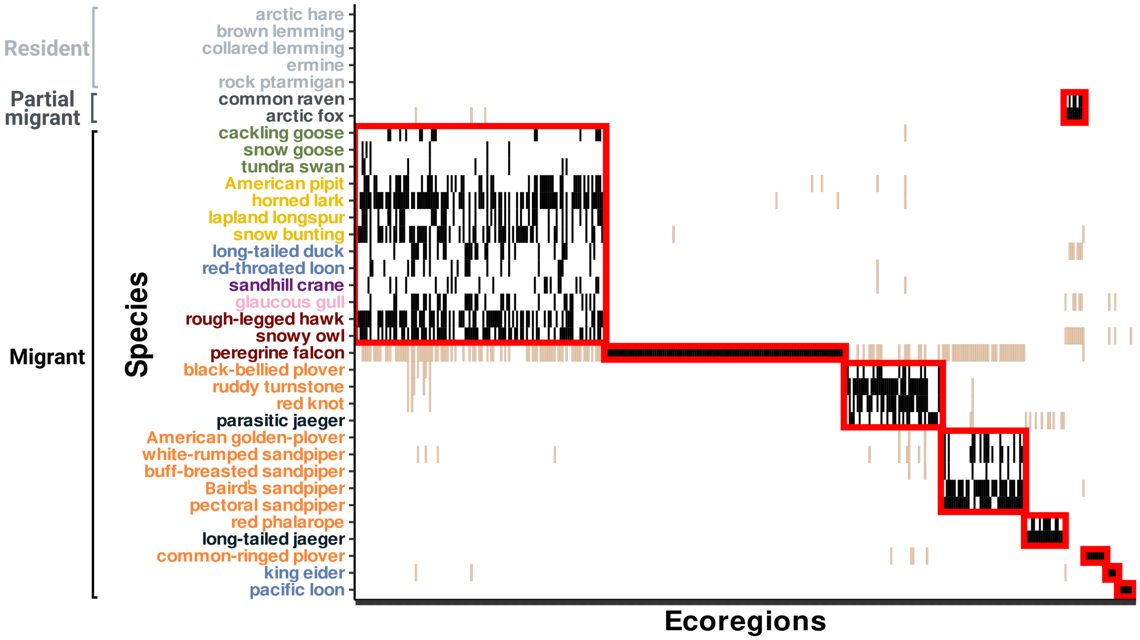

Figure 1.6 – Partition of the Bylot Island community migration network with the highest modularity based on the infomapecology algorithm (M=6.32, p<0.001), with nine modules of species and ecoregions sharing more edges between them than with other species and ecoregions of the network. Modules are represented 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).

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 1.7**). We illustrate that the shorebirds functional group composed of 10 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.

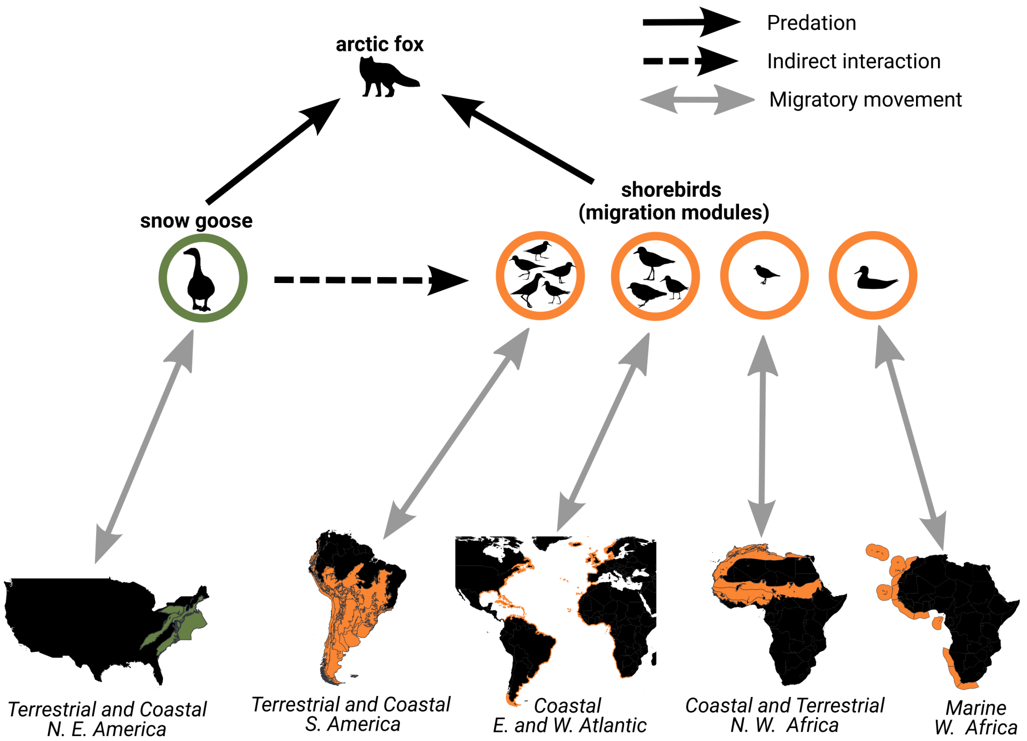

Figure 1.7 – Snow geese and shorebirds breeding on Bylot Island share a predator (Arctic fox), which may result in the spatial propagation of agricultural changes occurring in temperate ecoregions used by geese during the non-breeding period (green) to ecoregions used by shorebirds during the non-breeding 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.

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

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

Spatial cascades *via* migratory species have been described in well-known cases of animal migration, highlighting the diversity of mechanisms by which migratory species can propagate perturbations. Perturbations at geese non-breeding and staging grounds can alter nutrient subsidies (Hessen et al., 2017), trophic subsidies and associated indirect species interactions (Lamarre et al., 2017; Duchesne et al., 2021), and even cause drastic shifts in communities and ecosystems used for breeding (Jefferies, 2004). Springer et al. (2018) showed that hatchery-induced increases in salmon populations led to a decrease in available food for short-tailed shearwaters (*Ardenna tenuirostris*) at their non-breeding grounds, leading to a reduction in population size at their breeding grounds. As a result, nutrient subsidies would be reduced and this could lead to cascading changes in the insular communities used for breeding. In the well-known Seregenti system, Holdo et al. (2009) showed that a change in the population size of migratory wildebeest (*Connochaetes taurinus*) can influence fire frequency and forest cover at the meta-ecosystem level. Perturbations do not act in isolation in communities and may interact with each other and cause additive, synergistic, or antagonistic effects at the community level (Beauchesne et al., 2021). The diverse effects of migratory species on communities and ecosystems (Bauer and Hoye, 2014) highlight the difficulty of assessing the net effect of perturbations, which currently limits the applications of our approach.

The modular (non-random) network structure observed in our case study suggests that evolutionary and geographic constraints as well as ecological factors potentially shape the structure of migratory pathways at the community level. The proportion of migratory species is strongly correlated with the magnitude of seasonality, at least for terrestrial bird communities (Hurlbert and Haskell, 2003; Somveille et al., 2013). Also, migratory birds tend to relocate from breeding to non-breeding grounds by minimizing migration distance to reach suitable grounds in terms of climate and resources, akin to a refuge from the harsher conditions of the breeding ground (Somveille et al., 2015, 2019, 2021; Bonnet-Lebrun et al., 2021). Unsurprisingly, most migratory species from Bylot Island reach non-breeding grounds in temperate environments (intermediate migration distance from the focal community), suggesting an influence of community geographical location on the structure of migratory pathways. Somveille et al. (2019) also observed that trans-hemispheric migrants did not seem to respond to the same ecological drivers as migrants travelling within the same hemisphere. Interestingly, in the community migration network of Bylot Island, we observed a clear distinction between the functional groups performing trans-hemispheric migrations (shorebirds, jaegers and some raptors) and those who do not (geese and swans, passerines, cranes, gulls and ducks and loons and some raptors). The presence of modules composed of functionally similar species associated with common habitats (e.g., shorebirds in South American ecoregions) suggests that adaptive constraints on flight efficiency, environmental tolerance and diet may influence network structure by increasing the modularity. We could address the influence of phylogeny on migrations at the community level by linking phylogenetic distance, geographic distance and location of migratory destinations and species degree in the network. Within modules of functionally similar species, ecological factors such as interspecific interactions (mutualism or competition) could potentially increase or decrease the spatial overlap between species (Gotelli et al., 2010). Linking community and species traits, geography, phylogeny and species interactions with community migration network metrics will allow a better understanding of the factors and constraints shaping migratory patterns at 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. Our approach includes two sources of measurement uncertainty, the sampling of the community assemblage and the delineation of species ranges. We did not quantify either of these sources and therefore do not know the uncertainty of the observed metrics. A community surveyed with little effort would underestimate the number of migratory species, which could potentially influence network metrics in both directions (higher or lower). However, in our case, the surveyed community was heavily sampled. Despite the small sample size of our validation analysis, it suggests that using refined species range maps tends to overestimate the number of connected ecoregions, which could also influence network metrics in both directions. Developing an approach to measure these two sources of uncertainty, as well as their effects on community migration network metrics is a gap that needs to be filled in order to compare the structure of migratory pathways between communities. 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 population distribution (Smith et al., 2022; Center et al., 2022) will reduce uncertainty and 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, 2019, 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 allow for a better representation of connections at the meta-level, providing a more direct way to link migrations to ecosystem and community processes. This could be done by weighting edges with biomass to address energy, nutrient, and contaminant exchanges or by weighting edges with abundance to address parasite and disease exchanges and trophic effects. 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. This could involve integrating species traits and trophic position into community migration networks to identify distant regions and species more likely to generate spatial cascades. Scaling migrations at the community level is a first step towards assessing community vulnerability to changes occurring in distant locations connected through animal movement. To practically use our approach in a perturbation propagation context (e.g., conservation purposes), we will need to examine the relationship between community migration network metrics and community sensitivity, resilience, and vulnerability to distant changes. The development of community migration networks should thus improve our ability to anticipate the effects of global changes on ecosystems.

1.11 Data availability statement

Publicly available datasets were analyzed in this study. The data can be found here: eBird range maps: Long-tailed Jaegers: `https://www.movebank.org` Study ID = 1978212368. Common-ringed plovers: `https://www.movebank.org`, Study ID = 849807214. American Golden-Plovers: `https://www.movebank.org`, Study ID = 565443493. Snowy owls:`https://www.movebank.org`, Study ID = 12112706. King eiders: `https://www.movebank.org`, Study ID = 43747715. Terrestrial Ecoregions of the World: `https://www.worldwildlife.org/publications/terrestrial-ecoregions-of-the-world`. Freshwater Ecoregions of the World: `https://www.feow.org/download`. Marine and Coastal Ecoregions of the World: https://www.worldwildlife.org/publications/. Major Flyways of the World: `https://wpp.wetlands.org/downloads/downloads`. Scripts for data manipulation, analysis, and visualization can be found at: `https://github.com/Louis-Moisan/Community_Migration_Networks`. All other data are available on request from the corresponding author.

1.12 Ethics statement

Ethical review and approval was not required for the animal study because the study is based on published datasets approved by animal care committee.

1.13 Author contributions

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

1.14 Funding

This project was funded by (alphabetical order): Arctic Goose Joint Venture, Arctic Net, BIOS2 (NSERC CREATE Training Programs), Canadian Wildlife Service, EnviroNord (NSERC CREATE Training Program in Northern Environmental Sciences), Fonds de recherche du Québec - Nature et technologies (FRQNT), Indigenous and Northern Affairs Canada, Natural Resources Canada (PCSP), Natural Science and Engineering Research Council of Canada (NSERC), Nunavut Wildlife Management Board, Polar Knowledge Canada, Université Laval, Université du Québec à Rimouski and Centre d'Études Nordiques.

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1.16 Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest. The handling editor M-JF declared a past co-authorship with the author DG.

1.17 Publisher's note

All claims expressed in this article are solely those of the authors and do not necessarily represent those of their affiliated organizations, or those of the publisher, the editors and the reviewers. Any product that may be evaluated in this article, or claim that may be made by its manufacturer, is not guaranteed or endorsed by the publisher.

1.18 Supplementary information

1.18.1 Vertebrate community definition

We defined the vertebrate community at the species level with both standardized and non-standardized observations. We used annual records of vertebrates by field observations during the bird incubation period from late June to mid-July from 2010 to 2019. The observations were made from 500m linear transects (n= 145 to 295 per year), where all vertebrates were recorded within 150m of each side (Lamarre et al., 2017; Duchesne et al., 2021). We also used non-standardized daily incidental observations of vertebrates made by a single or a group of researchers from late May to late August each year from 2007 to 2019. Each species observed incidentally during field days was recorded. We apply the following criteria to each data set to exclude occasional visitors: i) species without confirmed breeding cases on the study site, ii) species observed only in a single year, and iii) species typically breeding and foraging in nearby marine or coastal habitats. After applying those criteria, we obtained 32 species with the standardized data and 35 with the daily incidental observations. We retained the largest number of species from these two lists (**Table 1.1**).

1.18.2 Non-breeding range delimitation

1.18.2.1 Range maps

The non-breeding range of most migratory species (22 of 28) was derived from species range maps defined by either a collection of diverse data sources, models of species occurrence based on amateur bird watching observations, or a combination of both.

Birdlife range maps (Migratory species)

We used the non-breeding range maps defined by BirdLife International and Handbook of the Birds of the World (2019) (hereafter **Birdlife**). The Birdlife range maps are based on a combination of individual localizations from scientific collections, field observations, published and unpublished literature, range maps and expert knowledge. All maps were reviewed between 2014 to 2017. Birdlife range maps include the intercontinental distribution of species in terrestrial, coastal and marine habitats. However, the precision and accuracy seem to vary between species, probably depending on the quality of the available data.

eBird range maps (Migratory species)

We used range maps defined by Fink et al. (2020*b*) (hereafter **eBird**) based on models of species occurrence built with amateur birdwatching observations and 79 environmental predictors, where 76 were derived from 19 land cover variables (Fink et al., 2020*a*). Species range maps defined by eBird have a high resolution (2.8 × 2.8 km) and are defined based on recent observations but are, for the moment, restricted to the Americas only. The eBird ranges do not extend to marine habitats since most observations are on land.

1.18.2.2 Tracking devices

Snowy owls

Snowy owls were captured at the study site and tracked for up to three consecutive years with ARGOS satellite transmitters in 2007 (n=9) and 2014 (n=3) (Therrien et al., 2012; Robillard et al., 2018). The non-breeding period was defined for each individual and year based on the daily distance traveled (Robillard et al., 2018). The non-breeding range of snowy owls was defined with a 95 % kernel density function of pooled non-breeding locations using the R package adehabitatHR (Calenge, 2006). The kernel was based on a bivariate normal kernel distribution with a fixed smoothing term, an automatic bandwidth selection with the ad hoc method, and the default software grid resolution.

Common-ringed plovers

Common-ringed plovers were captured at the study site and tracked from 2014 to 2016 (n= 14) with geolocators (Léandri-Breton et al., 2019). The non-breeding period was defined for each individual by considering the period where no apparent migration movement was observed for more than sixty days. The non-breeding range was defined with a 95 % kernel density function of pooled non-breeding locations using the R package adehabitatHR (Calenge, 2006). The kernel was based on a bivariate normal kernel distribution with a fixed smoothing term, bandwidth selection was done with a least-square cross-validation method (LSCV) because we did not observe convergence with the ad hoc method, and we used the default software grid resolution. We removed the marine part of the defined non-breeding range polygon since common-ringed plovers are associated to terrestrial and coastal habitats during the non-breeding period based on Billerman et al. (2021). The presence of a marine portion in the raw non-breeding range defined with geolocators could be explained by the uncertainty of the tracking devices, which located coastal individuals in the nearby marine environment.

Snow Geese

Snow geese were captured during migration at a staging site at Île-aux-Oies (St-Lawrence River, Québec, Canada) and equipped with GPS-GSM collars from 2019 to 2021 (Legagneux et al., unpublished data; LeTourneux et al. 2021). We selected only locations from geese that have bred on Bylot (n= 12) and filtered to keep only locations during January and February to represent the non-breeding range. We defined the non-breeding period for snow geese as January and February, based on a visual inspection of the individual movement to identify the longest period where individuals are relatively stationary. The non-breeding range of snow goose was also defined with a 95 % kernel density function of pooled non-breeding locations using the R package adehabitatHR (Calenge, 2006). The kernel was based on a bivariate normal kernel distribution with a fixed smoothing term, an automatic bandwidth selection with the ad hoc method, and the default software grid resolution. We removed the marine part of the defined non-breeding range polygon since snow geese are associated to terrestrial and coastal habitats during the non-breeding period based on Billerman et al. (2021). The presence of a marine portion in the raw non-breeding range defined with GPS could be explained by the uncertainty of the tracking devices, which located coastal individuals in the nearby marine environment. We compared the non-breeding range of snow geese defined with tracking devices to the non-breeding range defined with winter band recovery from individuals banded from Bylot Island (n= 7 156) and observed a highly similar range. The non-breeding of snow goose encompassed the boundaries of six ecoregions when defined with tracking devices and seven ecoregions when defined with banding data. The further analyses were performed with the tracking data.

Long-tailed jaegers

Long-tailed jaegers were captured in 2008 and from 2014 to 2019, equipped with geolocators or satellite transmitter devices, and tracked year-round (Seyer et al., 2021). Most individuals were tracked from Bylot Island (n= 50); however, two individuals were tracked from a site located around 400 km south of the study site (Seyer et al., 2021). The non-breeding range of long-tailed jaegers was also defined with a 95 % kernel density function of pooled non-breeding locations using the R package adeadehabitatHR (Calenge, 2006). The kernel was based on a bivariate normal kernel distribution and the least-square cross-validation method (LSCV) to select the smoothing parameters (Seyer et al., 2021).

American golden-plovers

American golden-plovers were captured at the study site from 2009 to 2015 and equipped with geolocators (Lamarre et al., 2021). Individuals were recaptured on Bylot 1 to 4 years after the first capture; we used the tracks of 19 individuals. The non-breeding locations were defined as the southernmost cluster of locations. The non-breeding range was defined with a 95 % kernel density estimation of pooled non-breeding locations using the kde function in the R package ks (Duong, 2007). We removed the marine part of the defined non-breeding range polygon since American golden-plovers are associated to terrestrial and coastal habitats during the non-breeding period based on Billerman et al. (2021). The presence of a marine portion in the raw non-breeding range defined with geolocators could be explained by the uncertainty of the tracking devices, which located coastal individuals in the nearby marine environment.

King eiders

King eiders were captured at East Bay in the Eastern Canadian subarctic around 1 000 km south of the study site (n= 6; Gilchrist et al. 2004). Subarctic and High-Arctic king eiders from the Canadian Eastern Arctic mixed on the same non-breeding grounds on the West coast of Greenland (Salomonsen, 1968). We defined the stationary non-breeding period for king eiders from November to March, based on a visual inspection of the individual movement to identify the longest period where individuals are relatively stationary. We filtered to keep only stationary non-breeding locations. The non-breeding range of king eiders was defined with a 95 % kernel density function of pooled non-breeding locations using the R package adehabitatHR (Calenge, 2006). The kernel was based on a bivariate normal kernel distribution with a fixed smoothing term, an automatic bandwidth selection with the ad hoc method, and the default software grid resolution. We removed the terrestrial portion of the defined non-breeding range polygon since king eiders are associated to coastal and marine habitats during the non-breeding period based on Billerman et al. (2021). The presence of a terrestrial portion in the raw non-breeding range could be explained by the uncertainty of the tracking devices, which located coastal individuals in the nearby terrestrial environment.

1.18.2.3 Buffer zones (Partially migratory species)

The non-breeding range of the partially migratory Arctic fox was delimited with a 500 km buffer around the study site based on the extent of the foraging trips documented by Lai et al. (2017). The non-breeding range of the partially migratory common raven was delimited with a 100 km buffer centered on the study site. We selected a 100 km radius around the study site which allow to encompass the nearest town and the nearby marine environment where ravens could scavenge on seals; based on winter foraging behavior documented by Temple (1974).

1.18.2.4 Selecting range data for each migratory species

We used the non-breeding ranges defined with tracking devices in priority if available. Otherwise, Birdlife range maps, eBird range maps, or the overlap between eBird and Birdlife range maps were used (**Table 1.1**). Birdlife range maps were selected over eBird range maps for species associated with marine habitats during the non-breeding season (6 species). Birdlife range maps were also prioritized for migratory species associated with the East Atlantic Flyway connecting the Canadian Arctic with European and African regions since eBird range maps are restricted to the Americas. Ebird range maps were chosen over Birdlife when the eBird range boundaries of a species fell inside the

Birdlife range because the resolution of eBird was higher (2.8 km × 2.8 km; 3 species). In other cases, a visual inspection of the correspondence between the Birdlife, eBird and the overlap between Birdlife and eBird non-breeding range maps with the non-breeding density defined by Fink et al. (2020*a*) was realized to select the most representative range data (11 species; **Figure 1.8A**).

1.18.2.5 Refining non-breeding range with species flyways

The non-breeding ranges of species were refined with the specific flyways used by the population or subspecies at the study site. The subspecies of polytypic migratory species were identified using the subspecies breeding range (Billerman et al., 2021). Populations of monotypic species with distinct geographic populations were identified with the literature available: research articles, unpublished tracking programs and animal movement database (Wikelski et al., 2021; Seaturtle, 2021). It allowed us to identify a single or multiple flyways encompassing the entire non-breeding range of each subspecies or population present at the study site (**Table 1.2**). We used the spatial extent of the major flyways of the world obtained from Wetlands International (2022). For each species, the area of the non-breeding range falling outside the boundaries of the identified flyway(s) was removed (**Figure 1.8B**). It allowed us to retain only areas of the non-breeding range where individuals from the study site have a higher occurrence probability.

1.18.3 Association between species non-breeding range and biogeographic ecoregions

1.18.3.1 Biogeographic ecoregions of the world

We used worldwide classifications of terrestrial, marine and coastal ecoregions (**Figure 1.9**) to determine the ecoregions where each migratory species is found during the non-breeding period. We used the well-known classifications of terrestrial ecoregions made by Olson et al. (2001) and marine ecoregions made by Spalding et al. (2007). An ecoregion represents a relatively homogeneous species assemblage at the regional scale (e.g., Bylot Island is located in the "High Arctic Tundra Ecoregion" and New York is located in the "Northeastern Coastal Forests Ecoregion"). The ecological relevance of terrestrial ecoregion boundaries has been shown for vertebrate and plant species assemblages (Smith et al., 2018). Ecoregion boundaries are caused by environmental conditions, topography and biogeographic history (Olson et al., 2001; Spalding et al., 2007). The absence of a worldwide classification of coastal ecoregions leads us to implement a classification consisting of narrow biogeographic regions along the coastline of the world. We refer to coastal regions as a region under the influence of the tide, so we defined a buffer of less than three km width on both sides of the coastline of the world. We delineated and named coastal ecoregions based on the adjacent marine ecoregions (Spalding et al., 2007). We removed the continental and coastal portions of the marine ecoregions since we defined a unique classification for coastal ecoregions. We decided to change the classification of mangroves from terrestrial to coastal ecoregion since tides influence them. Finally, large bodies of water were not assigned to specific ecoregions in the classification of terrestrial ecoregions (Olson et al., 2001), thus we assigned freshwater ecoregions to large inland bodies of water from the classification of freshwater ecoregions of the world

(Abell et al., 2008).

1.18.4 Filtering selected ecoregions based on species' non-breeding habitats

We filtered the ecoregions associated with each species during the non-breeding period based on the main type(s) of non-breeding habitat (terrestrial, marine or coastal). It allowed us to avoid the inclusion of edges that would represent weak ecological interaction between a species and an ecoregion. Single or multiple habitat types (terrestrial, marine and coastal) were assigned to each species based on the typical non-breeding habitat described in Billerman et al. (2021) (**Table 1.3**). Terrestrial habitats were defined as continental, including freshwater, but excluding coastal environments. Coastal habitats were defined as 3 km from both sides of the coastline to represent tidal environment and marine habitats were defined as the oceanic area located more than 3 km from the coastline. We removed the ecoregions associated with unassigned habitat types for each species. Using habitat type(s) as an ecological filter prevents the consideration of ecologically irrelevant associations between species and ecoregions during the geoprocessing based on a minor spatial overlap.

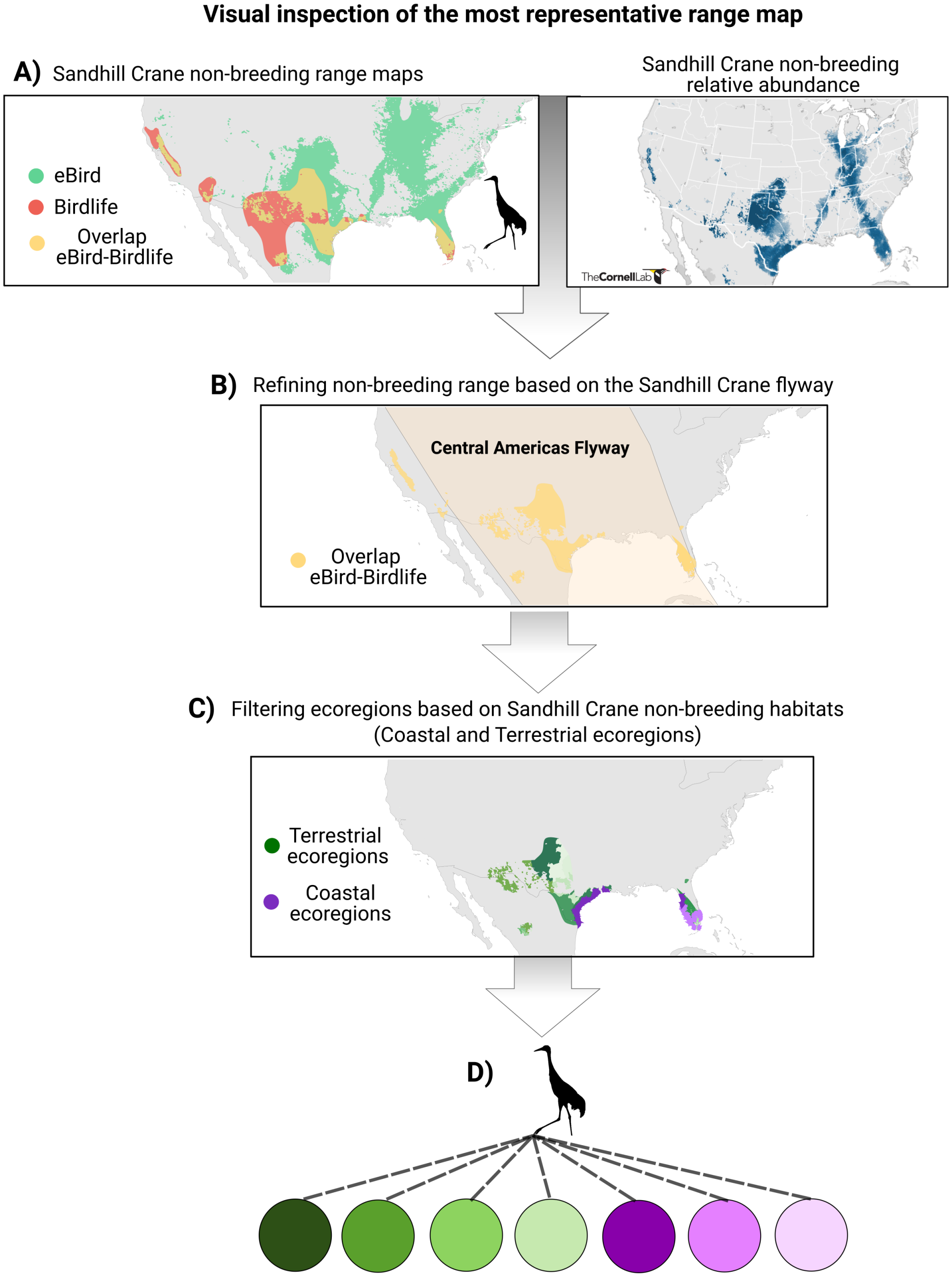
Visual inspection of the most representative range map
A) Sandhill Crane non-breeding range maps
eBird
Birdlife
Overlap eBird-Birdlife
Sandhill Crane non-breeding relative abundance
TheCornellLab
B) Refining non-breeding range based on the Sandhill Crane flyway
Central Americas Flyway
Overlap eBird-Birdlife
C) Filtering ecoregions based on Sandhill Crane non-breeding habitats (Coastal and Terrestrial ecoregions)
Terrestrial ecoregions
Coastal ecoregions
D)

Figure 1.8 – **(A)** Example of the visual inspection criteria to select the most representative non-breeding range data for sandhill crane. **(B)** Refinement of the selected non-breeding range map with the flyway used by sandhill crane from the study site population (i.e., Central Americas Flyway). **(C)** Refinement of the list of ecoregions associated with the sandhill crane population based on non-breeding habitat type. Based on the literature, we have assigned both terrestrial and coastal habitats to the sandhill crane population, which precludes association with marine ecoregions. **(D)** Bipartite representation of the migratory connections between the sandhill crane species node (crane icon) and the connected terrestrial ecoregions (green circles) and the coastal ecoregions (purple circles) used as non-breeding ground.

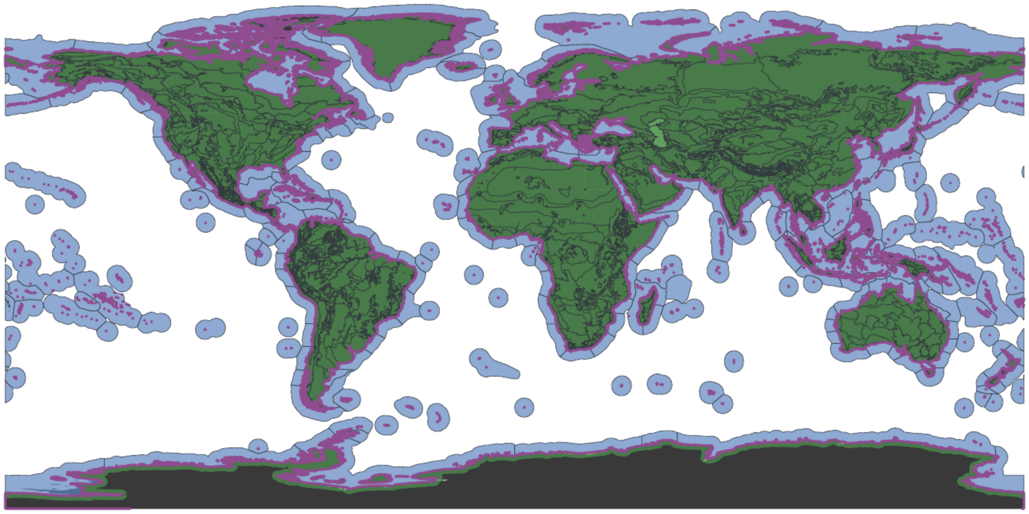

Figure 1.9 – Map of the ecoregions of the world delineated by dark gray lines and colored by type: terrestrial ecoregions in green (adapted from Olson et al. 2001), marine ecoregions in blue (adapted from Spalding et al. 2007) and coastal ecoregions in purple (adapted from Spalding et al. 2007). Since coastal ecoregions are extremely narrow, the delineation between ecoregions is not showed on the map, but the delineation between coastal ecoregions was based on the marine ecoregions.

1.18.5 Validation of the non-breeding range refinement with the flyways(s) and the non-breeding habitat type(s)

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). We compared the proportion of ecoregions filtered from general range maps using the non-breeding range defined with tracking data (**Figure 1.10**).

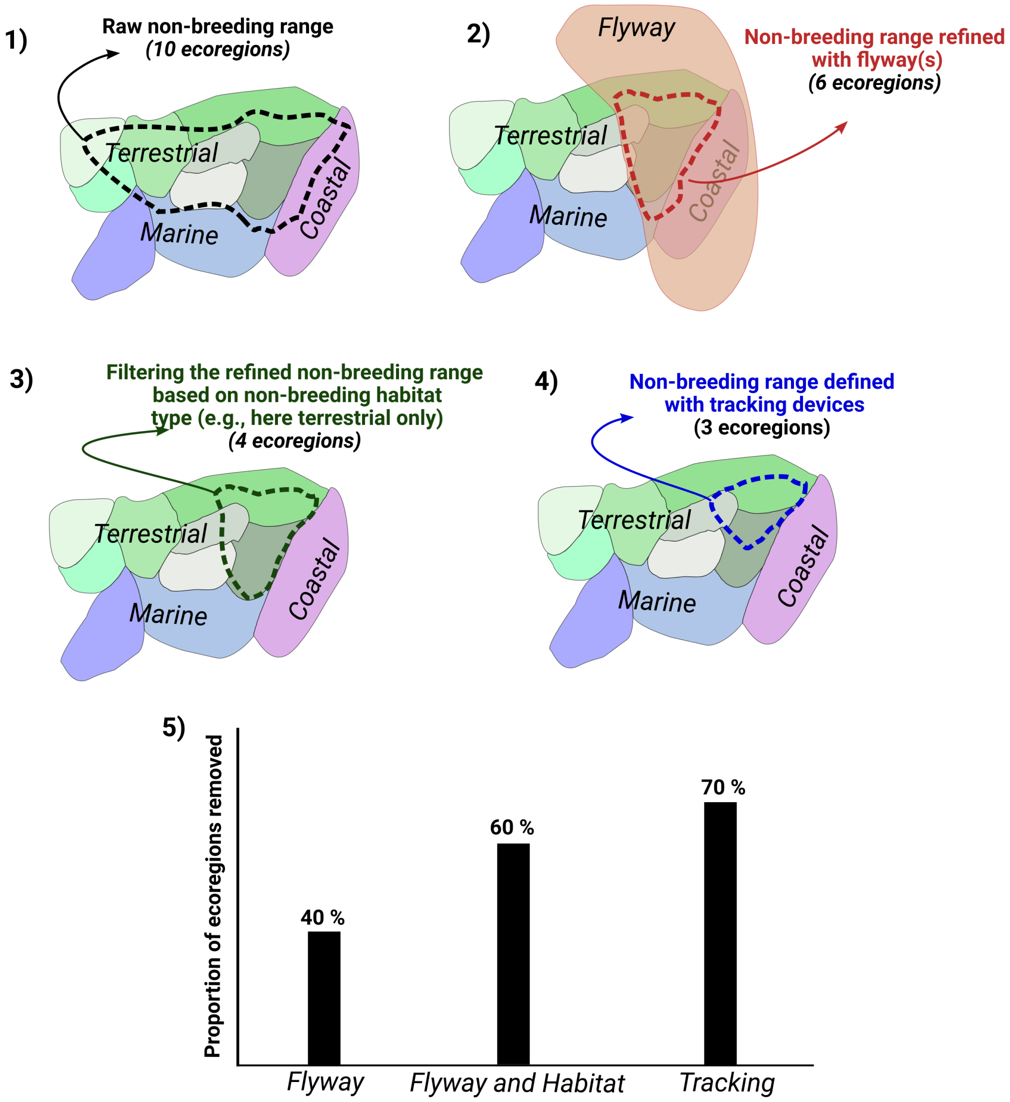

Figure 1.10 – Fictive example of the refinement of a non-breeding range with flyway(s) and filtering with habitat type(s) to illustrate the method employed to calculate the proportion of ecoregions removed. (**1**) Number of ecoregions overlapping with the raw species non-breeding range maps. (**2**) Number of ecoregions associated with the non-breeding range map refined with the flyway(s) used by the individuals from the study site. (**3**) Number of ecoregions associated with the non-breeding range map refined with the flyway(s) used by the individuals from the study site and their habitat type(s). (**4**) Number of ecoregions associated with the non-breeding range map defined with accurate and specific tracking data. (**5**) Comparison of the efficiency of each type of filter (Flyway(s), Habitat and Flyway(s) and Tracking data) measured by the proportion of removed ecoregions from the raw non-breeding range.

Despite the relatively low sample size of our reference data set (n=6 species; American golden-plover, common-ringed plover, snowy owl, long-tailed jaeger, snow goose and king eider), the validation analysis suggests that the use of flyway(s) and non-breeding habitat type(s) allow the removal of a considerable number of ecoregions, but still tend to overestimate the number of associated ecoregions (**Figure 1.11**). The eBird sample size is smaller than the Birdlife sample size because species with Old World ranges are not part of the eBird data set. The use of flyway(s) was more effective in refining Birdlife range maps than eBird range maps because it allows the removal of areas in the Old World which are not included in eBird range maps. Flyway(s) and habitat type(s) appear to have an additive effect on the removal of irrelevant species-ecoregion association (higher proportion of ecoregions removed with flyway+habitat than flyway only or habitat only). The wide variation observed in the proportion of ecoregions removed by flyway(s) and habitat type(s) suggests that the effectiveness of ecological filters in refining species range maps depends on the species involved. This means that for some species, filters have removed a large proportion of ecoregions (often species with intercontinental or global distributions) and for other species, filters have practically no effect (species with more localized ranges). The high proportion of ecoregions removed by using specific data (tracking) highlights the need to consider ecological filters to refine non-breeding ranges when focusing on a local or regional community. Note that the higher sample size with Birdlife range maps is explained by the presence of some species only outside of the Americas, thus for which eBird data are not available yet.

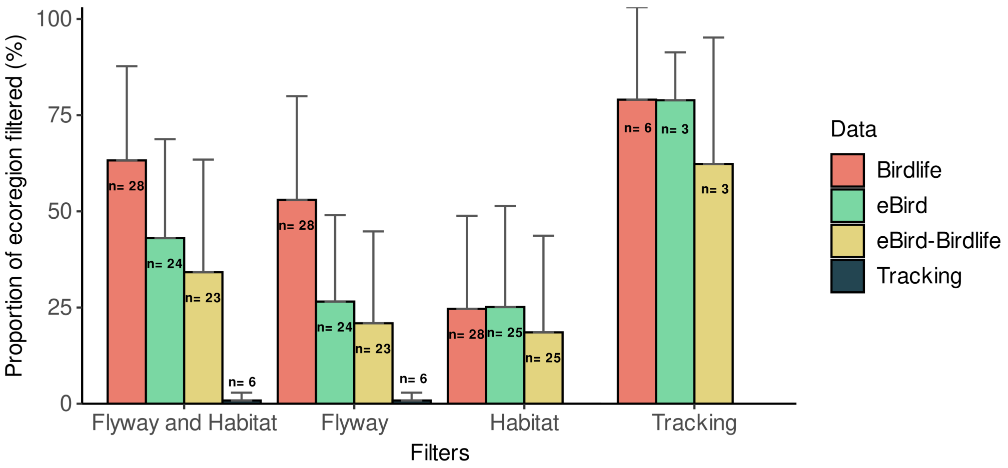

Figure 1.11 – Mean proportion of ecoregion removed from the raw non-breeding range maps by the refinement with flyway(s) and the filtering with habitat type(s), the refinement with the flyway(s) only, the filtering with habitat type(s) only and the filtering with non-breeding ranges defined with tracking data. Error bars represent standard deviation and the sample size represents the number of species considered.

Table 1.1 – Species of Bylot Island tundra food web and the non-breeding range map selected for migratory and partially migratory species based on the selection criteria used to retain the most representative non-breeding range data available.

Functional group	**Species**	**Non-breeding strategy**	**Range selected**	**Selection criteria**
Mosses	Polytrichum spp., Meesia triquetra	Resident	-	-
Forbs	Luzula spp., Saxifraga spp., Oxytropis maydelliana, Polygonum viviparum	Resident	-	-
Shrubs	Salix spp., Cassiope tetragona, Dryas integrifolia, Vaccinium uliginosum	Resident	-	-

Sedges and Grasses	Eriophorum scheuchzeri, Carex aquatilis, Dupontia fisheri	Resident	-	-
Arthropods	Chironomidae, Muscidae, Aranea, Lepidoptera, Ichneumonidae, Carabidae	Resident	-	-
Lemmings	Collared Lemming (Dicrostonyx groenlandicus)	Resident	-	-
Lemmings	Brown Lemming (Lemmus trimucronatus)	Resident	-	-
Hares	Arctic Hare (Lepus arcticus)	Resident	-	-
Ptarmigans	Rock ptarmigan (Lagopus muta)	Resident	-	-
Geese and Swans	Snow Goose (Anser caerulescens)	Migrant	Tracking	Legagneux et al., unpublished data
Geese and Swans	Cackling Goose (Branta hutchinsii)	Migrant	eBird-Birdlife	Visual inspection of the overlap with the Ebird relative abundance map
Geese and Swans	Tundra Swan (Cygnus columbianus)	Migrant	Birdlife	Visual inspection of the overlap with the Ebird relative abundance map
Passerines	Lapland Longspur (Calcarius lapponicus)	Migrant	eBird-Birdlife	Visual inspection of the overlap with the Ebird relative abundance map
Passerines	Horned Lark (Eremophila alpestris)	Migrant	eBird	Visual inspection of the overlap with the Ebird relative abundance map
Passerines	Snow Bunting (Plectrophenax nivalis)	Migrant	eBird-Birdlife	Visual inspection of the overlap with the Ebird relative abundance map
Passerines	American Pipit (Anthus rubescens)	Migrant	eBird-Birdlife	Visual inspection of the overlap with the Ebird relative abundance map
Shorebirds	American Golden-Plover (Pluvialis dominica)	Migrant	Tracking	Lamarre, J. F., Gauthier, G., Lanctot, R. B., Saalfeld, S. T., Love, O. P., Reed, E., et al., (2021). Timing of Breeding Site Availability Across the North American Arctic Partly Determines Spring Migration Schedule in a Long-Distance Neotropical Migrant. Front. Ecol. Evol. 9, 710007. https://doi.org/10.3389/fevo.2021.710007
Shorebirds	Black-bellied Plover (Pluvialis squatarola)	Migrant	eBird	Ebird range falls inside the boundary of the Birdlife range

Shorebirds	Common-ringed Plover (Charadrius hiaticula)	Migrant	Tracking	Léandri-Breton, D.-J., Lamarre, J.-F., and Bêty, J. (2019). Seasonal variation in migration strategies used to cross ecological barriers in a nearctic migrant wintering in Africa. J. Avian Biol. 50, e02101. https://doi.org/10.1111/jav.02101
Shorebirds	Ruddy Turnstone (Arenaria interpres)	Migrant	Birdlife	Birdlife range encompass palearctic distribution
Shorebirds	Red Phalarope (Phalaropus fulicarius)	Migrant	Birdlife	Species found mostly in marine habitats during non-breeding
Shorebirds	Red Knot (Calidris canutus)	Migrant	Birdlife	Birdlife range encompass palearctic distribution
Shorebirds	White-rumped Sandpiper (Calidris fuscicollis)	Migrant	eBird	Visual inspection of the overlap with the Ebird relative abundance map
Shorebirds	Buff-breasted Sandpiper (Calidris subruficollis)	Migrant	eBird	Visual inspection of the overlap with the Ebird relative abundance map
Shorebirds	Bairds Sandpiper (Calidris bairdii)	Migrant	eBird	Ebird range falls inside the boundary of the Birdlife range
Shorebirds	Pectoral Sandpiper (Calidris melanotos)	Migrant	eBird	Ebird range falls inside the boundary of the Birdlife range
Ducks and Loons	King Eider (Somateria spectabilis)	Migrant	Tracking	Gilchrist, G., Mosbech, A., and Sonne, C. (2004). Data available on movebank.org, study name "Common/King Eiders; East Bay Island, Nunavut; Gilchrist/Mosbech/Sonne 2001 and 2003", study ID 43747715).
Ducks and Loons	Long-tailed Duck (Clangula hyemalis)	Migrant	Birdlife	Species found mostly in marine habitats during non-breeding
Ducks and Loons	Pacific Loon (Gavia pacifica)	Migrant	Birdlife	Species found mostly in marine habitats during non-breeding
Ducks and Loons	Red-throated Loon (Gavia stellata)	Migrant	Birdlife	Species found mostly in marine habitats during non-breeding
Ermines	Ermine (Mustela erminea)	Resident	-	-
Cranes	Sandhill Crane (Antigone canadensis)	Migrant	eBird-Birdlife	Visual inspection of the overlap with the Ebird relative abundance map
Jaegers	Long-tailed Jaeger (Stercorarius longicaudus)	Migrant	Tracking	Seyer, Y., Gauthier, G., Bêty, J., Therrien, J.-F., and Lecomte, N. (2021). Seasonal variations in migration strategy of a long-distance Arctic-breeding seabird. Mar. Ecol. Prog. Ser. 677, 1-16. https://doi.org/10.3354/meps13905
Jaegers	Parasitic Jaeger (Stercorarius parasiticus)	Migrant	Birdlife	Species found mostly in marine habitats during non-breeding

Gulls	Glaucous Gull (Larus hyperboreus)	Migrant	Birdlife	Species found mostly in marine habitats during non-breeding
Ravens	Common Raven (Corvus corax)	Partial migrant	100 km buffer	Approximate distance from the nearest landfill: Temple, S. A. (1974). Winter food habits of ravens on the Arctic Slope of Alaska. Arctic 27 41-46. https://doi.org/10.14430/arctic2851
Raptors	Peregrine Falcon (Falco peregrinus)	Migrant	eBird	Visual inspection of the overlap with the Ebird relative abundance map
Raptors	Rough-legged Hawk (Buteo lagopus)	Migrant	eBird	Visual inspection of the overlap with the Ebird relative abundance map
Raptors	Snowy Owl (Bubo scandiacus)	Migrant	Tracking and eBird	Robillard, A., Gauthier, G., Therrien, J.-F., and Bêty, J. (2018). Wintering space use and site fidelity in a nomadic species, the snowy owl. J. Avian Biol. 49, jav−01707. https://doi.org/10.1111/jav.01707
Foxes	Arctic Fox (Vulpes lagopus)	Partial migrant	500 km buffer	Lai, S., Bêty, J., and Berteaux, D. (2017). Movement tactics of a mobile predator in a meta-ecosystem with fluctuating resources: the arctic fox in the High Arctic. Oikos 126, 937-947. https://doi.org/10.1111/oik.03948

Table 1.2 – Seasonal migratory species of Bylot Island with their assigned global avian flyway(s) (geographical grouping of annual ranges of avian migratory species). The assignment of flyway(s) was based on the available literature.

Species	**Subspecies**	**Flyway**	**Justification**	**Reference**
American Golden-Plover		Central Americas Atlantic Americas	Individuals tracked from study site (n=19)	Lamarre, J. F., Gauthier, G., Lanctot, R. B., Saalfeld, S. T., Love, O. P., Reed, E., et al., (2021). Timing of Breeding Site Availability Across the North American Arctic Partly Determines Spring Migration Schedule in a Long-Distance Neotropical Migrant. Front. Ecol. Evol. 9, 710007. https://doi.org/10.3389/fevo.2021.710007
American Pipit	A. r. rubescens	Central Americas Atlantic Americas	Subspecies non-breeding range: "se. United States and ne. Mexico, with records south to Guatemala"	Hendricks, P., and Verbeek, N. A. (2020). "American Pipit (Anthus rubescens), version 1.0", in Birds of the World, ed. Billerman, S. M. Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.amepip.01 [Accessed July 2020]
Bairds Sandpiper		Central Americas Pacific Americas	Annual range map	BirdLife International (2020). "Species factsheet: Calidris bairdii", in BirdLife Data Zone. http://datazone.birdlife.org [Accessed July 2020]
Black-bellied Plover		Atlantic Americas	Indivuals tracked from the Eastern Arctic	Canadian Wildlife Service (2020). "Black-bellied Plover Tracking (Canada)", in Seaturtle.org Satellite Tracking Data Repository. http://www.seaturtle.org/tracking/?project_id=1020 [Accessed July 2020]
Buff-breasted Sandpiper		Central Americas	Annual range map	Lanctot, R. B., Aldabe, J., Almeida, J. B., Blanco, D., Jorgensen, J., Rocca, P., et al. (2010). Conservation plan for the Buff-breasted Sandpiper (Tryngites subruficollis) Version 1.1. Manomet Center for Conservation Science, Manomet, Massachusetts, and U.S. Fish & Wildlife Service, Anchorage, Alaska.
Cackling Goose	B. h. hutchinsii	Central Americas	Subspecies non-breeding range: "south-central United States (chiefly Oklahoma and Texas) and south and northeastern Mexico (chiefly Tamaulipas)"	Mowbray, T. B., Ely, C. R., Sedinger J. S., and Trost, R. E. (2020). "Cackling Goose (Branta hutchinsii), version 1.0", in Birds of the World, ed. Rodewald, P. G., and Keeney, B. G. Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.cacgoo1.01 [Accessed July 2020]
Common-ringed Plover		East Atlantic	Individuals tracked from study site (n=14)	Léandri-Breton, D.-J., Lamarre, J.-F., and Bêty, J. (2019). Seasonal variation in migration strategies used to cross ecological barriers in a nearctic migrant wintering in Africa. J. Avian Biol. 50, e02101. https://doi.org/10.1111/jav.02101

Glaucous Gull	L. h. leuceretes	Atlantic Americas	"winters south to the ne. United States, with some reaching south to Florida, east to Bermuda, and west to the Great Plains, e. New Mexico, and s. Texas"	Weiser, E. and Gilchrist, H. G. (2020). "Glaucous Gull (Larus hyperboreus), version 1.0" in Birds of the World, ed. Billerman, S. M. Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.glagul.01 [Accessed July 2020]
Horned Lark	E. a. hoyti	Central Americas Atlantic Americas	"Subspecies non-breeding range: "Nevada to Michigan"	Beason, R. C. (2020). "Horned Lark (Eremophila alpestris), version 1.0" in Birds of the World, ed. Billerman, S. M. Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.horlar.01 [Accessed July 2020]
King Eider		East Atlantic	Individuals tracked from a subarctic Eastern Canadian arctic breeding site (n=6)	Gilchrist, G., Mosbech, A., and Sonne, C. (2004). Data available on movebank.org, study name “Common/King Eiders; East Bay Island, Nunavut; Gilchrist/Mosbech/Sonne 2001 and 2003”, study ID 43747715). Mosbech, A., and Boertmann, D. (1999). Distribution, relative abundance and reaction to aerial surveys of post-breeding king eiders (Somateria spectabilis) in western Greenland. Arctic 52, 188-203. https://doi.org/10.14430/arctic922
Lapland Longspur	C. l. subcalcaratus	Central Americas Atlantic Americas	Subspecies non-breeding range: "e. North America west to Nebraska, Colorado, Oklahoma, and Texas"	Hussell, D. J. T., and Montgomerie, R. (2020). "Lapland Longspur (Calcarius lapponicus), version 1.0", in Birds of the World, ed. Billerman S. M., Keeney, B. K., Rodewald, P. G., and Schulenberg, T. S. Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.laplon.01 [Accessed July 2020]
Long-tailed Duck		Atlantic Americas	Tracks of individuals from non-breeding sites	Sea Duck Joint Venture (2015). Atlantic and Great Lakes sea duck migration study: progress report June 2015.
Long-tailed Jaeger	S. l. pallescens	Atlantic Americas East Atlantic	Individuals tracked from study site (n=50)	Seyer, Y., Gauthier, G., Bêty, J., Therrien, J.-F., and Lecomte, N. (2021). Seasonal variations in migration strategy of a long-distance Arctic-breeding seabird. Mar. Ecol. Prog. Ser. 677, 1-16. https://doi.org/10.3354/meps13905
Pacific Loon		Pacific Americas	Species non-breeding range	Russell, R. W. (2020). "Pacific Loon (Gavia pacifica), version 1.0" in Birds of the World, ed. Rodewald, P. G. Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.pacloo.01 [Accessed July 2020]

Parasitic Jaeger		Atlantic Americas East Atlantic	"Widely distributed off both coasts of South America...Common near coasts of s. Africa from late Oct to early May, especially around the Benguela Current"	McCarty, J. P., L. L. Wolfenbarger, C. D. Laredo, P. Pyle, and R. B. Lanctot (2020). Buff-breasted Sandpiper (Calidris subruficollis), version 1.0. In Birds of the World (P. G. Rodewald, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.bubsan.01
Pectoral Sandpiper		Central Americas Atlantic Americas Pacific Americas	Annual range map	BirdLife International (2020). "Species factsheet: Calidris melanotos", in BirdLife Data Zone. http://www.birdlife.org [Accessed July 2020]
Peregrine Falcon	F. p. tundrius	Central Americas Atlantic Americas Pacific Americas	Individuals tracked from western Greenland	Burnham, K. K., Burnham, W.A., Newton, I., Johnson, J. A., and Gosler, A.G. (2012). The history and range expansion of peregrine falcons in the Thule Area, Northwest Greenland. Monographs on Greenland Bioscience. Museum Tusculanum Press
Red Knot	C. c. islandica C. c. rufa	Atlantic Americas East Atlantic	Study site is located in an overlap zone between the Atlantic Americas population and the East Atlantic population	Environment and Climate Change Canada (2017). Recovery Strategy and Management Plan for the Red Knot (Calidris canutus) in Canada. Ottawa.
Red Phalarope		East Atlantic	"Most birds nesting in e. Canadian Arctic thought to winter off w. and sw. Africa (Brown 1986)"	Tracy, D. M., Schamel, D., and Dale, J. (2020). "Red Phalarope (Phalaropus fulicarius), version 1.0", in Birds of the World, ed. Billerman, S. M. Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.redpha1.01 [Accessed July 2020]
Red-throated Loon		Atlantic Americas	Individuals tracked from non-breeding sites (n=31)	Spiegel, C.S., Berlin, A. M., Gilbert, A. T., Gray, C. O., Montevecchi, W.A., Stenhouse, I. J., et al. (2017). Determining Fine- scale Use and Movement Patterns of Diving Bird Species in Federal Waters of the Mid-Atlantic United States Using Satellite Telemetry. U.S. Department of the Interior, Bureau of Ocean Energy Management . OCS Study BOEM 2017-069.
Rough-legged Hawk	B. l. sanctijohannis	Central Americas Atlantic Americas	Individuals tracked from study site (n=2) and other arctic breeding sites	Paprocki, N. (n.d.). Year-round GPS movements of 77 Rough-legged Hawks .Idaho Cooperative Fish and Wildlife Research Unit. https://www.usgs.gov/media/images/year-round-gps-movements-77-rough-legged-hawks [Accessed July 2020]

Ruddy Turnstone	A. i. morinella A. i. interpres	Atlantic Americas East Atlantic	A. i. morinella: "Canadian arctic populations mainly migrate to and winter in Old World" A. i. interpres: "Winters mainly from s. U.S. along Atlantic and Gulf coasts south around Caribbean Sea, West Indies, and along both coasts of South America"	Nettleship, D. N. (2020). "Ruddy Turnstone (Arenaria interpres), version 1.0", in Birds of the World, ed. Billerman, S. M. Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.rudtur.01 [Accessed July 2020]
Sandhill Crane	A. c. canadensis	Central Americas	Individuals tracked from non-breeding sites	Krapu, G. L., Brandt, D. A., Jones, K. L., and Johnson, D. H. (2011). Geographic distribution of the mid-continent population of sandhill cranes and related management applications. Wildl. Monogr. 175, 1-38. https://doi.org/10.1002/wmon.1
Snow Bunting	P. n. nivalis	Central Americas Atlantic Americas	Low Canadian Arctic populations are associated to the Central Americas Flyway and the populations from western Greenland are associated to the Altantic Americas Flyway	Macdonald, C. A., Fraser, K. C., Gilchrist, H. G., Kyser, T. K., Fox, J. W., and Love, O. P. (2012). Strong migratory connectivity in a declining Arctic passerine. Anim. Migr. 1, 23-30. https://doi.org/10.2478/ami-2012-0003
Snow Goose	A. c. atlanticus	Atlantic Americas	Individuals tracked from study site (n=12)	Legagneux et al., unpublished data
Snowy Owl		Central Americas Atlantic Americas	Individuals tracked from study site (n=12)	Robillard, A., Gauthier, G., Therrien, J.-F., and Bêty, J. (2018). Wintering space use and site fidelity in a nomadic species, the snowy owl. J. Avian Biol. 49, jav–01707. https://doi.org/10.1111/jav.01707
Tundra Swan	C. c. columbianus	Atlantic Americas	Individuals banded and encountered across North America	Ely, C. R., Sladen, W. J., Wilson, H. M., Savage, S. E., Sowl, K. M., Henry, B., et al. (2014). Delineation of Tundra Swan Cygnus c. columbianus populations in North America: geographic boundaries and interchange. Wildfowl 64, 132-147.
White-rumped Sandpiper		Central Americas Atlantic Americas	Annual range map	BirdLife International (2020). "Species factsheet: Calidris fuscicollis", in BirdLife Data Zone. http://www.birdlife.org [Accessed July 2020]

Table 1.3 – Seasonal and partially migratory species of Bylot Island with their assigned primary non-breeding habitat type(s). The assignment of the non-breeding habitat type(s) was based on the available literature.

Species	**Habitat type**	**Justification**	**Reference**
Arctic Fox	Terrestrial Marine Coastal	Loop migration of several hundreads of kilometres in adjacent habitats	Lai, S., Bêty, J., and Berteaux, D. (2017). Movement tactics of a mobile predator in a meta-ecosystem with fluctuating resources: the arctic fox in the High Arctic. Oikos 126, 937-947. https://doi.org/10.1111/oik.03948
Rock Ptarmigan	Terrestrial	"Shrubby areas and margins of lakes and rivers"	Montgomerie, R., and Holder, K. (2020). "Rock Ptarmigan (Lagopus muta), version 1.0", in Birds of the World, ed. Billerman, S. M., Keeney, B. K., Rodewald, P. G., and Schulenberg, T. S. Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.rocpta1.01
Cackling Goose	Terrestrial Coastal	"Coastal areas, mudflats, shallow tidal waters, salt-water marshes, wet grasslands, freshwater marshes, lakes, reservoirs, rivers and agricultural fields"	Mowbray, T. B., Ely, C. R., Sedinger, J. S., and Trost, R. E. (2020). "Cackling Goose (Branta hutchinsii), version 1.0", in Birds of the World, ed. Rodewald, P G., and Keeney, B. K. Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.cacgoo1.01
Snow Goose	Terrestrial Coastal	"Coastal areas, estuarine marshes, inlets, bays, shallow tidal waters, coastal freshwater, brackish marshes, wet grasslands, freshwater marshes, coastal prairies and cultivated fields"	Mowbray, T. B., Cooke, F., and Ganter, B. (2020). "Snow Goose (Anser caerulescens), version 1.0", in Birds of the World, ed. Rodewald, P. G. Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.snogoo.01
Tundra Swan	Terrestrial Coastal	"Shallow estuarine tidal areas, freshwater lakes, ponds, rivers, agricultural fields and flooded pastures"	Limpert, R. J., Earnst, S. L., Carboneras, C., and Kirwan, G. M. (2020). "Tundra Swan (Cygnus columbianus), version 1.0", in Birds of the World, ed. Billerman, S. M. Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.tunswa.01
King Eider	Marine Coastal	"Southern edge of sea ice, polynyas in sea ice, coastal areas, shallow open waters, offshore waters"	Gerber, B. D., Dwyer, J. F., Nesbitt, S. A., Drewien, R. C., Littlefield, R. C., Tacha, T. C., and Vohs, P. A. (2020). "Sandhill Crane (Antigone canadensis), version 1.0", in Birds of the World, ed. Poole, A. F. Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.sancra.01
Long-tailed Duck	Terrestrial Marine Coastal	"Coastal marine waters, large freshwater lakes, with extensive sea ice, will use recurring polynyas and floe edges"	Robertson, G. J., and Savard, J.-P. L. (2020). "Long-tailed Duck (Clangula hyemalis), version 1.0", in Birds of the World, ed. Billerman, S. M. Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.lotduc.01
Pacific Loon	Marine	"Coastal water; nearshore open ocean, bays and estuaries"	Russell, R. W. (2020). "Pacific Loon (Gavia pacifica), version 1.0", in Birds of the World, ed. Rodewald, P G. Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.pacloo.01

Red-throated Loon	Terrestrial Marine Coastal	"Coastal upwellig, coastal estuaries, occasionally on large freshwater lakes and slow-moving rivers"	Rizzolo, D. J., Gray, C. E., Schmutz, J. A., Barr, J. F., Eberl, C., and McIntyre, J. W. (2020). "Red-throated Loon (Gavia stellata), version 2.0", in Birds of the World, ed. Rodewald, P. G., and Keeney, B. K. Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.retloo.02
Snowy Owl	Terrestrial Marine Coastal	"Snow-covered tundra, open water within the ice pack, rangelands, farmlands, coast lines, marshes, large forest clearings and cities and towns"	Holt, D. W., Larson, M. D., Smith, N., Evans, D. L., and Parmelee, D. F. (2020). "Snowy Owl (Bubo scandiacus), version 1.0", in Birds of the World, ed. Billerman, S. M. Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.snoowl1.01
Rough-legged Hawk	Terrestrial Coastal	"Prairies, shrub-steppes, semideserts, open fields, marshlands, bogs, dunes and coastal areas"	Bechard, M. J., Swem, T. R., Orta, J., Boesman, P. F. D., Garcia, E. F. J., and Marks, J. S. (2020). "Rough-legged Hawk (Buteo lagopus), version 1.0", in Birds of the World, ed. Billerman, S. M. Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.rolhaw.01
Peregrine Falcon	Terrestrial Coastal	"Extreme habitat variability: Open-relief, mangrove, coastal or wetland areas, major river valleys, lake shores, pasture lands and urban areas"	White, C. M., Clum, N. J., Cade, T. J., and Hunt, W. G. (2020). "Peregrine Falcon (Falco peregrinus), version 1.0", in Birds of the World, ed. Billerman, S. M. Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.perfal.01
Parasitic Jaeger	Marine Coastal	"Near shore to beyond the edge of the continental shelf and in estuaries"	Wiley, R. H., and Lee, D. S. (2020). "Parasitic Jaeger (Stercorarius parasiticus), version 1.0", in Birds of the World, ed. Billerman, S. M. Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.parjae.01
Long-tailed Jaeger	Marine	"Pelagic"	Wiley, R. H., and Lee, D. S. (2020). "Long-tailed Jaeger (Stercorarius longicaudus), version 1.0", in Birds of the World, ed. Billerman, S. M. Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.lotjae.01
Glaucous Gull	Terrestrial Marine Coastal	"Maritime coasts, freshwater lakes, agricultural fields, urban areas, garbage dumps, polynyas and open water"	Weiser, E., and Gilchrist, H. G. (2020). "Glaucous Gull (Larus hyperboreus), version 1.0", in Birds of the World, ed. Billerman, S. M. Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.glagul.01
Common Raven	Terrestrial Marine Coastal	"Extreme habitat generalist: forested and open coastal, steppe, mountain, desert, tundra, Arctic ice floes, mountains and cliff"	Boarman, W. I., and Heinrich, B. (2020). "Common Raven (Corvus corax), version 1.0", in Birds of the World, ed. Billerman, S. M. Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.comrav.01
Sandhill Crane	Terrestrial Coastal	"Shallow open water marshes, estuarine intertidal areas, wetland areas, croplands and pastures"	Gerber, B. D., Dwyer, J. F., Nesbitt, S. A., Drewien, R. C., Littlefield, C. D., Tacha, T. C., and Vohs, P. A. (2020). "Sandhill Crane (Antigone canadensis), version 1.0", in Birds of the World, ed. Poole, A. F. Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.sancra.01
American Pipit	Terrestrial Coastal	"Coastal beaches and marshes, stubble fields, recently-plowed fields, mud flats and river courses"	Hendricks, P., and Verbeek, N. A. (2020). "American Pipit (Anthus rubescens), version 1.0", in Birds of the World, ed. Billerman, S. M. Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.amepip.01

Horned Lark	Terrestrial Coastal	"Open barren country, shortgrass prairies, deserts, brushy flats, alpine habitats, shrub-steppes, sandy beaches, sand dunes, steppes, agricultural areas, areas grazed by livestock"	Beason, R. C. (2020). "Horned Lark (Eremophila alpestris), version 1.0", in Birds of the World, ed. Billerman, S. M. Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.horlar.01
Lapland Longspur	Terrestrial	"Prairies, open weedy and grassy fields, grain stubbles, shores"	Hussell, D. J. T., and Montgomerie, R. (2020). "Lapland Longspur (Calcarius lapponicus), version 1.0", in Birds of the World, ed. Billerman, S. M., Keeney, B. K., Rodewald, P. G., and Schulenberg, T. S. Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.laplon.01
Snow Bunting	Terrestrial Coastal	"Open weedy and grassy fields, grain stubbles, shores of lakes and rivers, farmyards, shingle beaches, salt marshes, sand dunes, tidelines, coastal lowlands"	Montgomerie, R., and Lyon, B. (2020). "Snow Bunting (Plectrophenax nivalis), version 1.0", in Birds of the World, ed. Billerman, S. M., Keeney, B. K., Rodewald, P. G., and Schulenberg, T. S. Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.snobun.01
American Golden-Plover	Terrestrial Coastal	"Grasslands, coastal wetlands and tidal areas"	Johnson, O. W., Connors, P. G., and Pyle, P. (2021). "American Golden-Plover (Pluvialis dominica), version 1.1", in Birds of the World, ed. Rodewald, P. G., Keeney, B. K., and Billerman, S. M. Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.amgplo.01.1
Black-bellied Plover	Coastal	"Coastal beaches and estuaries, flooded pastures and agricultural land near sea and bays, salt marshes, mangrove"	Poole, A. F., Pyle, P., Patten, M. A., and Paulson, D. R. (2020). "Black-bellied Plover (Pluvialis squatarola), version 1.0", in Birds of the World, ed. Billerman, S. M. Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.bkbplo.01
Common-ringed Plover	Coastal Terrestrial	"Beaches, sandbanks, mudflats, estuaries, rivers, lakes, lagoons, saltmarshes, grassland, flooded fields and artificial habitats (gravel pits, reservoirs, farmland and playing fields)"	Wiersma, P., Kirwan, G. M., and Boesman, P. F. D. (2020). "Common Ringed Plover (Charadrius hiaticula), version 1.0", in Birds of the World, ed. del Hoyo, J., Elliott, A., Sargatal, J., Christie, D. A., and de Juana, E. Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.corplo.01
Ruddy Turnstone	Coastal	"Almost exclusively coastal, shorelines, mudflats, sandflats and delta"	Nettleship, D. N. (2020). "Ruddy Turnstone (Arenaria interpres), version 1.0", in Birds of the World, ed. Billerman, S. M. Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.rudtur.01
Red Phalarope	Marine	"Pelagic"	Tracy, D. M., Schamel, D., and Dale, J. (2020). "Red Phalarope (Phalaropus fulicarius), version 1.0", in Birds of the World, ed. Billerman, S. M. Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.redpha1.01
Red Knot	Coastal	"Sandy beaches, peat banks, salt marshes, brackish lagoons, tidal mudflats, mangroves, sandflats"	Baker, A., Gonzalez, P., Morrison, R. I. G., and Harrington, B. A. (2020). "Red Knot (Calidris canutus), version 1.0", in Birds of the World, ed. Billerman, S. M. Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.redkno.01

White-rumped Sandpiper	Terrestrial Coastal	"Beaches, river banks, open fields, marshes, intertidal areas, salt-marsh/slough, stream and canal, pond/lagoon edge, flooded field"	Parmelee, D. F. (2020). "White-rumped Sandpiper (Calidris fuscicollis), version 1.0", in Birds of the World, Poole, A. F., Stettenheim, P. R., and Gill, F. B. Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.whrsan.01
Buff-breasted Sandpiper	Terrestrial Coastal	"Grasslands in the coastal portions of the Rio de La Plata Grasslands, the eastern portion of the Flooding Pampa of Argentina, and areas adjacent to lagoon complexes"	McCarty, J. P., Wolfenbarger, L. L., Laredo, C. D., Pyle, P., and Lanctot, R. B. (2020). "Buff-breasted Sandpiper (Calidris subruficollis), version 1.0", in Birds of the World, ed. Rodewald, P. G. Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.bubsan.01
Bairds Sandpiper	Terrestrial	"Habitats about 2,550-4,500 m elevation, dry areas with short vegetation, strongly grazed shore meadows with muddy, partly dry ponds, short-grass plains and slopes"	Moskoff, W., and Montgomerie, R. (2020). "Baird’s Sandpiper (Calidris bairdii), version 1.0", in Birds of the World, ed. Poole, A. F., and Gill, F. B. Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.baisan.01
Pectoral Sandpiper	Terrestrial	"Grasslands, marshy areas and wetlands, rarely tidal"	Farmer, A., Holmes, R. T., and Pitelka, F. A. (2020). "Pectoral Sandpiper (Calidris melanotos), version 1.0", in Birds of the World, ed. Billerman, S. Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.pecsan.01

1.18.6 Network analysis

1.18.6.1 Modularity analysis

The modularity analysis was performed with the package infomapecology based on network flow (Farage et al., 2021), representing the flow of migratory individuals between the focal community and non-breeding regions. The infomap algorithm is based on an iterative process of random walks (paths from node to node) to optimize the partition of nodes into groups (modules) with the minimum amount of information possible (Farage et al., 2021). A partition represents a specific organization of nodes into sub-groups (modules). At each iteration, the nodes are partitioned into modules, then the algorithm goes from node to node and applies an information cost and an additional cost for changing modules. Afterward, it calculates an index of the quality of the partition based on an objective function. In the next iteration, the algorithm proposes a slightly different partition and repeats the same walk, and so on, until reaching the optimal partition (i.e., the minimum index value).

1.18.7 Supplementary Results

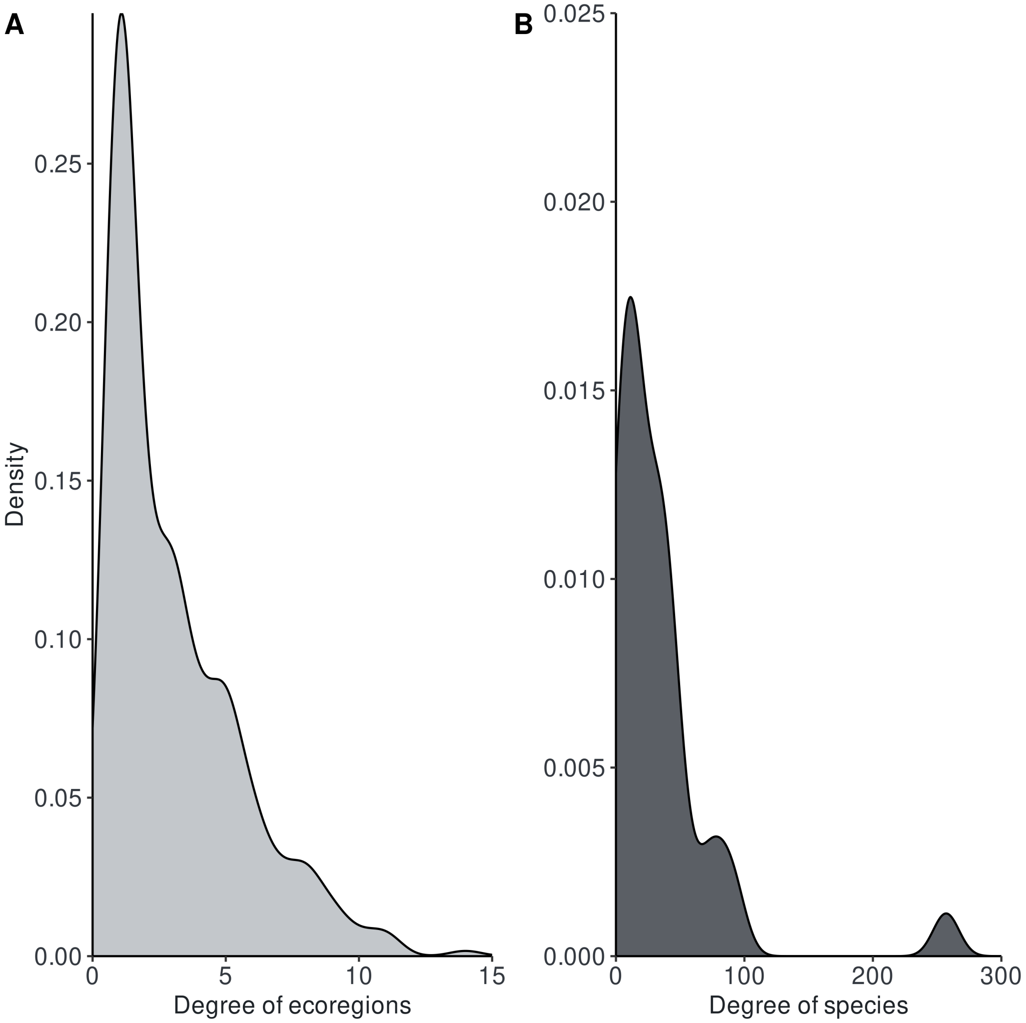

Figure 1.12 – Degree distributions (i.e., number of links) of the nodes representing species in the Bylot Island community (**A**) and the nodes representing ecoregions used as non-breeding grounds by the migratory and partially migratory species from Bylot Island (**B**).

ARTICLE 2

SÉRIES TEMPORELLES À LONG TERME DE L'ABONDANCE DE LA COMMUNAUTÉ DE VERTÉBRÉS TERRESTRES DU HAUT-ARCTIQUE DE L'ÎLE BYLOT, NUNAVUT

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DATA PAPER

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Long-term abundance time-series of the High Arctic terrestrial vertebratecommunity of Bylot Island, Nunavut

Louis Moisan | Azenor Bideault | Gilles Gauthier | Éliane Duchesne | Dominique Fauteux | Dominique Berteaux | Pierre Legagneux | Marie-Christine Cadieux | Joël Bêty

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2.1 Contexte et publication associée

L'article « *Long-term abundance time-series of the High Arctic terrestrial vertebrate community of Bylot Island, Nunavut* » a été accepté en août 2025 pour publication dans la revue *Ecology* en tant que « *Data paper* ». L'article est maintenant en processus de publication. L'éditrice en chef associée de l'article était Dr Kathryn L. Cottingham et l'éditeur spécialisé était Dr Hao Ye. L'article a été révisé par deux réviseurs anonymes. Cet article présente un jeu de données unique et rare sur la variation temporelle à long terme de la composition d'une communauté de vertébrés terrestres du Haut-Arctique canadien (île Bylot). Basé sur l'un des suivis de biodiversité en milieu terrestre les plus intensifs de l'Arctique, ce jeu de données constitue une référence pour modéliser de manière holistique la dynamique trophique d'une communauté de vertébrés et étudier les impacts des changements globaux sur une communauté de vertébrés arctiques. Les méthodes employées pour estimer l'abondance des différentes espèces de l'île Bylot ont été développées conjointement par moi-même, Joël Bêty, Éliane Duchesne, Azenor Bideault et Gilles Gauthier. En tant que premier auteur, j'ai rédigé la grande majorité de la première version du manuscrit et développé les codes nécessaires à la préparation, à l'analyse et à la visualisation des données. Azenor Bideault et Éliane Duchesne ont également contribué à la rédaction des codes pour la préparation des données. Joël Bêty, Pierre Legagneux, Gilles Gauthier, Dominique Berteaux et Marie-Christine Cadieux ont assuré le suivi à long terme de la biodiversité sur l'île Bylot. Gilles Gauthier, Joël Bêty, Dominique Berteaux, Pierre Legagneux, Dominique Fauteux et Éliane Duchesne ont contribué substantiellement à la collecte de données sur le terrain. Azenor, Joël, Gilles et Éliane ont apporté des commentaires approfondis sur le manuscrit à plusieurs reprises. L'ensemble des auteurs a relu et révisé le manuscrit avant sa publication. Joël, Gilles, Éliane et Azenor ont également révisé les modifications que j'avais apportées suite aux commentaires des réviseurs. J'ai échangé avec Joël Bêty tout au long de la réalisation de cet article.

2.2 Résumé de l'article en français

Les écosystèmes arctiques offrent des opportunités uniques pour le suivi à l'échelle des communautés, en partie grâce à leur richesse spécifique relativement faible. Cependant, la recherche dans ces milieux isolés pose des défis logistiques importants, ce qui rend les suivis à long terme extrêmement rares. Ici, nous nous concentrons sur le suivi écologique intensif à long terme mené sur la plaine sud de l'île Bylot (~400 km^2, Nunavut, Canada), qui a généré un jeu de données remarquable couvrant une période de 30 ans, une rareté dans les écosystèmes de toundra. Nos objectifs sont i) de fournir des séries temporelles à long terme de la densité annuelle des vertébrés, mesurées à différentes échelles spatiales et pour la plus grande diversité possible d'espèces et d'années, afin de permettre l'évaluation de la variabilité interannuelle et des tendances de densité des espèces ; et ii) estimer l'abondance annuelle des vertébrés, ou parfois les moyennes à long terme, à l'échelle du paysage (400 km^2) afin de permettre la modélisation du réseau trophique. Les données de suivi incluent des estimations de densité de lemmings dérivés de capture-marquage-recapture intensif sur des grilles de piégeage, le suivi systématique ou opportuniste des nids de toutes les espèces d'oiseaux à l'échelle de la zone d'étude ou de parcelles spécifiques, des transects de dénombrement de vertébrés répartis sur l'ensemble de la zone d'étude, des observations fortuites quotidiennes de vertébrés ainsi que le suivi satellitaire de renards. Nous avons standardisé les données obtenues par les différentes méthodes de terrain afin de fournir un jeu de données facilement utilisable par les écologistes des communautés. Les séries temporelles à long terme de densité de vertébrés s'étendent de 3 à 27 ans, avec une médiane de 16,5 ans pour 22 espèces. Nous avons estimé l'abondance à l'échelle du paysage pour les 35 espèces de vertébrés de la communauté, sur la base de séries temporelles annuelles pour 15 d'entre elles et de moyennes d'abondance à long terme pour les 20 restantes. De plus, nous fournissons la masse corporelle moyenne pour chaque espèce en utilisant des mesures empiriques sur le terrain pour 18 espèces et des mesures extraites de la littérature pour les autres. La masse corporelle est essentielle pour convertir l'abondance des espèces en biomasse dans les études sur les flux trophiques et les processus écosystémiques. Des données climatiques journalières enregistrées depuis 1992 par des stations météorologiques situées dans la zone d'étude sont également disponibles et complémentent le jeu de données sur la communauté de vertébrés. Les données écologiques présentées offrent une rare opportunité pour effectuer des études empiriques holistiques sur la structure et la dynamique des communautés. Étant donné que le site d'étude est une aire protégée, ayant subi un impact anthropique direct minimal, le jeu de donnée présenté constitue une référence idéale pour étudier les impacts des changements globaux sur les écosystèmes terrestres arctiques.

Les sections suivantes sont celles de l'article **publié**.

2.3 Title

Long-term abundance time-series of the High Arctic terrestrial vertebrate community of Bylot Island, Nunavut

2.4 Authors

Louis Moisan, Azenor Bideault, Gilles Gauthier, Éliane Duchesne, Dominique Fauteux, Dominique Berteaux, Pierre Legagneux, Marie-Christine Cadieux and Joël Bêty

Introduction

The composition of ecological communities, defined as the abundance of each species within a given community, is fundamental for understanding patterns and processes in community ecology. Variations in community composition can help to detect spatial patterns linked to environmental variations (Kemp et al., 1990), assess temporal trends of different groups of species after disturbances (Philippi et al., 1998; Magurran, 2007), and understand food web structures (Cohen et al., 2003). Additionally, species composition and their relative abundance are essential for modeling the dynamics of ecological communities. Dynamic community modelling allows addressing important issues and questions in ecology, such as: determining the relative strength of top-down versus bottom-up forces in communities (Krebs et al., 2003; Legagneux et al., 2014), assessing the ecological resilience of communities under climate change (Griffith et al., 2019) and evaluating the cascading effects of invasive species in food web (David et al., 2017; Goto et al., 2020). Dynamic community modelling can also be applied to address practical challenges, including fishery management (Plagányi, 2007) and the planning of protected areas (Okey et al., 2004; Dahood et al., 2020).

Modeling food webs requires adjusting trophic flows based on the functional or numeric responses of species, which necessitates time series data on the abundance of all species within a community. However, determining the abundance of all species within a community is rarely achievable. Consequently, empirical community models often reduce taxonomic resolution by grouping species into large functional or taxonomic categories. Additionally, food webs consist of species with varying body sizes depending on their trophic level, with top-level species often being highly mobile and having large home ranges (McCann et al., 2005). Therefore, community models must use landscape-wide estimates of species abundance to accurately represent trophic fluxes. Due to these constraints, empirical datasets with high taxonomic resolution that cover entire communities at broad spatial and temporal scales are rare and often include incomplete or rough estimates.

The composition of ecological communities is influenced by various factors acting at different temporal and spatial scales, leading to noisy data and emphasizing the need for long-term data sets (Magurran et al., 2010; Lindenmayer et al., 2012). Species abundances are influenced by stochastic effects (Hubbell, 2001), environmental changes (e.g., climate warming), and species interactions, contributing to data variability. For instance, the composition of a community could be driven simultaneously by intra-annual seasonal variations, multi-year cyclic variations (e.g., El Niño) and slow but directional long-term variations in the environment (Brown and Heske, 1990; Snyder and Tartowski, 2006). Therefore, long-term data series are required to untangle the relative effects of diverse abiotic and biotic factors on community composition (Magurran et al., 2010; Lindenmayer et al., 2012).

Arctic environments are highly valuable systems for studying community structure and dynamics due to their relatively low species richness (Payer et al., 2013; Legagneux et al., 2014). However, logistical challenges in the Arctic limit the number or length of biodiversity monitoring programs. Hence, the small number of Arctic communities with long-term monitoring serve as highly valuable sites for holistic and empirical community studies. Datasets on terrestrial communities are notably scarce, and this scarcity extends to Arctic communities as well (Ims et al., 2013).

The south plain of Bylot Island in the Canadian High Arctic (**Figure 2.1**) hosts one of the longest and most intensive vertebrate monitoring programs in the High-Arctic (Gauthier et al., 2024*b*). Monitoring on Bylot Island began in 1989 with a focus on the snow goose and it gradually expanded to other species over time. The program currently encompasses all vertebrate species in the community except for rare and occasional species (Gauthier et al., 2011; Legagneux et al., 2012), with continuous monitoring spanning more than a decade for several species (Gauthier et al., 2024*b*). Monitoring is also conducted at multiple spatial scales, including intensive and systematic observations conducted across a landscape spanning approximately 400 km^2. This approach enables local density measurements to be scaled to the landscape level by incorporating relative abundance across the landscape.

Previous work based on the tundra community of Bylot Island has already produced several influential papers (Gauthier et al., 2011, 2013; Legagneux et al., 2012, 2014; Hutchison et al., 2020; Duchesne et al., 2021; Gauthier et al., 2024*a*). These studies showed that tundra communities may experience stronger top-down regulation than bottom-up regulation (Legagneux et al., 2012, 2014). They also revealed a heterogeneous response of trophic levels to climate warming (Gauthier et al., 2013) and highlighted the effects of indirect trophic interactions on the occurrence of species across the landscape (Duchesne et al., 2021). However, those earlier papers were built on data from relatively short time series, they were not always scaled at the landscape level, and some species or functional groups were lacking abundance estimates.

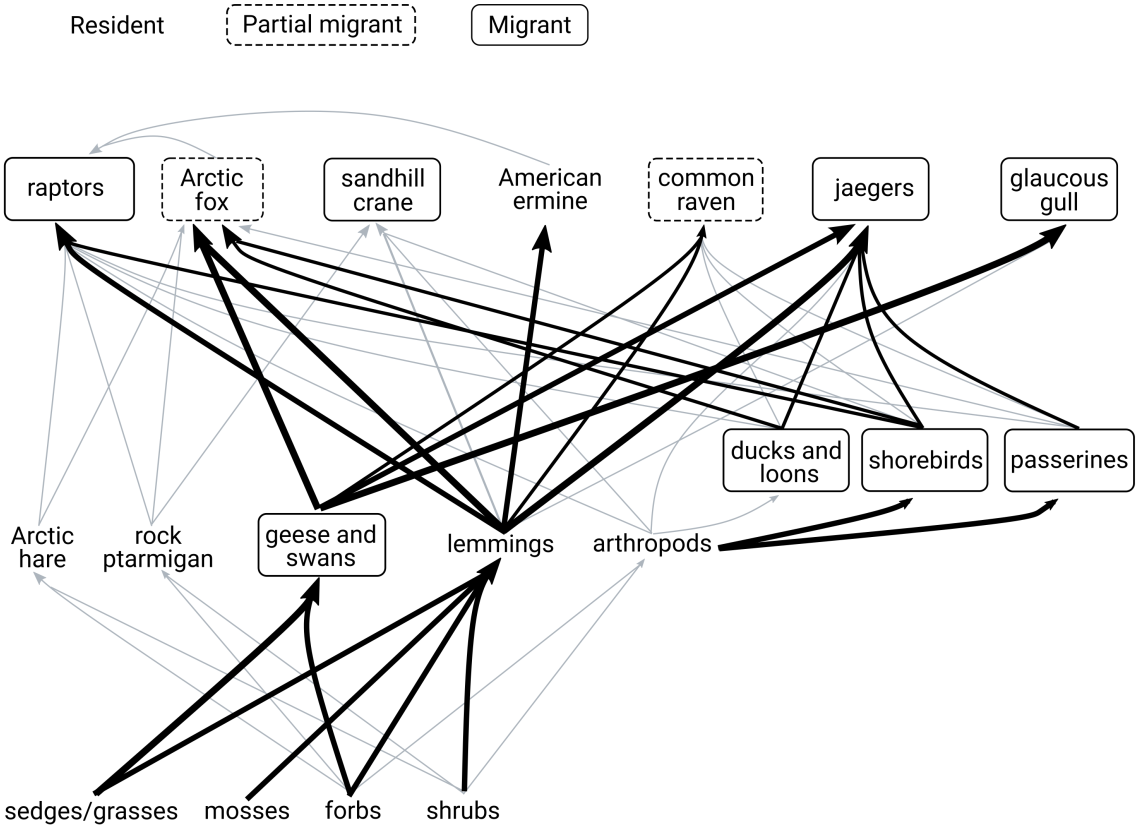
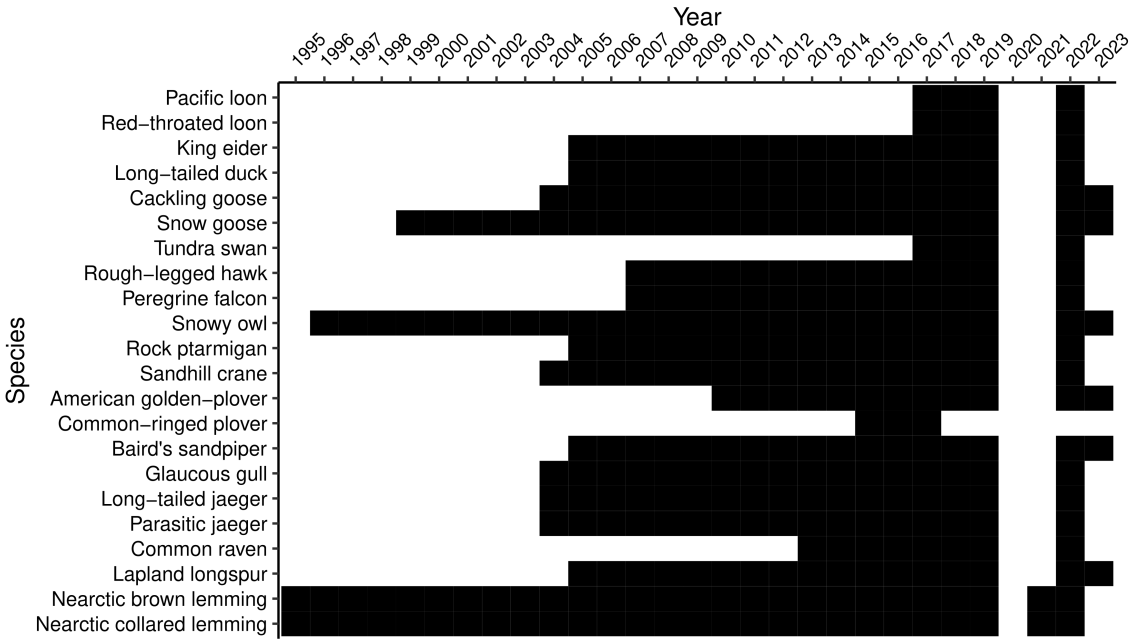


Figure 2.1 – Synthetic terrestrial vertebrate food web of the south plain of Bylot Island. The figure was adapted from Moisan et al. (2023) and Gauthier et al. (2011).

Objectives

With over a decade of additional community-wide monitoring compared to earlier studies, our goals are to i) provide long-term time series of annual vertebrate density measured at various spatial scales and for the broadest possible range of species and years, to allow the assessment of interannual variability and trends in species density; and ii) upscale annual vertebrate abundance or sometimes long-term averages to the landscape scale (400 km^2) to allow food web modelling (**Figure 2.2**). We focus on the breeding season (May to August) here because it is the most appropriate period to conduct surveys for most species, especially migratory birds. Although we recognize that ecological dynamics during the non-breeding period, for both resident (Hutchison et al., 2020) and migratory species (Moisan et al., 2023), can influence the food web during the breeding season, it was not possible to cover this period in the present study. The abundance estimates include both breeding and non-breeding individuals that remain in the study area for a significant period of time (e.g., territorial breeding or non-breeding foxes), and excludes non-breeding individuals that stop only briefly during migration (e.g., shorebirds using Bylot Island for a short stopover) or leave the area shortly after arrival without attempting to breed in some years (e.g. long-tailed jaegers). We focus on adults, except for lemmings for which we have not distinguished between juveniles and adults. Additionally, we aim to provide the average body mass for each species in the community, enabling the conversion of abundances into biomasses.

A) Species monitored most intensively at various spatial scales



B) Species abundance at the landscape scale (389 km²)

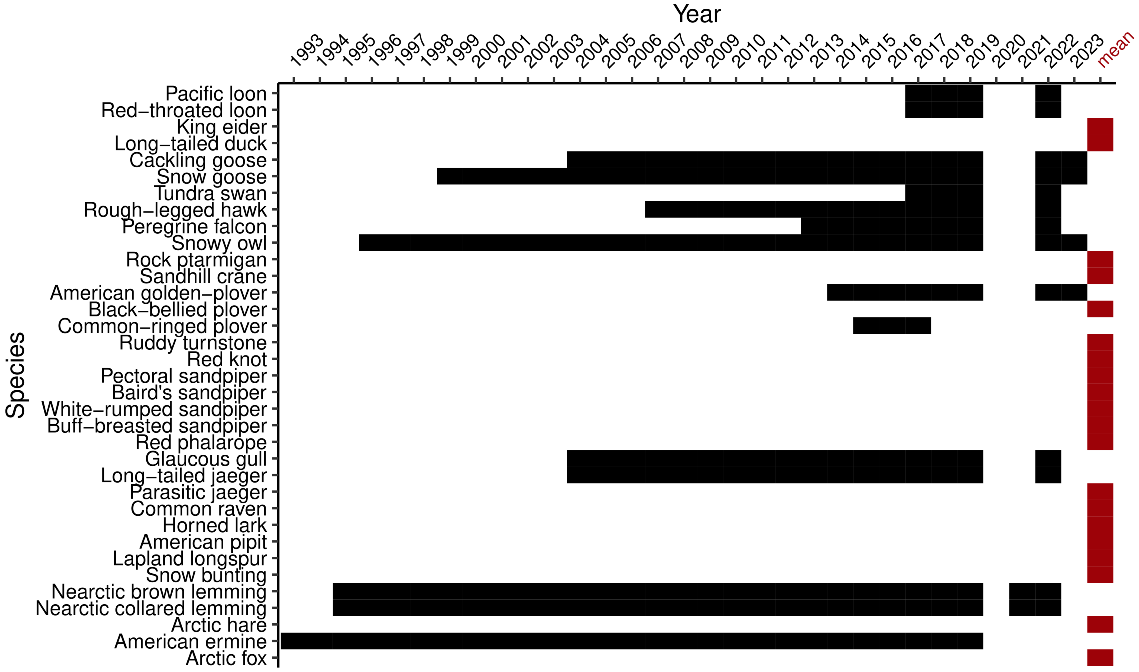


Figure 2.2 – **A)** Time series showing the longest available density records for 22 vertebrate species monitored in the community of Bylot Island. The spatial scale (i.e., zones of the study area) at which density was measured varies among species (see BYLOT-species_density_monitoring.csv). **B)** Time series of annual species abundance (black) or mean species abundance (red) at the landscape level (389 km^2) for all 35 vertebrate species in the community (see BYLOT-community_composition.csv).

Class I. Data Set Descriptors

A. Data set identity

Long-term abundance time-series of the High Arctic terrestrial vertebrate community of Bylot Island, Nunavut

B. Data set identification codes

`BYLOT-species_taxonomy.csv`

`BYLOT-species_density_monitoring.csv`

`BYLOT-species_abundance.csv`

`BYLOT-community_composition.csv`

`BYLOT-species_body_mass.csv`

C. Data set description

1. Originators

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2. Abstract

Arctic ecosystems present unique opportunities for community-wide monitoring, in part due to their relatively low species richness. However, conducting research in these remote environments poses significant logistical challenges, resulting in long-term monitoring being exceedingly rare. Here, we focus on the long-term, intensive ecological monitoring efforts conducted on the south plain of Bylot Island (~400 km^2, Nunavut, Canada), which has generated a remarkable dataset spanning up to 30 years, a rarity in

tundra ecosystems. Our goals are to i) provide long-term time series of annual vertebrate density measured at various spatial scales and for the broadest possible range of species and years, to allow the assessment of interannual variability and trends in species density; and ii) upscale annual vertebrate abundance or sometimes long-term averages to the landscape scale (400 km^2) to allow food web modelling. Monitoring data includes intensive capture-mark-recapture density estimates of lemmings on trapping grids, systematic or opportunistic nest monitoring conducted across the entire study area or within specific plots for all bird species, transects of vertebrate counts distributed throughout the study area, daily incidental observations of vertebrates and satellite tracking of foxes. We standardized data obtained with different field methods to provide a readily usable data set for community ecologists. Time series of vertebrate densities span 3 to 27 years, with a median of 16.5 years for 22 species. We estimated landscape-scale abundance for all 35 species of the community, using annual time series for 15 species and average abundance over different monitoring periods for the remaining 20 species. Furthermore, we provide body mass data for each species, based on empirical onsite measurements for 18 species and from the literature for the remaining species. Body mass is essential to convert species abundance into biomass for studies of trophic fluxes and ecosystem processes. Daily climatic data recorded since 1992 from weather stations within the study area are also available and complement the vertebrate dataset. The ecological data presented offer a rare opportunity for holistic empirical studies of community structure and dynamics. Considering that the study site is a pristine and protected area that has experienced minimal direct anthropogenic impact, it also provides an ideal baseline for investigating the impacts of global changes on high-latitude terrestrial ecosystems.

D. Key words/phrases

Arctic tundra, Biodiversity monitoring, Bylot Island, Canadian Arctic, Community composition, Community structure, Food web, Long-term monitoring, Species abundance, Species biomass, Species body mass

Class II. Research origin descriptors

A. Overall project description

1. Identity

Structure and functioning of Arctic terrestrial ecosystems

2. Originators

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3. Period of study

1989 - continuing

4. Objectives

i) Develop models for the Arctic tundra food web that incorporate seasonality, migratory connectivity and interactions with marine and southern ecosystems.
ii) Predict the effects of global changes on Arctic terrestrial food webs.

5. Abstract

Arctic terrestrial communities, characterized by relatively low species richness, offer unique opportunities for studying ecological patterns and community dynamics in simplified systems. Despite their relative simplicity, these ecosystems feature complex species interactions, extreme seasonal environmental changes, and a significant proportion of migratory species, making it difficult to identify the key factors shaping their structure and functioning. As global environmental changes accelerate, it is essential to understand the interacting processes driving these communities to eventually predict future impacts on Arctic ecosystems. Our research combines long-term biodiversity monitoring, a community-wide approach, and food web modeling to address these challenges.

6. Sources of funding

Natural Sciences and Engineering Research Council of Canada, Fonds Québécois de Recherche Nature et Technologies, Centre d'études nordiques, Natural Resources Canada (Polar Continental Shelf Program), Network of Centers of Excellence Canada (ArcticNet), Canada First Research Excellence Fund (Sentinel North Program), Polar Knowledge Canada, Environment and Climate Change Canada, Canada Foundation for Innovation, Parks Canada Agency, International Polar Year program of the Government of Canada, Crown–Indigenous Relations and Northern Affairs Canada (Northern Contaminant Program), Ducks Unlimited Canada, Kenneth M. Molson Foundation (Kenneth M. Molson Foundation's donation for wildlife research, conservation, and habitat), Garfield Weston Foundation, First Air-Canadian North, Nunavut Wildlife Management Board, Université Laval, Université du Québec à Rimouski

B. Specific subproject description

1. Site description

a. Site type

The study area (389 km^2) represents a relatively productive tundra ecosystem compared to other sites at similar latitudes in the eastern Canadian High Arctic (Gauthier et al., 2024*b*). An important biological characteristic of the area is the presence of a large snow goose (scientific names of most vertebrate species can be found in **Table 2.1**) colony of around 25 000 breeding pairs (Reed et al., 2002) spanning approximately 70 km^2. The vertebrate community within the study area comprises 30 bird species, with 29 of them being migratory or partially migratory, along with 5 mammal species (**Table 2.1**; Moisan et al. 2023; Gauthier et al. 2024*b*). The study area experiences significant temporal fluctuations in the population of small mammals (lemmings), which in turn impact the occurrence and abundance of their avian and mammalian predators such as snowy owls, rough-legged hawks, long-tailed jaegers and ermines (Therrien et al., 2014; Duchesne et al., 2021; Bolduc et al., 2025). We exclude occasional visitors, namely: i) species lacking confirmed breeding occurrences on the study site, ii) species observed solely within a single year, and iii) species primarily breeding and foraging in nearby marine or coastal habitats (Moisan et al., 2023). The case of the red fox (*Vulpes vulpes*) was ambiguous. While the presence of breeding pairs has been confirmed in the study area (Lai et al., 2022), the extent of population establishment remains unclear and sightings are rare. Therefore, we decided to exclude this species.

Table 2.1 – Species of the vertebrate community of Bylot Island and their corresponding migratory status (i.e., resident, partial migrant or migrant).

Functional group	Scientific name	English name	Migratory status
Ducks and loons	*Gavia pacifica*	Pacific loon	migrant
Ducks and loons	*Gavia stellata*	Red-throated loon	migrant
Ducks and loons	*Somateria spectabilis*	King eider	migrant
Ducks and loons	*Clangula hyemalis*	Long-tailed duck	migrant
Geese and swans	*Branta hutchinsii*	Cackling goose	migrant
Geese and swans	*Anser caerulescens*	Snow goose	migrant
Geese and swans	*Cygnus columbianus*	Tundra swan	migrant
Raptors	*Buteo lagopus*	Rough-legged hawk	migrant
Raptors	*Falco peregrinus*	Peregrine falcon	migrant
Raptors	*Bubo scandiacus*	Snowy owl	migrant
Ptarmigans	*Lagopus muta*	Rock ptarmigan	resident
Cranes	*Antigone canadensis*	Sandhill crane	migrant
Shorebirds	*Pluvialis dominica*	American golden-plover	migrant
Shorebirds	*Pluvialis squatarola*	Black-bellied plover	migrant
Shorebirds	*Charadrius hiaticula*	Common-ringed plover	migrant
Shorebirds	*Arenaria interpres*	Ruddy turnstone	migrant
Shorebirds	*Calidris canutus*	Red knot	migrant
Shorebirds	*Calidris melanotos*	Pectoral sandpiper	migrant
Shorebirds	*Calidris bairdii*	Baird’s sandpiper	migrant
Shorebirds	*Calidris fuscicollis*	White-rumped sandpiper	migrant
Shorebirds	*Calidris subruficollis*	Buff-breasted sandpiper	migrant
Shorebirds	*Phalaropus fulicarius*	Red phalarope	migrant
Gulls	*Larus hyperboreus*	Glaucous gull	migrant
Jaegers	*Stercorarius longicaudus*	Long-tailed jaeger	migrant
Jaegers	*Stercorarius parasiticus*	Parasitic jaeger	migrant
Ravens	*Corvus corax*	Common raven	partial migrant
Passerines	*Eremophila alpestris*	Horned lark	migrant
Passerines	*Anthus rubescens*	American pipit	migrant
Passerines	*Calcarius lapponicus*	Lapland longspur	migrant
Passerines	*Plectrophenax nivalis*	Snow bunting	migrant
Lemmings	*Lemmus trimucronatus*	Nearctic brown lemming	resident
Lemmings	*Dicrostonyx groenlandicus*	Nearctic collared lemming	resident
Hares	*Lepus arcticus*	Arctic hare	resident
Ermines	*Mustela richardsonii*	American ermine	resident
Foxes	*Vulpes lagopus*	Arctic fox	partial migrant

b. Geography

The 389 km^2 study area is located on the southern plain of Bylot Island, Nunavut, Canada (72.889 N, -79.906 W; **Figure 2.3**). This area is characterized by a rolling plain, mostly from 0 to 300 m above sea level, located between mountains (up to 1900 m) to the north and east and the sea to the west and south.

c. Habitat

The study area comprises a combination of mesic tundra mainly on hills and gentle slopes (64 %), upland plateaus of sedimentary rock with drier/rockier habitat at higher elevation (20 %), low-lying wetlands interspersed with ponds (10 %) and larger bodies of water such as lakes and rivers (6 %; **Figure 2.3**). The vegetation of mesic habitat is characterized by prostrate shrubs (*Salix* spp., *Vaccinium uliginosum*, and *Cassiope tetragona*), forbs (*Luzula* spp., *Oxytropis maydelliana*, *Astragalus alpinus*, *Oxyria digina*, and *Polygonum viviparum*), grasses (*Arctagrostis latifolia* and *Poa arctica*) and mosses (e.g., *Aulacomnium* spp.; Gauthier et al. 2013, 2024*b*). Wetlands are found near water bodies (streams, ponds and lakes) or in tundra polygons and present a vegetation typically associated with moss-covered fens with grasses and sedges (*Dupontia fisheri*, *Carex aquatilis*, and *Eriophorum scheuchzeri*; Gauthier et al. 2013, 2024*b*). See section *e. Hydrology* for details on wetlands and water bodies delineation. Upland habitat is drier and present a less abundant and rich vegetation with species such as *Dryas integrifolia* or *Saxifraga oppositifolia* (Gauthier et al., 2013, 2024*b*).

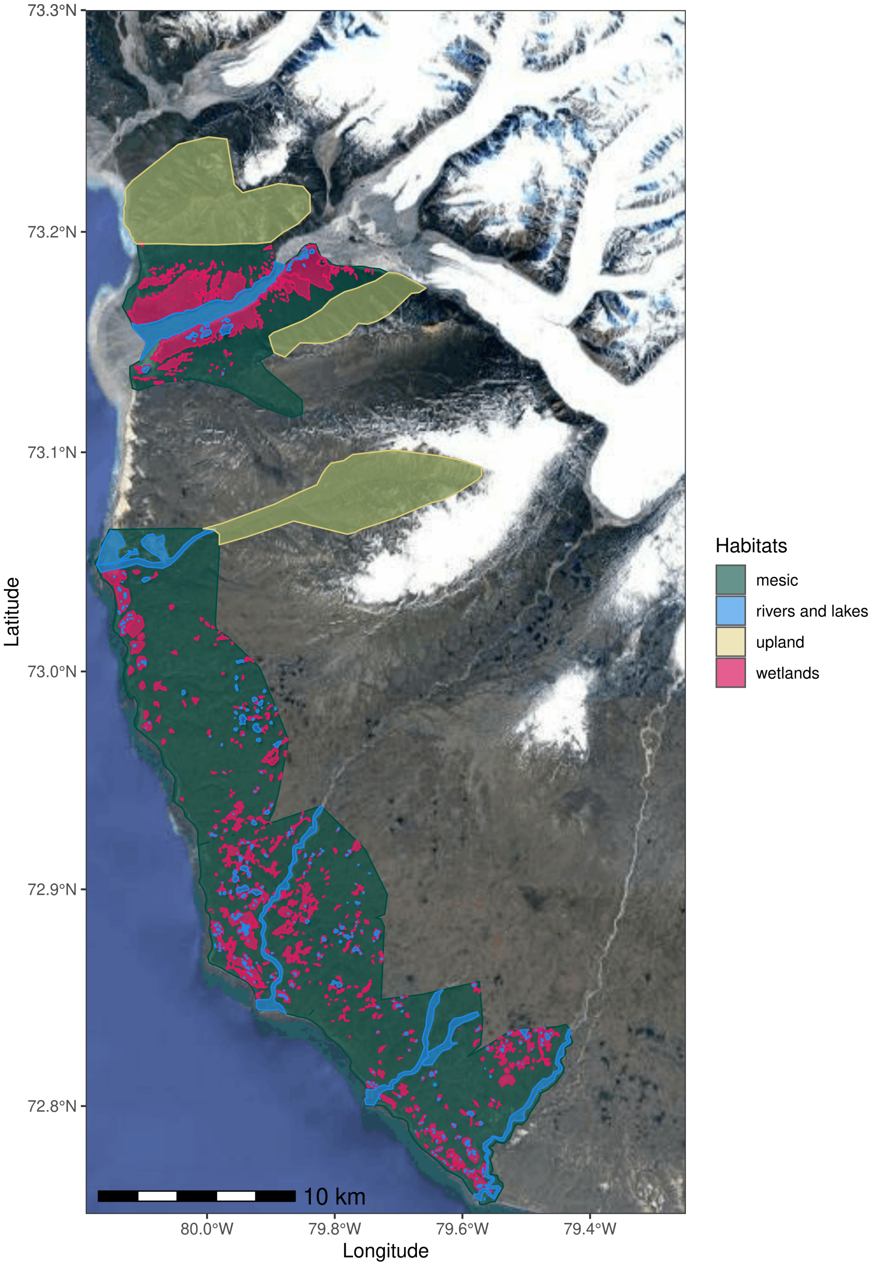


Figure 2.3 – Map of the main habitat types within the study area, including mesic tundra, upland areas, wetlands, and aquatic environments (rivers and lakes).

d. Geology

See Klassen (1993) for a detailed description of the geology of the study area.

e. Hydrology

Wetlands were delineated by photo-interpretation of high-resolution satellite images (30 cm; Louis-Pierre Ouellet, unpublished data). Lakes were delineated with aerial photos (see Corbeil-Robitaille et al. 2024), whereas rivers were delineated with google satellite images, resulting in a coarser delineation.

f. Site history

See Gauthier et al. (2024*b*,*a*) for a complete and detailed history of the site.

g. Climate

The mean annual air temperature since 1995 is -14.4°C, with mean seasonal temperature of 4.7°C in summer (June to August), -11°C in fall (September to November), -32.4°C in winter (December to February) and -19.4°C in spring (March to May; Centre of Northern Studies and Laval University 2019). The climate of the southern plain of Bylot Island is generally milder than that of the surrounding latitudes, as the plain present a southern exposure and the mountains to the north protect the plain from cold northerly winds (Gauthier et al., 2024*b*). In summer, the study area received on average 77.5 mm of precipitation. The study area typically remains free of snow from mid-June to late

September with an average of 106 frost-free days annually (Gauthier et al., 2013). From September to December, snow depth typically increases continuously to reach about 15 cm (Centre of Northern Studies and Laval University, 2019). Snow depth is relatively constant from December to February and starts increasing again in March to peak in late May (∼27 cm) before decreasing until disappearance in mid-June (Centre of Northern Studies and Laval University, 2019). The summary statistics presented here on the climate of the South plain of Bylot Island are derived from automated weather stations located in the Qarlikturvik valley, which have been recording data on air temperature, thawing degree days, frost-free days, summer precipitation, snow thickness, and wind speed on a daily basis since 1992 (Centre for Northern Studies, 2024). Raw data from these weather stations are openly accessible at `https://nordicana.cen.ulaval.ca/fr/publication.php?doi=45039SL-EE76C1BDAADC4890`.

2. Experimental or sampling design

Research activities on Bylot Island take place from mid-May, well before the snowmelt, which occurs in early June, to August 20, in part due to logistical constraints in the latter case. The period therefore covers the arrival of migratory species and the entire breeding cycle for most species. The timing of surveys was adapted to the breeding cycle of individual species to maximize detection rates. However, the sampling period does not encompass the departure of some migratory species (e.g., loons, snowy owl and sandhill crane).

a. Permanent plots

The study area is divided into nine zones based on the sampling method and the level of field effort applied in each zone (**Figure 2.4**). Long-term monitoring of the community began in the 1990s in the Qarlikturvik valley (Gauthier et al., 2013, 2024*b*), which represents the zone of the study area with the highest annual sampling effort. Within the Qarlikturvik valley, the sampling is concentrated on the southern side of the glacial river (**Figure 2.5**), where the main research infrastructure is located. Another zone with extensive sampling efforts is Camp 2, located at the core of the snow goose colony, where the primary focus is to monitor snow goose nests. However, nests of many other avian species are also monitored within and around the snow goose colony in this zone. Camp 3, Pointe Dufour, Goose Point, and Malaview are zones where intensive sampling efforts are conducted annually, albeit for a relatively brief period (approximately one week) during the breeding season of most species (Gauthier et al., 2024*b*). The upland zones in the study area (defined as areas approximately 300 meters above sea level or more) are the Black Plateau, Southern Plateau, and Camp 3 Plateau. These zones are primarily visited to assess raptor nesting activity (Beardsell et al., 2016). The zone between the Qarlikturvik valley and Camp 3 received very little sampling effort and is therefore excluded from the study area.

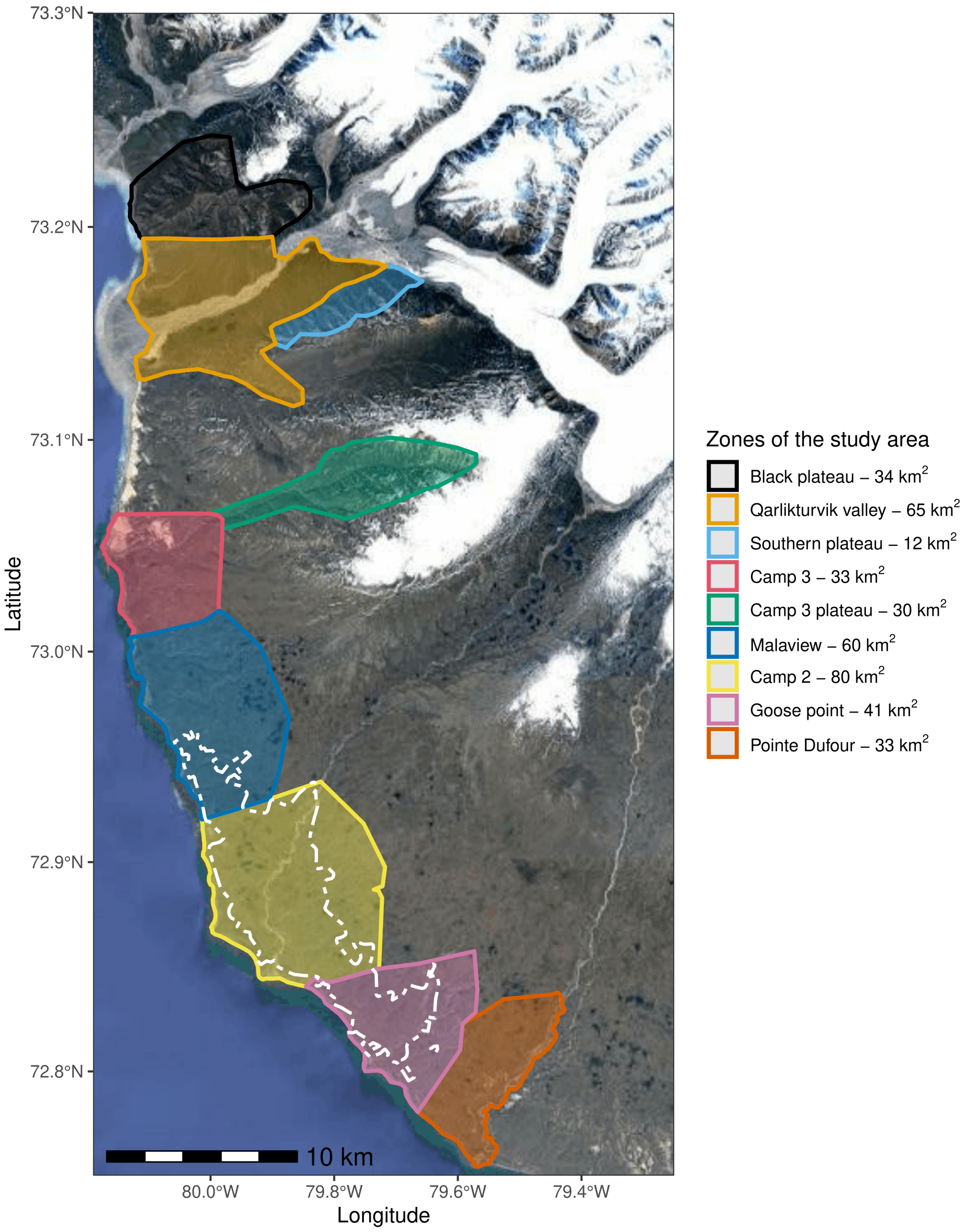


Figure 2.4 – Map of the different zones (colored polygons) of the 389 km^2 study area located on the south plain of Bylot Island, Nunavut Canada. The perimeter of the snow goose colony is delineated by white dashes; we highlighted the perimeter in 2017 since it represents the average colony area (74 km^2).

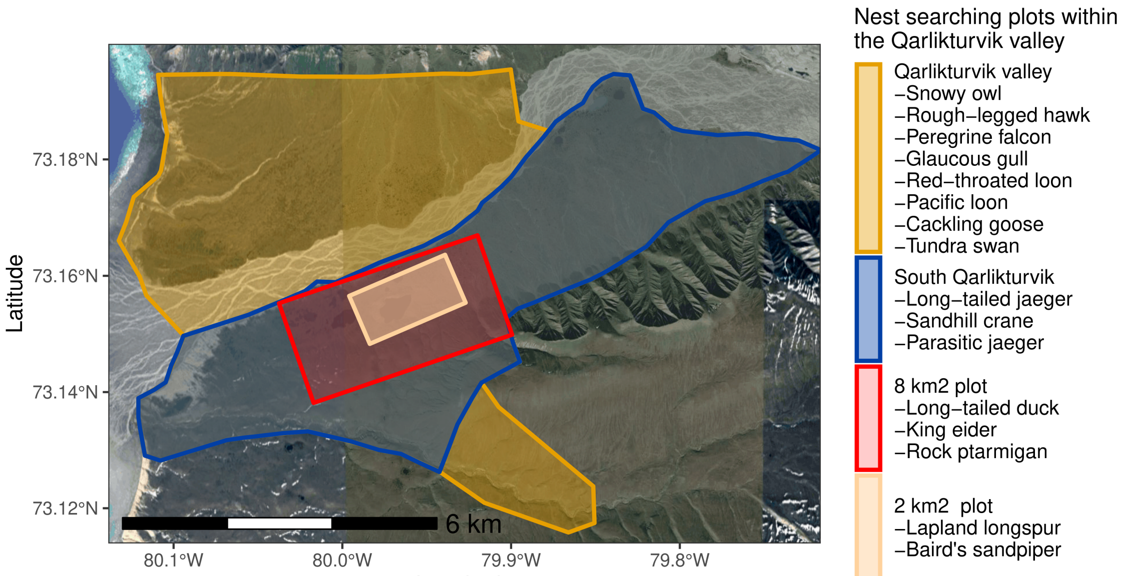


Figure 2.5 – Intensive nests searching plots within the Qarlikturvik valley.

b. Avian nest monitoring

Avian nest monitoring was not conducted in 2020 and 2021 due to logistical constraints imposed by the COVID-19 pandemic. Systematic nest monitoring refers here to a systematic sampling approach aimed at documenting all nests within a specified area (**Table 2.2**). Monitoring is considered opportunistic when there is a chance that some nests might not have been detected within a specific area. Nest densities derived from nest sampling could be underestimated due to early nest failure (i.e., failure that happened before our sampling period).

Table 2.2 – Summary of vertebrate species monitoring in the Bylot Island study area. In this paper, we excluded certain years for specific species due to reduced sampling efforts. As a result, duration of times series presented here may differ slightly from those in Gauthier et al. (2024b). The annual density values are provided in the file BYLOT-species_density_monitoring.csv.

Species	Zone	Years	Number of years	Monitoring
Pacific loon	Whole study area	2017-2019, 2022	(4)	systematic
Red-throated loon	Whole study area	2017-2019, 2022	(4)	systematic
King eider	Qarlikturvik (8 km2 plot)	2005-2019, 2022	(16)	opportunistic
Long-tailed duck	Qarlikturvik (8 km2 plot)	2005-2019, 2022	(16)	opportunistic
Cackling goose	Qarlikturvik valley	2004-2019, 2022-2023	(18)	systematic
Cackling goose	Whole study area	2017-2019, 2022-2023	(5)	systematic
Snow goose	Camp 2	1999-2019, 2022-2023	(23)	systematic
Tundra swan	Whole study area	2017-2019, 2022	(4)	systematic
Rough-legged hawk	Qarlikt., Black & South plat.	2007-2019, 2022	(15)	systematic
Rough-legged hawk	Whole study area	2013-2019, 2022	(8)	systematic
Peregrine falcon	Qarlikt., Black & South plat.	2007-2019, 2022	(15)	systematic
Peregrine falcon	Whole study area	2013-2019, 2022	(8)	systematic
Snowy owl	Qarlikt., Black & South plat.	1996-2019, 2022-2023	(26)	systematic
Snowy owl	Whole study area	2012-2019, 2022-2023	(10)	systematic
Rock ptarmigan	Qarlikturvik (8 km2 plot)	2005-2019, 2022	(16)	opportunistic
Sandhill crane	South Qarlikturvik valley	2004-2019, 2022	(17)	opportunistic
Common-ringed plover	Whole study area	2015-2017	(3)	systematic
Baird's sandpiper	Qarlikturvik (2 km2 plot)	2005-2019, 2022-2023	(17)	systematic
Glaucous gull	Qarlikturvik valley	2004-2019, 2022	(17)	systematic
Glaucous gull	Whole study area	2017-2019, 2022	(4)	systematic
Long-tailed jaeger	South Qarlikturvik valley	2004-2019, 2022	(17)	systematic
Parasitic jaeger	South Qarlikturvik valley	2004-2019, 2022	(17)	systematic
Parasitic jaeger	Whole study area	2009-2019, 2022	(12)	opportunistic
Common raven	Whole study area	2013-2019, 2022	(8)	systematic
Lapland longspur	Qarlikturvik (2 km2 plot)	2005-2019, 2022-2023	(17)	systematic
Nearctic brown lemming	Qarlikturvik (trapping grids)	1995-2019, 2021-2022	(27)	systematic
Nearctic collared lemming	Qarlikturvik (trapping grids)	1995-2019, 2021-2022	(27)	systematic
American ermine	Whole study area	1993-2019	(27)	opportunistic
Arctic fox	Whole study area	2008-2016	(9)	systematic

Pacific loon, red-throated loon, cackling goose, tundra swan and glaucous gull

Between 2004 and 2016, systematic searches for glaucous gull and cackling goose nests were conducted in the wetlands of the Qarlikturvik alley. Starting in 2017, nest searches in wetlands were carried out systematically across the entire study area. Since then, nest locations of other large wetland-nesting species—including tundra swans, red-throated loons, and Pacific loons—have also been recorded systematically, as these species nest in similar habitats (Duchesne et al., 2021; Gauthier et al., 2024*b*). Each year, all known or potential nesting sites were revisited. Observers detected nests by walking and scanning around ponds and lakeshores to identify any active nesting sites. These large species can be seen from a relatively long distance sitting on the nest or when flushing from the nest. Most of them (geese, swans and gulls) can also reveal their presence with alarm calls or nest defense displays. We are confident that nest detection probability was high for these species given the open landscape.

Snow goose

Snow geese nest in a large colony in the study area (**Figure 2.4**), but also in small aggregations distributed on the island, especially in years when snowy owls are nesting (Lepage et al., 1996; Reed et al., 2002). Since 1994, goose nests were systematically monitored on a 0.24 km^2 wetland at the center of the colony. Since 1999, nests were also systematically monitored on a variable number of plots, measuring 0.01 km^2 in wetland habitat and 0.04 km^2 in mesic habitat, randomly distributed throughout the goose colony (Gauthier and Cadieux, 2020*a*). The total area covered by the randomly distributed plots averaged 0.79 ±0.37 km^2 per year. From 2010 onwards, except in 2020 and 2021, we opportunistically traced sections of the approximate boundary of the goose colony using a GPS receiver aboard a helicopter, taking advantage of regular flights across the study area whenever the flight path passed over the colony border (Duchesne et al., 2021).

Rough-legged hawk, peregrine falcon and common raven

Peregrine falcons, rough-legged hawks and common ravens nest on cliffs, near ravines, and on large rocky outcrops and tend to reuse the same nesting sites from one year to the next (Beardsell et al., 2016). Systematic monitoring of every known or potential nesting site has been carried out in the Qarlikturvik valley, Black plateau and Southern plateau since 2007 and throughout the study area since 2013 (Beardsell et al., 2016; Gauthier et al., 2020). Observers walked along ridges and scanned surrounding areas from vantage points to detect nesting birds. These large species can be seen from a relatively long distance sitting on the nest or when flushing from the nest. They can also reveal their presence with alarm calls or nest defense displays. We are confident that nest detection probability was high for these species. Each year the observers use slightly different paths to sample the areas, but locate the nests in the same positions, which supports a high probability of detection for these species. Most nesting sites were located in the upland zones of the study area, which include the Black Plateau, Southern Plateau and Camp 3 Plateau.

Snowy owl

Snowy owls predominantly nest in habitats similar to other raptors, favoring ridges in mountainous or hilly regions, although they can occasionally be found nesting on mounds in lowland areas (Seyer et al., 2020). Since 1996, searches for snowy owl nests have been conducted in the Black and Southern plateaus, as well as during searches for jaeger nests on the southern side of the glacial river in the Qarlikturvik Valley. Additionally, since 2012, nests have been recorded across the entire study area by scanning the landscape from hills and ridges during the nesting period (Duchesne et al., 2021). Given that snowy owls nest on elevated mounds, exhibit contrasting colors with the landscape, emit alarm calls, and display defensive behaviors, active nesting sites have a high probability of detection.

Long-tailed jaeger, parasitic jaeger and sandhill cranes

Since 2004, observers have walked parallel transects spaced 400 meters apart, covering the entire southern side of the glacial river in the Qarlikturvik Valley (33 km^2; **Figure 2.5**), during the nesting period. The aim of those transects was to record nests of long-tailed jaegers, parasitic jaegers, and sandhill cranes. Observers listened for alarm calls to detect territorial birds, and then located nests by observing the birds returning to their nests from elevated vantage points. We consider the sampling to be systematic for long-tailed and parasitic jaeger, since those species tend to leave their nest relatively far from the observer to perform mobbing behavior, and thus increasing their detection probability. We consider the sampling to be opportunistic for sandhill cranes, as individuals display defensive behaviors only at relatively close distances from their nests (see *Opportunistic nest monitoring* below).

Common-ringed plover

Between 2015 and 2019, observers conducted surveys of the primary nesting areas of the common-ringed plover. The survey involved walking in stony and sandy shores and gravel bars with scarce vegetation along rivers. Nests were found by detecting individuals exhibiting reproductive behaviors, such as incubation, alarm calls, or distraction displays. The sampling effort was particularly intensive between 2015 and 2017. Small areas along the coast or on the banks of smaller rivers that could potentially serve as nesting sites may have been overlooked.

Lapland longspur and Baird's sandpiper

Since 2005, nests of passerines and sandpipers have been extensively monitored across an 8 km^2 (4x2 km) area in the Qarlikturvik valley. We considered the sampling to be most systematic within a core 2 km^2 (2x1 km) plot in this area (**Figure**

2.5). We excluded relatively large water bodies (0.26 km^2) to calculate nest density in the plot due to the presence of a large lake, which leaves an area of 1.74 km^2 available for nesting. An observer conducted systematic searches of this plot during the entire breeding season to locate and monitor as many passerine and shorebird nests as possible. Assuming the observer can detect all nests within a 5 or 10 meter radius, analysis of daily GPS tracks shows that the observer covered a minimum area of 0.72 ±0.12 (5 m) or 1.09 ±0.17 km^2 (10 m) of the core area annually (n= 3 years). Additionally, several other observers conducting related field work in the same zone reported all passerine and shorebird nests found opportunistically.

Opportunistic nest monitoring

Since 2005, we also noted the nest location of any other bird species encountered opportunistically during travel or while carrying out the protocols for the previously described species. The sampling was particularly intensive in the defined 8 km^2 area in the Qarlikturvik valley. The accuracy of nest monitoring in this plot thus depends on the species detection probability. We are confident to obtain a realistic order of magnitude for the number of nests present for relatively large bodied species in this area (i.e., sandhill crane, rock ptarmigan, long-tailed duck and king eider). Additionally, starting in 2009, a significant effort has been made each year, though not systematically, to visit known nesting territories of parasitic jaegers throughout the study area.

c. Observation of individuals

Vertebrate count transects

From 2010 to 2023, observers walked 500-meter linear transects where all vertebrate individuals observed within 150 meters on either side were counted (146 to 320 transects per year). Transects were distributed across all lowland zones of the study area, typically in mesic habitat, and were carried out during the nesting period (between June 21 and July 14; Lamarre et al. (2017); Duchesne et al. (2021); **Figure 2.6**). As a calibration exercise, all observers were trained to estimate a distance of 150 m using a rangefinder prior to data collection. Furthermore, specifically for American golden-plovers, we measured the distance of each observed individual to the transect path. Observations of species considered as occasional visitors (i.e., species lacking confirmed breeding occurrences on the study site, or species observed solely within a single year, or species primarily breeding and foraging in nearby marine or coastal habitats) were removed.

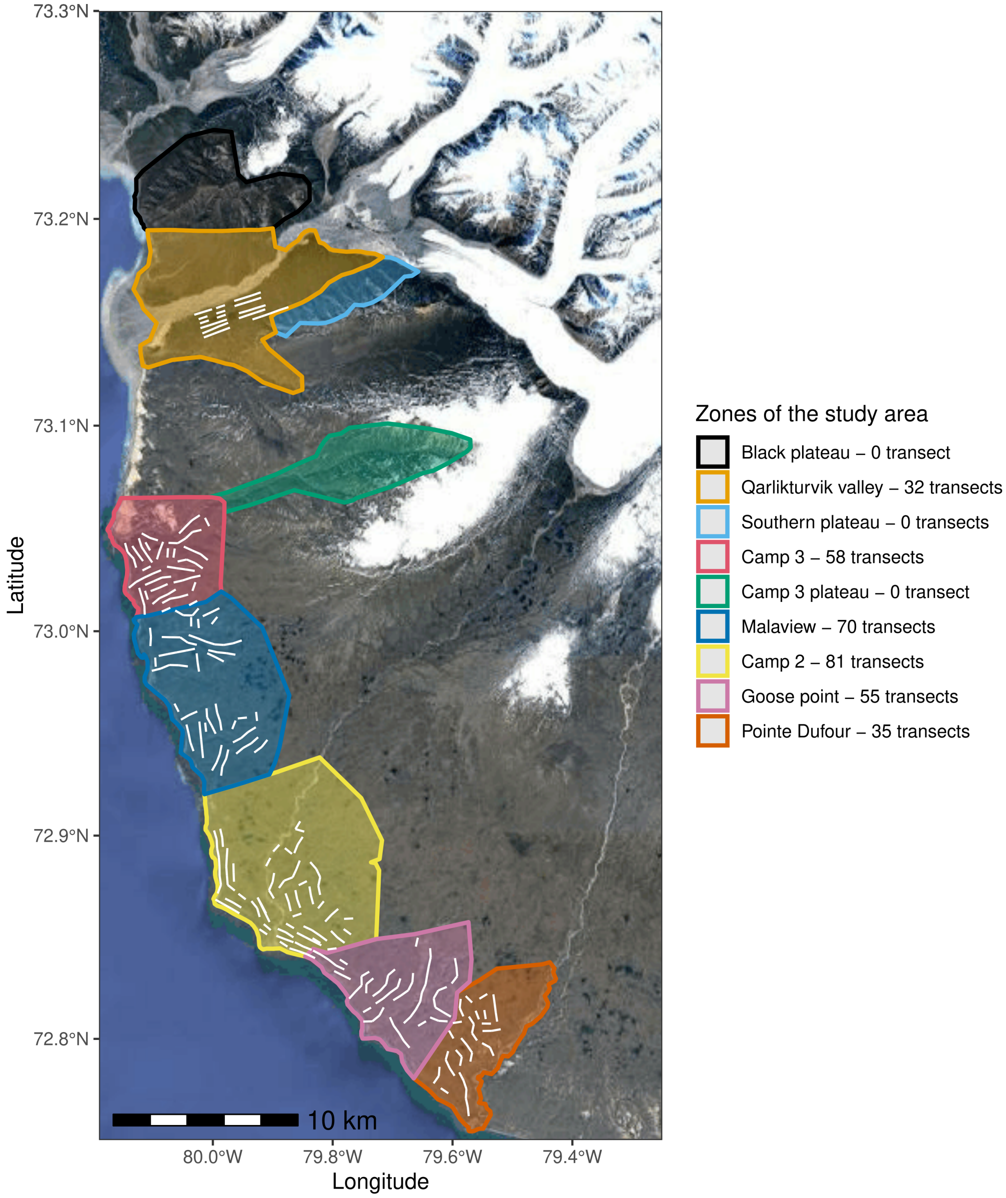


Figure 2.6 – Spatial distribution of vertebrate count transects (white lines) on the south plain of Bylot Island (146 to 320 transects per year).

Snow goose point count

At the start, middle, and end of each vertebrate count transect, a point count with a radius of 125 meters was conducted to determine the number of snow goose breeding pairs. On average, 613 ±142 point counts were sampled each year, covering an area of 30 ±7 km^2. Observers were trained with a rangefinder to estimate a distance of 125 m prior to data collection.

Incidental observations

Since 2007, observers have recorded all vertebrate species observed opportunistically during field work and tallied the total number of individuals at the end of each day (Gauthier and Cadieux, 2020*b*; Gauthier et al., 2024*b*). Observations are made from mid-May to late August, but the effort is highest during late June and early July. The number of hours spent in the field served as a proxy for the sampling effort. Observations of species considered as occasional visitors (i.e., species lacking confirmed breeding occurrences on the study site, or species observed solely within a single year, or species primarily breeding and foraging in nearby marine or coastal habitats) were removed (see Gauthier et al. 2024*b* for a comprehensive list of all species observed in the study area over the years). The original data, as well as any future updates, can be accessed at: `https://nordicana.cen.ulaval.ca/fr/publication.php?doi=45645CE-A24D883A6676492E`. We used the number of individuals observed per hour spent in the field calculated by Gauthier et al. (2024*b*) as an index of relative abundance for each species. Moreover, we separated observations made in lowland from those in upland zones to have a relative abundance of each species in each of these two broad categories (**Table 2.3**). Given that incidental observations lacked georeferencing, we opted to extract upland observations by focusing on observations made during visits to rough-legged hawk nests, which are mostly located in upland areas.

Table 2.3 – Index of relative abundance (i.e., number of individuals observed per hour) derived from incidental daily observations for selected vertebrate species in lowland (i.e., Qarlikturvik valley, Camp 3, Malaview, Camp 2, Goose point and Pointe Dufour) and upland (i.e., Black plateau, Southern plateau and Camp 3 plateau) zones of the Bylot Island study area. The ratio compares relative abundance indexes between these two types of zones, calculated by dividing the upland by the lowland index of relative abundance.

	Individuals/hour		
Species	Upland	Lowland	Ratio
Rock ptarmigan	0.03	0.03	1
Sandhill crane	0.42	0.287	1.5
American golden-plover	0.26	0.394	0.7
Black-bellied plover	0.02	0.032	0.6
Ruddy turnstone	0.01	0.007	1.3
Red knot	0.00	0.033	0
Pectoral sandpiper	0.02	0.034	0.6
Baird's sandpiper	0.31	0.32	1
White-rumped sandpiper	0.04	0.137	0.3
Buff-breasted sandpiper	0.00	0.001	0
Red phalarope	0.01	0.038	0.2
Horned lark	0.24	0.154	1.6
American pipit	0.34	0.024	14.2
Lapland longspur	1.93	2.641	0.7
Snow bunting	0.59	0.092	6.4
Arctic hare	0.02	0.009	2

Testimonials of ermine sightings

There was no direct estimation of ermine abundance on Bylot Island as they are quite difficult to obtain. The density estimates for ermine were derived from an annual abundance index established by Bolduc et al. (2023), which relied on testimonials provided by observers across the whole study area from 1993 to 2019. The testimonials provided by observers were used to create an abundance index ranging from 0 to 3 (Bolduc et al., 2023). In this index, a score of 0 corresponds to the absence of ermine sightings, 1 indicates a single sighting of a lone individual, 2 represents multiple sightings of lone individuals, and 3 signifies at least one sighting of a family group. Scores of individual participants were averaged annually as detailed in Bolduc et al. (2023).

d. Capture of individuals

Lemming trapping

Since 2004, Nearctic brown and collared lemmings were live-trapped 3 times during the summer (mid-June, mid-July, and mid-August) in two 11-ha grids. Each grid is made of 144 traps separated by 30 m according to a cartesian plane, one in mesic habitat and the other in wet habitat, located in the Qarlikturvik valley (Fauteux et al., 2015; Gauthier, 2020). Density of each species was estimated at each occasion using spatially explicit capture-recapture methods (Fauteux et al., 2015). From 1995 to 2016 snap-trapping was performed once a year (mid-July) along 2 groups of transects located in the same habitats than the trapping grids (Gruyer et al., 2008). Abundance indices derived from snap-trapping (i.e., number of animals caught per 100 trap-nights) were converted to density estimates using a linear model based on data from 2004 to 2016, when both snap-trapping and live-trapping were conducted concurrently (Fauteux et al., 2018). Separate regressions were performed for mesic and wetland habitats. Both live-trapping densities and snap-trapping indices were log-transformed to reduce large variations and improve model fit.

In some years, no lemming was captured on our trapping grids. However, this does not mean that lemmings were totally absent from the study area when extrapolating to the landscape level. In those years, we thus replaced zeros by half of the lowest lemming density that our sampling scheme could have detected, which corresponded to a situation where only a single lemming would have been captured. Prior to 2004, half of the minimum detectable density was 0.07 lemming/ha and after that, 0.025 lemming/ha (the difference was due to the change in trapping method in 2004). Therefore, zeros were replaced by these values in the dataset.

Arctic fox movement tracking

In order to assess fox abundance based on the size of their home range, 109 Arctic foxes were fitted with Argos Platform Transmitter Terminals mounted on collars between 2008 and 2016 (Lai et al., 2015; Christin et al., 2015; Dulude-de Broin et al., 2023). Foxes were captured between May and August across the study area, within and outside the goose colony (Dulude-de Broin et al., 2023). Sampling of animal locations was set for an interval of 1 or 2 days and only locations between May 1 and October 30 were retained (Dulude-de Broin et al., 2023).

Parasitic jaeger banding

In 2009, a significant effort was made to band as many parasitic jaegers as possible within the study area. This effort resulted in the banding of 17 adult individuals (Therrien and Gauthier, unpublished data).

e. Species body mass

All vertebrate individuals captured for marking purposes were systematically weighed: snow goose (G. Gauthier, M.-C. Cadieux and J. Lefebvre, unpublished data), snowy owl (Therrien et al., 2012; Robillard et al., 2018), American-golden plovers (Lamarre et al., 2021), common-ringed plovers (Léandri-Breton et al., 2019), other shorebirds (J. Bêty, unpublished data), glaucous gulls (Gauthier et al., 2015), long-tailed jaeger (Seyer et al., 2019), parasitic jaegers (J.-F. Therrien and G. Gauthier, unpublished data), Lapland longspurs (J. Bêty and G. Gauthier, unpublished data), lemmings (Gauthier, 2020), American ermine (Bilodeau and Bolduc, unpublished data) and Arctic foxes (Lai et al., 2015). We retrieved the mean body mass of cackling geese captured and banded on Baffin Island presented in Neufeld (2021). When not available, we extracted mean body mass from the literature (Wilman et al., 2014).

3. Research methods

a. Field/laboratory

The methods used to estimate annual or mean species abundance at the landscape scale are summarized in **Table 2.4**.

Pacific loon, red-throated loon, cackling goose, tundra swan and glaucous gull

Based on the systematic and intensive search for the glaucous gull, cackling goose, tundra swan, red- throated loon and Pacific loon nests in wetlands, we are confident that we have found nearly all nests across the study area from 2017 to 2019 and in 2022. We observed a relatively strong correlation between the nest density of glaucous gulls in the Qarlikturvik valley and the nest density across the entire study area (R^2= 0.7, p = 0.16, n= 4). Consequently, we estimated the density of glaucous gulls at the scale of the study area between 2004 and 2016 based on the nest density in the Qarlikturvik valley ($y = 0.12409x + 0.13774$). We used a similar approach for cackling geese with the following equation $y = 0.60236x + 0.02019$ considering the strong correlation observed between the nest density in the Qarlikturvik valley and the nest density across the entire study area (R^2= 0.75, p = 0.06, n= 5). The first cackling goose nest was found in the study area in 1996. Since then, the total number of nests found annually appears to have increased exponentially (**Figure 2.7**). It is important to note that the substantial increase in monitoring effort from 2017 onward may have influenced the observed trend in nest numbers. Nest monitoring of loons and swans was not considered systematic in the Qarlikturvik valley before 2017, therefore we did not extend the time series for those species. Since annual abundance estimates for these species are derived from nest monitoring, they reflect only breeding individuals.

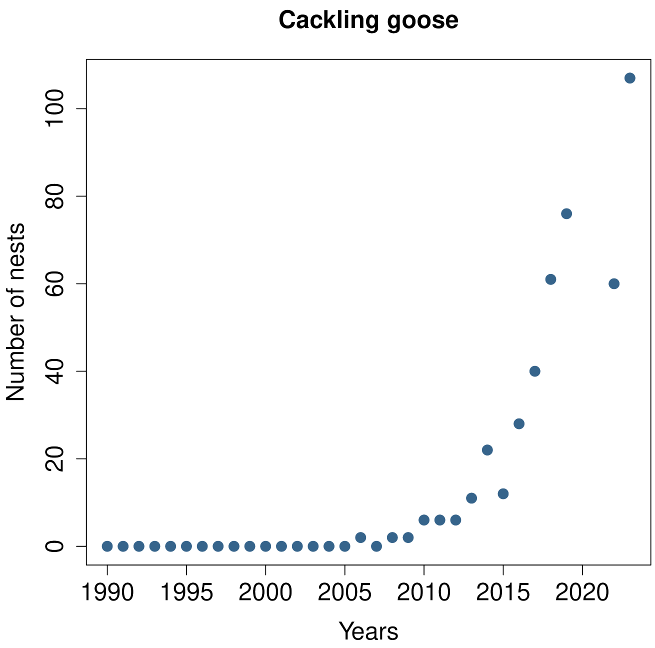


Figure 2.7 – Number of cackling goose nests found across the study area over time. The first nest was found and 1996 and nest monitoring effort increase substantially across the study area since 2017.

Snow goose

Between 1999 and 2023, we assessed the abundance of snow geese in the study area through a multi-step process. We calculated the mean annual density of snow goose nests separately in the mesic and wetland habitats of the area occupied by the goose colony annually. We made slight adjustments to the goose colony perimeter defined from helicopter flights to include all snow goose point counts where at least one breeding pair had been observed (**Figure 2.8**). To determine the mean density of nesting geese in wetlands, we divided two times (assuming two individuals per nest) the total number of nests found during systematic nest searches by the total area of wetlands sampled. Systematic nest search plots cover in average 4% of the wetland habitat within the goose colony. The density of geese nesting in mesic habitat, a less preferred nesting habitat (Lecomte et al., 2008), was averaged from three independent methods: systematic nest searches, vertebrate count transects, and snow goose point counts; **Figure 2.9**). Systematic nest searches were highly precise, but covered a relatively small area (on average, 1% of the mesic habitat within the goose colony), whereas transects and point counts were less precise but covered larger areas, averaging 20% and 12% of the mesic habitat, respectively. For each method, we calculated the mean density of breeding individuals in mesic habitat by dividing the number of birds (or nests) recorded by the area sampled. We found a strong and statistically significant correlation between density estimates derived from vertebrate count transects and point counts (Sperman's rank correlation r_s= 0.8; p=0.003). However, there was no significant correlation between density estimates from nest sampling plots and either the transect data (r_s=0.37; p=0.24) or the point counts (r_s=0.22; p= 0.5). Despite the lack of correlation between observations (transects and point counts) and nest sampling, we chose to average the estimates from all three methods since observations and nest monitoring present complementary strengths and limitations. Transects and point counts offer broader spatial coverage but lower precision, while nest sampling provides higher precision but with a more restrained spatial coverage. Averaging the three methods allows us to balance these trade-offs and produce estimates that are less precise individually, but likely more accurate overall. Lastly, to transform the densities in total abundance, we determined the annual proportion of wetland and mesic habitats within the goose colony and multiplied the area of each habitat by the density of breeding individuals. For the period 1999 to 2009, we used the average limits of the colony over the period 2010 to 2023 because we did not conduct aerial survey of the colony. Moreover, during the same period, nest density in the mesic habitat was derived only from systematic nest search (**Figure 2.9**). All annual estimates of snow goose abundance represent breeding individuals.

Figure 2.8 – Map showing the region occupied by the snow goose colony in 2017 (green polygon) as an example. The perimeter was first defined opportunistically using a GPS receiver aboard a helicopter, taking advantage of regular flights across the study area whenever the flight path passed over the colony border. The perimeter was then slightly adjusted to include all snow goose point counts where at least one breeding pair had been observed in that year (green dots). Snow goose point counts where no breeding geese were observed in that year are presented as red dots.

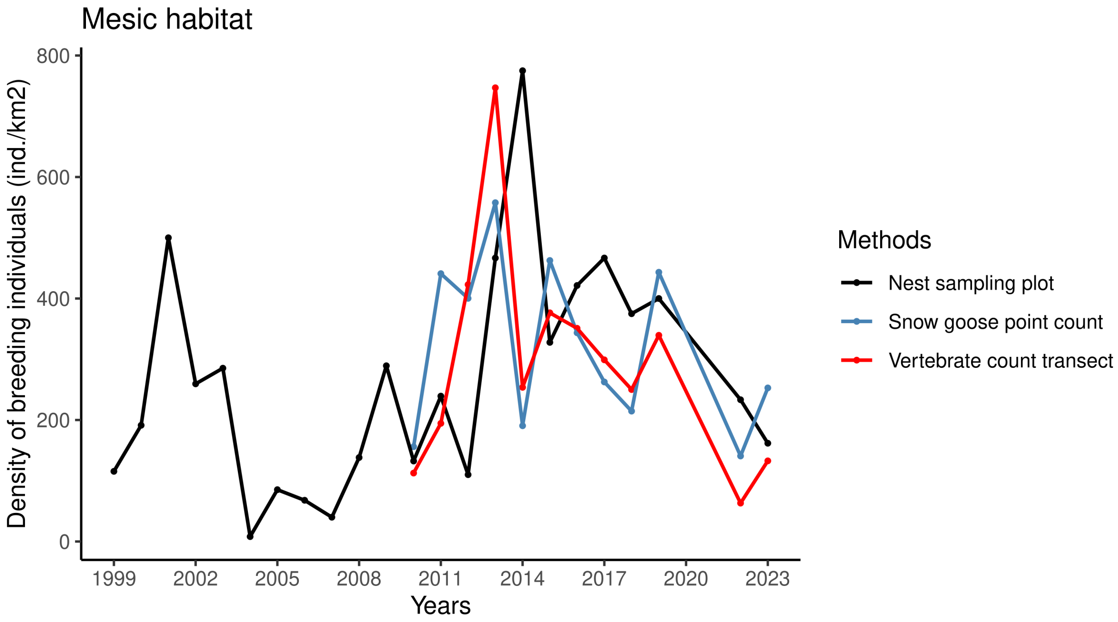


Figure 2.9 – Estimates of breeding goose density in mesic habitat within the Bylot Island snow goose colony using three independent methods: Nest sampling plot, Snow goose point count, Vertebrate count transect.

King eider and long-tailed duck

We first estimated the abundance of both king eiders and long-tailed ducks at the scale of the study area based on the annual nest density of each species found in the 8 km^2 extensive nest search area located in the Qarlikturvik valley. We extrapolated the mean nest density in the wetlands of the Qarlikturvik valley to the wetlands of the study area (38.35 km^2). We transformed nest density to abundance of breeding individuals by multiplying it by a factor of two (assuming two individuals per nest). We acknowledge that the opportunistic monitoring of these species likely underestimated their true nest density. However, considering the extensive sampling effort deployed annually within this area, we are confident to obtain a realistic order of magnitude for the number of nests present. Because duck sightings are frequent throughout the breeding period, yet only a few nests are found, we believe there may be a significant portion of non-breeding individuals. Therefore, we employed an additional method to estimate the overall duck populations without differentiating between breeding and non-breeding individuals.

As an alternative approach, we estimated the abundance of ducks based on the indices of relative abundance (i.e., the number of individuals observed per 100 hours) presented by Gauthier et al. (2024*b*). We assumed that the ratios between relative and actual abundance are the same (i.e., similar detection probability) in duck and loon species. We therefore derived the absolute abundance of long-tailed ducks and king eiders from their relative abundances using the ratio between relative and absolute abundances of red-throated loons as a reference. In summary, duck abundance estimates based on nest monitoring reflect only breeding individuals, while those based on observations may include non-breeding individuals.

Rough-legged hawk, peregrine falcon and snowy owl

We estimated the abundance of breeding rough-legged hawks, peregrine falcons and snowy owls based on systematic nest monitoring conducted throughout the study area for these species. To convert the number of nests into breeding abundance, we multiplied it by two (assuming two individuals per nest). For snowy owls, we extended the time series from 1996 to 2011 based on a linear regression between nest density in the Qarlikturvik valley and nearby plateaus (Black and Southern plateaus) and nest density across the entire study area ($y = 0.68867x - 0.00173$; $R^2 = 0.98$; $p < 0.0001$, n= 10). The linear regression included only three years in which snowy owls were present. To avoid overestimating the strength of the correlation, we restricted the analysis to those years and still observed a strong relationship despite the very small sample size (R^2= 0.98, p= 0.096, n= 3). We used the same approach for rough-legged hawks ($y = 0.49851x$, R^2= 0.99, p < 0.0001, n= 8) to extend the time series from 2007 to 2012. As with snowy owls, the correlation remained strong when considering only the years in which hawks were present (R^2= 0.98, p< 0.0001 n= 7). We did not extend the time series for peregrine falcons because the correlation was not as strong (R^2= 0.20, p= 0.27, n=8). Since annual abundance estimates for these species are derived from nest monitoring, they reflect only breeding individuals.

Rock ptarmigan

We estimated the abundance of rock ptarmigans based on the mean annual nest density measured in the 8 km^2 extensive nest search area of the Qarlikturvik valley. While we acknowledge that the opportunistic monitoring of this species likely underestimates nest density, the extensive sampling effort deployed annually within this area gives us confidence in obtaining a realistic number of nests. We then extrapolate the density to the whole study area, without distinction between mesic, wetland and upland habitats (**Table 2.3**). Among the 6 nests found in the study area, 4 were located in mesic habitat, while one nest was found in a wetland and another in an upland habitat. Nest site selection by rock ptarmigan has not been well documented in the Canadian Arctic; however, a study conducted at Sarcpa Lake (n= 7 nests) also highlight that rock ptarmigans can nest in a variety of habitats (Montgomerie et al., 1983). To convert the number of nests into abundance, we multiplied it by two (assuming two individuals per nest). Since the estimate of rock ptarmigan abundance is based on nest monitoring, it reflects only breeding individuals.

Sandhill crane

We determined the mean nest density of sandhill cranes from the nest sampling between 2004 and 2023 on the southern side of the glacial river in the Qarlikturvik valley. We determined mean nest density by dividing the mean annual number of nests recorded by the area of the surveyed zone (33 km^2). We estimated total abundance by multiplying mean nest density by the total area of the study area. We assumed a uniform density across the study area, as sandhill crane nests have been observed in wetland, mesic, and upland habitats. Since the estimate of sandhill crane abundance is based on nest monitoring, it reflects only breeding individuals.

American golden-plover and black-bellied plover

We used a distance sampling approach to estimate the abundance of American golden-plovers in the lowland zones of the study area between 2014 and 2023. Observations of plovers were made along vertebrate count transects mainly in mesic habitat. Perpendicular distance between detected individuals and the transect path were used (n= 1015) to estimate a detection function with the *ds* function from the *Distance* package (Miller et al., 2019). To determine the detection function, we applied a truncation distance of 150 m (i.e., maximum distance on either side of the observer where observations have been considered) and selected the model with the lowest AIC, which included a "hn" key and a single "cos" adjustment term. We excluded observations of groups with more than four individuals, as these likely indicated groups of non-breeders. We did not estimate abundance in wetland habitat because American golden-plovers nest almost exclusively in mesic habitat (Parmelee et al., 1967). We estimated the abundance in the upland zones (i.e., plateaus) by applying a correction factor to the abundance in lowland zones. This correction factor was based on the relative abundance ratio between the upland and lowland zones (**Table 2.3**). Since groups of non-breeding individuals (>4 individuals) were excluded from the analysis, the estimates represent the abundance of breeding individuals.

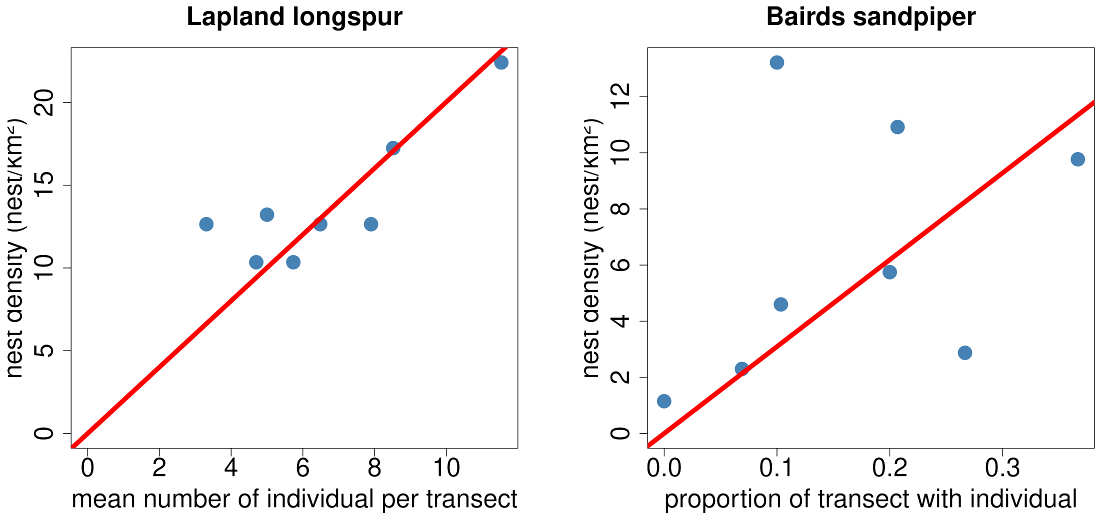
To determine the abundance of black-bellied plovers, we used the mean number of black-bellied plovers and American golden-plovers observed per transect as an index of relative abundance. For both species, observations of groups with more than four individuals were removed. We assumed that the ratios between relative and actual abundance are the same (i.e., similar detection probability) among those species. This assumption is realistic as those species present similarities in size, color, and reproductive behavior. We therefore derived the absolute abundance of black-bellied plovers from their relative abundance using the ratio between relative and absolute abundances of American golden-plover as a reference. As an alternative approach to determine black-bellied plover abundance, we used the same approach as previously described, but with the indices of relative abundance presented by Gauthier et al. (2024*b*), which was derived from incidental daily observations. The estimate of abundance derived from transect observations reflects breeding individuals, as groups of non-breeding individuals (>4 individuals) were excluded. However, the estimate based on incidental observations may include non-breeding individuals.

Common-ringed plover

To estimate the abundance of common-ringed plovers in the study area, we relied on the total number of nests recorded annually from 2015 to 2017, during which the primary nesting sites underwent intensive sampling. We multiplied the total nest count by two (assuming two individuals per nest). Since abundance estimates for the common-ringed plover are based on nest monitoring, they reflect only breeding individuals.

Lapland longspur and Baird's sandpiper

We estimated the abundance of Lapland longspurs in the different lowland zones of the study area based on a relation between nest density and the number of individuals observed per transect (**Figure 2.10**). For Baird's sandpiper, we employed a similar approach, but instead of using the mean number of individuals observed per transect, we used the mean proportion of transects where at least one individual was detected. We made this adjustment because this species was less frequently observed. Observations of Baird's sandpiper groups containing more than four individuals were removed to exclude potential non-breeding individuals. In this relationship, nest density for these two species came from the intensive nest sampling conducted within the core 2 km^2 area of the Qarlikturvik valley and observations of individuals from transects carried out in the larger 8 km^2 area in which the core area was located (**Figure 2.5**). This approach allowed us to incorporate a larger sample size from the transects while focusing on a measure of nest density determined systematically. Transects observations in lowland were then converted into nest density using the regressions equation, and then in total number of individuals by multiplying by the area and a factor 2. We estimated the density of both species in the upland zones by applying a correction factor to the annual mean density in lowland zones. This correction factor was based on the relative abundance ratio between the upland and lowland zones (**Table 2.3**). We acknowledge that the relation for Baird's sandpiper is weaker. However, incorporating spatial information derived from transect observations should offer some refinement and result in more accurate estimates compared to assuming uniform density across zones (which is a common assumption in food web modeling studies). Since abundance estimates for these species are based on a correlation between observations and nest density, they reflect the abundance of breeding individuals.



(a) (b)

Figure 2.10 – a) The red line shows the linear relation between nest density and the number of individuals observed per transect, described by the equation nest density = 2.0031 × number of individuals per transect. The relation was forced through the origin. Blue dots represent annual values (2014–2019 and 2022–2023) of nest density and mean number of individuals per transect from the core sampled area of the Qarlikturvik Valley. We assumed that the relation between nest density and observations on transects is linear. b) The red line shows the linear relation between nest density and the proportion of transects with at least an individual, described by the equation nest density= 30.9519 x proportion of transects with at least one individual. The relation was forced through the origin. Blue dots represent annual values (2014–2019 and 2022–2023) of nest density and mean proportion of transects with at least an individual from the core sampled area of the Qarlikturvik Valley. We assumed that the relation between nest density and observations on transects is linear.

Other passerines and sandpipers

We estimated the abundance of other passerines (horned lark, American pipit, and snow bunting) in the lowland zones of the study area with the regression equation between number of individuals per transect and nest density of the Lapland longspur (see section *Lapland longspur and Baird's sandpiper*). We assumed here a similar detection probability for all species. We used the same approach for other sandpiper species (white-rumped sandpiper, pectoral sandpiper, buff-breasted sandpiper, red knot, ruddy turnstone and red phalarope) based on the regression equation for the Baird's sandpiper (see section *Lapland longspur and Baird's sandpiper*). For all these species, we estimated the density in the upland zones by applying a correction factor to the mean density in lowland zones. This correction factor was based on the relative abundance ratio between the upland and lowland zones (**Table 2.3**). Nest density was then converted in number of individuals by multiplying by the area and a factor 2. As an alternative approach, we estimated the abundance of other passerines and sandpipers based on the indices of relative abundance (i.e., the number of individuals observed per 100 hours) presented by Gauthier et al. (2024*b*). We assumed that the ratios between relative and actual abundance are the same (i.e., similar detection probability) among both passerine and sandpiper species. We therefore derived the absolute abundance of other passerine and sandpiper species from their relative abundances using respectively, the ratios between relative and absolute abundances of Lapland longspur (passerines) and Baird's sandpiper (sandpipers) as references. For passerines, we assumed that all individuals observed were breeding, so abundance estimates represent breeding individuals. For shorebirds, observations of groups larger than four individuals were excluded from transects, meaning transect-based estimates represent breeding individuals. However, estimates derived from daily incidental observations may include non-breeding individuals.

Long-tailed jaeger

We determined the annual nest density of long-tailed jaegers from the systematic nest sampling between 2004 and 2023 on the southern side of the glacial river in the Qarlikturvik valley. We determined nest density by dividing the annual number of nests recorded by the area of the surveyed zone (33 km^2). As long-tailed jaegers typically nest in mesic habitat (Andersson, 1971), we multiplied the area occupied by mesic habitat across the study area by the nest density obtained in the surveyed zone and by two to obtain the total abundance of individuals (assuming two individuals per nest). Since abundance estimates for the long-tailed-jaeger are based on nest monitoring, they reflect only breeding individuals.

Parasitic jaeger

Based on the opportunistic nest monitoring of parasitic jaegers across the study area, an average of 4 nests is found annually, a small number considering that parasitic jaegers were frequently observed at the study site (Gauthier et al., 2024*b*). This suggests that there may be non-breeding individuals present at the study site, or alternatively, individuals may regularly travel long distances, potentially from outside the study area, to forage during the breeding season. Due to limited data availability for estimating the abundance of non-breeding parasitic jaegers, we relied on the maximum number of adults banded (breeding and non-breeding) during a single year (17 individuals in 2009; Therrien, unpublished data) as the minimum abundance on the study area. This corresponds to a density of 0.04 individuals/km^2. For comparison, Taylor (1974) measured a density of 0.06 individual/km^2 on Bathurst Island.

Common raven

Despite the intensive nest searches for raptors in upland zones, we never found more than one common raven nest each year, a small number considering the frequent raven observations at the study site (Gauthier et al., 2024*b*). This indicates the potential presence of non-breeding individuals or individuals that breed outside the study area but use it for foraging throughout the breeding period. Therefore, we opted for alternative approaches based on individual counts to estimate the abundance of both breeding and non-breeding ravens. As a first approach, we based our estimate of ravens on the number of glaucous gulls observed per transect. We assumed that the ratios between relative and actual abundance are the same (i.e., similar detection probability) among those species. This assumption is reasonable as those species present similarities in size and foraging strategy. We therefore derived the absolute abundance of common ravens from their relative abundance using the ratio between relative and absolute abundances of glaucous gulls as a reference.

Independently, we estimated the abundance of common ravens with the same approach but using the indices of relative abundance presented by Gauthier et al. (2024*b*), which was derived from incidental daily observations, rather than observations from the transects. Potential non-breeding individuals are included in all estimates of common raven abundance.

Nearctic brown and collared lemming

Between 1995 and 2003, we used the density estimates derived from the snap-trapping indices obtained in late July in each habitat. Between 2004 and 2007, annual abundance of each lemming species was based on the late-July density estimates on trapping grid in wet and mesic habitats. However, starting from 2008, estimates were derived from the mean density recorded in mid-July and mid-August, except for two instances: 2019 and 2021. In 2019, due to an exceptionally early snowmelt and thus an early decline in lemmings during the summer, we only retained value from mid-July. In 2021, we relied solely on data gathered in August because it was the only trapping period carried out that year. To scale the estimated densities from the wet and mesic grids to the entire study area, we used the proportions of mesic habitats (64%) and wet habitats (10%) measured within the study area. Lemming abundance estimates include juveniles and therefore reflect both breeding and non-breeding individuals.

Arctic hare

Arctic hares are primarily observed in the upland zones of the study area, where sampling effort is limited. We thus derived abundance of hares from the estimated abundance of Arctic foxes based on indices of relative abundance presented in Gauthier et al. (2024*b*), which were derived from incidental daily observations. We doubled the density of Arctic hares in the upland zones (i.e., plateaus), as twice as many individuals were observed per hour of fieldwork there compared to lowland zones (**Table 2.3**). However, it is worth noting that assuming a similar detection probability between foxes and hares might lead to an overestimation of hare detection probability due to behavioral differences between the species. Therefore, we most likely underestimate the actual abundance of Arctic hares in the study area. Breeding and non-breeding hares are not distinguished in incidental observations; therefore, the abundance estimate may include non-breeding individuals.

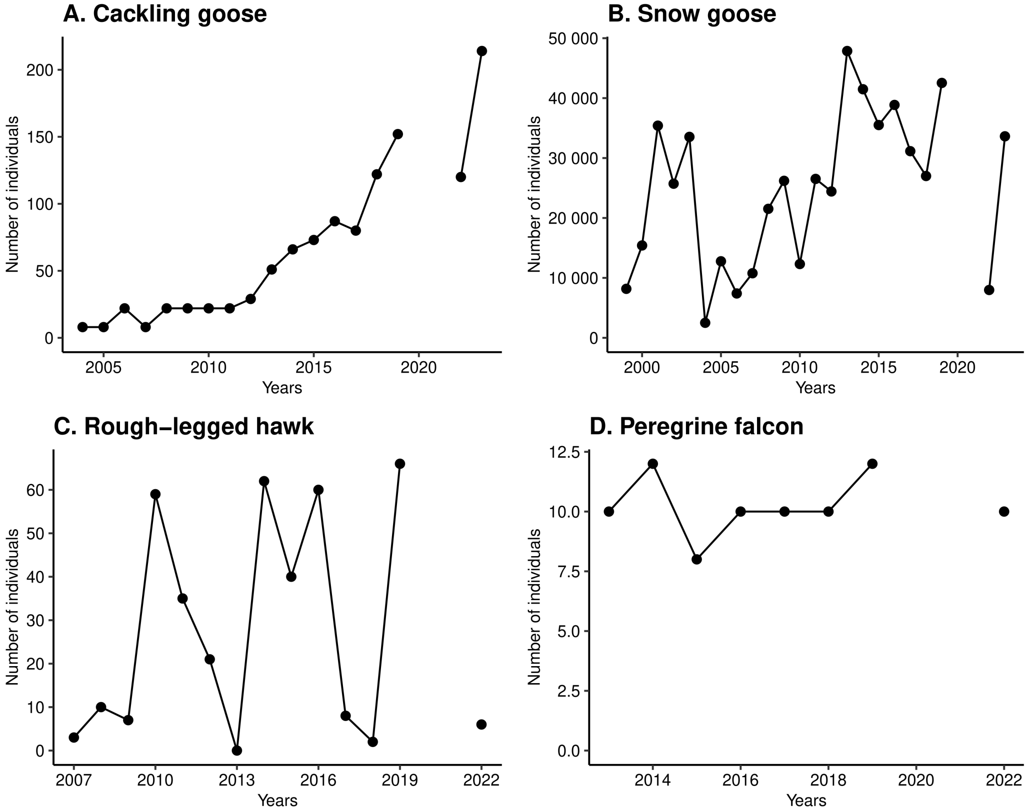
American ermine

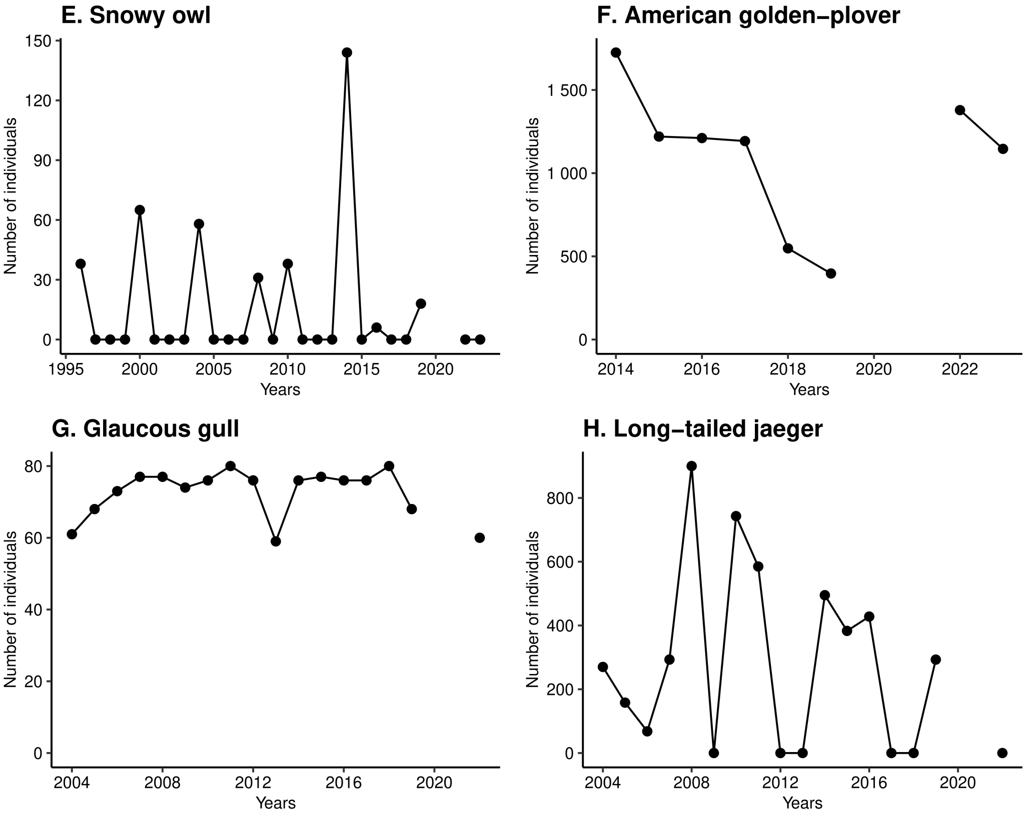
We estimated the annual abundance of ermines by transforming the annual index of relative abundance provided in Bolduc et al. (2023) into individual density. Annual values ranged from 0, indicating no ermine sighting, to 2.88, which signifies that nearly all observers observed at least one family group during their field season. We independtly obtained measures of minimum (0.02 ind./km^2) and maximum (0.4 ind./km^2) ermine density, which were determined from estimates of individual home range obtained from radio-tracking data, observations on Bylot Island, and existing literature (Legagneux et al., 2012; Bilodeau, 2013). We associated the minimum and maximum scores of relative abundance with the minimum and maximum density of individuals, respectively. Ultimately, we calculated the ermine density by linearly interpolating between these two density extremes using the annual index of relative abundance. The index of ermine abundance is derived from observations that include both breeding and potentially non-breeding individuals; consequently, the corresponding estimates of absolute abundance include potential non-breeding individuals.

Arctic fox

We estimated the abundance of Arctic foxes in the study area based on their estimated home range size inside and outside the goose colony. We used the data and methodologies outlined in Dulude-de Broin et al. (2023) to estimate home range size of territorial foxes. However, here, we did not account for annual variations in lemming density as presented in Dulude-de Broin et al. (2023) in order to obtain mean fox home range. Given that foxes are territorial and exhibit an average spatial overlap with adjacent territories of 18% (Clermont et al., 2021), we converted home range size into individual density using the following formula: $\textit{density of individuals} = \frac{2}{0.82 \times \textit{home range}}$. We used two as numerator because we assumed each territory was held by a pair of fox, either breeding or non-breeding fox pair, without accounting for potential nomadic or transient individuals. We used values of 12.26 km^2 to represent the mean home range of foxes within the goose colony and 20.02 km^2 for foxes outside the goose colony. We estimated the mean density of foxes in each zone of the study area according to the mean proportion of the zone covered by the goose colony. We derived the mean annual proportion of each zone covered by the goose colony from the colony outline between 2010 and 2023. We estimated a mean density of 0.14 individuals/km^2 for the study area. Previously, the minimum density of foxes in the study area was estimated to be between 0.03 and 0.13 individuals per km^2 based on camera traps (Royer-Boutin, 2015). Since breeding and non-breeding individuals are both territorial (Lai et al., 2017), the provided estimate of fox abundance includes both breeding and non-breeding individuals.

Figure 2.11 – Time series of the estimated annual abundance of vertebrate species on the southern plain of Bylot Island (389 km^2). Estimated abundance represents adult individuals, with the exception of lemmings, for which juveniles were also included in the estimate. Time series shorter than 5 years are not presented.




E. Snowy owl
Number of individuals
150
120
90
60
30
0
1995
2000
2005
2010
2015
2020
Years
F. American golden−plover
Number of individuals
1 500
1 000
500
0
2014
2016
2018
2020
2022
Years
G. Glaucous gull
Number of individuals
80
60
40
20
0
2004
2008
2012
2016
2020
Years
H. Long−tailed jaeger
Number of individuals
800
600
400
200
0
2004
2008
2012
2016
2020
Years

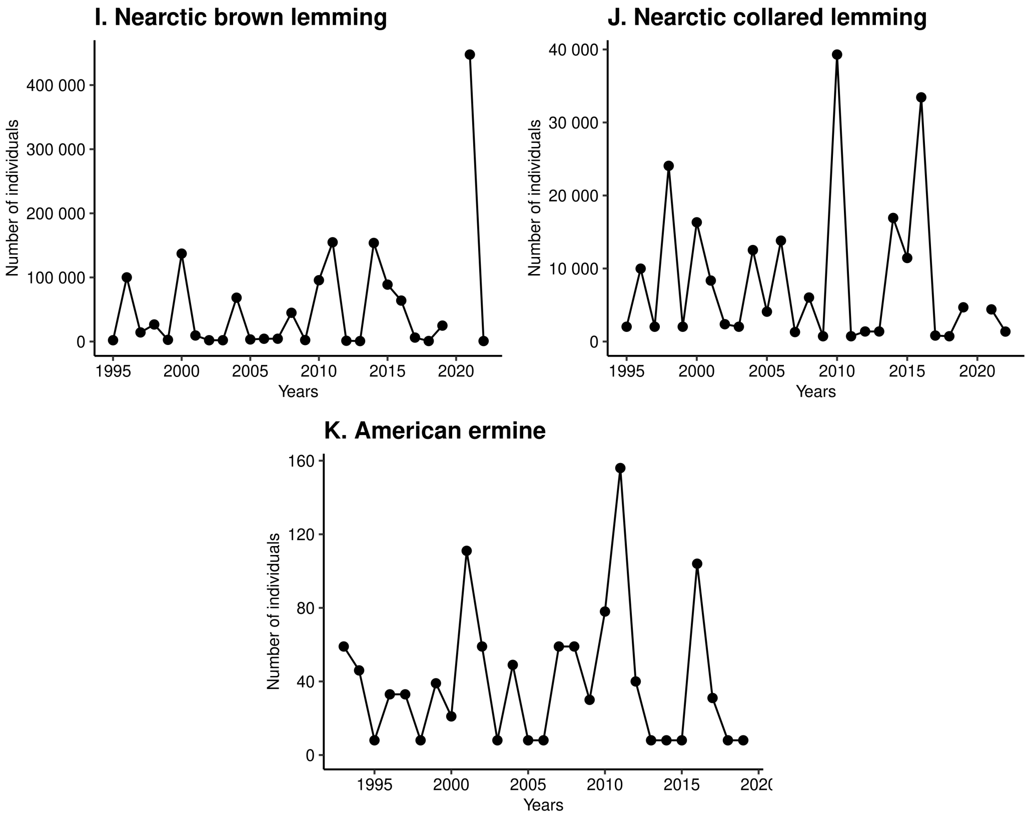

I. Nearctic brown lemming
Number of individuals
400 000
300 000
200 000
100 000
0
1995
2000
2005
2010
2015
2020
Years
J. Nearctic collared lemming
Number of individuals
40 000
30 000
20 000
10 000
0
1995
2000
2005
2010
2015
2020
Years
K. American ermine
Number of individuals
160
120
80
40
0
1995
2000
2005
2010
2015
2020
Years

Table 2.5 – Due to the absence of confidence intervals in our abundance estimates, we present uncertainty intervals based on field expert judgment. Experts derived these intervals by considering the given abundance estimate, estimates for other species for comparaison, and their field expertise. For species with time series data (several years of estimates), the intervals are presented for the lowest and highest abundance reached within the given time series. These intervals reflect the interval within which the actual abundance lies according to field experts. For species without time series, the intervals are presented for the mean only.

		Annual abundance (individuals)		
Species	Period	Lowest	Highest	Mean
Pacific loon	2017-2019, 2022	[0-6]	[6-10]	
Red-throated loon	2017-2019, 2022	[42-62]	[75-100]	
King eider	Mean abundance			[60-250]
Long-tailed duck	Mean abundance			[80-300]
Cackling goose	2004-2016	[8-30]	[87-110]	
Cackling goose	2017-2019, 2022-2023	[80-110]	[214-244]	
Snow goose	1999-2009	[2500-10000]	[35000-60000]	
Snow goose	2010-2019, 2022-2023	[6000-10000]	[45000-60000]	
Tundra swan	2017-2019, 2022	[0-2]	[2-6]	
Rough-legged hawk	2007-2012	[0-8]	[50-90]	
Rough-legged hawk	2013-2019, 2022	[0-4]	[66-86]	
Peregrine falcon	2013-2019, 2022	[8-12]	[12-20]	
Snowy owl	1996-2011	0	[50-100]	
Snowy owl	2012-2019, 2022-2023	0	[144-170]	
Rock ptarmigan	Mean abundance			[10-60]
Sandhill crane	Mean abundance			[15-45]
American golden-plover	2014-2019, 2022-2023	[300-600]	[1000-2500]	
Black-bellied plover	Mean abundance			[6-30]
Common-ringed plover	2015-2017	[44-60]	[60-100]	
Ruddy turnstone	Mean abundance			[10-30]
Red knot	Mean abundance			[10-30]
Pectoral sandpiper	Mean abundance			[20-100]
Baird's sandpiper	Mean abundance			[1500-3500]
White-rumped sandpiper	Mean abundance			[1000-2000]
Buff-breasted sandpiper	Mean abundance			[2-10]
Red phalarope	Mean abundance			[20-80]
Glaucous gull	2004-2016	[50-80]	[70-100]	
Glaucous gull	2017-2019, 2022	[60-80]	[80-100]	
Long-tailed jaeger	2004-2019, 2022	[0-10]	[300-900]	
Parasitic jaeger	Mean abundance			[15-50]
Common raven	Mean abundance			[30-75]
Horned lark	Mean abundance			[200-600]
American pipit	Mean abundance			[50-300]
Lapland longspur	Mean abundance			[6000-10000]
Snow bunting	Mean abundance			[50-300]
Nearctic brown lemming	1995-2019, 2021-2022	[100-2000]	[200000-450000]	
Nearctic collared lemming	1995-2019, 2021-2022	[100-2000]	[20000-50000]	
Arctic hare	Mean abundance			[15-50]
American ermine	1993-2019	[0-10]	[50-200]	
Arctic fox	Mean abundance			[30-60]

Table 2.4 – Summary of the lowest, highest, mean and standard deviation of the estimated abundance of each vertebrate species in the vertebrate community of the southern plain of Bylot Island (389 km^2). In some cases, two independent approaches have been used to estimate the abundance of the same species as a proxy for uncertainty. We provide a qualitative measure of the method quality based on data available, method used for extrapolation (if necessary), and in some cases, from the fit of statistical models to estimate density. The asterisk (*) indicates that the estimate reflects breeding individuals only. The absence of an asterisk means the abundance estimate may include non-breeding individuals.

Species	**Method**	**Method quality**	**Justification**	**Lowest abundance**	**Highest abundance**	**Mean abundance**	**sd**	**n**
Pacific loon	Intensive study area-wide nest monitoring (389 km2)	high	No extrapolation	0*	6*	4*	3	4 (2017-2019, 2022)
Red-throated loon	Intensive study area-wide nest monitoring (389 km2)	high	No extrapolation	42*	76*	64*	15	4 (2017-2019, 2022)
King eider	Intensive, but opportunistic nest monitoring (8 km2) extrapolated by habitat	very low	Intensive, but opportunistic monitoring at relatively small spatial scale, but does not include potential non-breeding individuals			25*		
King eider	Derived from the abundance estimate of red-throated loon using incidental observations	low	Derived from high quality estimate of another species			106		
Long-tailed duck	Intensive, but opportunistic nest monitoring (8 km2) extrapolated by habitat	very low	Intensive, but opportunistic monitoring at relatively small spatial scale, but does not include potential non-breeding individuals			20*		
Long-tailed duck	Derived from the abundance estimate of red-throated loon using incidental observations	low	Derived from high quality estimate of another species			191		

Species	**Method**	**Method quality**	**Justification**	**Lowest abundance**	**Highest abundance**	**Mean abundance**	**sd**	**n**
Cackling goose	Extrapolation from intensive nest monitoring (111 km2, R2= 0.75, p = 0.06, n= 5)	high	Strong correlation with study area-wide nest density	8*	87*	34*	26	13 (2004-2016)
Cackling goose	Intensive study area-wide nest monitoring (389 km2)	high	No extrapolation	80*	214*	138*	50	5 (2017-2019, 2022-2023)
Snow goose	Nest monitoring plots extrapolated to mean goose colony area	moderate	Relatively small sample size and uncertainty on goose colony area	2505*	35404*	18129*	11037	11 (1999-2009)
Snow goose	Intensive study area-wide monitoring based on a combination of methods (transects, point counts and nest monitoring plots) and annual colony outline	high	Multiple independent methods and annual colony outline	7982*	47859*	30771*	11962	12 (2010-2019, 2022-2023)
Tundra swan	Intensive study area-wide nest monitoring (389 km2)	high	No extrapolation	0*	2*	1*	1	4 (2017-2019, 2022)
Rough-legged hawk	Extrapolation from intensive nest monitoring (111 km2, R2=0.99, p<0.0001, n=8)	high	Strong correlation with study area-wide nest density	3*	59*	22*	21	6 (2007-2012)
Rough-legged hawk	Intensive study area-wide nest monitoring (389 km2)	high	No extrapolation	0*	66*	30*	29	8 (2013-2019, 2022)
Peregrine falcon	Intensive study area-wide nest monitoring (389 km2)	high	No extrapolation	8*	12*	10*	1	8 (2013-2019, 2022)
Snowy owl	Extrapolation from intensive nest monitoring (111 km2, R2=0.98, p<0.0001, n=10)	high	Strong correlation with study area-wide nest density	0*	65*	14*	23	16 (1996-2011)
Snowy owl	Intensive study area-wide nest monitoring (389 km2)	high	No extrapolation	0*	144*	17*	45	10 (2012-2019, 2022-2023)

Species	Method	Method quality	Justification	Lowest abundance	Highest abundance	Mean abundance	sd	n
Rock ptarmigan	Intensive, but opportunistic nest monitoring (8 km2) extrapolated to study area	very low	Intensive, but opportunistic monitoring at relatively small spatial scale and prime nesting habitat not well sampled			24*		
Sandhill crane	Intensive nest monitoring (33 km2) extrapolated to study area	moderate	Nest density is extrapolated uniformly across the study area			69*		
American golden-plover	Distance sampling throughout lowland (313 km2)	high	Large sample size	397*	1725*	1102*	432	8 (2014-2019, 2022-2023)
Black-bellied plover	Derived from the abundance estimate of American golden-plover using transects observations	low	Derived from high quality estimate of another species			29*		
Black-bellied plover	Derived from the abundance estimate of American golden-plover using incidental observations	very low	Derived from high quality estimate of another species, but potentially includes transient migratory individuals			87		
Common-ringed plover	Nest monitoring on the main breeding sites	moderate	Intensive monitoring, but not exhaustive to study area	44*	62*	55*	9	3 (2015-2017)
Ruddy turnstone	Derived from the abundance estimate of Bairds sandpiper using transects observations	low	Derived from moderate quality estimate of another species			36*		
Ruddy turnstone	Derived from the abundance estimate of Bairds sandpiper using incidental observations	very low	Derived from moderate quality estimate of another species, but potentially includes transient migratory individuals			47		
Red knot	Derived from the abundance estimate of Bairds sandpiper using transects observations	low	Derived from moderate quality estimate of another species			59*		
Red knot	Derived from the abundance estimate of Bairds sandpiper using incidental observations	very low	Derived from moderate quality estimate of another species, but potentially includes transient migratory individuals			206		

Species	Method	Method quality	Justification	Lowest abundance	Highest abundance	Mean abundance	sd	n
Pectoral sandpiper	Derived from the abundance estimate of Bairds sandpiper using transects observations	low	Derived from moderate quality estimate of another species			71*		
Pectoral sandpiper	Derived from the abundance estimate of Bairds sandpiper using incidental observations	very low	Derived from moderate quality estimate of another species, but potentially includes transient migratory individuals			226		
Baird’s sandpiper	Extrapolation from intensive nest monitoring (2 km2) and transects observations	moderate	Uncertain relation between nest density and transects observations			2170*		
White-rumped sandpiper	Derived from the abundance estimate of Bairds sandpiper using transects observations	low	Derived from moderate quality estimate of another species			878*		
White-rumped sandpiper	Derived from the abundance estimate of Bairds sandpiper using incidental observations	very low	Derived from moderate quality estimate of another species, but potentially includes transient migratory individuals			1005		
Buff-breasted sandpiper	Derived from the abundance estimate of Bairds sandpiper using transects observations	low	Derived from moderate quality estimate of another species			5*		
Buff-breasted sandpiper	Derived from the abundance estimate of Bairds sandpiper using incidental observations	very low	Derived from moderate quality estimate of another species, but potentially includes transient migratory individuals			7		
Red phalarope	Derived from the abundance estimate of Bairds sandpiper using transects observations	low	Derived from moderate quality estimate of another species			124*		
Red phalarope	Derived from the abundance estimate of Bairds sandpiper using incidental observations	very low	Derived from moderate quality estimate of another species, but potentially includes transient migratory individuals			240		
Glaucous gull	Extrapolation from intensive nest monitoring (111 km2, R2=0.7, p=0.16, n=4)	high	Strong correlation with study area-wide nest density	59*	80*	73*	6	13 (2004-2016)

Species	Method	Method quality	Justification	Lowest abundance	Highest abundance	Mean abundance	sd	n
Glaucous gull	Intensive study area-wide nest monitoring (389 km2)	high	No extrapolation	60*	80*	71*	9	4 (2017-2019, 2022)
Long-tailed jaeger	Intensive nest monitoring (33 km2) extrapolated by habitat	high	Relatively large spatial coverage of sampling	0*	900*	272*	285	17 (2004-2019, 2022)
Parasitic jaeger	Maximum number of individuals banded in a year	low	Based on a single year and potentially not all individuals were captured			17		
Parasitic jaeger	Maximum number of nest found annually during study area-wide opportunistic nest monitoring	very low	Monitoring does not include potential non-breeding individuals			8*		
Common raven	Derived from the abundance estimate of glaucous gull using transects observations	very low	Derived from moderate quality estimate of another species, but potential difference in detectability between species			14		
Common raven	Derived from the abundance estimate of glaucous gull using incidental observations	very low	Derived from moderate quality estimate of another species, but potential difference in detectability between species			18		
Horned lark	Derived from the abundance estimate of Lapland longspur using transects observations	low	Derived from moderate quality estimate of another species			310*		
Horned lark	Derived from the abundance estimate of Lapland longspur using incidental observations	low	Derived from moderate quality estimate of another species			352*		
American pipit	Derived from the abundance estimate of Lapland longspur using transects observations	very low	Derived from moderate quality estimate of another species and prime nesting habitat not sampled			46*		
American pipit	Derived from the abundance estimate of Lapland longspur using incidental observations	low	Derived from moderate quality estimate of another species and prime nesting habitat not well sampled			74*		

Species	Method	Method quality	Justification	Lowest abundance	Highest abundance	Mean abundance	sd	n
Lapland longspur	Extrapolation from intensive nest monitoring (2 km2) and transects observations	moderate	Uncertain relation between nest density and transects observations			6080*		
Snow bunting	Derived from the abundance estimate of Lapland longspur using transects observations	very low	Derived from moderate quality estimate of another species and prime nesting habitat not sampled			15*		
Snow bunting	Derived from the abundance estimate of Lapland longspur using incidental observations	low	Derived from moderate quality estimate of another species and prime nesting habitat not well sampled			236*		
Nearctic brown lemming	Rigorous density estimates at small spatial scale (0.22 km2) extrapolated by habitat	moderate	Intensive sampling, but small spatial coverage and extrapolation by habitat	724	447630	54170	93455	27 (1995-2019, 2021-2022)
Nearctic collared lemming	Rigorous density estimates at small spatial scale (0.22 km2) extrapolated by habitat	moderate	Intensive sampling, but small spatial coverage and extrapolation by habitat	724	39302	8306	10202	27 (1995-2019, 2021-2022)
Arctic hare	Derived from the abundance estimate of Arctic fox using incidental observations	very low	Derived from moderate quality estimate of another species, prime nesting habitat not well sampled and difference in detectability between species			6		
American ermine	Indices of relative abundance derived from testimonials converted to abundance using home range size	moderate	Indirect indices and uncertainty on ermine home range size estimates	8	156	40	37	27 (1993-2019)
Arctic fox	Derived from extensive fox home range size studies (n=109)	moderate	Indirect indices, but large sample size			53		

b. Taxonomy and systematics

Birds taxonomy was obtained from the IOC World Bird List 14.2 (Gill et al., 2024) and mammals taxonomy from the Mammal species of the world: a taxonomic and geographic reference (Upham et al., 2024).

c. Permit history

All research involving animals on Bylot Island has been approved by an institutional Animal Care Committee. In 1999, the study area became part of Sirmilik National Park, managed by Parks Canada. Since then, all research activities in the park have been approved by a Joint Park Management Committee.

d. Project personnel

Principal and associated investigators

Gilles Gauthier, Austin Reed, Jean-François Giroux, Dominique Berteaux, Joël Bêty, Josée Lefebvre, Dominique Gravel, Jean-François Therrien, Nicolas Lecomte, Dominique Fauteux, Pierre Legagneux (see Gauthier et al. 2024*a*)

Students

By combining animal and plant ecology, 24 doctoral theses and 56 master theses have been completed in relation to the study area located on the south plain of Bylot Island (see Gauthier et al. 2024*a*).

Class III. Data set status and accessibility

A. Status

1. Latest update

August 11, 2025

2. Latest archive date

August 11, 2025

3. Metadata status

August 11, 2025

4. Data verification

The methods employed to estimate species abundance were subject to several rounds of revision by the authors.

B. Accessibility

1. Storage location and medium

The complete data set is available as Supporting Information. The complete data set, including raw data, is also archived in Dryad: `https://doi.org/10.5061/dryad.44j0zpcnt`. The code and the complete R project used to estimate species abundance are archived in Zenodo: `https://doi.org/10.5281/zenodo.13993826`.

2. Contact persons

Overall project

Joël Bêty; *joel_bety@uqar.ca*; 418 723-1986 #1701; 300 allée des Ursulines, Rimouski, Québec, Canada, G5L 3A1, Office B-002

Specific subproject description

Louis Moisan, *louis.moisan.bio@gmail.com*

3. Copyright restrictions

None

4. Proprietary restrictions

a. Release date

None

b. Citation

Please refer to the data paper version published in *Ecology* Moisan et al. (2025*a*).

c. Disclaimer

None

5. Costs

None, the data can be used free of charge.

Class IV. Data structural descriptors

A. Data set file

1. Identity

a. `BYLOT-species_taxonomy.csv`

b. `BYLOT-species_density_monitoring.csv`

c. `BYLOT-species_abundance.csv`

d. `BYLOT-community_composition.csv`

e. `BYLOT-species_body_mass.csv`

2. Size

a. 35 records, not including header row (4.1 kB)

b. 1186 records, not including header row (128.5 kB)

c. 261 records, not including header row (35.6 kB)

d. 35 records, not including header row (4.3 kB)

e. 54 records, not including header row (3.8 kB)

3. Format and storage mode

All files are in a comma-separated value format (.csv).

4. Header information

a. `BYLOT-species_taxonomy.csv`

`class`; `order`; `family`; `genus`; `species_scientific`; `species_en`; `species_fr`; `functional_group`; `migratory_status`

b. `BYLOT-species_density_monitoring.csv`

`species_en`; `year`; `zone`; `area_sampled_km2`; `habitat`; `method`; `monitoring`; `breeding_status`; `ind_density_km2`

c. `BYLOT-species_abundance.csv`

`species_en`; `year`; `breeding_status`; `abundance`; `method_description`; `method_quality`; `spatial_extrapolation`

d. `BYLOT-community_composition.csv`

`species_en`; `1993` ... `2023`; `mean`

e. `BYLOT-species_body_mass.csv`

`species_en`; `site`;`mean_body_mass_g`; `sample_size`; `reference`

5. Alphanumeric attributes

Mixed

6. Special characters/fields

Unavailable values are indicated by NA.

7. Authentication procedures

Sums of the numeric columns:

b. `BYLOT-species_density_monitoring.csv`: year= 2389178; area_sampled_km2= 62017.96; ind_density_km2= 31269.65

c. `BYLOT-species_abundance.csv`: year= 456443; abundance= 2286541

d. `BYLOT-community_composition.csv`: 1993= 59; 1994= 46; 1995= 4060; 1996= 110133; 1997= 16284; 1998= 50661; 1999= 12880; 2000= 168935; 2001= 53306; 2002= 30172; 2003= 37592; 2004= 83856; 2005= 20380; 2006= 25726; 2007= 16886; 2008= 73475; 2009= 29315; 2010= 148246; 2011= 182925; 2012= 27161; 2013= 50088; 2014= 214747; 2015= 137586; 2016= 138211; 2017= 39625; 2018= 29379; 2019= 73157; 2021= 452032; 2022= 11778; 2023= 34986; mean= 10575

e. `BYLOT-species_body_mass.csv`: body_mass_g= 51256; sample_size= 14138

B. Variable information

1. Variable identity

See **Table 2.6**

2. Variable definition

See **Table 2.6**

3. Units of measurement

See **Table 2.6**

Table 2.6 – Summary of variable definition and unit of measurement.

Data file	**Variable identity**	**Variable definition**	**Units**
a.	class	Taxonomic class for birds (Gill et al., 2024) and mammals species (Upham et al., 2024).	NA
a.	order	Taxonomic order for birds (Gill et al., 2024) and mammals species (Upham et al., 2024).	NA
a.	family	Taxonomic family for birds (Gill et al., 2024) and mammals species (Upham et al., 2024).	NA
a.	genus	Taxonomic genus for birds (Gill et al., 2024) and mammals species (Upham et al., 2024).	NA
a.	species_scientific	Taxonomic species for birds (Gill et al., 2024) and mammals species (Upham et al., 2024).	NA
a.	species_en	Common names of species in English.	NA
a.	species_fr	Common names of species in French.	NA
a.	functional_group	Functional group for each species. The classification of species into functional groups is based on Moisan et al. (2023).	NA
a.	migratory_status	Migratory status of each species. The classification of species migratory status is based on Gauthier et al., (2011) and Moisan et al. (2023).	NA
b.	species_en	Common names of species in English.	NA
b.	year	Year in which species density was monitored in the corresponding zone.	years
b.	zone	Zone of the study area in which density was measured.	NA
b.	area_sampled_km2	Area (in square kilometers) sampled to measure species density.	square kilometers
b.	habitat	Habitat in which species density was measured.	NA
b.	method	Method used to measure species density.	NA
b.	monitoring	Type of monitoring conducted, distinguishing between systematic (planned, standardized data collection) and opportunistic (irregular or incidental).	NA
b.	breeding_status	Reproductive status of the individuals.	NA
b.	ind_density_km2	Density of individuals (number of individuals per square kilometer) measured in the corresponding year and zone of the study area.	individuals per square kilometer
c.	species_en	Common names of species in English.	NA
c.	year	Year corresponding to the estimate of annual abundance. If abundance has not been calculated for a given series of years, but rather as a general average, then NA has been assigned.	years
c.	breeding_status	Reproductive status of the individuals.	NA
c.	abundance	Estimate of the annual number of individuals found within the 389 km2 study area located on the southern part of Bylot Island during the breeding season (May to August). The estimates only consider adults, with the exception of lemmings, for which no distinction has been made between juveniles and adults.	individuals
c.	method_description	Brief overview of the method used to estimate the species abundance.	NA
c.	method_quality	Qualitative measure of the method quality based on data available, method used for extrapolation (if necessary), and in some cases, from the fit of statistical models to estimate density.	NA

c.	spatial_extrapolation	Indicates whether the abundance estimate was derived from monitoring across the entire study area ("no") or was spatially extrapolated ("yes").	NA
d.	species_en	Common names of species in English.	NA
d.	1993 – 2023	Estimate of the annual number of individuals within the 389 km2 study area located on the southern part of Bylot Island during the breeding season (May to August) for the corresponding year. The estimates represent only breeding individuals, except for lemmings, for which the estimates include both breeding and non-breeding individuals. The estimates exclude non-breeding individuals that stop for only a few days during their migration. The estimates only consider adults, with the exception of lemmings, for which no distinction has been made between juveniles and adults. Note that 2020 does not appear since fieldwork was not possible due to Covid-19 restrictions.	individuals
d.	mean	Estimate of the long-term average annual number of individuals within the 389 km2 study area located on the southern part of Bylot Island during the breeding season (May to August). This includes both breeding and non-breeding individuals that stay in the study area for a significant period of time, and excludes non-breeding individuals that stop for only a few days during their migration. The estimates only consider adults. For species where abundance was estimated using multiple methods, we selected the method determined to be of the highest quality. In cases where multiple methods yielded equivalent quality, the mean value of their estimates was retained.	individuals
e.	species_en	Common names of species in English.	NA
e.	site	Site where body mass measurements were taken.	NA
e.	mean_body_mass_g	Mean individual body mass.	grams
e.	sample_size	Number of individuals measured.	individuals
e.	reference	Reference from which estimate of mean body mass were derived.	NA

4. Data type

a. Storage type

See **Table 2.7**

b. List and definition of variable codes

See **Table 2.7**

c. Range for numeric values

See **Table 2.7**

d. Missing value codes

Unavailable values are indicated by NA.

e. Number of digits

See **Table 2.7**

Table 2.7 – Summary of variable storage type, code definition, range and number of digit.

Data file	Variable identity	Storage type	Definition variable codes	Range	Number digits
a.	class	string	NA	NA	NA
a.	order	string	NA	NA	NA
a.	family	string	NA	NA	NA
a.	genus	string	NA	NA	NA
a.	species_scientific	string	NA	NA	NA
a.	species_en	string	NA	NA	NA
a.	species_fr	string	NA	NA	NA
a.	functional_group	string	NA	NA	NA
a.	migratory_status	string	resident: Individuals performing movements within the study area throughout the annual cycle. \ partial migrant: A combination of resident and migratory and/or individuals performing long-distance foraging trips outside the study area during the non-breeding period. \ migrant: Individuals performing seasonal and highly synchronous movements between the study area and a distant non-breeding ground.	NA	NA
b.	species_en	string	NA	NA	NA
b.	year	integer	NA	1995-2023	0
b.	zone	string	see Figure 4 and 5 in MetadataS1.pdf or file study_area/study_area.shp for spatial delineation of the zones.	NA	NA
b.	area_sampled_km2	numeric	NA	0.11-388.80	2
b.	habitat	string	see section c. Habitat for a detailed description of mesic, wetland and upland habitats. mixed is used to represent a combination of different habitats.	NA	NA
b.	method	string	nest sampling: Total number of nests found within a given zone or plot. / trapping: Capture-mark-recapture of individuals within a trapping grid to estimate density. / distance sampling: Observations of individuals along vertebrate count transects analyzed using a distance detection function to estimate density.	NA	NA
b.	monitoring	string	opportunistic: irregular or incidental data collection. \ systematic: planned and standardized data collection.	NA	NA
b.	breeding_status	string	breeding: Individuals present in the study area during the breeding period (June to August) and having attempted and/or completed breeding. \ undetermined: Individuals present on the study area during the breeding period (June to August) that might have breed or not.	NA	NA
b.	ind_density_km2	numeric	NA	0.000-1550.000	3
c.	species_en	string	NA	NA	NA

c.	year	integer	If abundance has not been calculated for a given series of years, but rather as a general average, then NA has been assigned.	1993-2023	0
c.	breeding_status	string	breeding: Individuals present in the study area during the breeding period (June to August) and having attempted and/or completed breeding. \ undetermined: Individuals present on the study area during the breeding period (June to August) that might have breed or not.	NA	NA
c.	abundance	integer	NA	0-447630	0
c.	method_description	string	NA	NA	NA
c.	method_quality	string	very low: Sampling might not encompasses prime nesting habitat, excludes transient migratory individuals or includes potential non-breeding individuals. If abundance is derived from the abundance estimate of another species based relative abundance, detection probabilities may differ. \ low: Abundance is derived from the estimate of another species based on indices of relative abundance. \ moderate: Small to intermediate scale sampling with spatial extrapolation. \ high: Large scale intensive sampling, with some spatial extrapolation in a few cases.	NA	NA
c.	spatial_extrapolation	binary	yes: Some form of spatial extrapolation has been applied to estimate species abundance at the landscape scale. / no: Monitoring was performed at the landscape scale without requiring spatial extrapolation.	NA	NA
d.	species_en	string	NA	NA	NA
d.	1993	integer	NA	59-59	0
d.	1994	integer	NA	46-46	0
d.	1995	integer	NA	8-2026	0
d.	1996	integer	NA	33-100080	0
d.	1997	integer	NA	0-14225	0
d.	1998	integer	NA	0-26590	0
d.	1999	integer	NA	0-8175	0
d.	2000	integer	NA	21-137110	0
d.	2001	integer	NA	0-35404	0
d.	2002	integer	NA	0-25715	0
d.	2003	integer	NA	0-33532	0
d.	2004	integer	NA	8-68378	0
d.	2005	integer	NA	0-12773	0
d.	2006	integer	NA	0-13817	0

d.	2007	integer	NA	0-10778	0
d.	2008	integer	NA	10-44827	0
d.	2009	integer	NA	0-26199	0
d.	2010	integer	NA	22-95615	0
d.	2011	integer	NA	0-154805	0
d.	2012	integer	NA	0-24424	0
d.	2013	integer	NA	0-47859	0
d.	2014	integer	NA	8-153753	0
d.	2015	integer	NA	0-88772	0
d.	2016	integer	NA	6-63865	0
d.	2017	integer	NA	0-31147	0
d.	2018	integer	NA	0-27001	0
d.	2019	integer	NA	2-42535	0
d.	2021	integer	NA	4402-447630	0
d.	2022	integer	NA	0-7982	0
d.	2023	integer	NA	0-33626	0
d.	mean	integer	NA	5-6080	0
e.	species_en	string	NA	NA	NA
e.	site	string	bylot: Southern plain of Bylot Island, Nunavut, Canada.\ baffin: Baffin Island (65.421 N, 70.966 E), Nunavut, Canada. \ undetermined: Data were not retrieved from original publications.	NA	NA
e.	mean_body_mass_g	integer	NA	21-6378	0
e.	sample_size	integer	NA	1-6405	0
e.	reference	string	NA	NA	NA
e.	species_en	string	NA	NA	NA

C. Data anomalies: Description of missing data, anomalous data, calibration errors, etc.

c. `BYLOT-species_abundance.csv`

`year`: If abundance has not been calculated for a given series of years, but rather as a general average, then NA has been assigned.

d. `BYLOT-community_composition.csv`

`1993 - 2023`: For the years 1993 to 2023, NA values in the respective columns indicate that no annual abundance estimates were available for the study area.
`mean`: The 'mean' column displays values only when annual estimates (i.e., time series data) were unavailable.

e. `BYLOT-species_body_mass.csv`

`sample_size`: NA is used when sample size was not specified.

Class V. Supplemental descriptors

A. Data acquisition

1. Data forms or acquisition methods

See Section **2. Experimental or sampling design**

2. Location of completed data forms

The complete data set is available as Supporting Information. The complete data set, including raw data, is also archived in Dryad: `https://doi.org/10.5061/dryad.44j0zpcnt`. Also, part of the raw monitoring data for the key species of the food web are also available at the NordicanaD data repository (`https://nordicana.cen.ulaval.ca/en/list-of-publications.php`; Lemming monitoring on Bylot Island; Monitoring of Greater Snow Goose reproduction on Bylot Island; Monitoring of Lapland longspur reproduction on Bylot Island; Monitoring of shorebirds reproduction on Bylot Island; Monitoring of arctic and red fox reproduction on Bylot Island; Monitoring of avian predator reproduction on Bylot Island; Relative abundance of tundra bird and mammal species encountered daily on Bylot Island) and are periodically updated as the field studies continue on Bylot Island.

3. Data entry verification procedures

The methods used to extract final species abundance estimates were subject to several rounds of revision by the authors.

B. Quality assurance/quality control procedures

The authors revised the presented measures of species density and abundance estimates. Following comments from two anonymous reviewers in April 2025, the methods, dataset, and MetadataS1 document were updated accordingly.

C. Computer programs and data-processing algorithms

1. Program

R version 4.4.1 (2024-06-14)

2. Operating system

Data preparation was performed on x86_64-pc-linux-gnu (64-bit) with Ubuntu 22.04.3 LTS.

3. Packages

dplyr 1.1.4 (Wickham et al., 2023*a*)
tidyr 1.3.1 (Wickham et al., 2024)
sf 1.0-20 (Pebesma, 2018)
stringr 1.5.1 (Wickham, 2023)
xtable 1.8-4 (Dahl et al., 2019)
Distance 1.0.9 (Miller et al., 2019)
ggplot2 3.5.1 (Wickham, 2016)
lme4 1.1-35.3 (Bates et al., 2015)
AICcmodavg 2.3-3 (Mazerolle, 2023)
scales 1.3.0 (Wickham et al., 2023*b*)
ggmap 4.0.1 (Kahle and Wickham, 2013)
ggspatial 1.1.9 (Dunnington, 2023)

4. Code

The code and the complete R project used to estimate species abundance are archived in Zenodo: `https://doi.org/10.5281/zenodo.13993826`.

D. Archiving

1. Archival procedures

The complete data set is available as Supporting Information. The complete data set, including raw data, is also archived in Dryad: `https://doi.org/10.5061/dryad.44j0zpcnt`. The code and the complete R project used to estimate species abundance are archived in Zenodo: `https://doi.org/10.5281/zenodo.13993826`.

2. Redundant archival sites

The complete data set is available as Supporting Information, on Dryad `https://doi.org/10.5061/dryad.44j0zpcnt` and within the complete R project on Zenodo `https://doi.org/10.5281/zenodo.13993826`.

E. Publications and results

The presented estimates of species abundance and body mass are used in:
Moisan, L., D. Gravel, G. Gauthier, P. Legagneux and J. Bêty, 2025. Arctic migrations shape

global meta-communities: contrasting insights from species occurrence, abundance and biomass. *Global Ecology And Biogeography*. `https://doi.org/10.1111/geb.70074`

Previous estimates of species abundance on the southern plain of Bylot Island were presented by Legagneux et al. (2012), however, the temporal series presented here is longer, the methods are refined and the taxonomic resolution is higher.

F. History of data set usage

1.Data request history

None

2.Data set update history

The first version of the dataset was archived on Dryad prior to submission to a peer-reviewed journal on November 19, 2024. Following comments from anonymous reviewers, a revised version of the dataset was archived on June 23 2025. Minor details were corrected on August 11 2025 following a final review by the subject-matter editor, the authors and the editorial staff. On August 12, 2025, the hyperlink to the complete R project, which previously redirected to version 1 of the repository (`https://zenodo.org/records/13993827`), was updated to point to the general software repository containing the up-to-date version (`https://doi.org/10.5281/zenodo.13993826`).

3.Review history

Following comments from two anonymous reviewers in April 2025, the methods, dataset, and MetadataS1 document were updated accordingly. Minor details were corrected on August 11 2025 following a final review by the subject-matter editor, the authors and the editorial staff.

4.Questions and comments from secondary users

None

Acknowledgements

We are deeply appreciative of the extensive data gathered over the decades by generations of students and researchers during their fieldwork at the Bylot Island research station, which made this project possible. Our gratitude also extends to the Center of Northern Studies for providing research facilities, as well as to the Polar Continental Shelf Program and Sirmilik National Park (Parks Canada) for their logistical support throughout the years. Additionally, we would like to express our special thanks to the Mittimatalik community and the Mittimatalik Hunters and Trappers Organization for their ongoing support of ecological monitoring on Bylot Island and for permitting us to conduct research on their land.

ARTICLE 3

LES MIGRATIONS ARCTIQUES FAÇONNENT DES MÉTA-COMMUNAUTÉS GLOBALES: PERSPECTIVES CONTRASTÉES SELON L'OCCURRENCE, L'ABONDANCE ET LA BIOMASSE DES ESPÈCES

Global Ecology and Biogeography

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

Louis Moisan | Dominique Gravel | Gilles Gauthier | Pierre Legagneux | Joël Bêty

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3.1 Contexte et publication associée

L'article « *Arctic Migrations Shape Global Meta-Communities: Contrasting Insights From Species Occurrence, Abundance and Biomass* » a été publié en juin 2025 dans la revue *Global Ecology and Biogeography*. L'éditeur associé était Dr Kevin Healy, et deux réviseurs anonymes ont évalué l'article. Dans cet article, nous avons quantifié pour la première fois les connexions migratoires maintenues par les espèces migratrices d'une communauté avec l'abondance et la biomasse des espèces. Cela a permis de montrer que l'occurrence, l'abondance et la biomasse des espèces fournissent de l'information complémentaire sur la structure des réseaux de migration des communautés, autant sur le rôle structural des espèces au sein du réseau de migration qu'au niveau des propriétés émergentes du réseau. Cette observation suggère que différents types de perturbations environnementales (ex. introduction de contaminants, exposition à un nouveau pathogène ou changements d'abondance) se propagent différemment au sein des réseaux de migration des communautés. L'idée d'intégrer l'abondance et la biomasse au sein du réseau de migration de l'île Bylot provient de discussions entre moi-même, Joël Bêty et Dominique Gravel. En tant qu'auteur principal, j'ai écrit la première version du manuscrit et les codes nécessaires afin de préparer, analyser et visualiser les données. Joël Bêty, Pierre Legagneux et Gilles Gauthier ont assuré la continuité à long terme du suivi sur l'île Bylot. Tous les auteurs ont révisé en profondeur le manuscrit. J'ai échangé avec Joël et Dominique tout au long de la réalisation de cet article. Le contenu de l'article a été présenté à la Conférence de la Société Internationale de Biogéographie, tenu en janvier 2024 en République tchèque, sous la forme d'une présentation orale.

3.2 Résumé de l'article en français

Objectif: Les espèces migratrices saisonnières génèrent d'importants mouvements d'organismes et de biomasse entre des sites de reproduction et de non-reproduction distants. Cependant, notre compréhension de la manière dont ces espèces génèrent des réseaux de communautés interconnectées (métacommunautés) reste limitée. Les liens migratoires entre communautés peuvent être mesurés de différentes façons (par exemple, l'occurrence, l'abondance ou la biomasse des espèces), chacune apportant une information complémentaire en modulant l'importance relative des espèces dans les métacommunautés. Nous visons à étudier dans quelle mesure quantifier les liens migratoires via l'abondance ou la biomasse des espèces peut révéler des structures alternatives à celle générée par l'occurrence au sein d'une métacommunauté reliant une communauté arctique à des aires d'hivernage éloignées.

Localisation: Nous utilisons comme cas d'étude la communauté de vertébrés de l'île Bylot (Haut-Arctique, Nunavut, Canada), ainsi que les écorégions d'Amérique du Nord et du Sud, d'Europe et d'Afrique.

Période étudiée: Actuelle.

Principaux taxons étudiés: Oiseaux (30 espèces) et mammifères (5 espèces) terrestres arctiques.

Méthodes: Nous considérons d'abord l'occurrence des espèces sur les zones de non-reproduction (hivernage) pour définir les liens migratoires au sein de la métacommunauté. Ensuite, nous mesurons le nombre d'individus et la quantité de biomasse circulant le long de ces liens. Enfin, nous comparons la structure de la métacommunauté dans chaque scénario en utilisant une représentation par réseau.

Résultats: Les patrons d'occurrence, d'abondance et de biomasse révèlent que les écoré-

gions tempérées de l'Amérique du Sud et surtout de l'Amérique du Nord, maintiennent de fortes connexions écologiques avec la communauté de vertébrés de l'île Bylot. Cependant, le rôle structurel des espèces dans le réseau peut varier considérablement selon la métrique utilisée pour déterminer le poids relatif des liens migratoires (c'est-à-dire des anomalies topologiques contrastées). L'utilisation de l'abondance ou de la biomasse des espèces conduit à une division plus fine du réseau en modules, comparé à l'utilisation de l'occurrence.

Conclusions principales: Nous montrons que l'utilisation de différentes métriques pour mesurer les liens migratoires révèle des caractéristiques structurelles uniques et complémentaires des métacommunautés. Ces résultats contribuent à évaluer la vulnérabilité des communautés face aux perturbations survenant dans des environnements éloignés, mais connectés via la migration.

Les sections suivantes sont celles de l'article **publié**.

3.3 Title

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

3.4 Authors

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3.5 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.

3.6 Introduction

The seasonal movements of migratory species couple distant communities and ecosystems of the globe (Polis et al., 1997; Jefferies, 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, 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, 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*a*) 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.

3.7 Methods

3.7.1 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; **Figure 3.7**). This area is characterised by a relatively simple terrestrial vertebrate community (30 bird species and 5 mammal species, Moisan et al. 2025*a*; see **Table 3.2**). 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*b*; Moisan et al., 2025*a*). 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*b*; Moisan et al., 2025*a*). 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*a*).

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*a*). 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*a*).

3.7.2 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 of different species (**Figure 3.1**). 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.

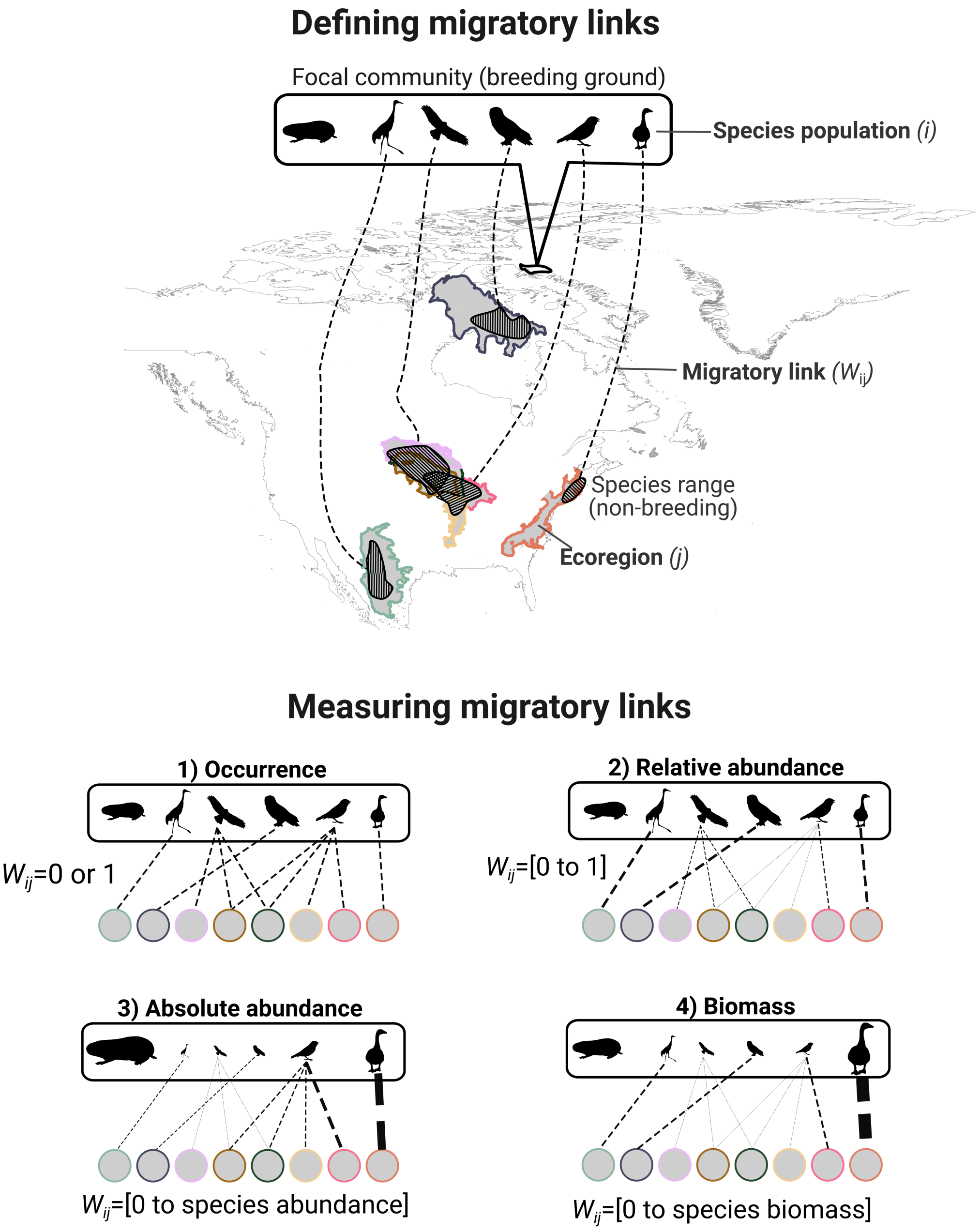

Defining migratory links
Focal community (breeding ground)
Species population (i)
Migratory link (W_{ij})
Species range (non-breeding)
Ecoregion (j)
Measuring migratory links
1) Occurrence
W_{ij}=0 or 1
2) Relative abundance
W_{ij}=[0 to 1]
3) Absolute abundance
W_{ij}=[0 to species abundance]
4) Biomass
W_{ij}=[0 to species biomass]

Figure 3.1 – **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.

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 3.1**). 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 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; 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 Supplementary material *Non-breeding range*). 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.

3.7.3 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 3.1**). 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 Supplementary material *Non-breeding relative abundance*). 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 3.2** 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 Supplementary material *Non-breeding relative abundance*). 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 3.1**).

Thirdly, we measured migratory links based on the number of individuals (i.e., absolute abundance of the species in the study area; **Figure 3.1**). 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 3.2**) 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 3.1**). 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 3.2**) 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 Supplementary material *Sensitivity analysis – methods of calculating relative abundance*).

3.7.4 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 Supplementary material *Link diversity Shannon diversity index*). 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 Supplementary material *Module assignment algorithm Infomap*). 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 Supplementary material *Similarity module composition Normalized Mutual Information*) implemented in the *com-*

pare 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*a*), spatial data processing ('sf' 1.0–16: Pebesma 2018; 'raster' 3.6–26: Hijmans 2018), 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.

3.8 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 3.2**) 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 3.2**). When snow geese are excluded, migratory species represent 16% of the total abundance and 39% of the biomass (see **Figure 3.9**). 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 3.8**). The Shannon diversity index is 1.37 when migratory links are calculated using species abundance and 0.51 when using species biomass.

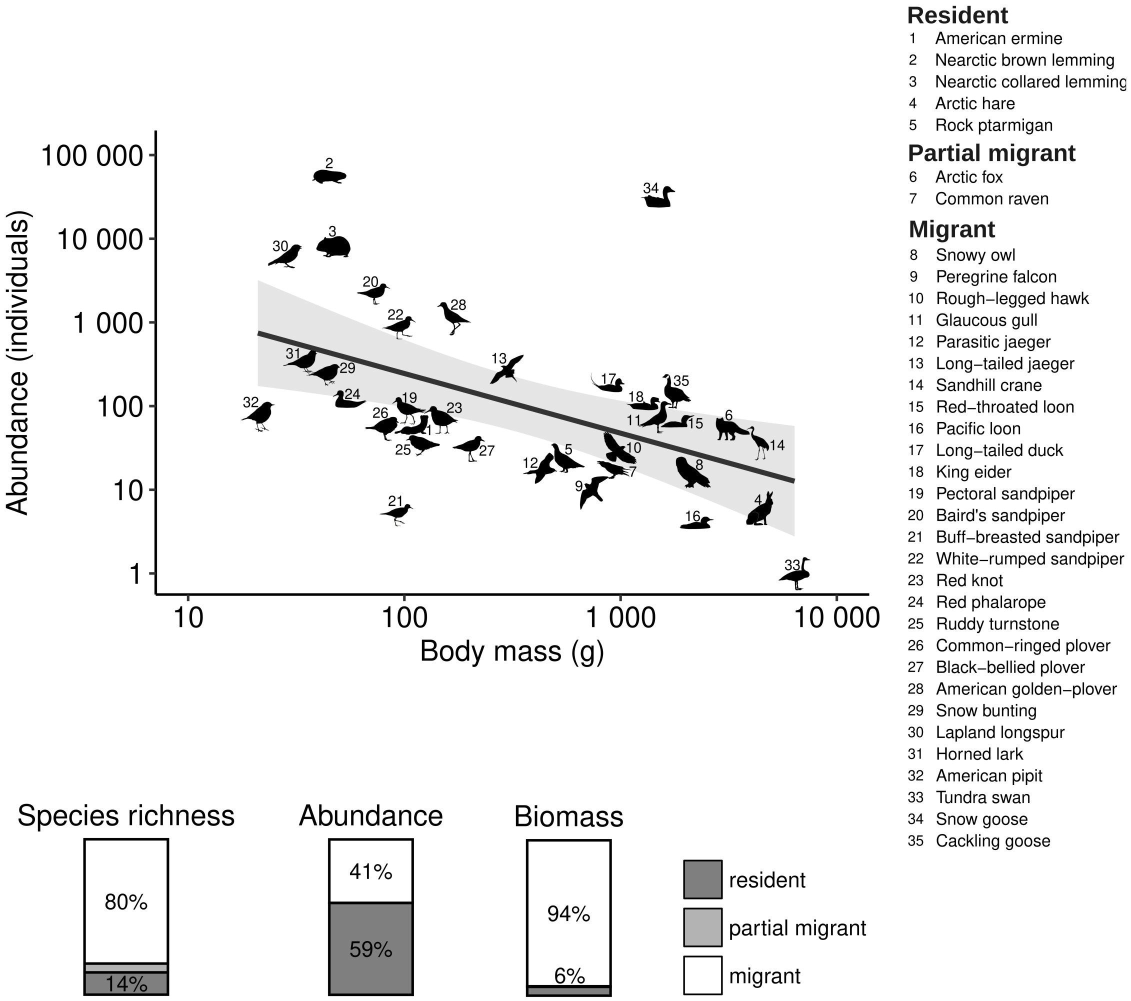
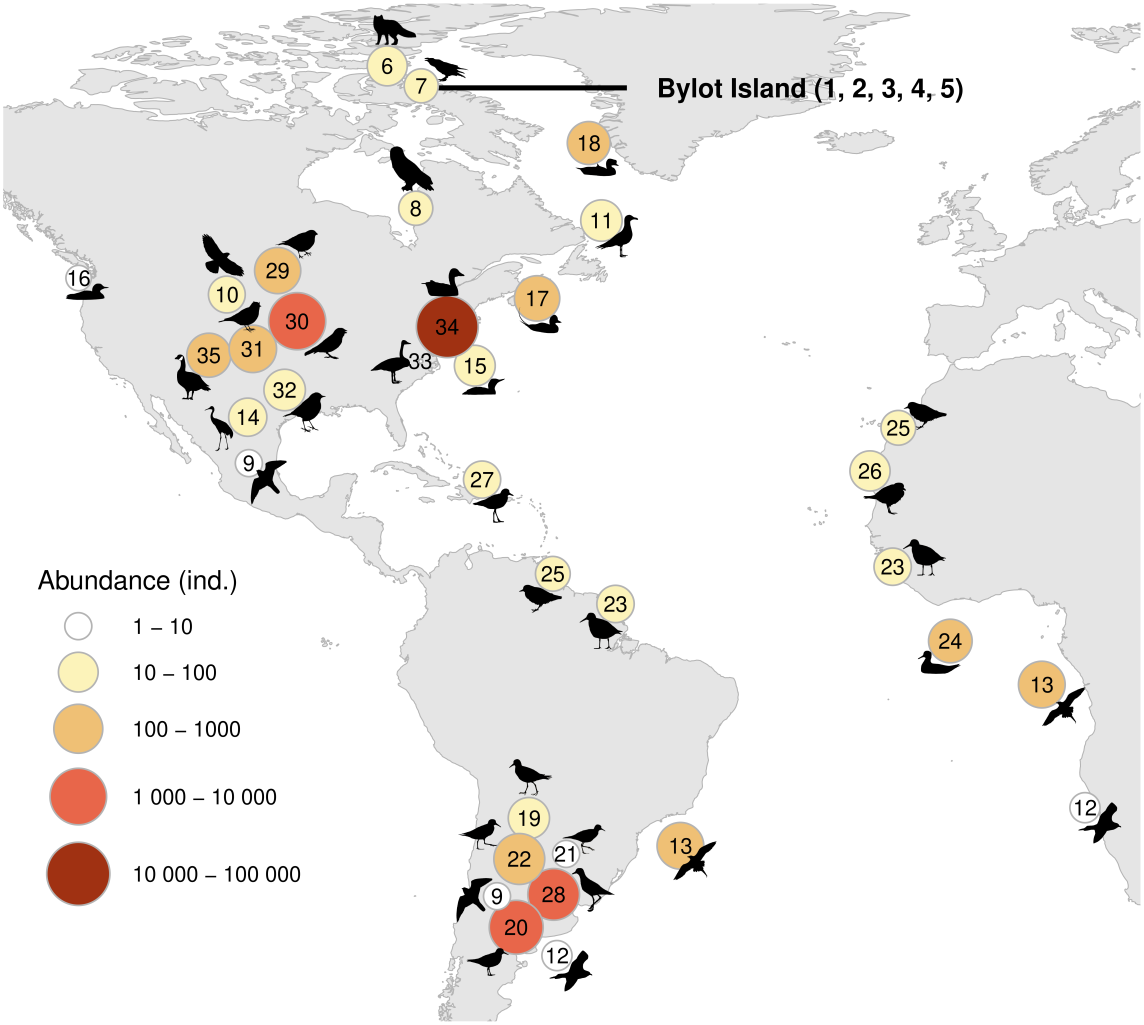


Figure 3.2 – **Top**: Relationship between mean species abundance and mean adult body mass in the Bylot Island vertebrate community during the breeding period (May–August). Juveniles are considered in the abundance and body mass of lemmings. Both variables are depicted on logarithmic scales, and each 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.

Migratory species breeding on Bylot Island migrate across a broad latitudinal and longitudinal range, but most individuals are found in relatively restricted areas (**Figure 3.3**). 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).



Resident
1 American ermine
2 Nearctic brown lemming
3 Nearctic collared lemming
4 Arctic hare
5 Rock ptarmigan

Partial migrant
6 Arctic fox
7 Common raven

Migrant
8 Snowy owl
9 Peregrine falcon
10 Rough–legged hawk
11 Glaucous gull
12 Parasitic jaeger
13 Long–tailed jaeger
14 Sandhill crane
15 Red–throated loon
16 Pacific loon
17 Long–tailed duck
18 King eider
19 Pectoral sandpiper
20 Baird's sandpiper
21 Buff–breasted sandpiper
22 White–rumped sandpiper
23 Red knot
24 Red phalarope
25 Ruddy turnstone
26 Common–ringed plover
27 Black–bellied plover
28 American golden–plover
29 Snow bunting
30 Lapland longspur
31 Horned lark
32 American pipit
33 Tundra swan
34 Snow goose
35 Cackling goose

Figure 3.3 – 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).

Ecoregions in temperate North and South America host the highest species richness and biomass of migratory vertebrates originating from Bylot Island (**Figure 3.4**). 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 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 3.10**). 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.

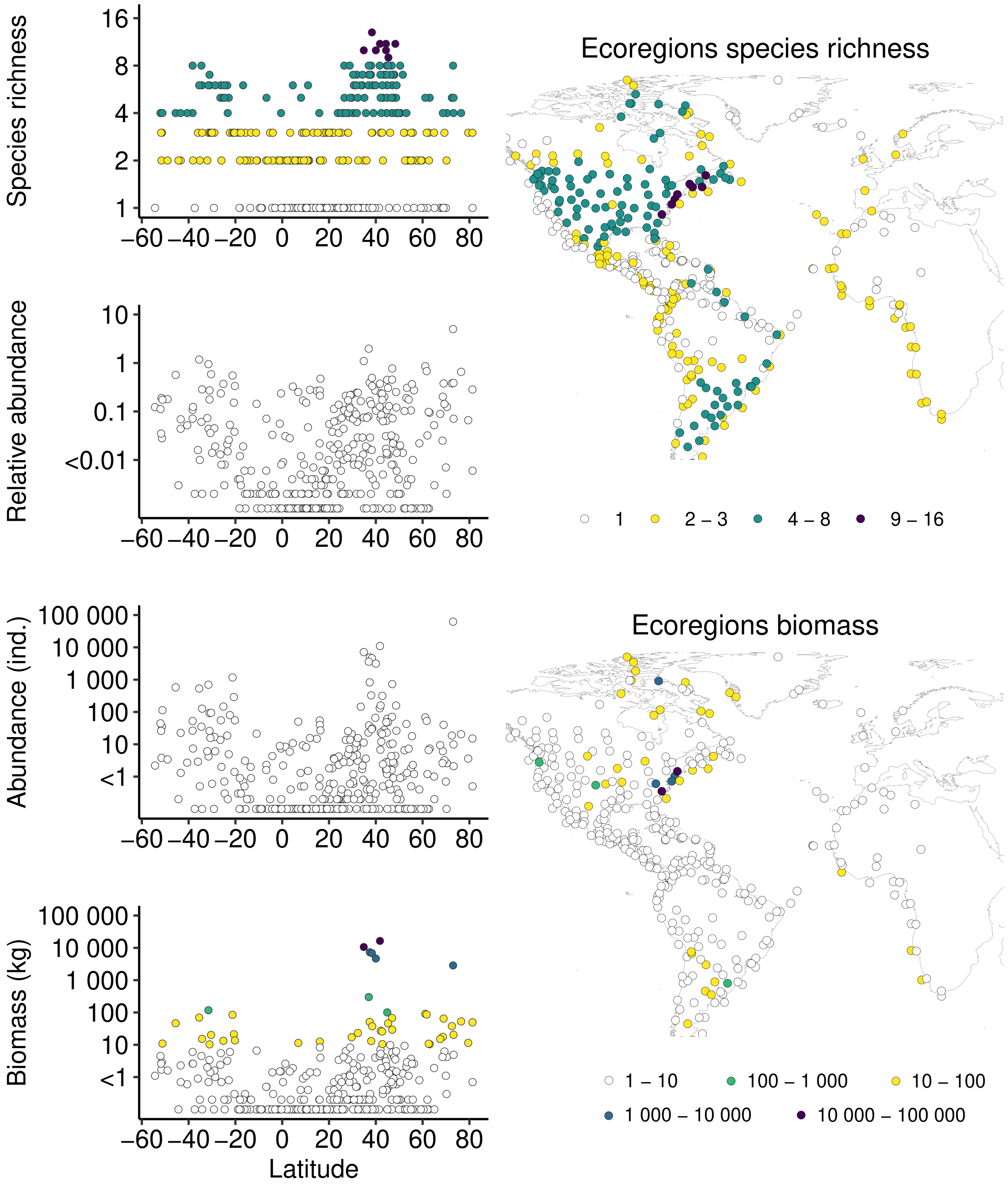
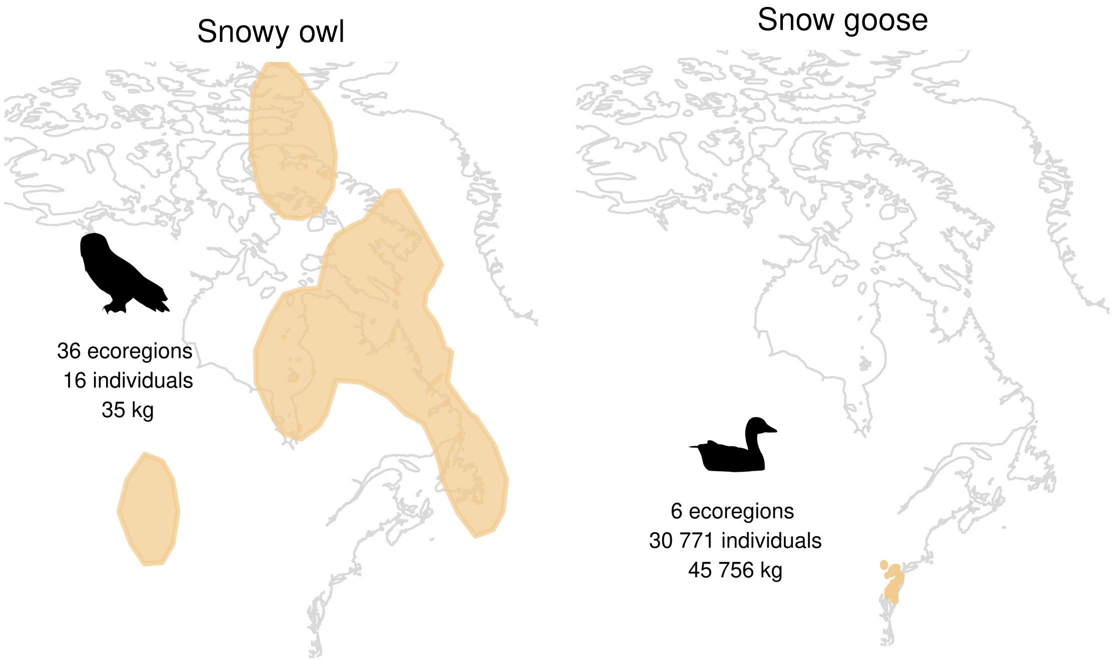

Species richness
16
8
4
2
1
Relative abundance
10
1
0.1
<0.01
Abundance (ind.)
100 000
10 000
1 000
100
10
<1
Biomass (kg)
100 000
10 000
1 000
100
10
<1
−60 −40 −20 0 20 40 60 80
Latitude
Ecoregions species richness
○ 1
● 2 – 3
● 4 – 8
● 9 – 16
Ecoregions biomass
○ 1 – 10
● 100 – 1 000
● 10 – 100
● 1 000 – 10 000
● 10 000 – 100 000

Figure 3.4 – **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.

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 3.5**). 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.


Snowy owl

Snow goose

Figure 3.5 – 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.

We observe some differences in the structure of the Bylot Island migration network depending on how migratory links are measured (**Table 3.1**). 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 3.5**). The composition of modules based on species occurrence shows the greatest contrast of all pairwise comparisons among scenarios (**Table 3.1**, **Figure 3.11**).

Table 3.1 – 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	17	0.85	0.7
Biomass	1.96	15	0.88	0.69

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 3.6**). When distributing migratory flow proportionally to relative abundance, we observe a division of these modules into more geographically constrained modules (**Figure 3.6**).

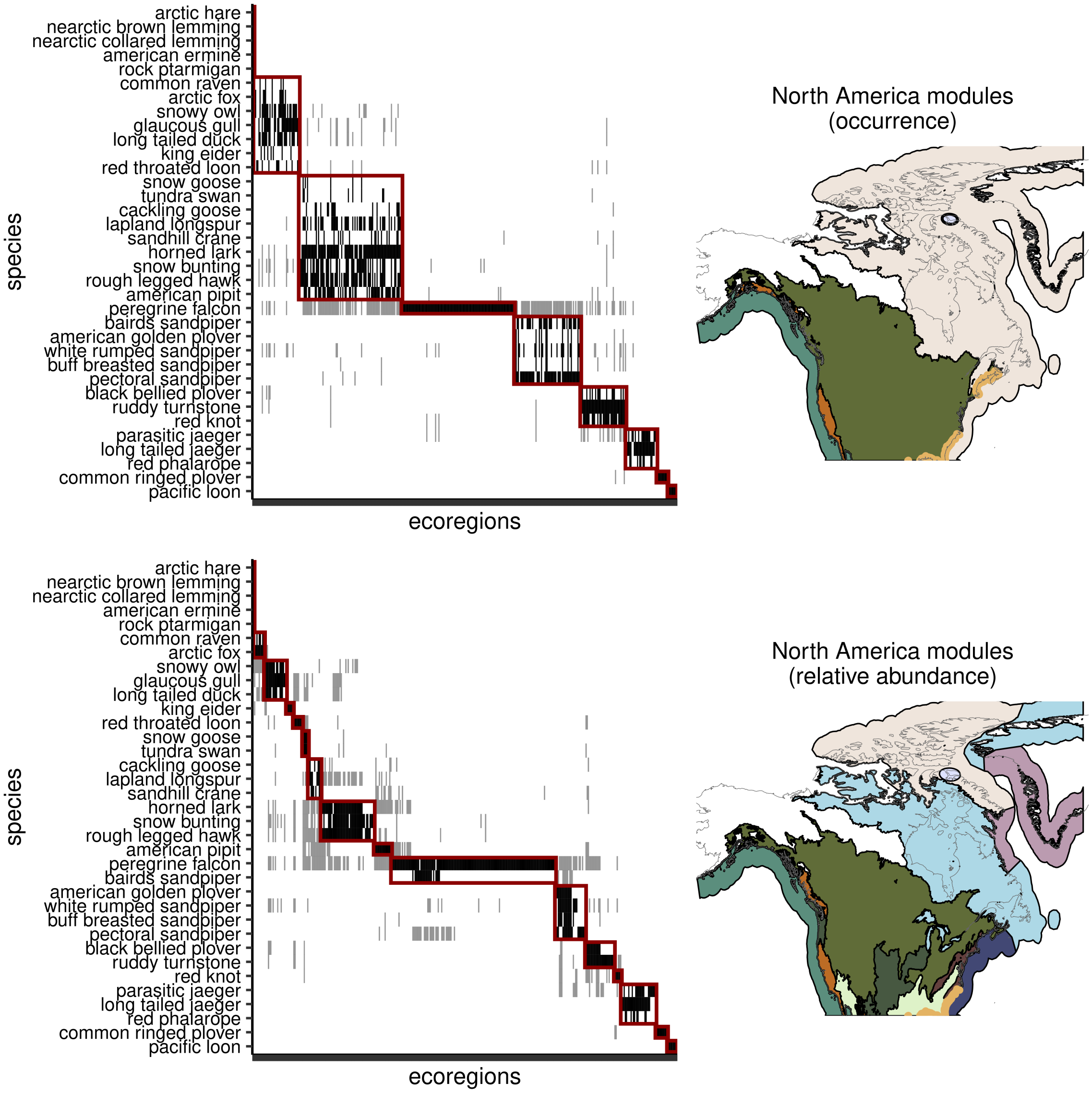


Figure 3.6 – **Left**: Matrix representation of the modules of species and ecoregions within the Bylot Island migration network when migratory flows are measured with species occurrence (top) and species relative abundance (bottom). In each matrix, species and ecoregions are ordered by modules (red boxes), 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.

3.9 Discussion

Understanding the structure of migratory links within meta-communities is crucial for assessing the vulnerability of local communities to distant perturbations. Our results show that measuring migratory links using species occurrence, abundance 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*b*; Moisan et al., 2025*a*) 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.

3.10 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.

3.11 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.

3.12 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.

3.13 Conflicts of interest

The authors declare no conflicts of interest.

3.14 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`.

3.15 Supplementary information

3.15.1 Bylot Island community composition

We used the same criteria outlined in Moisan et al. (2023) to identify the species comprising the Bylot Island vertebrate community. Specifically, we excluded occasional visitors based on the following criteria: i) species without confirmed breeding records at the study site, ii) species observed exclusively in a single year, and iii) species that primarily breed and forage in nearby marine or coastal habitats. Although recent breeding pairs of red foxes (*Vulpes vulpes*) have been documented (Lai et al., 2022), we excluded this species due to the uncertainty surrounding its population establishment on the island and the rarity of sightings.

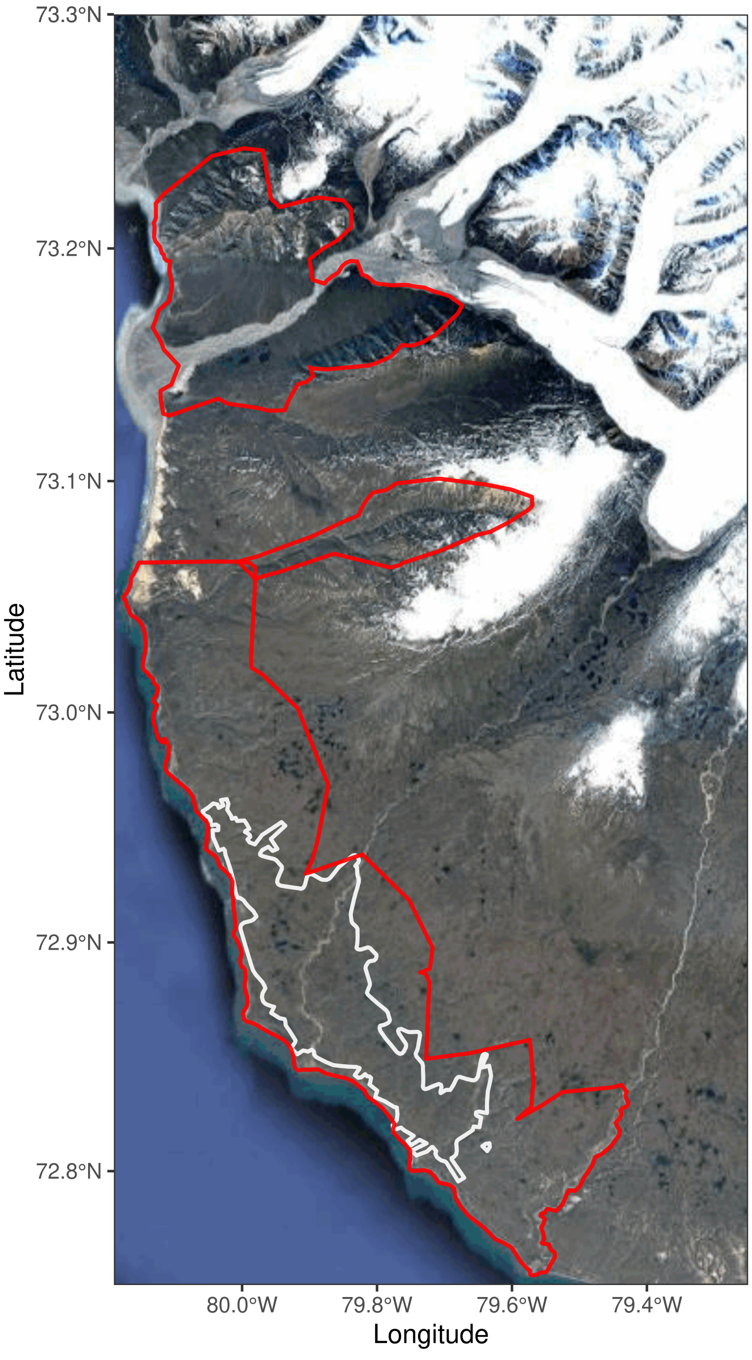


Figure 3.7 – Map of the 389 km^2 study area located on the south plain of Bylot Island, Nunavut Canada (red) and the average perimeter of the snow goose colony (74 km^2; white). The study area consists of a mix of habitats, including mesic tundra (64%), upland plateaus of sedimentary rock (20%), low-lying wetlands (10%; Ouellet unpublished data) and water bodies such as lakes and rivers (6%; see Moisan et al. 2025*a* for more details).

Table 3.2 – Composition of the vertebrate community of Bylot Island. Body mass, absolute abundance and biomass (product of body mass and absolute abundance) represents the mean values of adult individuals of each species, except for lemmings which also considers juveniles. The 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. Data were extracted from (Moisan et al., 2025*a*).

Species (en)	**Species**	**Migratory status**	**Body mass (g)**	**Abundance (ind.)**	**Biomass (kg)**
Pacific loon	*Gavia pacifica*	migrant	2251	4	9
Red-throated loon	*Gavia stellata*	migrant	1486	64	95.1
King eider	*Somateria spectabilis*	migrant	1617	106	171
Long-tailed duck	*Clangula hyemalis*	migrant	871	191	166
Cackling goose	*Branta hutchinsii*	migrant	2812	138	388
Snow goose	*Anser caerulescens*	migrant	1487	30771	45756
Tundra swan	*Cygnus columbianus*	migrant	6378	1	6.4
Rough-legged hawk	*Buteo lagopus*	migrant	950	27	25.6
Peregrine falcon	*Falco peregrinus*	migrant	760	10	7.6
Snowy owl	*Bubo scandiacus*	migrant	2169	16	34.7
Rock ptarmigan	*Lagopus muta*	resident	535	24	12.8
Sandhill crane	*Antigone canadensis*	migrant	4296	36	155
American golden-plover	*Pluvialis dominica*	migrant	170	1102	187
Black-bellied plover	*Pluvialis squatarola*	migrant	210	29	6.1
Common-ringed plover	*Charadrius hiaticula*	migrant	86	55	4.7
Ruddy turnstone	*Arenaria interpres*	migrant	136	36	4.9
Red knot	*Calidris canutus*	migrant	145	59	8.6
Pectoral sandpiper	*Calidris melanotos*	migrant	88	71	6.2
Baird's sandpiper	*Calidris bairdii*	migrant	72	2170	156
White-rumped sandpiper	*Calidris fuscicollis*	migrant	94	878	82.5
Buff-breasted sandpiper	*Calidris subruficollis*	migrant	92	5	0.46
Red phalarope	*Phalaropus fulicarius*	migrant	56	124	6.9
Glaucous gull	*Larus hyperboreus*	migrant	1500	73	110
Long-tailed jaeger	*Stercorarius longicaudus*	migrant	298	272	81.1
Parasitic jaeger	*Stercorarius parasiticus*	migrant	461	17	7.8
Common raven	*Corvus corax*	partial migrant	928	16	14.8
Horned lark	*Eremophila alpestris*	migrant	33	331	10.9
American pipit	*Anthus rubescens*	migrant	21	74	1.6
Lapland longspur	*Calcarius lapponicus*	migrant	28	6080	170
Snow bunting	*Plectrophenax nivalis*	migrant	42	236	9.9
Nearctic brown lemming	*Lemmus trimucronatus*	resident	45	54043	2432
Nearctic collared lemming	*Dicrostonyx groenlandicus*	resident	47	8128	382
Arctic hare	*Lepus arcticus*	resident	4405	6	26.4
American ermine	*Mustela richardsonii*	resident	134	40	5.4
Arctic fox	*Vulpes lagopus*	partial migrant	3300	53	175

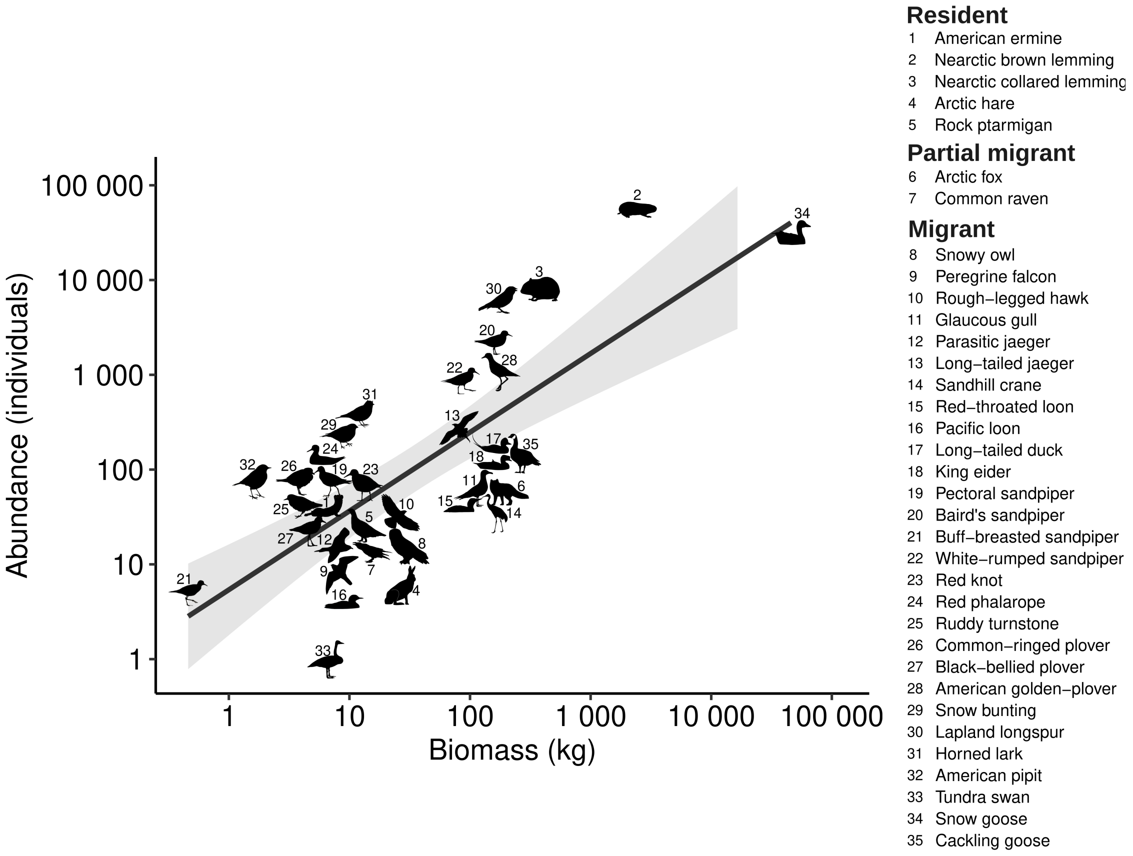


Figure 3.8 – Relationship between mean species biomass and mean species abundance in the Bylot Island vertebrate community during the breeding period (May to August). Juveniles are considered only in the calculations of the abundance and biomass of lemmings. Both variables are depicted on logarithmic scales and each icon and label represents different species. Labels represent each species' rank in absolute abundance within the Bylot Island community.

3.15.2 Spatial distribution of species

3.15.2.1 Non-breeding range

We used the methods presented in Moisan et al. (2023) (see their supplementary material for more details) to define the non-breeding range of each migratory and partially migratory species from Bylot Island. First, when available, we prioritized locations of individuals equipped with tracking devices (satellite or geolocators) during the non-breeding period to extract a 95 % kernel polygon (n= 6 species). Alternatively, we used species non-breeding range maps (BirdLife International and Handbook of the Birds of the World, 2019; Fink et al., 2021) refined based on the non-breeding distribution of Eastern Canadian Arctic populations or subspecies (n= 28 species). Note that here we used the 2020 version (Fink et al., 2021) of eBird non-breeding range maps instead of the 2019 version (Fink et al., 2020*b*) as presented in Moisan et al. (2023). The more recent eBird range maps represent the only difference with the analysis presented in Moisan et al. (2023). The refinement of species range maps consists in assigning major flyway(s) of the globe (Wetlands International, 2022) and non-breeding habitat type(s) (terrestrial, coastal and marine) to each species based on the literature. We then cropped the extent of the species non-breeding range on the map based on the delimitation of the flyway(s) used by individuals present on Bylot Island. By doing so, we were able to remove areas of the species non-breeding range, and thus ecoregions where individuals from Bylot Island have a quasi-null probability of occurrence. For instance, we removed the Pacific and central part of a species non-breeding range if individuals from the Eastern Canadian Arctic population are known to migrate solely to the Atlantic part of the non-breeding range. For partial migrants (Arctic fox and common raven), we used a buffer zone centered on the study area with a width determine from movements described in the literature (Lai et al., 2017) or their foraging ecology (Temple, 1974).

3.15.2.2 Non-breeding relative abundance

We used various methods to estimate the relative abundance of species in ecoregions during the non-breeding period, selecting the approach based on the quality of the available data (see **Table 3.3**). We prioritized using the locations of individuals equipped with tracking devices (n = 6 species) to derive a probability density function (kernel) across the species non-breeding range. The kernel was used as an index of abundance of Bylot Island-related individuals over the defined non-breeding range of a species. We therefore assumed that the distribution of individual locations reflected the distribution of individuals at population level.

Alternatively, we used abundance distribution model based on citizen observations (i.e., eBird) with a resolution of 3 km x 3 km cell (n= 16 species; Sullivan et al. 2009; Fink et al. 2021). Here, observations are used as an index of abundance. For each species, we summed the index of abundance of every cell found within the defined species range to as an index of total abundance. Then, we extracted index of abundance per ecoregion by summing the index of abundance of each cell found in the overlapping area of the ecoregion and the species range. We transformed the index of abundance per ecoregions to proportion (i.e. relative abundance) by dividing by the index of total abundance across the defined species range. By using abundance distribution model, we assumed that distribution of individuals from the study site reflects the distribution of individuals at the species level in the defined species range. An assumption that might not be far-fetched, since the non-breeding range have been refined to represent Eastern Arctic populations or subspecies.

In cases where no individual was equipped with tracking devices or abundance distribution models were not available, we assumed that individuals were distributed proportionally to the area of overlap between the ecoregion and the defined non-breeding range (n= 8 species).

Table 3.3 – Summary of the methods used to define relative abundance of partially migratory and strictly migratory species in ecoregions during the non-breeding period. For resident species, we assumed that all individuals remain within the study area throughout the non-breeding period. The scientific names of species can be found in **Table 3.2**

Species	**Most accurate data available on non-breeding relative abundance**	**Method used to determine relative abundance in ecoregion**
Common raven Arctic fox Red phalarope Long-tailed duck Pacific loon Red-throated loon Parasitic jaeger Glaucous gull	None	We assumed that the relative abundance of a species in an ecoregion is proportional to the overlap between the ecoregion boundaries and the species defined range. For example, if an ecoregion overlaps with 25% of the species range, we assumed that 25% of individuals from Bylot are present in that ecoregion during the non-breeding period.
Cackling goose Tundra swan Lapland longspur Horned lark Snow bunting American pipit Black-bellied plover Ruddy turnstone Red knot White-rumped sandpiper Buff-breasted sandpiper Baird’s sandpiper Pectoral sandpiper Sandhill crane Peregrine falcon Rough-legged hawk	Abundance distribution model (eBird observations)	We determined species relative abundance in a given ecoregion as the proportion of the index of total abundance found within the area of overlap between the defined species range and the ecoregion boundaries. We used abundance distribution models based on eBird observations (3km x 3km). This method thus considers the area of the ecoregion within the defined species range and the species index of abundance within this area.
Snow goose American golden-plover Common-ringed plover King eider Long-tailed jaeger Snowy owl	Kernel density function (tracking of individuals)	We determined species relative abundance in an ecoregion using a kernel density function based on the locations of tracked individuals during the non-breeding period. This method takes into account both the area of the ecoregion within the species defined range and the species index of abundance within that area.

3.15.2.3 Sensitivity analysis – methods of calculating relative abundance

Calculations of relative abundance based on either kernel density function (for tracked birds) or abundance distribution models (eBird observations) relied on several assumptions (see Section 2.2). We determined the sensitivity of our results to these assumptions by calculating relative abundance for all species with the simplest method, which considers that individuals are distributed proportionally to the area of overlap between the ecoregion and the defined non-breeding range. Comparison of the two approaches is presented in **Table 3.4**.

Table 3.4 – Emerging structural properties of the Bylot Island migration networks when migratory flows are measured by species occurrence, relative or absolute abundance, and biomass. For each scenario, we report results based on two approaches to estimate relative abundance: i) Using tracking of individuals (n= 6 species), eBird index of abundance distribution models (n=16 species) and abundance proportional to the overlap between the ecoregion boundaries and the species defined range (n= 8 species) and ii) for all species that relative abundance was proportional to the overlap between the ecoregion boundaries and the species defined range (n=30 species). The similarity in module composition is assess with the Normalized Mutual Information (NMI) index, with the partition based on species occurrence as a reference. Values range from 0 (completely different partitions) to 1 (the composition of a partition can be predicted perfectly from another one; see methods for details).

Scenario of migratory flow	**Approaches to estimate relative abundance**	**Edge diversity**	**Number of modules**	**Similarity module composition (species)**	**Similarity module composition (ecoregions)**
Occurrence	NA	7.04	9	1	1
Relative abundance	Tracking, eBird and proportional to area	5.24	16	0.83	0.67
Relative abundance	Proportional to area	5.66	14	0.85	0.7
Absolute abundance	Tracking, eBird and proportional to area	2	17	0.85	0.7
Absolute abundance	Proportional to area	2.13	17	0.85	0.74
Biomass	Tracking, eBird and proportional to area	1.96	15	0.88	0.69
Biomass	Proportional to area	2	15	0.87	0.71

3.15.3 Network analysis methods

3.15.3.1 Link diversity (Shannon diversity index)

Where E is the set of edges (i.e., links) in the network and $pWij$ represents the proportion of the total weight of migratory links for a species that travels between species i and ecoregion *j*. For instance, in a scenario where migratory links are measured with biomass, if $pWij$ = 0.5, this indicates that 50 % of the biomass of species i is found in ecoregion *j* during the non-breeding period.

$$H' = -\sum_{(i,j)\in E} p_{W_{ij}} \ln\left(p_{W_{ij}}\right) \tag{3.1}$$

3.15.3.2 Module assignment algorithm (Infomap)

The *Infomap* algorithm models the flow of information in a network through iterative random walks (see Farage et al. 2021 for a comprehensive method description). It starts with an initial random classification of nodes into modules and evaluates the amount of information required to describe the flow in the network. The amount of information necessary to describe network flow is quantified using the map equation, which considers entry and exit costs when the walker goes from nodes of different modules. By assigning densely connected clusters of nodes as modules, the algorithm reduces the amount of information necessary to model the flow because the random walker tends to spend more time within these clusters, resulting in fewer transitions between modules. Conversely, grouping weakly connected nodes together in a module increases the amount of information required to describe network flow due to more frequent transitions between modules. Therefore, at each iteration, the algorithm adjusts the module composition to minimize the map equation, ultimately finding the classification of nodes into modules that requires the least amount of information to represent the flow in the network.

3.15.3.3 Similarity module composition (Normalized Mutual Information)

$$NMI(A,B) = \frac{-2\sum_{a=1}^{C_A}\sum_{b=1}^{C_B} N_{ab}\log\left(N_{ab}n \div N_a N_b\right)}{\sum_{a=1}^{C_A} N_a \log\left(N_a \div n\right) + \sum_{b=1}^{C_B} N_b \log\left(N_b \div n\right)}$$

Where NMI(A;B) represents the NMI value between partition A and B, CA and CB represent the number of modules in partition A and B, Na is the number of nodes in module a of partition A and Nb is the number of nodes in module b of partition B, Nab represents the number of nodes shared between the a^{th} module of partition A and the b^{th} module of partition B, finally n represents the number of nodes in each partition (Beckett, 2016).

3.15.4 Sensitivity analysis – Excluding snow geese

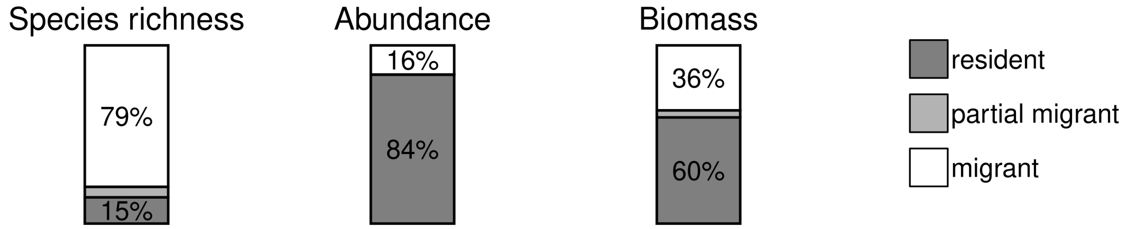


Figure 3.9 – Proportion of species richness, mean abundance and mean biomass represented by migrants, partial migrants and resident species of the Bylot Island vertebrate community, when snow geese are excluded. Partial migrants represent 6 % of the species richness, 0.09 % of the abundance and 4 % of the biomass.

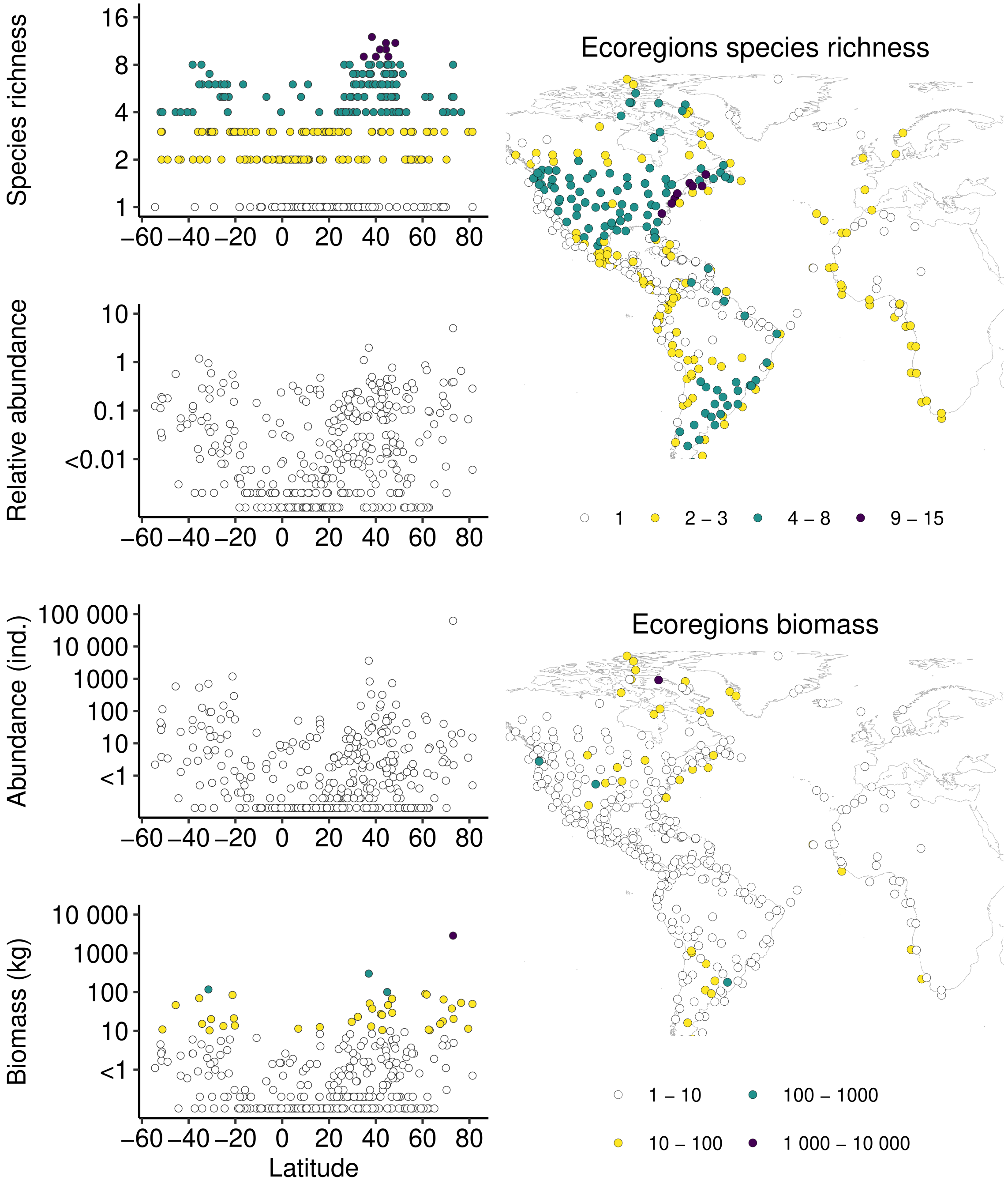

Species richness
16
8
4
2
1
−60 −40 −20 0 20 40 60 80
Relative abundance
10
1
0.1
<0.01
−60 −40 −20 0 20 40 60 80
Abundance (ind.)
100 000
10 000
1000
100
10
<1
−60 −40 −20 0 20 40 60 80
Biomass (kg)
10 000
1000
100
10
<1
−60 −40 −20 0 20 40 60 80
Latitude
Ecoregions species richness
1
2 – 3
4 – 8
9 – 15
Ecoregions biomass
1 – 10
100 – 1000
10 – 100
1 000 – 10 000

Figure 3.10 – **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, when snow geese are excluded. Each point represents a distinct ecoregion, with the latitude taken from its centroid. All y-axes are presented on a logarithmic scale. We use colors to visualize logarithmic classes of species richness and biomass, enabling clear cartographic visualization 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, when snow geese are excluded. The coordinates of ecoregion represent the ecoregion centroid.

Table 3.5 – Emerging structural properties of the Bylot Island migration networks when snow geese are excluded or not in the network and when migratory links are measured by species occurrence, relative or absolute abundance, and biomass. The similarity in modules composition is assess with the Normalized Mutual Information (NMI) index, with the partition based on species occurrence (including the snow goose) as a reference. Values range from 0 (completely different partitions) to 1 (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	1.00	1.00
Occurrence (snow goose excluded)	7.04	10	0.98	0.99
Relative abundance	5.24	16	0.84	0.67
Relative abundance (snow goose excluded)	5.24	16	0.84	0.67
Absolute abundance	2.00	17	0.85	0.70
Absolute abundance (snow goose excluded)	1.35	16	0.86	0.70
Biomass	1.95	15	0.89	0.69
Biomass (snow goose excluded)	2.75	15	0.89	0.69

3.15.5 Modules composition (NMI)

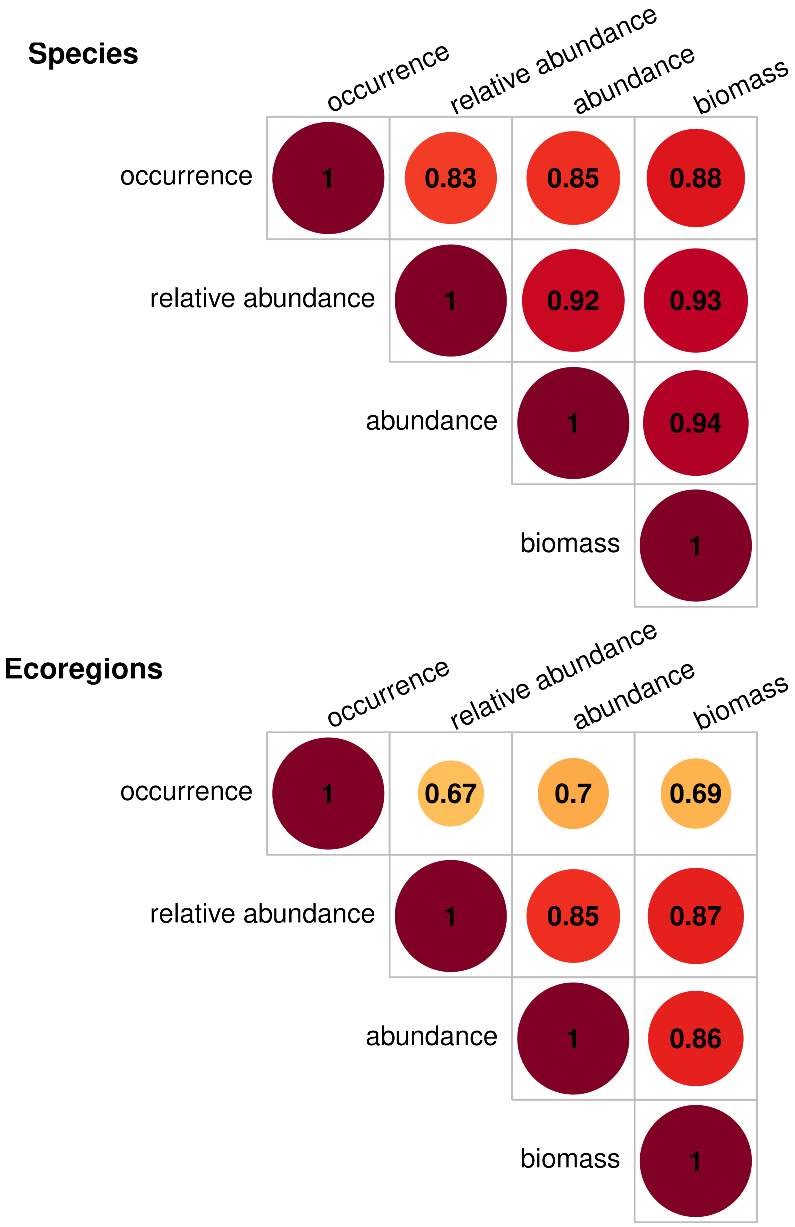


Figure 3.11 – Matrix of Normalized Mutual Information index (NMI) representing the similarity in module composition under the different scenarios of migratory links (occurrence, relative abundance, absolute abundance and biomass). Values range from 0 (completely different partitions) to 1 (the composition of a partition a can be predicted perfectly from another one). We compare the classification of species and ecoregions into modules separately to facilitate interpretation, despite that modules are composed of both species and ecoregions.

ARTICLE 4

LES MIGRATIONS SAISONNIÈRES EXPOSENT UNE COMMUNAUTÉ DE VERTÉBRÉS ARCTIQUES À DE MULTIPLES FACTEURS DE CHANGEMENT DE LA BIODIVERSITÉ

RESEARCH ARTICLE

Seasonal migrations expose an Arctic vertebrate community to multiple drivers of biodiversity change

Louis Moisan | **Silke Bauer** | **Dominique Gravel** | **Gilles Gauthier** | **Pierre Legagneux** | **Joël Bêty**

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4.1 Contexte et publication associée

L'article « *Seasonal migrations expose an Arctic vertebrate community to multiple drivers of biodiversity change* » est en préparation pour soumission dans la revue *Ecography*. Dans cet article, nous avons utilisé les aires de non-reproduction des espèces afin de caractériser pour la première fois l'exposition à des perturbations environnementales d'une communauté via les destinations migratoires des espèces. Nous avons montré que malgré une faible exposition apparente aux pressions anthropiques directes, les communautés de vertébrés terrestres arctiques peuvent tout de même être exposées à diverses perturbations environnementales via les sites de non-reproduction des espèces migratrices. L'approche conceptuelle initiale a été développée conjointement entre moi-même, Joël Bêty et Dominique Gravel. Ensuite, j'ai collaboré étroitement avec Silke Bauer dans le cadre d'une visite de recherche de trois mois à l'Institut Fédéral Suisse de Recherches sur la Forêt, la Neige et le Paysage (WSL) afin d'écrire la majorité du manuscrit et réaliser la visualisation des résultats. Joël Bêty, Pierre Legagneux et Gilles Gauthier ont assuré la continuité à long terme du suivi sur l'île Bylot. Silke Bauer, Joël Bêty, Gilles Gauthier et Dominique Gravel ont révisé le manuscrit. En tant que premier auteur, j'ai écrit la première version du manuscrit et les codes nécessaires afin de préparer, analyser et visualiser les données. J'ai également révisé le manuscrit et intégré les modifications proposées par les autres auteurs. J'ai échangé avec Joël et Dominique tout au long de la réalisation de cet article.

4.2 Résumé de l'article en français

Les espèces migratrices modifient périodiquement la structure et la dynamique des communautés locales par leur arrivée et leur départ saisonniers. Comme les espèces migratrices des communautés locales dépendent d'environnements distants et distincts pour compléter leur cycle annuel, elles peuvent être exposées à des facteurs de changement de la biodiversité contrastés selon les saisons. Même des espèces présentant des traits fonctionnels et des rôles similaires au sein d'une communauté peuvent être soumises à des pressions environnementales différentes si elles migrent vers des régions distinctes. Ainsi, évaluer de manière exhaustive l'exposition aux facteurs de changement de la biodiversité dans les communautés locales comprenant des espèces migratrices nécessite de prendre en compte la distribution spatiale annuelle des espèces. Ici, nous caractérisons l'exposition à diverses perturbations environnementales durant l'hiver boréal pour l'ensemble des vertébrés d'une communauté de la toundra arctique. Nous évaluons également si les espèces migratrices ayant des traits fonctionnels similaires tendent à migrer vers les mêmes aires d'hivernage et sont exposées à des types et intensités similaires de perturbations environnementales. Nous nous concentrons sur la communauté de vertébrés de l'île Bylot, pour laquelle les aires d'hivernage de toutes les espèces migratrices ont été délimitées, et nous utilisons ces aires pour évaluer l'exposition relative des espèces aux perturbations liées aux changements climatiques, à l'utilisation humaine et à la pollution. Nous observons que la communauté de l'île Bylot est principalement exposée à des perturbations environnementales se produisant dans les environnements tempérés terrestres, en particulier des changements climatiques et des perturbations liées aux activités agricoles (p. ex., cultures, et application de pesticides et d'engrais). Les espèces migratrices au sein des groupes fonctionnels montrent généralement une concordance intermédiaire à élevée dans leur exposition aux perturbations environnementales, malgré un chevauchement spatial relativement faible durant la période de non-reproduction. Nos résultats suggèrent que les communautés toundriques pourraient être particulièrement vulnérables aux activités agricoles et au réchauffement climatique se produisant dans les régions tempérées, en particulier dans l'hémisphère Nord. Nous proposons que l'adaptation des espèces migratrices de la toundra aux milieux ouverts pourrait les prédisposer à l'exposition aux activités agricoles pendant la période de non-reproduction.

4.3 Title

Seasonal migrations expose an Arctic vertebrate community to multiple drivers of biodiversity change

4.4 Authors

Louis Moisan, Silke Bauer, Dominique Gravel, Gilles Gauthier and Joël Bêty

4.5 Abstract

Migratory species periodically shift the structure and dynamics of local communities through their seasonal arrival and departure. Because migratory species from local communities depend on distant and distinct environments to complete their annual cycle, they may be exposed to contrasting drivers of biodiversity change across seasons. Even migratory species with similar functional traits and roles within a community may be subjected to contrasting environmental pressures if they migrate to distinct areas. Therefore, comprehensively assessing the exposure to drivers of biodiversity change in local communities comprising migratory species requires accounting for the full annual spatial distributions of species. Here, we characterize the exposure to diverse environmental perturbations for all vertebrates of an Arctic tundra community during the boreal winter. In addition, we examine whether migratory species with similar functional traits tend to migrate to the same non-breeding destinations and are exposed to similar types and intensity of environmental perturbations. We focus on the vertebrate community of Bylot Island, for which the non-breeding ranges of all migratory species have been

delineated, and use these ranges to assess species relative exposure to climate change, human use, and pollution-related perturbations. We observe that the High Arctic community of Bylot Island is primarily exposed to environmental perturbations occurring in terrestrial temperate environments, especially climate changes and perturbations related to agricultural activity (e.g., cropland, and pesticide and fertilizer application). Migratory species within functional groups generally show intermediate to high concordance in their exposure to environmental perturbations, despite relatively low spatial overlap during the non-breeding period. Our findings suggest that Arctic tundra communities may be especially vulnerable to agricultural activity and climate warming taking place in temperate regions, especially in the Northern Hemisphere. We propose that the adaptation of tundra migratory species to open habitats could predispose them to exposure to agricultural activities during the non-breeding period.

4.6 Introduction

Seasonal migratory species occur in ecosystems worldwide and play a crucial role in shaping the structure and dynamics of local communities by consuming or being consumed by other species (Holdo et al., 2011; Bauer and Hoye, 2014; Furey et al., 2018). As migrants undertake regular, bidirectional, and seasonally synchronized movements between distinct and spatially distant breeding and non-breeding grounds (Webster et al., 2002; Mueller and Fagan, 2008; Winger et al., 2019), the fate of their populations depends on environmental conditions at all of these sites. Depending on the migrant traits and position in a local food web, changes in their populations influence interactions with other species and may cascade through the entire food web (Jefferies, 2000). Therefore, a perturbation of environmental conditions in one location can generate cascading effects in distant, but connected communities via migration (i.e, **spatial cascades**; García-Callejas et al. 2019). For instance, agricultural subsidies on the non-breeding ground of migratory herbivores can lead to population increase, causing cascading effects on distant breeding grounds (Jefferies, 2000; Dulude-de Broin et al., 2023). Thus, the structure and dynamics of any local food web that comprises migratory species can be influenced by perturbations occurring in other parts of the globe (Winemiller and Jepsen, 1998; Jefferies, 2004).

The Anthropocene is characterized by profound and diverse environmental perturbations that fundamentally alter habitats and ecosystems, driving biodiversity change globally (Jaureguiberry et al., 2022). Importantly, these perturbations are neither spatially nor temporally uniform (Bowler et al., 2020; Mu et al., 2022) and can affect species in different ways, with varying magnitudes and directions (Pacifici et al., 2017). Unlike resident species, the mobile lifestyle of migratory species expose them to a variety of potentially contrasting anthropogenic drivers of biodiversity changes when they use seasonally changing sites (Small-Lorenz et al., 2013; Seavy et al., 2025). For instance, forest passerines migrating to Central America generally experience strong human use on their non-breeding grounds, while facing pronounced warming on their breeding grounds (La Sorte et al., 2017). At the community level, migratory species can experience similar or contrasting drivers during parts of their annual cycle, depending on their migratory strategies (Lisovski et al., 2021). We could expect species with similar functional traits to migrate to similar non-breeding grounds due to shared dietary and habitat preferences, and thus to be exposed to similar environmental perturbations. In such cases, some ecological functions of communities may be particularly vulnerable to distant environmental perturbations. Moreover, when multiple species from a given community are affected by perturbations, trophic interactions can either amplify or buffer the resulting effects on the food web (Beauchesne et al., 2021). Thus, characterizing exposure to anthropogenic drivers of biodiversity changes across the full annual cycle of locally co-occurring migratory species is a critical step in assessing food web vulnerability to spatial cascades.

We aim here to i) characterize the exposure to global anthropogenic drivers of biodiversity changes during the boreal winter for all species of an Arctic food web, which includes a high proportion of migratory species that co-occur only during the boreal summer, and ii) assess whether functionally similar migratory species, based on migratory status, habitat, and diet, tend to converge in their migratory destinations and are exposed to similar global anthropogenic drivers of biodiversity changes. We focus on the stationary non-breeding period or the wintering period (hereafter referred to as the **non-breeding period**) and exclude the breeding and non-breeding migratory periods. During the breeding period all species co-occur and are exposed to the same environmental perturbations, and data for the migratory period are too scarce to cover the entire food web. We examine how diversity in migratory strategies may generate heterogeneity in exposure to distant environmental perturbations. Moreover, we assess how incorporating species abundance and biomass can modulate community exposure to various environmental perturbations. We define **species exposure to anthropogenic drivers of biodiversity change** as the average speed or intensity at which abiotic and biotic conditions are altered within a species range, caused directly or indirectly by human activities. Identifying species and migratory destinations experiencing strong environmental perturbations can improve our ability to detect those at higher risk of triggering spatial cascades. This is especially true if multiple species, a large number of individuals or a substantial proportion of the local food web biomass migrate to the same destinations. Moreover, we describe exposure to drivers of biodiversity change within functional groups since they can support distinct functions and energy pathways within local communities.

Modeling the spread of spatial cascades via migration is a long-term goal, and characterizing species exposure to distant environmental perturbations within a community represents a first essential step toward achieving this goal, which is the focus of the current study. Perturbation of environmental conditions can influence individuals directly (e.g., through thermoregulation) or indirectly by modifying the abundance of interacting species or the structure of the habitat (Simmons et al., 2021). Thus modelling spatial cascades via migration would also require quantifying species-specific responses to anthropogenic drivers of biodiversity change, which depend not only on exposure but also on species sensitivity (Dickinson et al., 2014), as well as the strength of trophic interactions. Although species responses to individual stressors can often be assessed, current knowledge remains insufficient to support a comprehensive, quantitative analysis of species responses to multiple drivers, including their potential interactions and the resulting consequences at the food-web level. We therefore limit our scope to the characterization and comparison of exposure levels among species within the community, as a necessary first step toward modelling the spread of spatial cascades mediated by migration.

We focus on the vertebrate tundra food web of Bylot Island, located in the Eastern Canadian High-Arctic (**Figure 4.1**). The relatively low species richness, but high proportion of migratory species in terrestrial Arctic ecosystems (Gauthier et al., 2011; Legagneux et al., 2012; Somveille et al., 2013) represents a great opportunity to identify migratory destinations of all species in this food web and the severity of global anthropogenic drivers of biodiversity change occurring in these destinations. The present study builds on previous contributions made on Bylot Island which aimed to define the non-breeding range of all species in the food web (Moisan et al., 2023) and quantify the number of individuals and the amount of biomass that transit between Bylot Island and distant ecoregions (Moisan et al., 2025*b*). We first use species non-breeding range to characterize seasonal exposure to climate change (6 variables), human use (4 variables), and pollution (4 variables) in both terrestrial and marine environments used by all species of the tundra food web. Next, using estimated species abundance and biomass, we calculated, for each environmental perturbation, the proportion of individuals and total biomass in the community exposed to varying levels of exposure. Finally, to test if functionally similar species converge on their migratory destinations and are exposed to similar or contrasting drivers of biodiversity changes, we measure spatial overlap and concordance in the exposure to drivers among species within functional groups.

4.7 Methods

4.7.1 Bylot Island food web

The study area (~400 km^2) is located on the south plain of Bylot Island in the Eastern Canadian High-Arctic (73°N, 80°W; **Figure 4.7**). The study area has been under conservation protection since 1965, when it was first designated as part of a Migratory Bird Sanctuary, and even more so since 1999, when it became part of Sirmilik National Park (Gauthier et al., 2024*b*). The landscape represents a mixture of mesic tundra (~65 %), dryer upland plateaus (~20 %) and lowland wetlands (~10 %; Moisan et al. 2025*a*). The core vertebrate community of Bylot Island is composed of 30 bird and 5 mammal species, when considering only species occurring in the study area for most of the breeding season and regularly observed throughout the years (Moisan et al. 2023; Gauthier et al. 2024*b*; **Figure 4.1** and **Table 4.2**). The main predator is the Arctic fox (*Vulpes lagopus*) and the main herbivore is the snow goose (*Anser caerulescens*); large mammalian herbivores have been largely absent from the area for at least several decades (Gauthier et al., 2024*b*). Most of the vertebrates (80 %; 28 bird species) are migratory, the Arctic fox and the common raven (*Corvus corax*) are considered partial migrants since some individuals stay in the area year-round and others travel to surrounding environments during the non-breeding period (Lai et al., 2017). The American ermine (*Mustela richardsonii*), nearctic brown (*Lemmus trimucronatus*) and collared lemmings (*Dicrostonyx groenlandicus*), Arctic hare (*Lepus arcticus*) and rock ptarmigan (*Lagopus muta*) are considered residents (Gauthier et al., 2011).

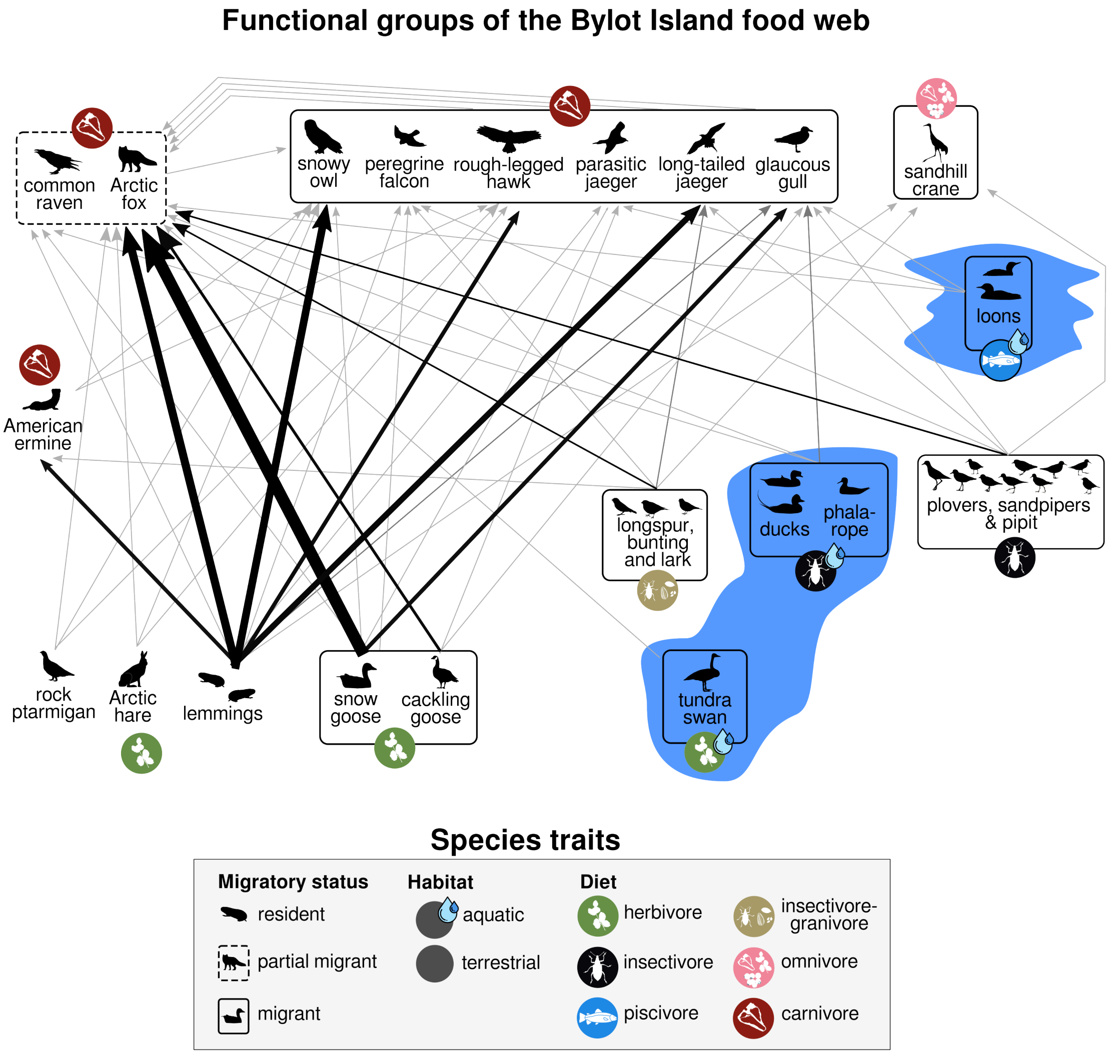
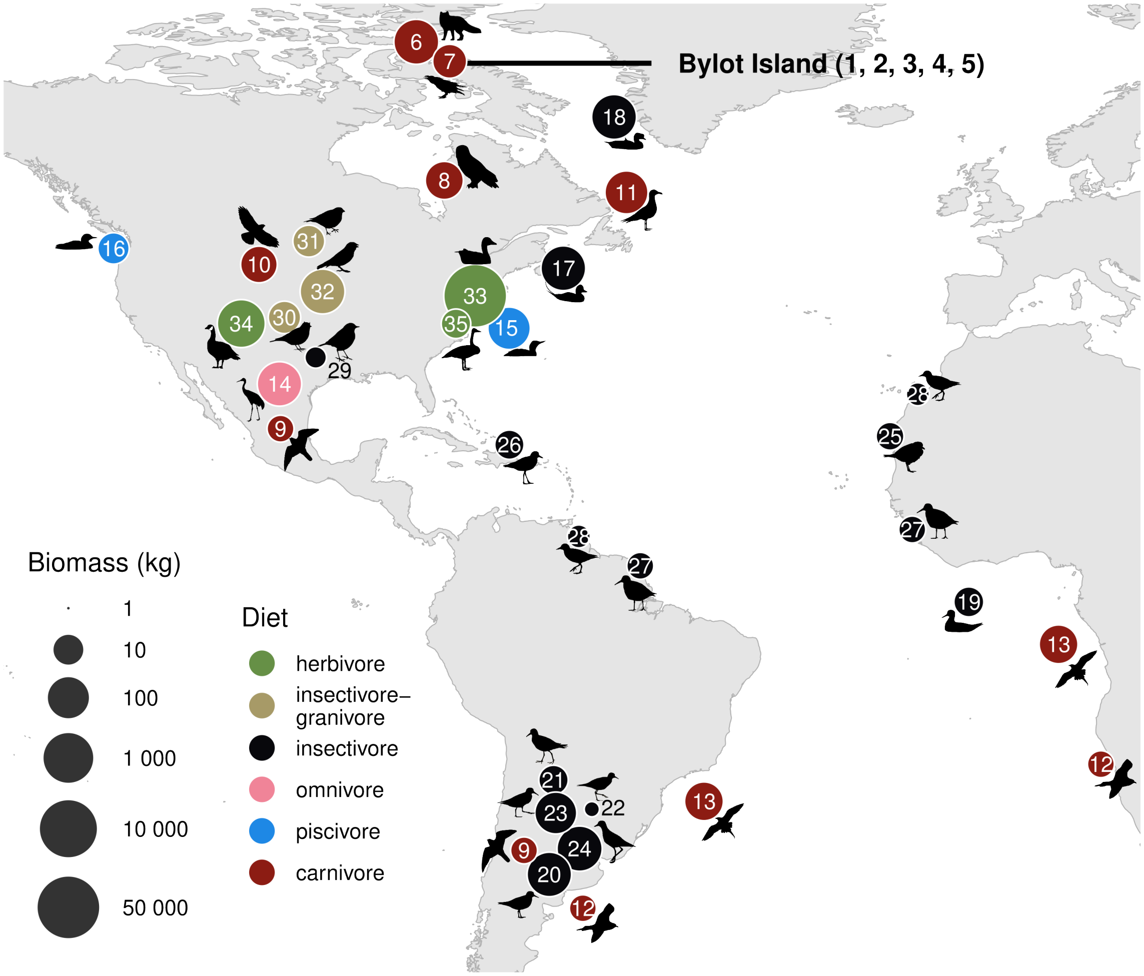


Figure 4.1 – Simplified schematic representation of the Bylot Island terrestrial vertebrate food web, with functional groups defined by unique combinations of species migratory status, breeding habitat, and diet. Trophic interactions are shown as arrows: black arrows indicate major trophic flows, while gray arrows represent weaker or less important flows within the food web in terms of energy. Some rare interactions have been omitted to simplify the figure. Trophic interactions and energy flows were derived from diet matrices (Legagneux et al., 2012) and previous food web representations (Gauthier et al., 2011; Moisan et al., 2023). Here, the term insectivore refers to species that feed on relatively small arthropods, including insects, spiders, and other small non-insect terrestrial or freshwater arthropods. A complete list of species associated with each functional group is provided in **Table 4.2**. Species icons were extracted from Moisan et al. (2025*a*) and diet icons were extracted from Saulnier-Talbot et al. (2024) with the authors' permission. The fish icon was created by Lars Meiertoberens and extracted from the Noun project (`https://thenounproject.com/icon/trout-4720251/`). The water drop icon was created by Freepik - Flaticon.

4.7.2 Species non-breeding range, abundance and biomass

The non-breeding ranges of migratory and partially migratory species were previously determined either from the locations of individuals equipped with tracking devices (n = 6 species; Gilchrist et al. 2004; Therrien et al. 2014; Robillard et al. 2018; Léandri-Breton et al. 2019; LeTourneux et al. 2021; Seyer et al. 2021; Lamarre et al. 2021) or from species range maps refined using existing literature on the annual distribution of individuals breeding in the Eastern Canadian Arctic (BirdLife International and Handbook of the Birds of the World 2019; Fink et al. 2021; Moisan et al. 2023; **Figure 4.2**). The mean species abundance and biomass on Bylot Island were estimated from nesting density, capture–marking of individuals, or field observations (for detailed information on data collection and estimation methods, see Moisan et al. 2025*a*). Estimates represent adults that spend a substantial portion of time (i.e., several weeks) in the Bylot Island study area during the breeding period (June to August), but exclude individuals present only for a few days during migration. Estimates for lemmings also include juveniles.



Resident

1 American ermine
2 Nearctic brown lemming
3 Nearctic collared lemming
4 Arctic hare
5 Rock ptarmigan

Partial migrant

6 Arctic fox
7 Common raven

Migrant

8 Snowy owl
9 Peregrine falcon
10 Rough−legged hawk
11 Glaucous gull
12 Parasitic jaeger
13 Long−tailed jaeger
14 Sandhill crane
15 Red−throated loon
16 Pacific loon
17 Long−tailed duck
18 King eider
19 Red phalarope
20 Baird's sandpiper
21 Pectoral sandpiper
22 Buff−breasted sandpiper
23 White−rumped sandpiper
24 American golden−plover
25 Common−ringed plove
26 Black−bellied plover
27 Red knot
28 Ruddy turnstone
29 American pipit
30 Horned lark
31 Snow bunting
32 Lapland longspur
33 Snow goose
34 Cackling goose
35 Tundra swan

Figure 4.2 – Distribution during the non-breeding period of the Bylot Island resident, partially migratory and migratory species, illustrated by the centroid of each species non-breeding range (except for lemmings, which also reproduce during winter). Circle sizes are proportional to the log of the biomass of adults in the Bylot Island food web. Two centroids are used for species with non-continuous range, for instance when individuals can migrate to different continents (i.e., long-tailed jaeger, parasitic jaeger, peregrine falcon, ruddy turnstone and red knot). The figure was adapted from Moisan et al. (2025*b*), but labels were modified to order species by functional groups and facilitate interpretation of the exposure to environmental perturbations. Here, the term insectivore refers to species that feed on relatively small arthropods, including insects, spiders, and other small non-insect terrestrial or freshwater arthropods. Species icons were extracted from Moisan et al. (2025*b*).

4.7.3 Drivers of biodiversity changes

We selected environmental perturbations representing, as much as possible, the contemporary exposure to global drivers of biodiversity changes (**Table 4.1**). We note that these drivers can act directly on individuals, for example by causing mortality (e.g., entanglement in fishing gear) or reducing fecundity (e.g., fecundity-reducing pollutants), or indirectly by modulating thermoregulation costs, altering habitat structure, or changing the abundance of interacting species (Simmons et al., 2021), which in turn can affect survival or fecundity in subsequent seasons through carry-over effects. Drivers of biodiversity changes were measured in both terrestrial and marine environments. We used the terrestrial ecoregions of the world defined by Olson et al. (2001), including large continental bodies of water, to delineate terrestrial areas, and classified all remaining grid cells as marine. Climate change perturbations were quantified as temporal trends, estimated from the slope of linear regressions, representing the rate of change in abiotic conditions within species ranges. Human use and pollution perturbations are calculated as fixed or annual values and represent the intensity of perturbations to abiotic and/or biotic conditions within species range. We did not include perturbations related to alien species, as Billerman et al. (2025) did not highlight alien species as a main driver of biodiversity change affecting the selected species. We acknowledge the direct exploitation (i.e., hunting) of several of the selected migratory species (e.g., snow goose, cackling goose, long-tailed duck, king eider and sandhill crane). Estimating hunting pressure on the non-breeding grounds of these species is however beyond the scope of this paper.

Climate change

We used monthly near-surface air temperature over land at a 0.5°resolution (CRU TS4.08 ;University of East Anglia Climatic Research Unit et al. 2024) and sea surface temperature at a 1°resolution (HadISST1; Rayner et al. 2003) to extract annual average temperatures during the non-breeding period (i.e., December to April). We acknowledge that the timing of the non-breeding period varies among species, but the defined period is conservative and should encompass the core of the non-breeding period for all species. We followed the approach described in Bowler et al. (2020) and performed a linear regression of the annual average temperature from 1950 to 2023 (land) or 2024 (ocean) to estimate the warming trend. The slope of the regression in each grid cell was used to represent the temperature trend, irrespective of statistical significance. We used the average temperature between December and April to represent trends during the non-breeding period. We selected 1950 as the starting point to represent the start of the Anthropocene (as performed in Bowler et al. (2020); see Waters et al. 2016). Only positive temperature trends were retained to represent climate warming, with negative trends set to zero. We applied a similar approach to sea ice concentration (i.e., the proportion of each grid cell covered by sea ice), snow cover duration, and ocean pH; however, for these variables, only negative trends were retained to represent declines, and positive trends were set to zero. Negative trends were then converted to positive values to facilitate interpretation, such that larger values indicate more rapid change. Specifically, we used sea ice concentration between December to May from 1950 to 2024 at a 1°resolution (Rayner et al., 2003), annual snow cover duration between September 1st to August 31st from 2001 to 2024 at a resolution of 500 meters (Dietz et al., 2015), and, for ocean acidification, the mean annual seawater pH trend from 1985 to 2023 at 1°resolution, provided by the Chau et al. (2023). We did not consider trends in aridity or precipitation because their ecological interpretation differs substantially between temperate/arctic regions and subtropical/tropical regions.

Human use

We selected cropland, pasture and urban cover derived from satellite imagery and empirical data as human use perturbations. In the marine environment we selected fishing efforts to represent human use. The proportion of pasture and cropland cover in ~10 km grid cell for 2015 was extracted from Mehrabi et al. (2025). Pastures are defined as “land in permanent meadows and pastures, land that is used permanently (5 years or more) to grow herbaceous forage crops through cultivation or naturally (wild prairie or grazing land)” and cropland as “land used for cultivation of crops, including areas under arable land and permanent crops”. We used urban cover, which encompasses “any roofed structure erected above ground for any use”, at a 1 km resolution for 2020 (Pesaresi et al., 2024). We selected these land cover data sets to capture continuous variation in grid cell values (proportion of cover, 0 to 1) rather than using binary values (0 or 1) derived from a threshold. Fishing activities can act directly on individuals by causing mortality through entanglement, drowning or ingestion of dangerous objects such as a fishhook, but could also have indirect effects by modulating the abundance of prey or competing species (Tasker et al., 2000). Therefore, we retained a general index of fishing effort, expressed as the number of hours fished per square kilometer, regardless of the fishing gear used. Fishing effort was estimated from vessel locations tracked by the Automatic Identification System (AIS; Kroodsma et al. 2018) and obtained from Global Fishing Watch (2025) at a 0.1°spatial resolution.

Pollution

We focused on fertilizer and pesticide use as indicators of pollution in both terrestrial and coastal environments, as global-scale datasets are available (Tilman et al., 2001; Potter et al., 2010; Maggi et al., 2019; Tang et al., 2021). In the terrestrial environment, we used the mean fertilizer application rate between 1994 and 2001 (expressed in kg of Nitrogen per hectare of cropland) at a resolution of 0.5°(Potter et al., 2010). We used the pesticide (i.e., herbicides, insecticides, and fungicides) pollution risk index (Tang et al., 2021), which accounts for both the concentration of components (Maggi et al., 2019) and their ecotoxicities (e.g., see Nagai 2016). We used pesticide and fertilizer runoff for coastal areas, modeled as diffusive plumes in coastal areas at the mouths of large rivers, for the period 2007 to 2010 at a 1 km resolution (Halpern et al., 2015).

Table 4.1 – List of the selected anthropogenic drivers of biodiversity change and associated environmental perturbations with their corresponding realm, resolution, year or period and reference.

Realm	**Anthropogenic driver of biodiversity change**	**Environmental perturbation**	**Resolution**	**Year(s)**	**Reference**
Terrestrial	Climate change	Temperature increase	0.5°	1950 to 2024	University of East Anglia Climatic Research Unit et al. 2024
		Snow cover duration decrease	500m	2001 to 2024	Dietz et al. 2015
	Human use	Cropland cover	3km	2015	Mehrabi et al. 2025
		Pasture cover	3km	2015	Mehrabi et al. 2025
		Urban cover	1km	2020	Pesaresi et al. 2024
	Pollution	Pesticide pollution risk	10km	(2015)	Tang et al. 2021
		Nitrogen fertilizer application	0.5°	(1994-2001)	Potter et al. 2010
Marine	Climate change	Sea temperature increase	1°	1950 to 2024	Rayner et al. 2003
		Sea acidification	1°	1985-2023	Chau et al. 2023
		Sea ice concentration decrease	1°	1950 to 2024	Rayner et al. 2003
	Human use	Fishing effort	0.1°	(2024)	Kroodsma et al. 2018
	Pollution	Pesticide coastal pollution	1km	(2007-2010)	Halpern et al. 2015
		Fertilizer coastal pollution	1km	(2007-2010)	Halpern et al. 2015

4.7.4 Analysis

We quantify specific exposure to each environmental perturbation as the average value across the non-breeding range (grid cell resolution varies depending on the perturbation). Missing grid cell values were set to 0 for each environmental perturbation to prevent cases where only a small number of grid cells with data overlap with a species' range, which could otherwise inflate the estimated average exposure across the entire range. Environmental perturbations were all scaled between 0 and 1, where 1 represents the maximum exposure among species in the Bylot Island community, and 0 represents the lowest. We scaled values to facilitate comparisons between species; it does not however assess whether a given species is exposed to high or low values in absolute terms. The distribution of the scaled values are provided in **Figure 4.8**. We then classified relative exposure into semi-quantitative categories: low (0 to 0.2), intermediate-low (0.2 to 0.4), intermediate (0.4 to 0.6), intermediate-high (0.6 to 0.8) and high (0.8 to 1). Note that the interpretation of these categories is relative to the species within the Bylot Island community. For each perturbation, we used the assigned exposure categories along with estimated species abundance and biomass to calculate the proportion of community richness, total abundance, and biomass in each exposure category. We also repeated the analysis excluding snow geese, as they are the most dominant migratory species in the community in terms of both abundance and biomass, and therefore strongly influence proportions.

We investigated if species with similar functional traits migrate to similar destinations during the non-breeding period using the proportion of overlap between their non-breeding ranges. For each functional group, we computed pairwise overlap values between all species. Because species can have ranges of different sizes, the overlap is directional and potentially asymmetric. For instance, if species A's range is entirely contained within the range of species B, the overlap from A $\rightarrow$ B is complete (i.e., 1). However, the reverse (B $\rightarrow$ A) would yield a value less than 1, since species B's range extends beyond that of species A (see **Figure 4.9** for an empirical example).

To evaluate similarity in species' exposure to environmental perturbations within functional groups, we used the Concordance Correlation Coefficient (CCC). This metric compares the exposure values of two species across all environmental perturbations with non-zero values. The CCC captures both the strength of the linear relationship and the degree to which the relationship approaches a 1:1 line (i.e., perfect agreement; see **Figure 4.9** for an empirical example). Values range from -1, indicating completely opposing exposure patterns, to 1, indicating that species present exactly the same exposure to each perturbation.

4.8 Results

4.8.1 Community exposure to environmental perturbations

Terrestrial environments

Species from the vertebrate community of Bylot Island are mostly exposed to drivers of biodiversity changes affecting terrestrial environments during the non-breeding period (**Figure 4.3**). Climate warming is the perturbation to which the highest number of species are exposed. However, human use and pollution associated with agriculture are those to which the highest number of species are exposed at relatively high levels. Species migrating to temperate terrestrial environments in North America present relatively high exposure to several environmental perturbations (i.e., temperature increase, snow cover duration decrease, built-up cover, cropland cover, pesticide pollution risk and nitrogen fertilizer application; **Figure 4.4** and **4.11**). In contrast, species migrating to temperate environments in South America are generally exposed to less intensive agricultural activities, characterized by more pasture, less cropland, and lower fertilizer and pesticide application. Most environmental perturbations are positively correlated together in terrestrial environments, with varying strength (**Figure 4.10**). Cropland cover, pesticide pollution risk and nitrogen fertilizer application present a particularly high correlation (Spearman's ρ = 0.84 to 0.92; $p < 0.05$). When accounting for species abundance and biomass, the proportion of the community exposed to high levels of temperature increase, changes in snow cover duration, built-up cover, pesticide pollution risk and nitrogen fertilizer application increases substantially (**Figure 4.5** and **4.12**). For these perturbations, accounting for abundance increases the proportion of the community exposed to high levels by 24 ± 4 % (SD) on average, and accounting for biomass increases it by 82 ± 6% (SD). However, when snow geese are excluded, the proportion of the community exposed to high levels of environmental perturbations is much lower, and no substantial differences are observed between the proportion of species, individuals, and biomass (**Figure 4.13**).

Marine environments

Species occurring predominantly in marine environments during the non-breeding season are primarily exposed to climate change during this period (**Figure 4.3**). Exposure to environmental perturbations are generally less correlated in marine than in terrestrial environments (**Figure 4.10**). However, correlations are strong when they do occur in marine environments (Spearman's $\rho > 0.80$). For instance, exposure to ocean acidification, sea temperature increase, and fishing effort are strongly positively correlated (ρ = 0.80). Although exposure to coastal pesticides and fertilizers is highly correlated (ρ = 0.99), it remains generally low in the community. Pelagic species migrating to tropical or subtropical Atlantic (i.e., jaegers and the red phalarope) experience high exposure to sea temperature increase, sea acidification and fishing effort during the non-breeding period (**Figure 4.4**). Species migrating to coastal marine environments of North America generally exhibit lower exposure to these perturbations. Accounting for species abundance and biomass reduces community exposure to environmental perturbations in marine environments (**Figure 4.5** and **4.12**).

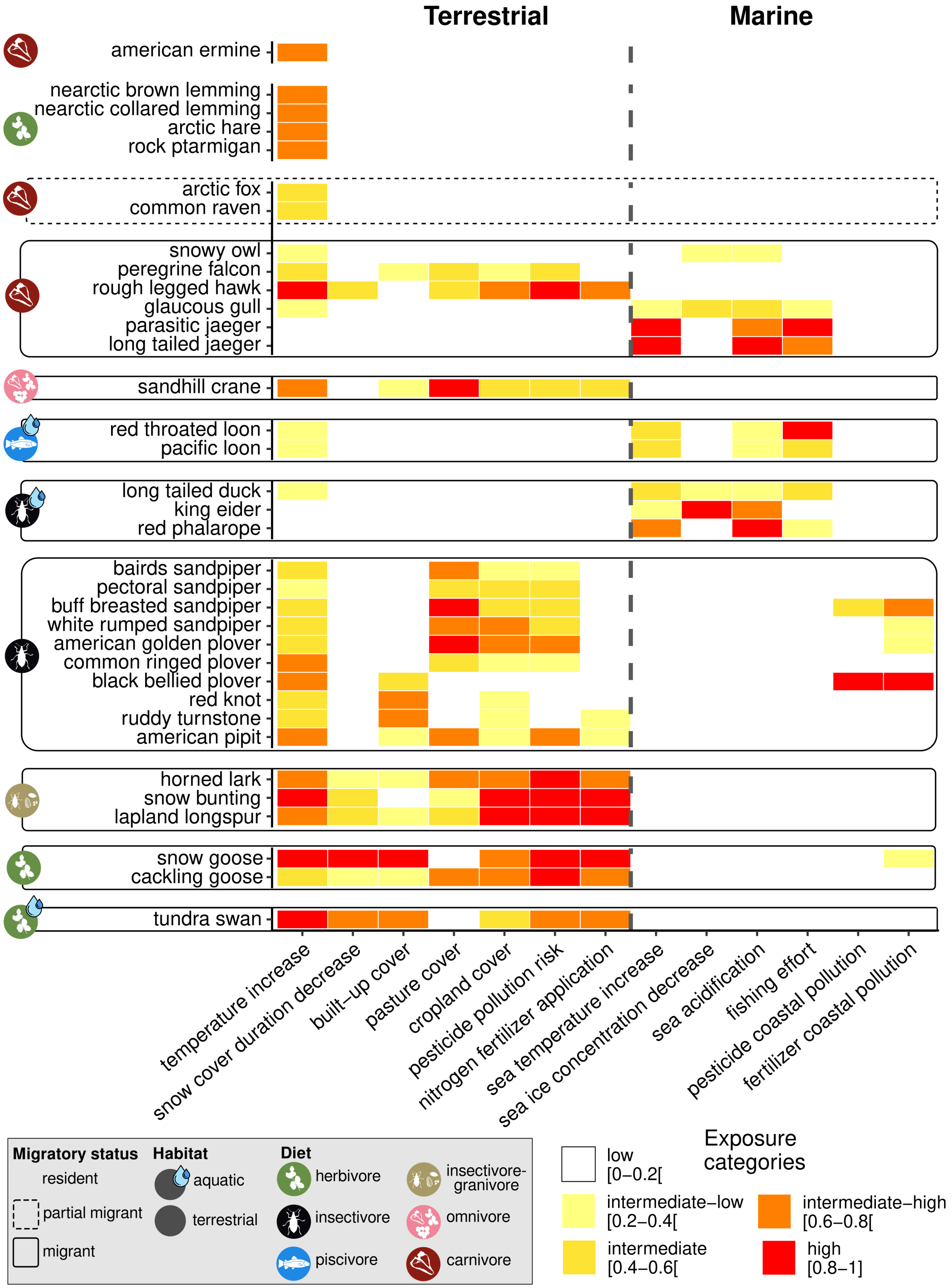

Terrestrial
Marine
american ermine
nearctic brown lemming
nearctic collared lemming
arctic hare
rock ptarmigan
arctic fox
common raven
snowy owl
peregrine falcon
rough legged hawk
glaucous gull
parasitic jaeger
long tailed jaeger
sandhill crane
red throated loon
pacific loon
long tailed duck
king eider
red phalarope
bairds sandpiper
pectoral sandpiper
buff breasted sandpiper
white rumped sandpiper
american golden plover
common ringed plover
black bellied plover
red knot
ruddy turnstone
american pipit
horned lark
snow bunting
lapland longspur
snow goose
cackling goose
tundra swan
temperature increase
snow cover duration decrease
built-up cover
pasture cover
cropland cover
pesticide pollution risk
nitrogen fertilizer application
sea temperature increase
sea ice concentration decrease
sea acidification
fishing effort
pesticide coastal pollution
fertilizer coastal pollution
Migratory status
resident
partial migrant
migrant
Habitat
aquatic
terrestrial
Diet
herbivore
insectivore
piscivore
insectivore-granivore
omnivore
carnivore
Exposure categories
low [0–0.2[
intermediate–low [0.2–0.4[
intermediate [0.4–0.6[
intermediate–high [0.6–0.8[
high [0.8–1]

Figure 4.3 – Exposure of vertebrate species of the Bylot Island food web to environmental perturbations during the non-breeding period. Exposure values were scaled between 0 and 1 for each environmental perturbation and then classified into semi-quantitative categories. Diet icons were extracted from Saulnier-Talbot et al. 2024 with the authors' permission. The fish icon was created by Lars Meiertoberens and extracted from the Noun project (`https://thenounproject.com/icon/trout-4720251/`). The water drop icon was created by Freepik - Flaticon.

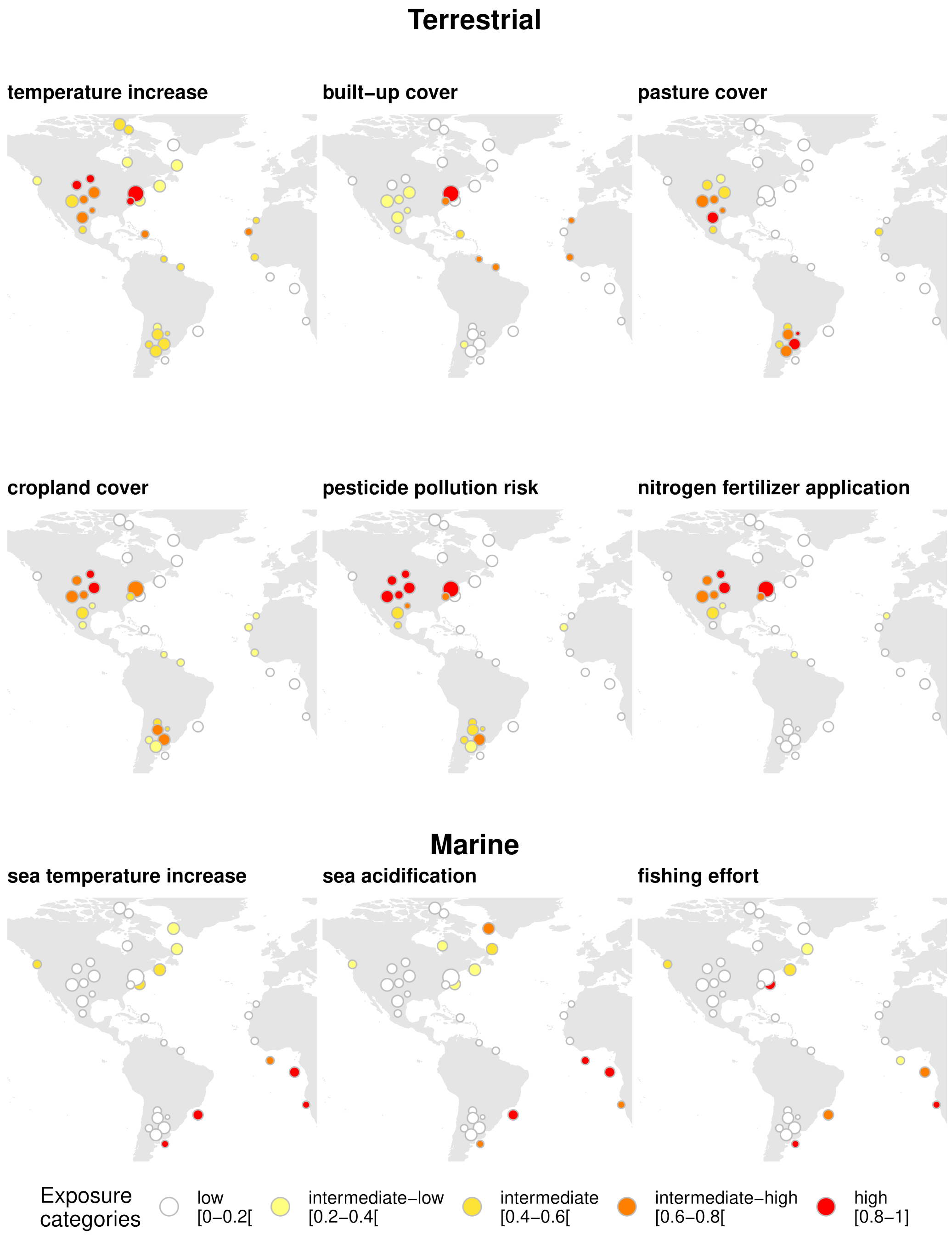


Figure 4.4 – Maps of the non-breeding range centroid of partially migratory and migratory species from the Bylot Island community (circles) colored by their relative exposure to different environmental perturbations in terrestrial and marine environments. Circle size is proportional to the log-transformed biomass of adults in the Bylot Island food web.

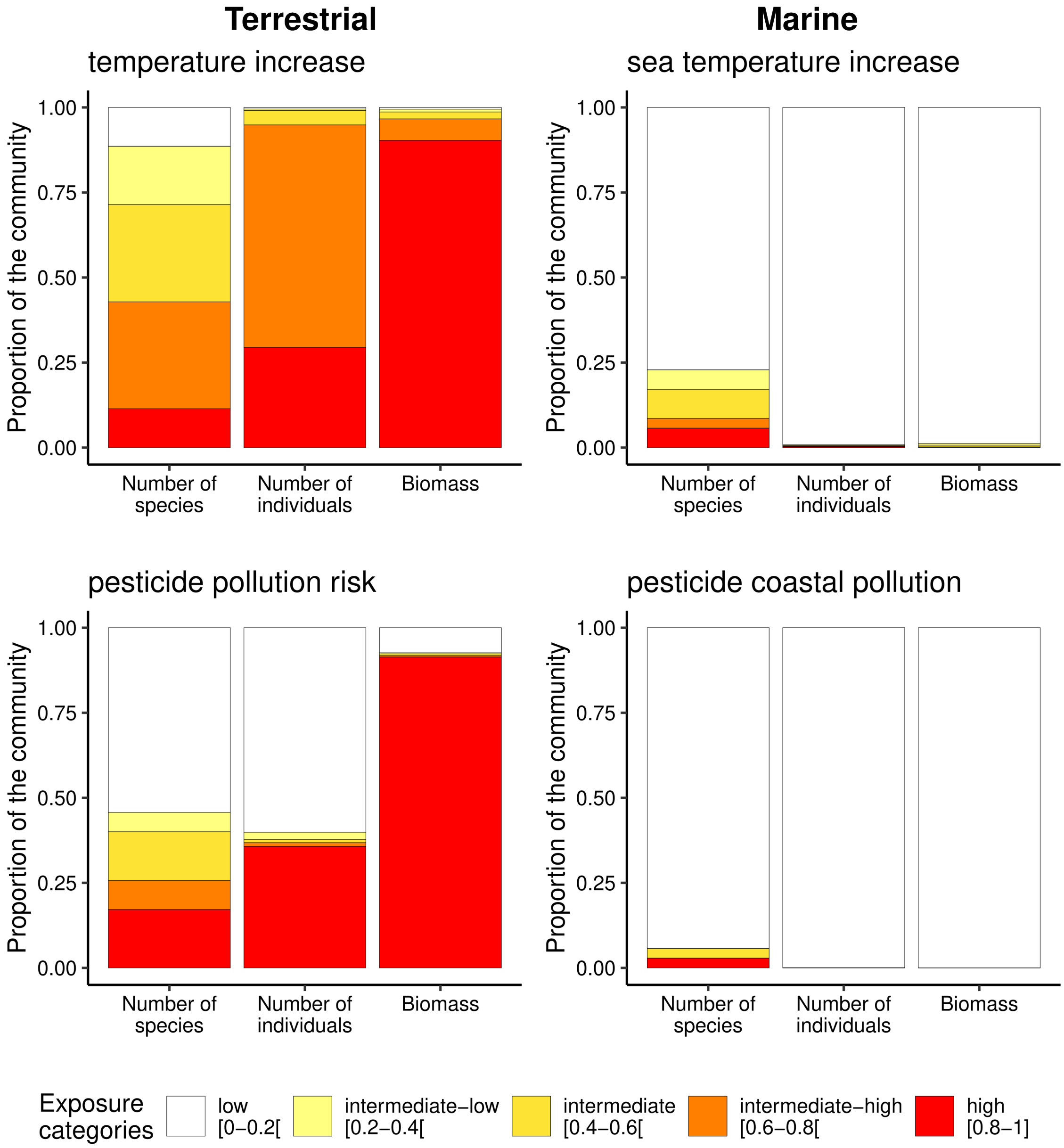


Figure 4.5 – Proportion of species, number of individuals and amount of biomass from the Bylot Island vertebrate community assigned to each category of relative exposure for different environmental perturbations in terrestrial and marine environments. Species associated with terrestrial habitats during the non-breeding period are included in the calculation of proportions for environmental perturbations in marine environments, and vice versa.

4.8.2 Exposure of functional groups to environmental perturbations

There is a strong contrast between resident/partially migratory species and fully migratory species. The former are primarily exposed to climate change, while their exposure to pollution and human use perturbations remains minimal (**Figure 4.3**). Some functional groups of migratory species, such as insectivores-granivores and herbivores, experience similar or greater temperature increases than Arctic residents during the non-breeding period. These groups also show high exposure to human use and pollution perturbations, particularly those linked to agricultural activities (e.g., cropland, pesticides, and fertilizers). Migratory species within functional groups generally show intermediate to high concordance in their exposure to environmental perturbations, despite relatively low spatial overlap during the non-breeding period. An exception is migratory carnivores, which exhibit a high variability in their exposure to environmental perturbations and a low spatial overlap (**Figure 4.6**).

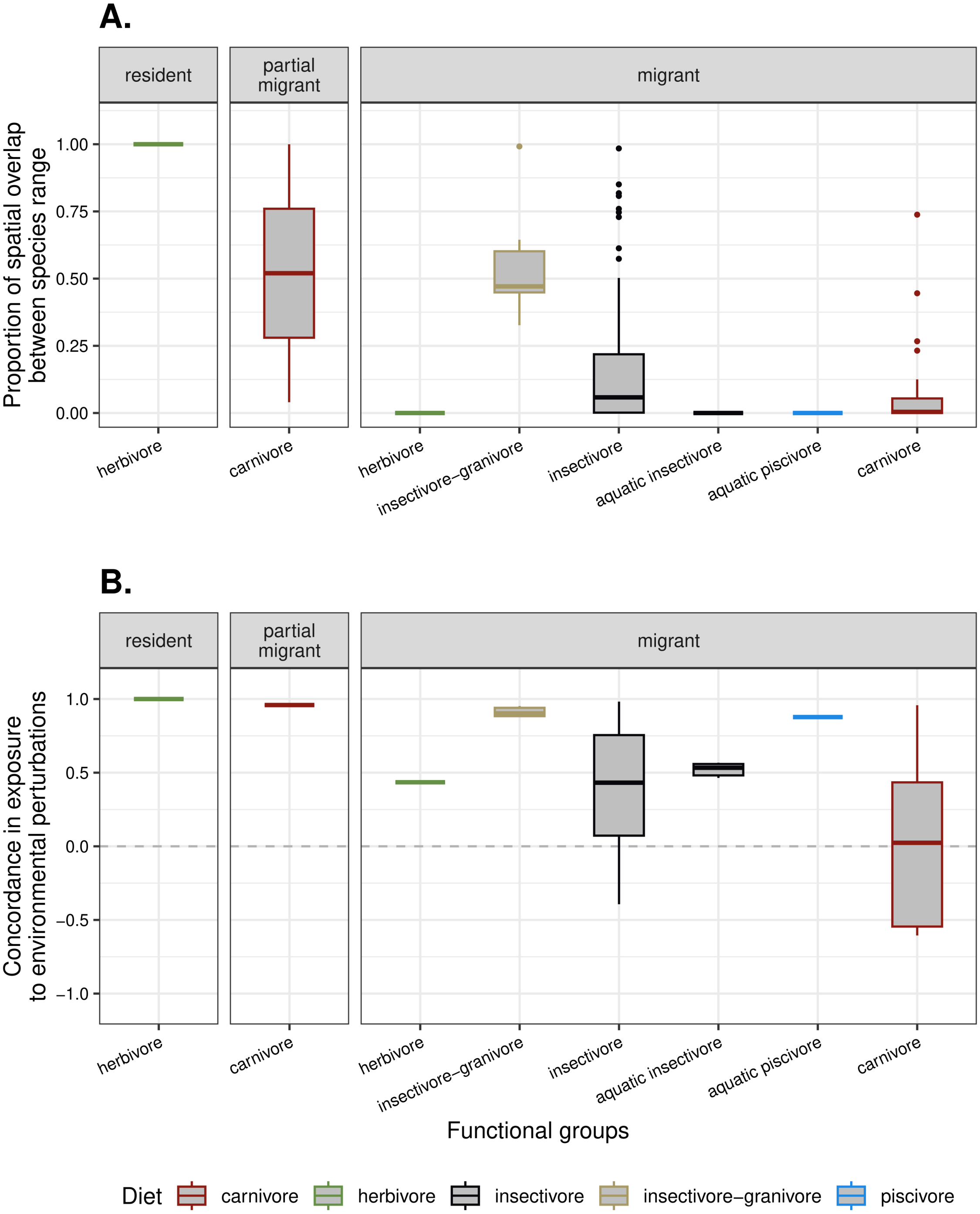

A.
resident
partial migrant
migrant
Proportion of spatial overlap between species range
1.00
0.75
0.50
0.25
0.00
herbivore
carnivore
herbivore
insectivore–granivore
insectivore
aquatic insectivore
aquatic piscivore
carnivore
B.
resident
partial migrant
migrant
Concordance in exposure to environmental perturbations
1.0
0.5
0.0
−0.5
−1.0
herbivore
carnivore
herbivore
insectivore–granivore
insectivore
aquatic insectivore
aquatic piscivore
carnivore
Functional groups
Diet
carnivore
herbivore
insectivore
insectivore–granivore
piscivore

Figure 4.6 – **A.** Proportion of spatial overlap between the non-breeding ranges of species within functional groups of the Bylot Island food web. **B.** Concordance in exposure to environmental perturbations within functional groups is represented by the distribution of pairwise Concordance Correlation Coefficients (CCC) between species. Concordance Correlation Coefficient measures how much two vectors differ from each other by taking into account the strength of the correlation but also the deviation from a 1:1 relationship (y=x). Values range from -1, representing variables perfectly correlated along a y=-x line, to 1 representing values perfectly correlated along a y=x line.

4.9 Discussion

Migratory species within local communities can spend a substantial portion of their annual cycle in distant environments, where exposure to drivers of biodiversity change may exert heterogeneous pressures on species. Through the Bylot Island case study, we show that most vertebrate species breeding in a protected Arctic ecosystem, where direct anthropogenic pressures are minimal, are migratory and thus face multiple anthropogenic pressures of varying intensity during a substantial part of their annual cycle. Migratory species within the same functional group tend to experience similar environmental perturbations during the non-breeding period, even though they generally migrate to different destinations. Climate warming and agricultural activity in temperate regions of South, but especially North America, emerged as exerting substantial pressure on the Bylot Island vertebrate community. This is especially true in regions of intensive agriculture in North America (e.g., cropland management, pesticide and fertilizer use), where migratory herbivores, insectivore-granivores, and one carnivore species show relatively high exposure. Together, these groups account for a substantial proportion of the community abundance and biomass.

Assessing species exposure to environmental perturbations during the non-breeding period improves our understanding of the vulnerability of the Bylot Island community to distant perturbations. It was previously shown that the Bylot Island community is strongly connected to terrestrial temperate ecosystems of South, but especially North America, since a substantial portion of species, individuals and biomass migrate to those areas (Moisan et al., 2025*b*). Here, we highlight that species migrating to temperate terrestrial environments of North America are exposed to relatively high levels of environmental perturbations across multiple dimensions (e.g., climate change, human use, and pollution). Therefore, based on exposure, the Bylot Island community would be more vulnerable to perturbations originating from temperate terrestrial environments of North America. Drivers of biodiversity change at the global scale are more correlated in terrestrial than in marine environments (Bowler et al., 2020). The high exposure of the Bylot Island community to environmental perturbations associated with agriculture suggest that changes in agriculture practices could act as a potential source of spatial cascades for the Bylot Island food web. Since a substantial portion of the community biomass present a relatively high exposure to agrochemical pollution, Arctic migratory species represent a considerable pathway for introducing pollutants in the Arctic food web. Fortunately, the most abundant migratory species in the community is herbivore and concentration of pollutants is apparently generally low in Arctic migratory species of lower trophic level (Tsuji et al., 2007; Hitchcock et al., 2019). However, pesticide compounds are degraded into pesticide transformation products in natural environments through various processes, which can sometimes be more toxic than the original compounds (Mitra et al., 2024). Consequently, tracking pesticide concentrations in organisms is challenging and should also account for these derivative compounds.

The Bylot Island vertebrate community could be especially exposed to agricultural activity because of their adaptations to open tundra habitat with low vegetation. Adaptations to the breeding ground habitat could influence migratory species to select similar habitats during the non-breeding season, which include natural grassland, pasture and cropland. Habitat conservatism through seasons, may thus partly explain why migratory species with similar functional traits, despite migrating to distinct non-breeding grounds, tend to exhibit a relatively high concordance in their exposure to environmental changes. Supporting this, at the global scale, long-distance migratory species tend to select similar environmental niches across seasons, with land-cover type identified as a strong determinant of niche conservatism (Zurell et al. 2018, but see Somveille et al. 2019). We thus hypothesized that Arctic tundra vertebrate communities are likely to be exposed to environmental perturbations associated with agricultural activity, given the similarity in habitat characteristics between some agricultural landscapes and tundra habitats.

Environmental perturbations occurring in distant but connected environments are more likely to propagate to the Bylot Island food web via lower trophic levels. The high abundance of geese in the study area has been linked to changes in the functional or numerical response of the main predator, the Arctic fox, with indirect effects on several other species (Duchesne et al., 2021; Beardsell et al., 2023). Insectivore-granivores and insectivores are considered alternative prey for most predators and thus make up only a relatively small proportion of predator diets, resulting in a lesser influence on vertebrate food web dynamics (Legagneux et al., 2012; Beardsell et al., 2025). Several main predators in the food web (e.g., American ermine, Arctic fox, and snowy owl; Legagneux et al. 2012) remain in polar latitudes during the boreal winter (Lai et al., 2017; Robillard et al., 2018) and therefore experience relatively low direct anthropogenic pressures. Nevertheless, some migratory predators (e.g., rough-legged hawks, long-tailed and parasitic jaegers) experience relatively high exposure to multiple environmental perturbations during the non-breeding period.

The diversity of migratory strategies within functional groups suggests that species are not necessarily affected simultaneously by localized (tens to hundreds of kilometers) and short-term perturbations on their non-breeding range. This diversity of migratory strategy within functional groups may help reduce the vulnerability of Arctic communities to localized and short-term distant environmental perturbations. For instance, among migratory herbivores, the cackling goose migrates to the central portion of North America and the snow goose to the Atlantic coast, thus extreme weather events in a given winter, such as drought in the Central area would probably not influence both species simultaneously. However, species within functional groups experience similar exposure to the different perturbations. For instance, despite migrating to completely distinct non-breeding grounds, both geese species experience substantial agricultural activity on their non-breeding ranges. Therefore, given the global distribution of drivers of biodiversity change, with more direct pressures from anthropogenic activities in temperate than in Arctic ecosystems (Bowler et al., 2020), seasonal migrations may increase the vulnerability of Arctic communities as species move from breeding grounds with minimal direct pressures to non-breeding areas under higher direct pressure.

Considering species exposure alone is not enough to predict the magnitude and direction of species responses to change. Environmental perturbations on the non-breeding grounds of migratory species can directly influence survival outside the breeding season and indirectly affect both survival and fecundity during breeding through carry-over effects (Harrison et al., 2011). For Arctic species, the breeding season is critical since all reproduction occurs within a short period (mostly June to August), yet they spend a much larger portion of their annual cycle on non-breeding grounds. Therefore, species that are particularly sensitive to changes in adult survival, such as shorebirds (Hitchcock and

Gratto-Trevor, 1997; Weiser et al., 2020), may be especially vulnerable to environmental perturbations on their non-breeding grounds (Weiser et al., 2018). Within the non-breeding period, the migratory phases, a period not considered here, are suggested to strongly influence adult survival in migratory species (Sillett and Holmes, 2002; Klaassen et al., 2014). In some cases, environmental perturbations at staging or stopover sites have been shown to drive species population trends (Studds et al., 2017). For instance, shorebird species that rely heavily on the Yellow Sea mudflats as staging grounds, a region experiencing intense land conversion (Ma et al., 2014), show stronger population declines (Studds et al., 2017). Moreover, environmental perturbations can affect species through different mechanisms, for example habitat loss reducing adult survival (Studds et al., 2017) and pollution reducing fecundity (Goutte et al., 2014), which may also interact.

In some cases, species sensitivity to environmental perturbations occurring on their non-breeding ground has been documented, which allows us to anticipate species response considering exposure. Several empirical studies have shown that geese have benefited from the intensification of agricultural activities on their non-breeding and staging grounds by foraging on crop residues (Jefferies, 2004; Gauthier et al., 2005; Hessen et al., 2017), which has contributed to the increase in geese populations across North America and Europe (Ganter et al., 2013). Since both geese species present on Bylot Island experience relatively high exposure to cropland, pesticide, and fertilizer, we can expect migratory herbivores in the food web to benefit from these environmental perturbations on their non-breeding grounds. However, the positive effects of agricultural activity on snow goose populations are now offset by hunting pressure aimed at preventing overgrazing in Arctic ecosystems (Lefebvre et al., 2017). Interestingly, the cackling goose population on Bylot Island is recently showing signs of rapid increase (Moisan et al., 2025*a*).

On the other hand, insectivorous species such as shorebirds, appear to be negatively impacted by agricultural intensification, especially the conversion of natural grasslands or pastures to cropland and the use of agrochemicals (Clay et al., 2010; Lanctot et al., 2010). We observe that species migrating to temperate terrestrial environments in South America are generally exposed to less intensive agriculture than species migrating to temperate terrestrial environments in North America, with lower cropland extent and agrochemical use. However, because cropland area is increasing in South America but remains relatively stable in North America (Potapov et al., 2022), temperate terrestrial species migrating to South America may experience stronger habitat conversion on their non-breeding grounds than those migrating to North America. Moreover, species migrating to South America may also be more vulnerable to agrochemical use, likely due to a stronger temporal overlap with the growing season. This emphasizes that the temporal overlap between species seasonal occurrence and environmental perturbations could be an important factor to include in future exposure assessments (Jackson et al., 2021). In addition, the effects of environmental perturbations on shorebirds can be amplified through indirect trophic interactions within the community. For instance, shifts in agricultural practices have been linked to increases in snow goose populations on Bylot Island (Gauthier et al., 2005), which in turn contribute to higher fox densities (Dulude-de Broin et al., 2023) and, consequently, increased predation on shorebird nests (Lamarre et al., 2017; Duchesne et al., 2021; Beardsell et al., 2023).

We are confident that our observations remain robust despite the inherent limitations of the data and the methodological approach employed. First, species' non-breeding ranges were derived from data of varying quality, from precise individual tracking to coarse range maps (Moisan et al., 2023), which can influence our assessment of species exposure to environmental perturbations. However, given the relatively high concordance in exposure among species migrating to similar regions (see **Figure 4.11**), it is probable that more accurate and precise species ranges would yield similar interpretations. Second, scaling exposure values based on the maximum observed for a Bylot Island species prevents assessment of the absolute magnitude of environmental perturbations faced during the non-breeding period. Assessing species' absolute exposure to environmental perturbations would require comparison to specific reference points, which we considered beyond the scope of this study. Finally, the results are based on a selection of common variables of environmental perturbation, thus representing only a subset of all the dimensions of environmental perturbations. This provides an incomplete picture of community exposure, a limitation inherent to multi-stressor studies (Bowler et al., 2020). A future and more comprehensive assessment could include for example the frequency of extreme weather events, legal and illegal hunting pressure, collision risk with vehicles and land-cover conversion rate. While not exhaustive, our approach represents a first step toward assessing exposure to environmental perturbations in local vertebrate communities with seasonal migration.

Describing species exposure to environmental perturbations during the non-breeding period in a single tundra community provides valuable insight into the vulnerability of other Arctic communities to global environmental changes. Tundra species adapted to open, low-vegetation habitats are predisposed to exposure to agricultural activity when migrating outside the Arctic. Therefore, other tundra vertebrate communities can be expected to show relatively high exposure to cropland, pasture, and agrochemical applications. Extending this reasoning, boreal migratory bird communities might be particularly exposed to disturbances associated with forest environments during the non-breeding season. Moreover, we suggest that the high diversity of migratory strategy within functional groups could help desynchronize the effects of distant, localized, and short-term environmental perturbations on food web energy pathways. In the Bylot Island study case, most Arctic breeding species spend the non-breeding period in terrestrial temperate environments experiencing intermediate to high climate change and anthropogenic pressures. Thus, Arctic migratory species could be more exposed to global drivers of biodiversity change during the non-breeding than the breeding period, at least in Eastern Arctic communities, which may increase community vulnerability to distant perturbations. Our study illustrates that some migratory species breeding in protected Arctic environments can move to southern non-breeding grounds where they face higher environmental pressures. Assessing migratory species exposure to environmental perturbations in other tundra communities could test whether our observations hold at larger spatial scales and help guide conservation efforts in southern ecosystems to protect Arctic biodiversity.

4.10 Data availability statement

The code used to prepare and analyze the data will be archived in Zenodo upon acceptance of the manuscript for publication. The raw data used to conduct the analyses and generate the figures presented here are available at the following repositories. Species non-breeding range: link; Species abundance and biomass: link; Monthly land surface temperature: link; Yearly snow cover duration: link; Cropland and pasture cover: link; Built-up area cover: link; Pesticides risk pollution: link; Fertilizers application rate: link; Monthly sea surface temperature and sea ice concentration: link; Sea water acidification trend: link; Fishing pressure: link; Coastal pesticides and fertilizers pollution: link.

4.11 Supplementary material

Table 4.2 – Composition of the vertebrate community of Bylot Island. Body mass, absolute abundance and biomass (product of body mass and absolute abundance) represents the mean values of adult individuals of each species, except for lemmings which also considers juveniles. The 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. Data were extracted from Moisan et al. (2025*a*).

Species (en)	**Species**	**Migratory status**	**Body mass (g)**	**Abundance (ind.)**	**Biomass (kg)**
Pacific loon	*Gavia pacifica*	migrant	2251	4	9
Red-throated loon	*Gavia stellata*	migrant	1486	64	95.1
King eider	*Somateria spectabilis*	migrant	1617	106	171
Long-tailed duck	*Clangula hyemalis*	migrant	871	191	166
Cackling goose	*Branta hutchinsii*	migrant	1639	138	388
Snow goose	*Anser caerulescens*	migrant	1487	30771	45756
Tundra swan	*Cygnus columbianus*	migrant	6378	1	6.4
Rough-legged hawk	*Buteo lagopus*	migrant	950	27	25.6
Peregrine falcon	*Falco peregrinus*	migrant	760	10	7.6
Snowy owl	*Bubo scandiacus*	migrant	2169	16	34.7
Rock ptarmigan	*Lagopus muta*	resident	535	24	12.8
Sandhill crane	*Antigone canadensis*	migrant	4296	36	155
American golden-plover	*Pluvialis dominica*	migrant	170	1102	187
Black-bellied plover	*Pluvialis squatarola*	migrant	210	29	6.1
Common-ringed plover	*Charadrius hiaticula*	migrant	86	55	4.7
Ruddy turnstone	*Arenaria interpres*	migrant	136	36	4.9
Red knot	*Calidris canutus*	migrant	145	59	8.6
Pectoral sandpiper	*Calidris melanotos*	migrant	88	71	6.2
Baird’s sandpiper	*Calidris bairdii*	migrant	72	2170	156
White-rumped sandpiper	*Calidris fuscicollis*	migrant	94	878	82.5
Buff-breasted sandpiper	*Calidris subruficollis*	migrant	92	5	0.46
Red phalarope	*Phalaropus fulicarius*	migrant	56	124	6.9
Glaucous gull	*Larus hyperboreus*	migrant	1500	73	110
Long-tailed jaeger	*Stercorarius longicaudus*	migrant	298	272	81.1
Parasitic jaeger	*Stercorarius parasiticus*	migrant	461	17	7.8
Common raven	*Corvus corax*	partial migrant	928	16	14.8
Horned lark	*Eremophila alpestris*	migrant	33	331	10.9
American pipit	*Anthus rubescens*	migrant	21	74	1.6
Lapland longspur	*Calcarius lapponicus*	migrant	28	6080	170
Snow bunting	*Plectrophenax nivalis*	migrant	42	236	9.9
Nearctic brown lemming	*Lemmus trimucronatus*	resident	45	54043	2432
Nearctic collared lemming	*Dicrostonyx groenlandicus*	resident	47	8128	382
Arctic hare	*Lepus arcticus*	resident	4405	6	26.4
American ermine	*Mustela richardsonii*	resident	134	40	5.4
Arctic fox	*Vulpes lagopus*	partial migrant	3300	53	175

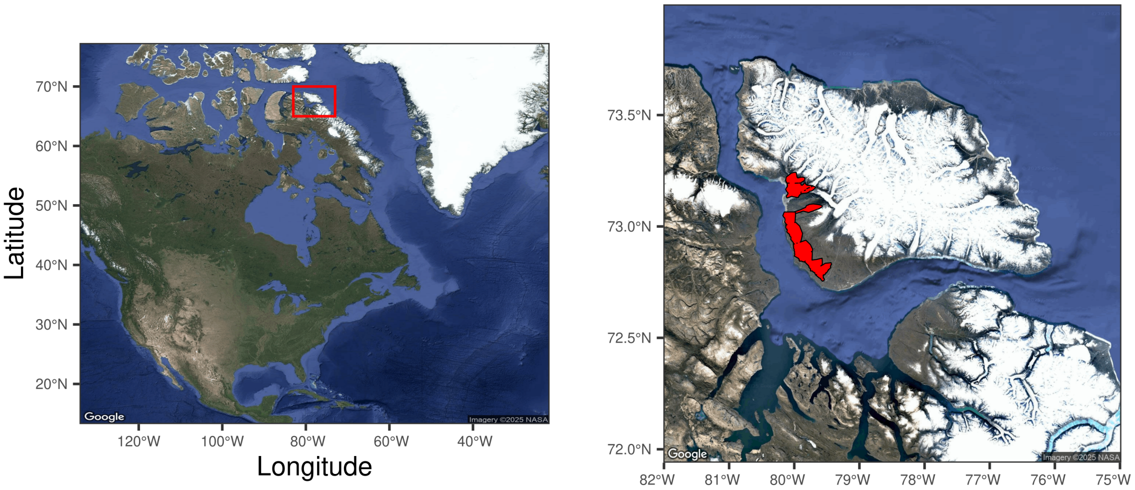
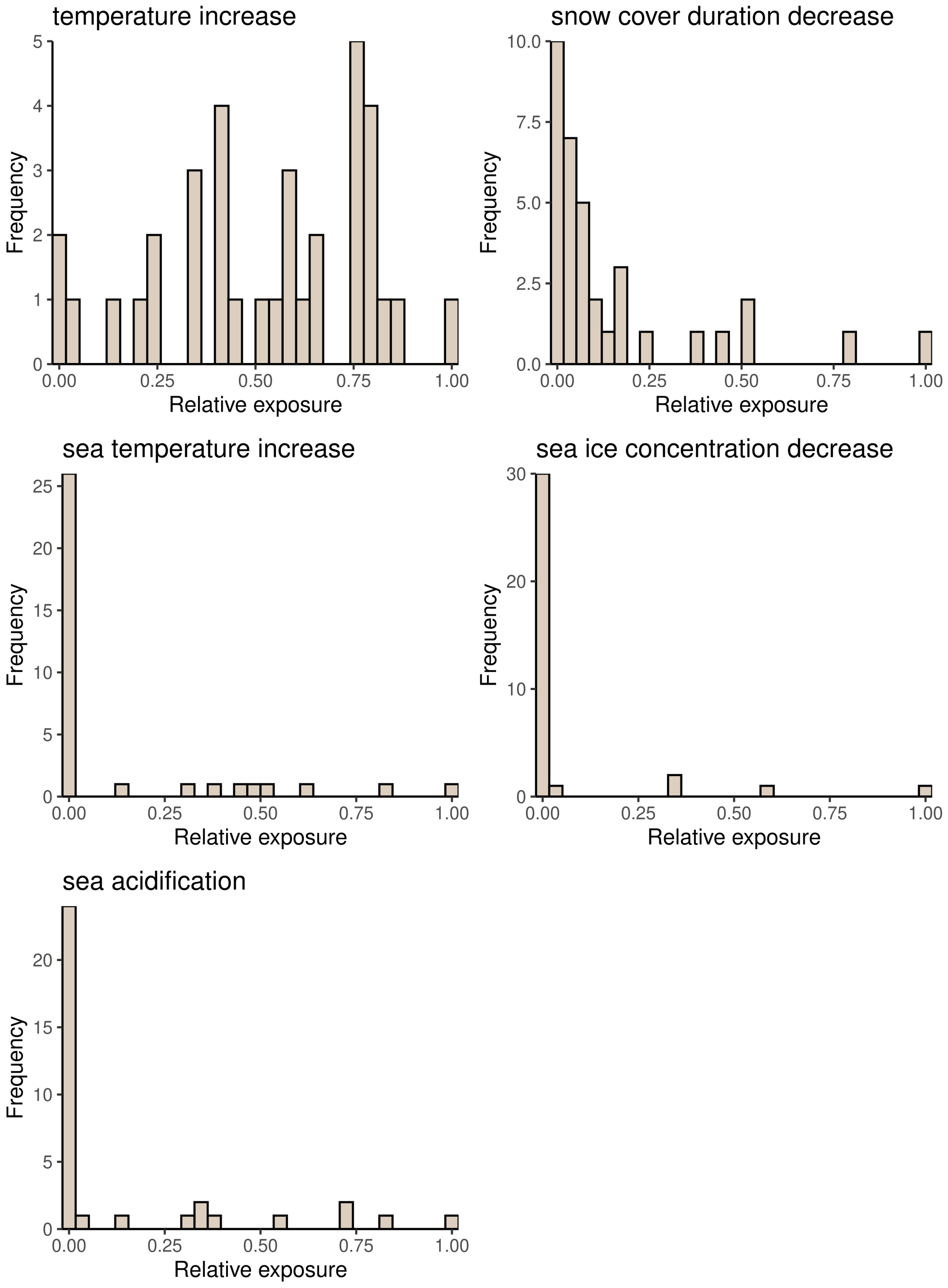
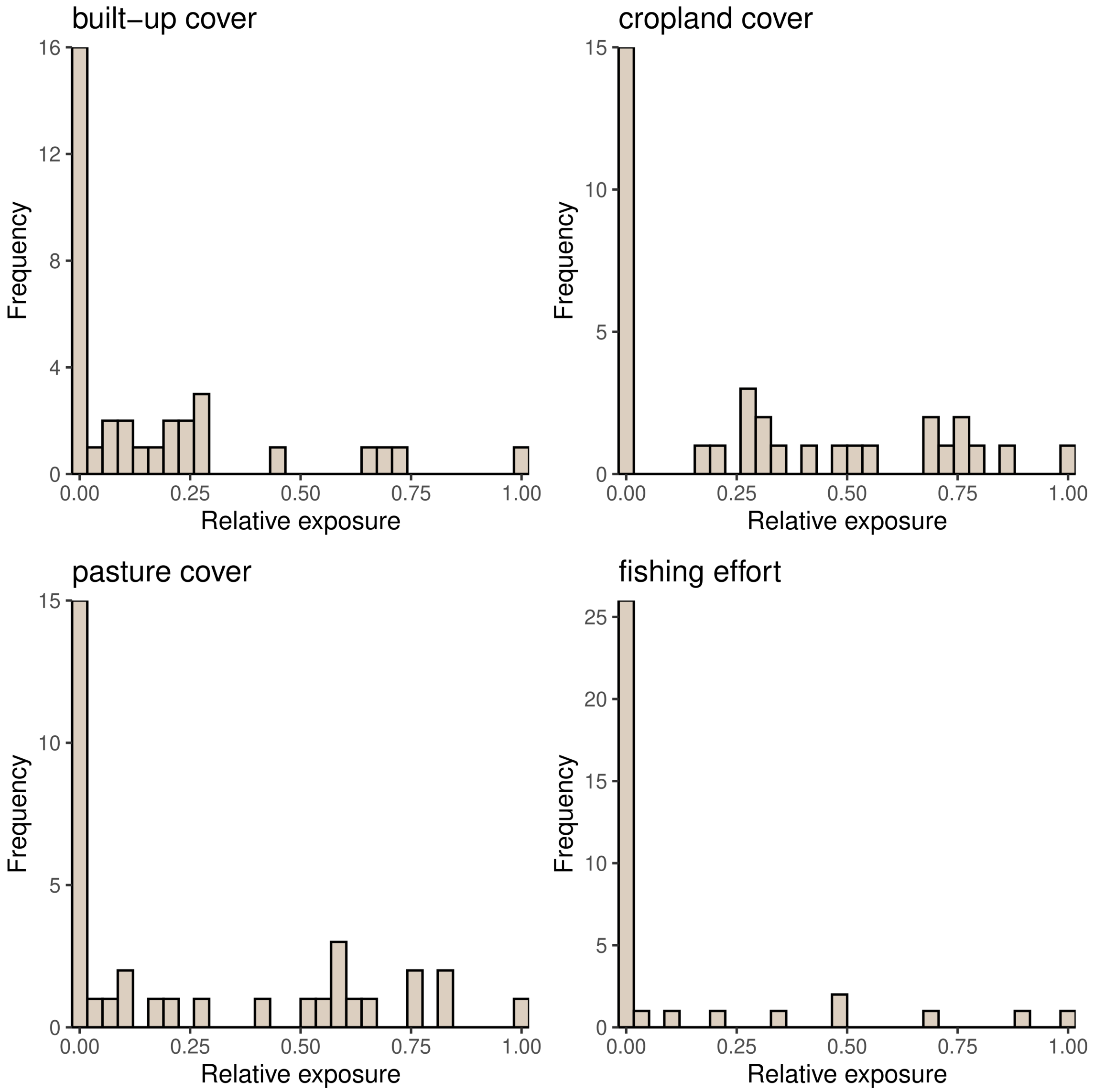


Figure 4.7 – *Left*: Location of the Bylot Island study area in North America, indicated by a red rectangle. *Right*: Delimitation of the study area on the southern plain of Bylot Island, shown as a red polygon.


temperature increase
Frequency
0
1
2
3
4
5
0.00
0.25
0.50
0.75
1.00
Relative exposure
snow cover duration decrease
Frequency
0.0
2.5
5.0
7.5
10.0
0.00
0.25
0.50
0.75
1.00
Relative exposure
sea temperature increase
Frequency
0
5
10
15
20
25
0.00
0.25
0.50
0.75
1.00
Relative exposure
sea ice concentration decrease
Frequency
0
10
20
30
0.00
0.25
0.50
0.75
1.00
Relative exposure
sea acidification
Frequency
0
5
10
15
20
0.00
0.25
0.50
0.75
1.00
Relative exposure


built−up cover
Frequency
16
12
8
4
0
0.00
0.25
0.50
0.75
1.00
Relative exposure
cropland cover
Frequency
15
10
5
0
0.00
0.25
0.50
0.75
1.00
Relative exposure
pasture cover
Frequency
15
10
5
0
0.00
0.25
0.50
0.75
1.00
Relative exposure
fishing effort
Frequency
25
20
15
10
5
0
0.00
0.25
0.50
0.75
1.00
Relative exposure

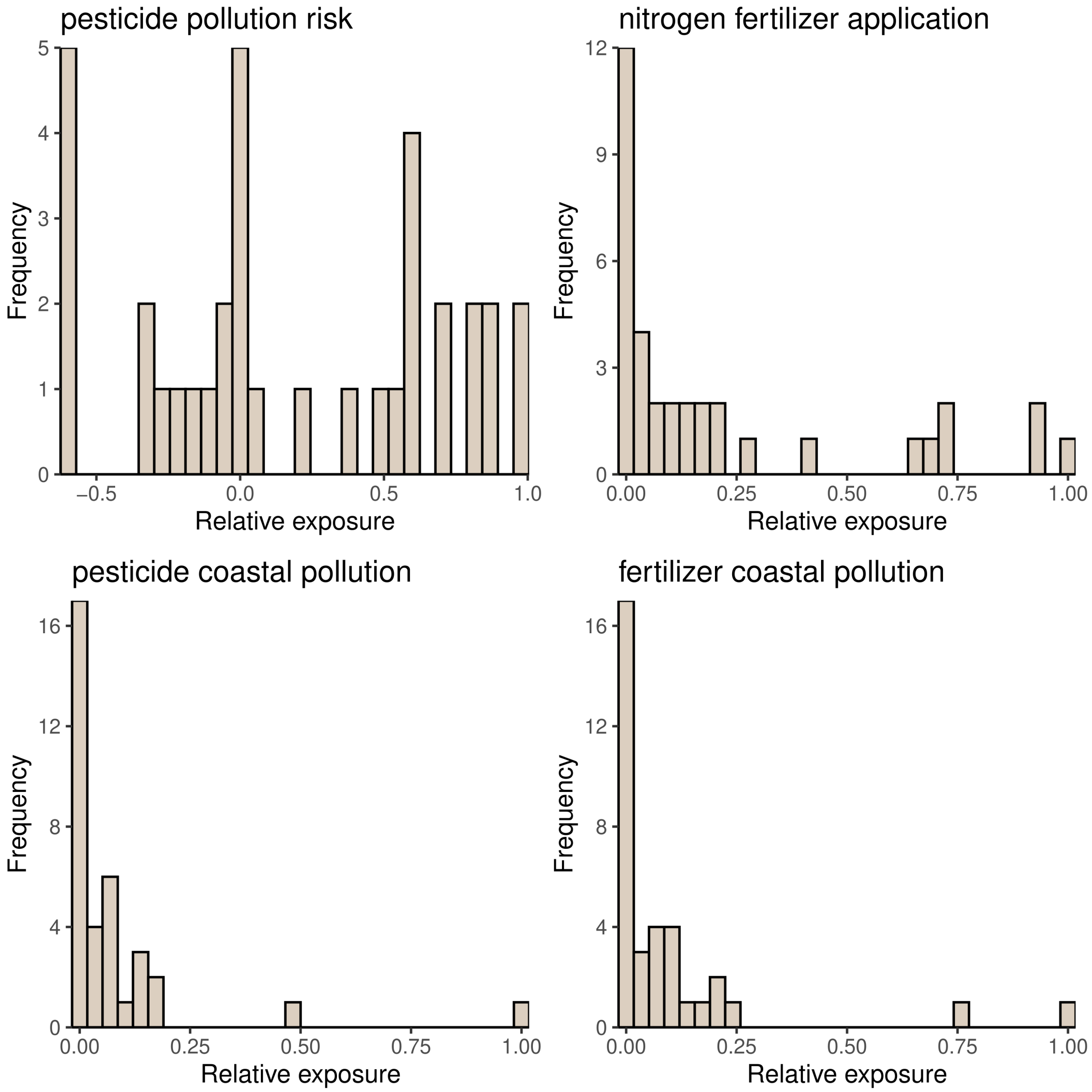
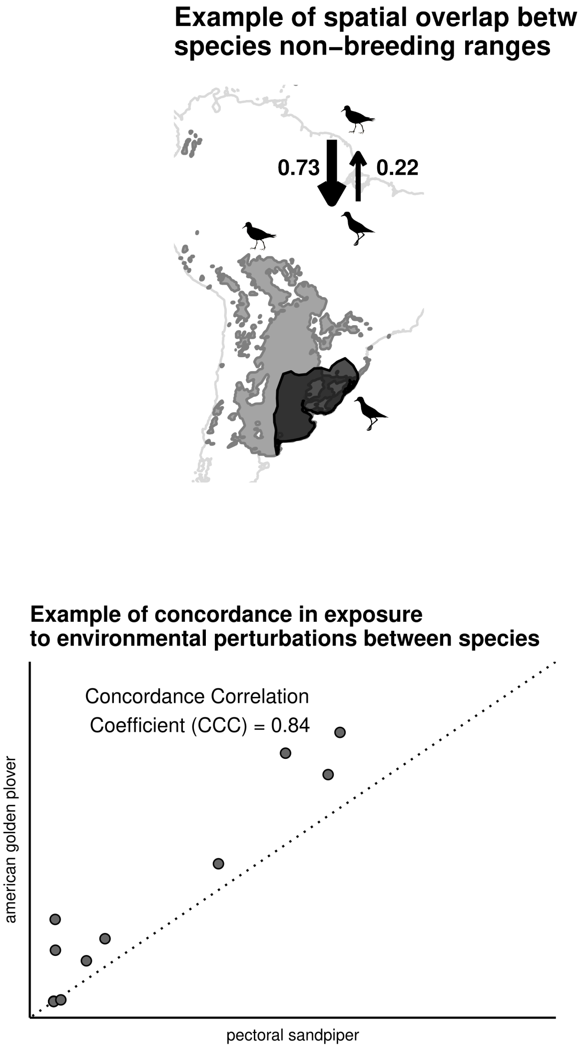


Figure 4.8 – Distribution of scaled exposure values to various environmental perturbation variables for species in the Bylot Island vertebrate community.



Example of spatial overlap between species non−breeding ranges

Example of concordance in exposure to environmental perturbations between species

Figure 4.9 – **Top**: As an example of the method used to quantify the spatial overlap between species non-breeding ranges, we illustrate the case for the American golden-plover (dark gray) and the pectoral sandpiper (light gray) to highlight that overlap can be asymmetric, depending on the relative size of each species' non-breeding range. **Bottom**: Example of the Concordance Correlation Coefficient (CCC) between the exposure to environmental perturbations between the American Golden-Plover and the Pectoral sandpiper. Each point represents a unique environmental perturbation.

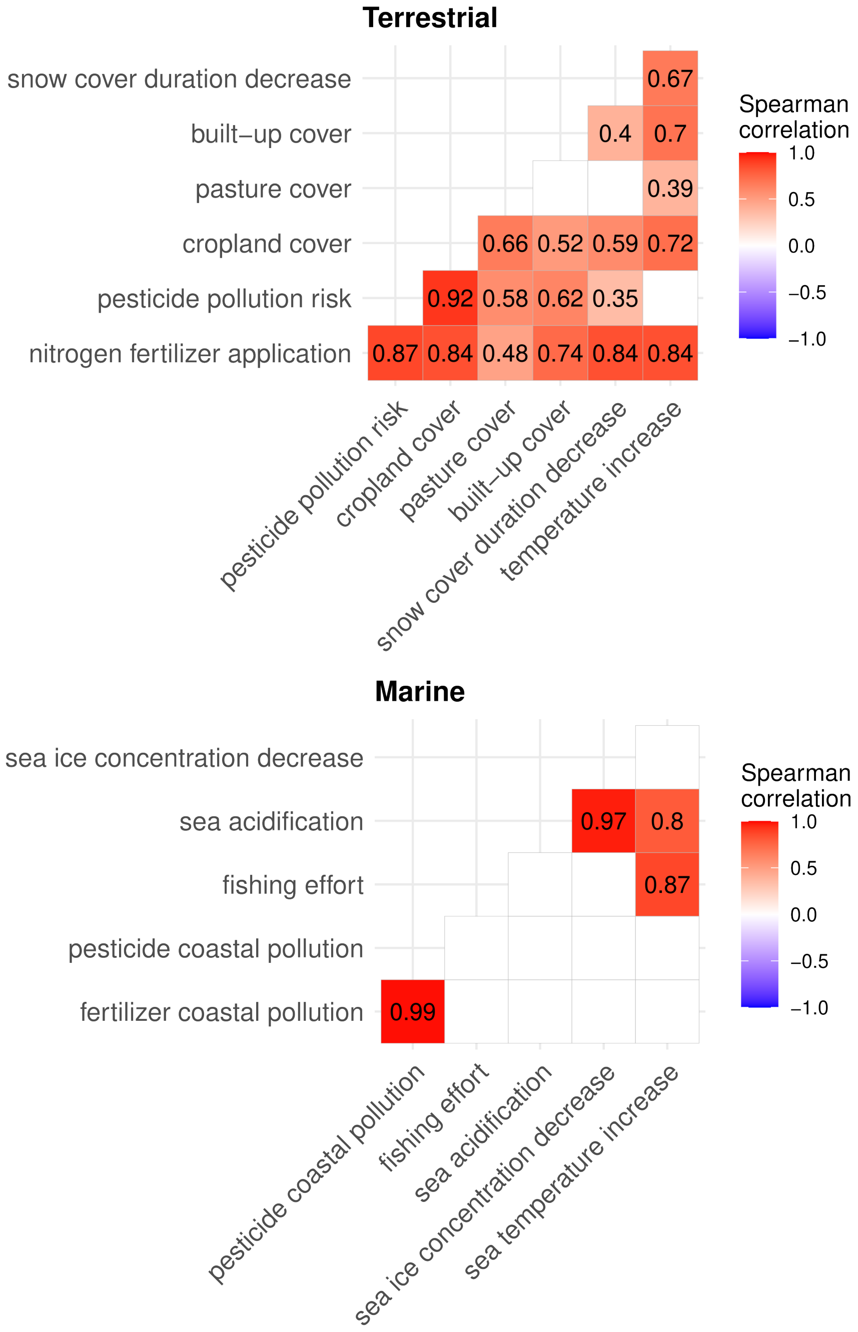
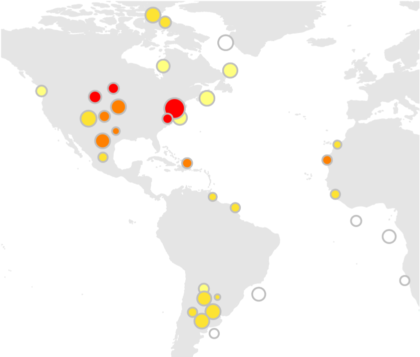


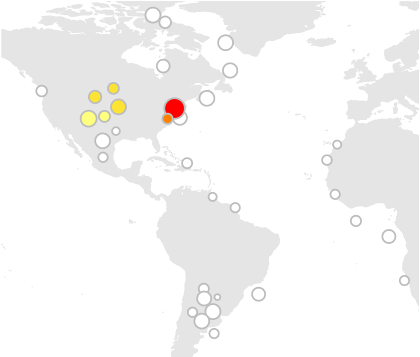
Figure 4.10 – Spearman rank correlation coefficient (ρ) among the exposure of Bylot Island species to multiple variables of environmental changes. Cases in which species showed pairwise null exposure were excluded from the correlation coefficient calculation. Only significant correlations ($p<0.05$) are presented.

Terrestrial

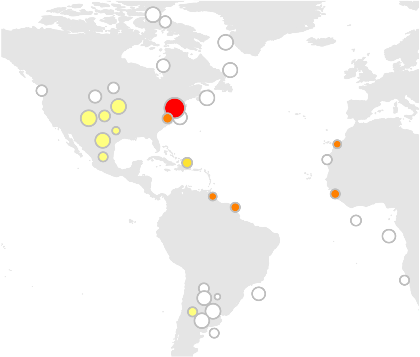
temperature increase



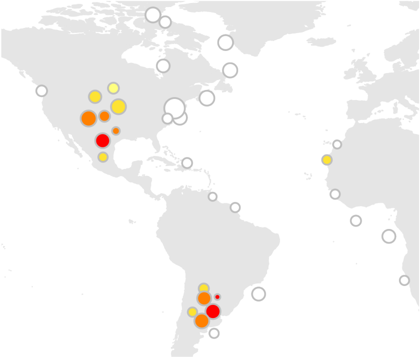
snow cover duration decrease



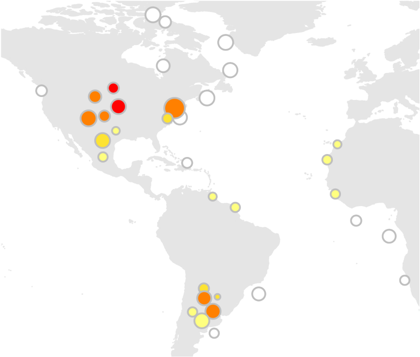
built−up cover



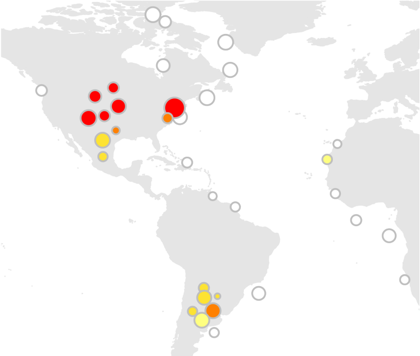
pasture cover



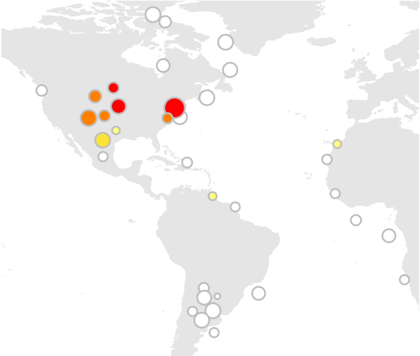
cropland cover



pesticide pollution risk



nitrogen fertilizer application



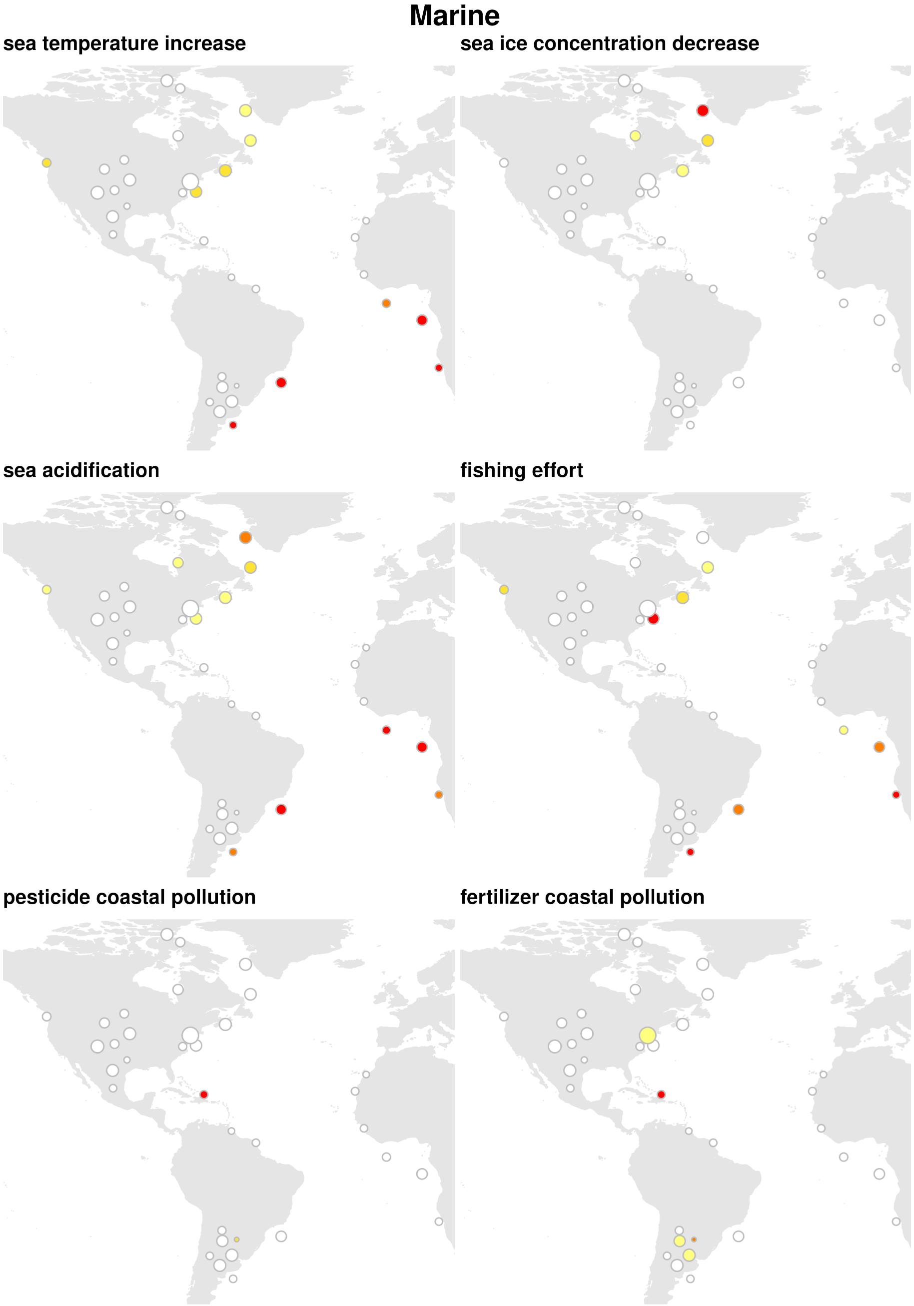
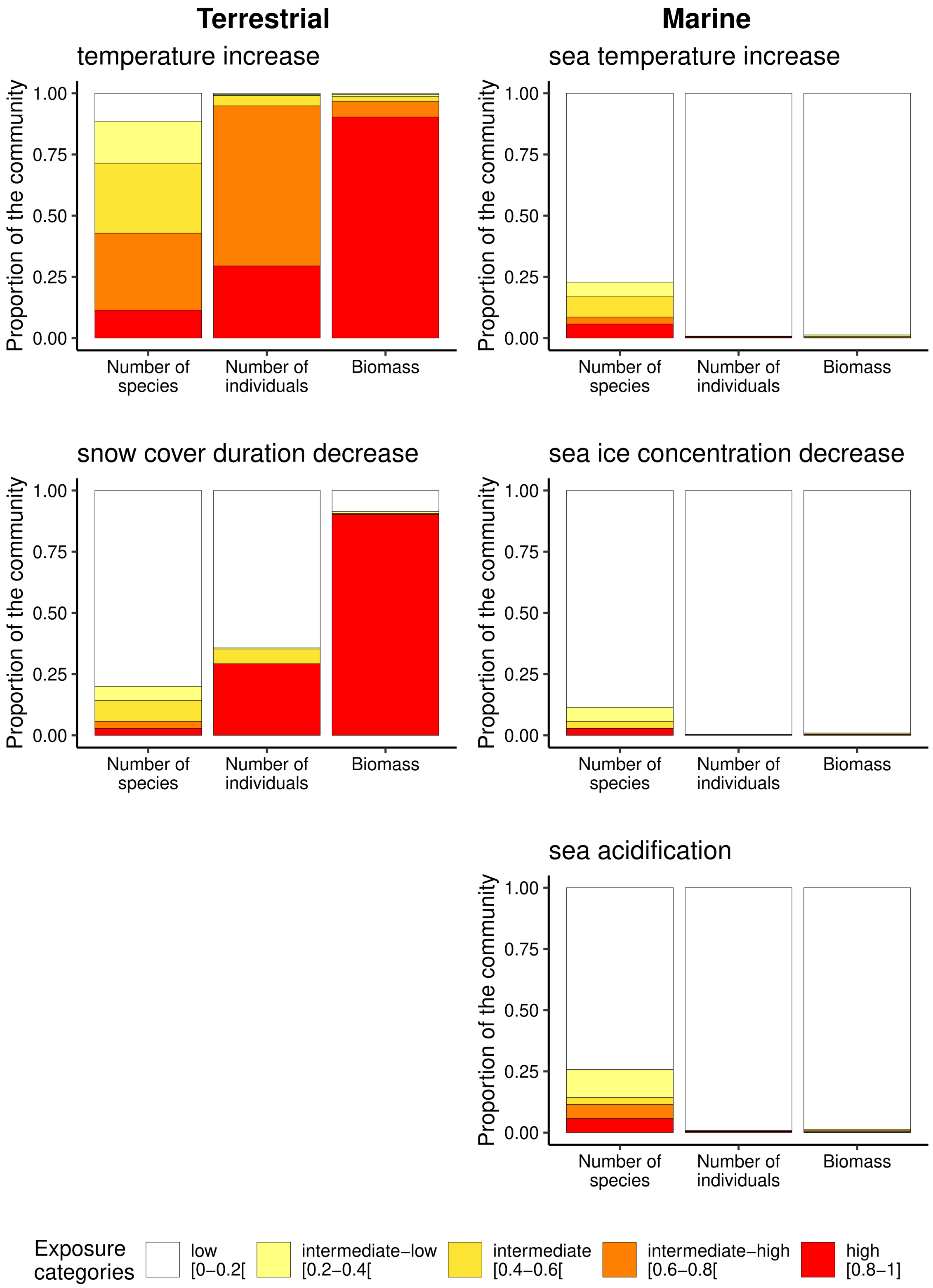
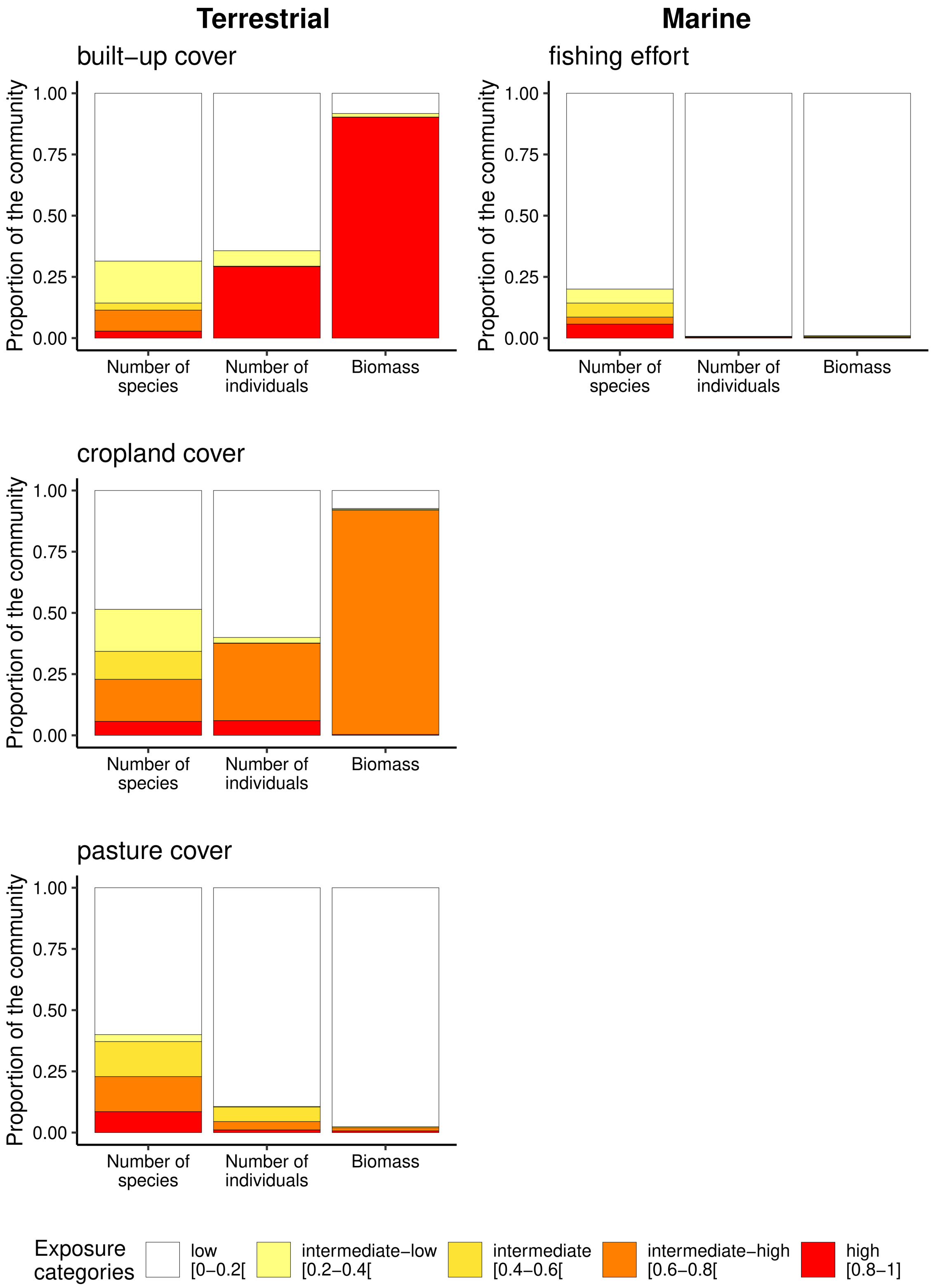


Figure 4.11 – Maps of the non-breeding range centroid of partially migratory and migratory species from the Bylot Island community colored by their relative exposure to different variables of environmental perturbations in terrestrial and marine environments. Circle colors indicate exposure categories: white = low [0-0.2[, pale yellow = intermediate-low [0.2-0.4[, light orange = intermediate [0.4-0.6[, orange = intermediate-high [0.6-0.8[, and red = high [0.8-1]. Circle size is proportional to the log-transformed biomass of adults in the Bylot Island food web.


Terrestrial
Marine
temperature increase
sea temperature increase
snow cover duration decrease
sea ice concentration decrease
sea acidification
Proportion of the community
0.00
0.25
0.50
0.75
1.00
Number of species
Number of individuals
Biomass
Exposure categories
low [0–0.2[
intermediate–low [0.2–0.4[
intermediate [0.4–0.6[
intermediate–high [0.6–0.8[
high [0.8–1]


Terrestrial
Marine
built−up cover
fishing effort
cropland cover
pasture cover
Proportion of the community
1.00
0.75
0.50
0.25
0.00
Number of species
Number of individuals
Biomass
Exposure categories
low [0−0.2[
intermediate−low [0.2−0.4[
intermediate [0.4−0.6[
intermediate−high [0.6−0.8[
high [0.8−1]

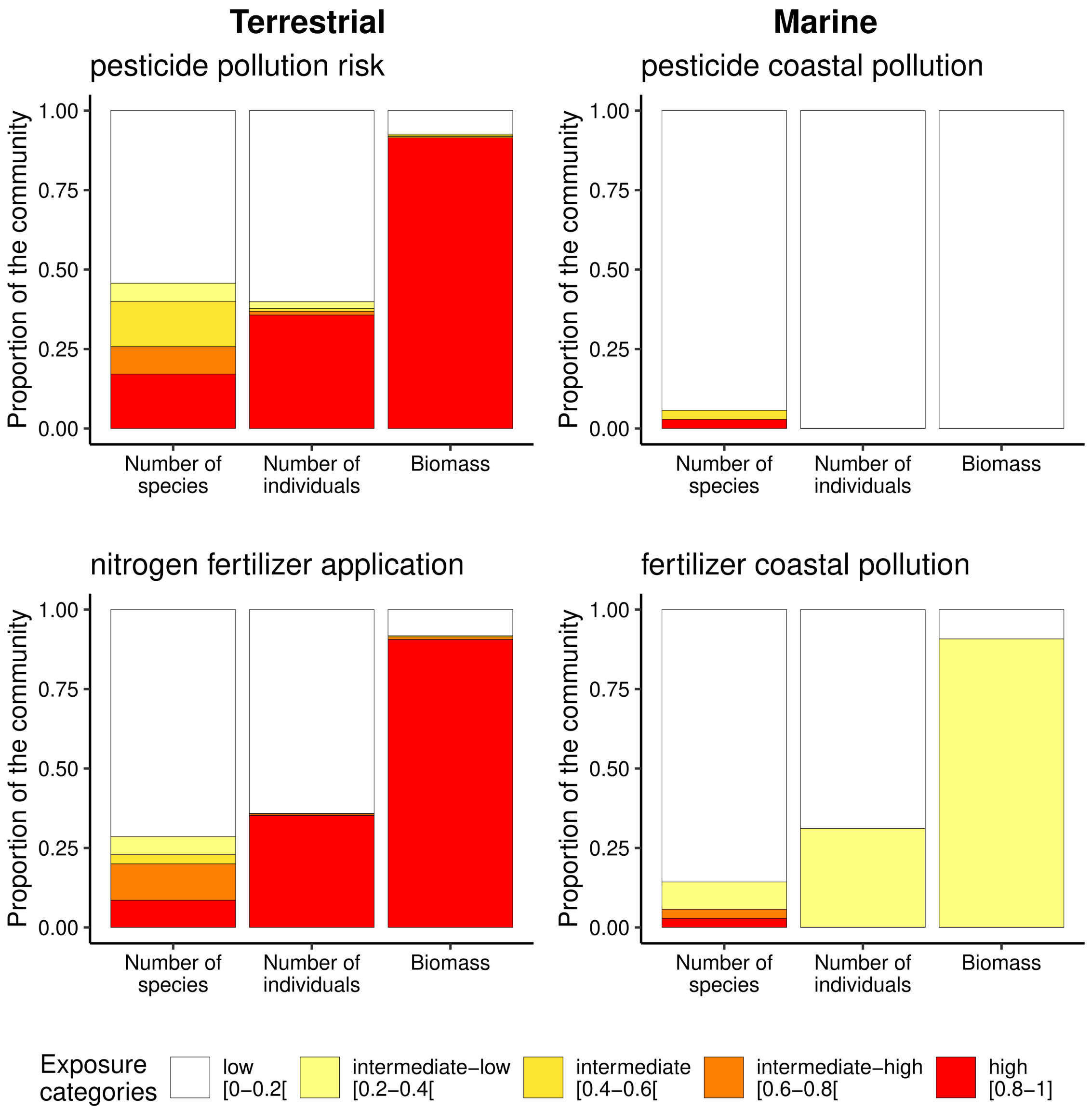
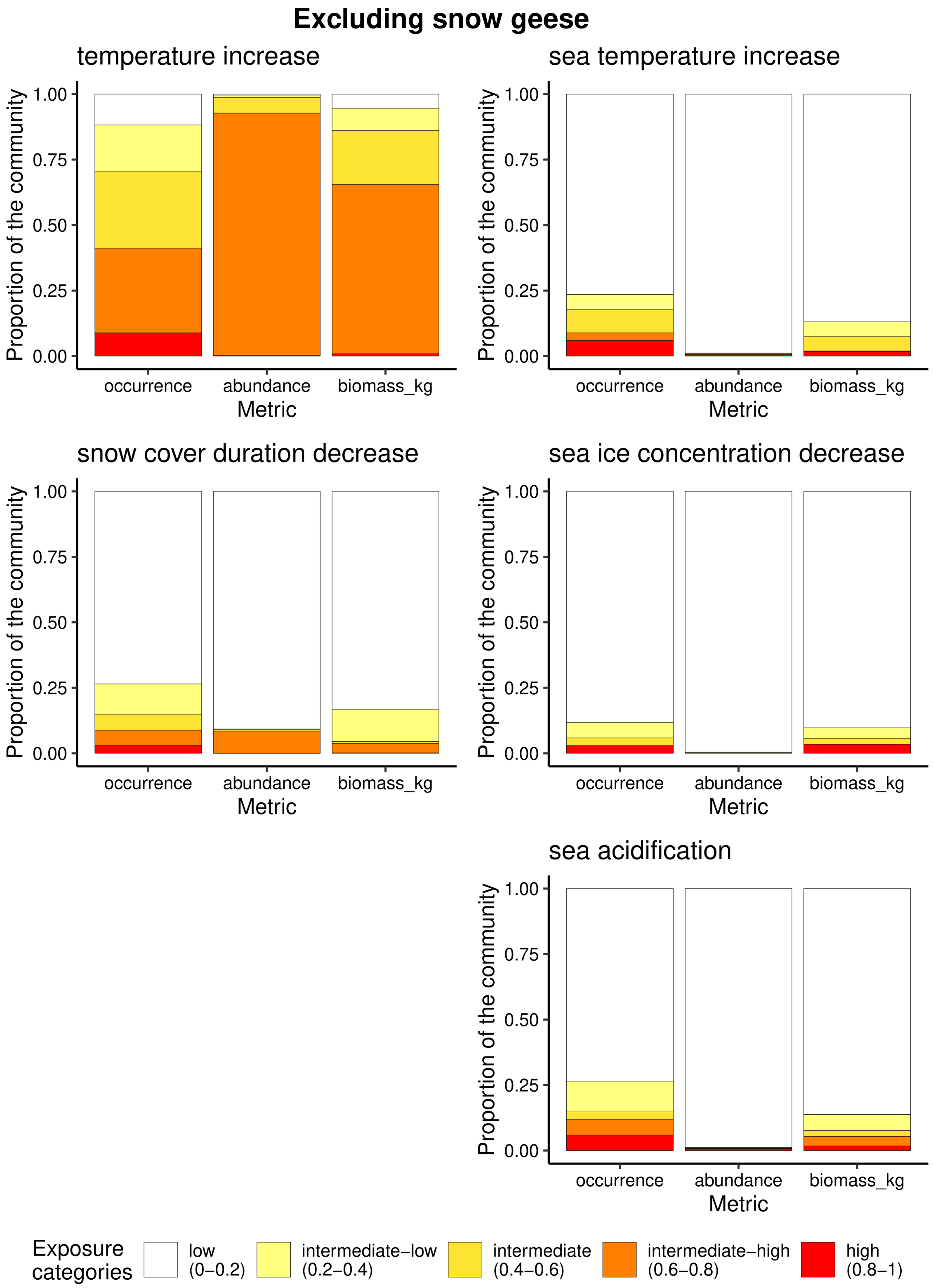
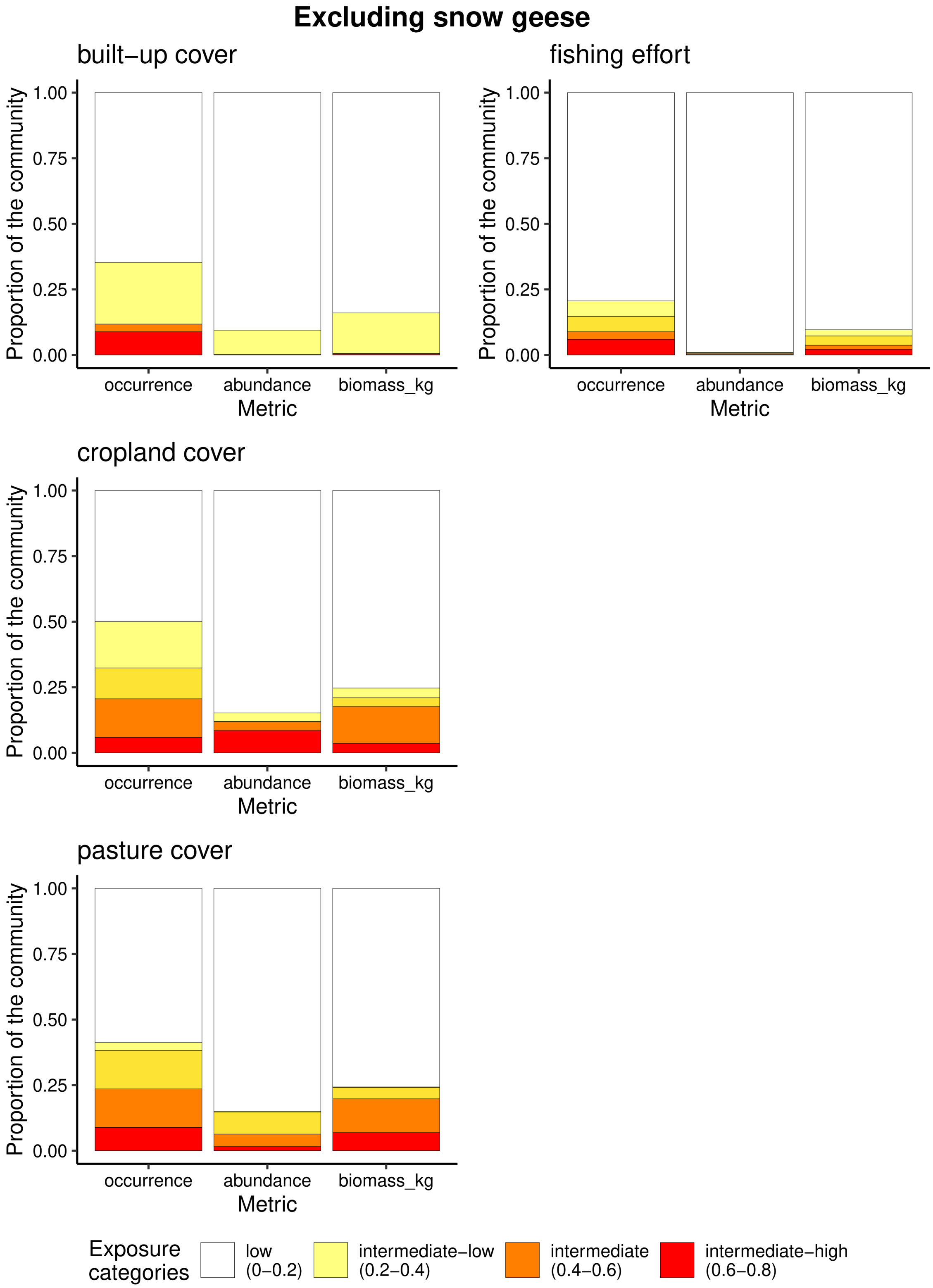


Figure 4.12 – Proportion of the Bylot Island community in terms of number of species, individuals and biomass assigned to each category of relative exposure for different variables of environmental perturbations in terrestrial and marine environments.


Excluding snow geese
temperature increase
sea temperature increase
snow cover duration decrease
sea ice concentration decrease
sea acidification
Proportion of the community
1.00
0.75
0.50
0.25
0.00
occurrence
abundance
biomass_kg
Metric
Exposure categories
low (0–0.2)
intermediate−low (0.2–0.4)
intermediate (0.4–0.6)
intermediate−high (0.6–0.8)
high (0.8–1)


Excluding snow geese
built−up cover
fishing effort
cropland cover
pasture cover
Proportion of the community
1.00
0.75
0.50
0.25
0.00
occurrence
abundance
biomass_kg
Metric
Exposure categories
low (0−0.2)
intermediate−low (0.2−0.4)
intermediate (0.4−0.6)
intermediate−high (0.6−0.8)

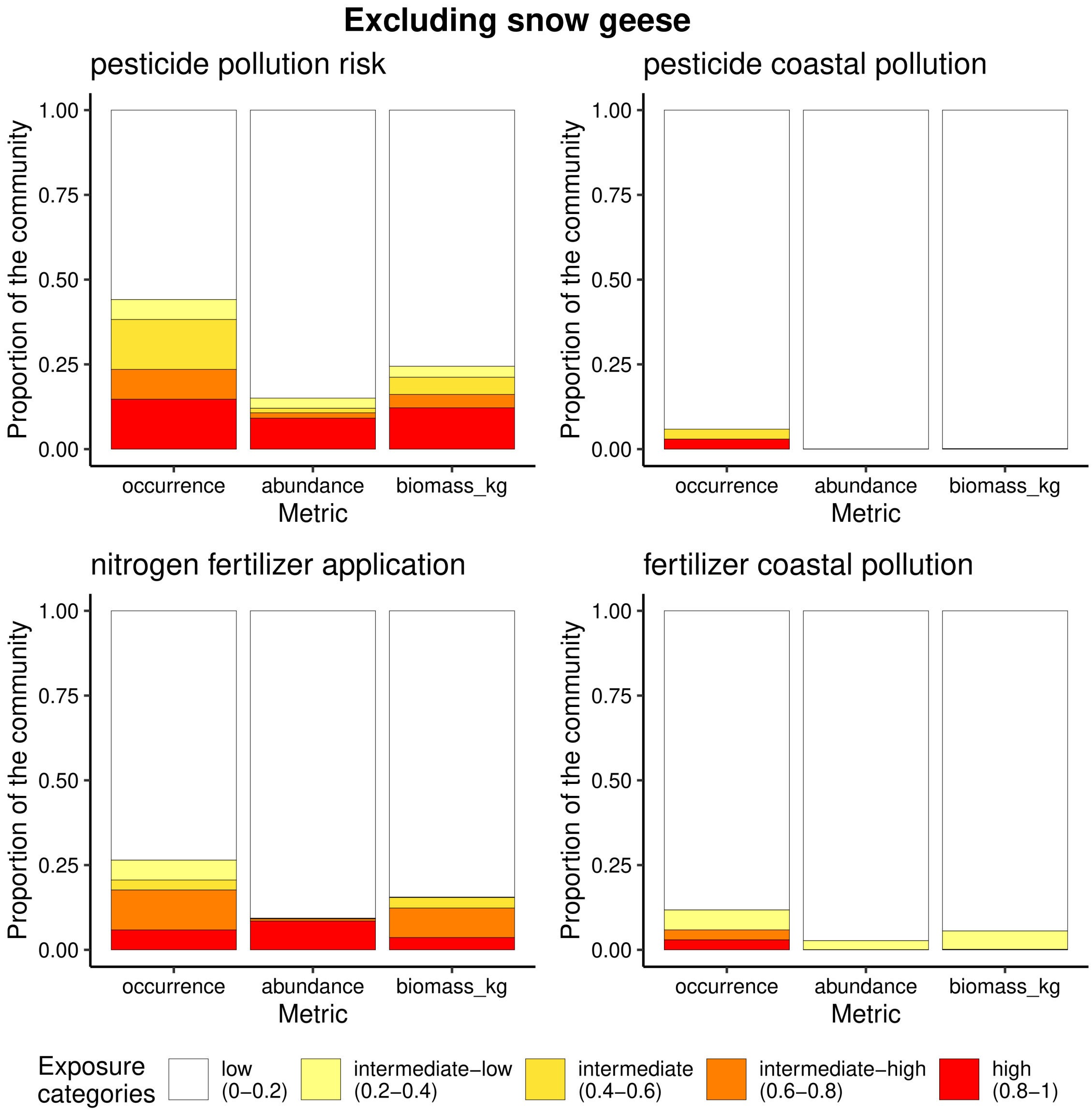


Figure 4.13 – Proportion of the Bylot Island community in terms of number of species, individuals and biomass assigned to each category of relative exposure for different variables of environmental perturbations in terrestrial and marine environments, when snow geese are excluded.

CONCLUSION GÉNÉRALE

4.12 Contexte

Au cours de leur cycle annuel, les espèces migratrices transportent de l'énergie et de la matière entre les écosystèmes qu'elles visitent, et interagissent avec les espèces des réseaux trophiques locaux (Holdo et al., 2011; Bauer and Hoye, 2014). Des changements dans les conditions environnementales d'un site utilisé pendant la période de non-reproduction d'une espèce migratrice peuvent ainsi moduler l'abondance de cette espèce et conséquemment générer des effets en cascades sur le site de reproduction (Jefferies, 2004; Hessen et al., 2017; Springer et al., 2018). De plus, des contaminants ou des pathogènes présents sur une aire d'hivernage peuvent se propager aux sites de reproduction *via* les espèces migratrices (Madigan et al., 2012; Hill et al., 2016). La structure et la dynamique des communautés comprenant des espèces migratrices peuvent être influencées par des perturbations environnementales qui surviennent dans des environnements éloignés, mais connectés par la migration. Toutefois, les patrons de migration ont été rarement étudiés à l'échelle des communautés, tant empiriquement que théoriquement. Ce manque de connaissances limite actuellement notre compréhension de l'influence des espèces migratrices sur la vulnérabilité des systèmes naturels face aux perturbations environnementales. Les objectifs de cette thèse sont de proposer un cadre d'étude de la connectivité générée par les migrations animales à l'échelle des communautés, et de l'appliquer à la communauté de vertébrés arctiques de l'île Bylot pour en illustrer l'intérêt empirique.

4.13 Contributions principales

Dans le premier chapitre de cette thèse, nous proposons une avancée conceptuelle majeure en combinant la représentation traditionnelle d'un réseau de migration à l'échelle d'une espèce avec celle d'un réseau écologique d'une communauté pour obtenir un réseau de migration d'une communauté « *community migration network* ». Cette représentation originale est accompagnée d'une interprétation spécifique des métriques traditionnelles des réseaux dans le contexte de migration à l'échelle des communautés. L'approche conceptuelle proposée est simple et généralisable et donc peut facilement être appliquée à d'autres communautés à travers l'Arctique ou bien à d'autres types d'écosystèmes. Nous avons également caractérisé pour la première fois la structure des patrons migratoires pour une communauté entière de vertébrés, montrant ainsi que les communautés de vertébrés de la toundra peuvent faire partie intégrante de vastes réseaux écologiques comprenant des centaines d'écorégions réparties à travers le globe par le biais des espèces migratrices.

Dans le cadre du deuxième chapitre, nous avons bénéficié d'un des suivis les plus intensifs pour une communauté de vertébrés terrestres en Arctique (Gauthier et al., 2024*b*) afin d'estimer l'abondance et la biomasse annuelle ou moyenne de l'ensemble des espèces. Les séries temporelles à long terme de l'abondance de proies et prédateurs sont relativement rares en milieu terrestre, et particulièrement en Arctique où la logistique associée à la collecte de données terrain est difficile et coûteuse (Mallory et al., 2018). Le jeu de données résultant représente une opportunité unique pour les écologistes des communautés afin d'évaluer les changements de biodiversité passés, actuels et futurs, ainsi que modéliser la dynamique trophique au sein d'une communauté terrestre arctique.

Dans le troisième chapitre, nous avons combiné les aires de non-reproduction des espèces migratrices définies au premier chapitre (voir **Annexe 1**) et l'abondance et la biomasse moyenne des espèces estimées au deuxième chapitre, afin de quantifier pour la première fois les connexions migratoires maintenues par les espèces migratrices d'une communauté (**Figure 4.14**). Cela nous a permis de montrer que l'occurrence, l'abondance et la biomasse des espèces fournissent de l'information complémentaire sur la structure des réseaux de migration des communautés, autant sur le rôle structural des espèces au sein du réseau de migration qu'au niveau des propriétés émergentes du réseau. Cette observation suggère que différents types de perturbations environnementales (ex. introduction de contaminants, exposition à un nouveau pathogène ou changements d'abondance) se propagent différemment au sein des réseaux de migration des communautés. L'évaluation exhaustive de la vulnérabilité d'une communauté face aux perturbations externes requiert alors la prise en compte conjointe de l'occurrence, de l'abondance et de la biomasse des espèces. Dans le cadre du quatrième chapitre, nous avons utilisé les aires de non-reproduction des espèces afin de caractériser pour la première fois l'exposition à des perturbations environnementales d'une communauté via les destinations migratoires des espèces. Nous avons montré que malgré une faible exposition apparente aux pressions anthropiques directes, les communautés de vertébrés terrestres arctiques peuvent tout de même être exposées à diverses perturbations environnementales via les sites de non-reproduction des espèces migratrices. La thèse propose ainsi une approche conceptuelle novatrice pour étudier la migration à l'échelle des communautés, appuyée par des cas empiriques originaux rendus possibles grâce à un jeu de données unique issu de décennies de collectes sur le terrain.

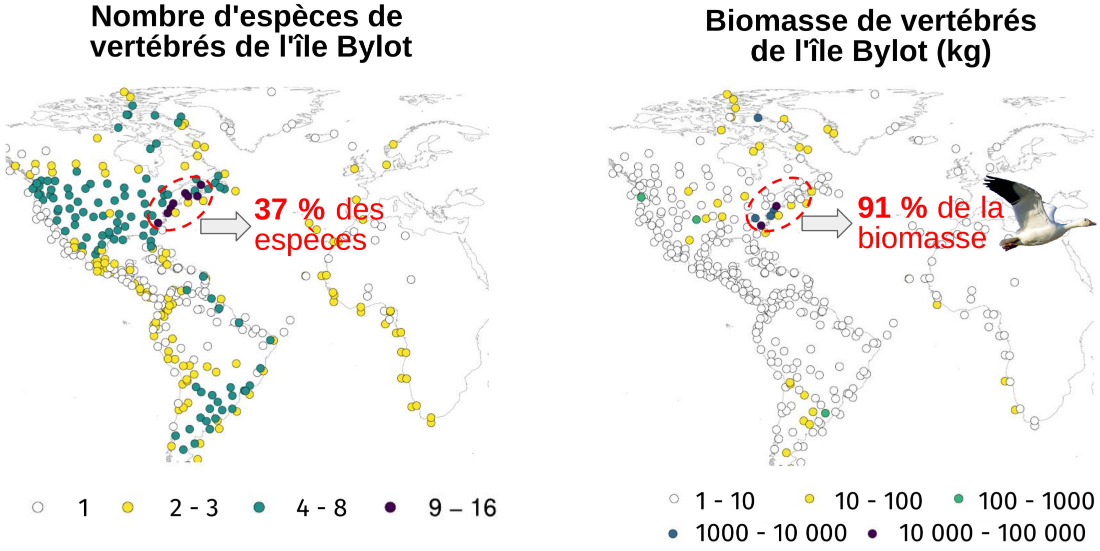


FIGURE 4.14 – Répartition géographique du nombre d'espèces de vertébrés (à gauche) et de la biomasse (à droite) de l'île Bylot au sein des écorégions pendant la période de non-reproduction. Chaque point représente le centroïde géographique d'une écorégion distincte. Les couleurs correspondent à des classes logarithmiques de richesse spécifique et de biomasse.

4.14 Interprétations des principaux résultats

La variabilité intra et interspécifique relativement élevée des stratégies migratoires observées dans la communauté de l'île Bylot pourrait expliquer le grand nombre de connexions migratoires ainsi que la faible connectance du réseau de migration. Il est commun que les oiseaux migrateurs d'une même population présentent une grande variation dans leur destination de migration et se retrouvent souvent à plusieurs centaines de kilomètres les un des autres en période de non-reproduction (Finch et al., 2017). Cela pourrait expliquer le nombre relativement élevé de connexions migratoires maintenues par chaque espèce (33 ± 46 écorégions) au sein du réseau de migration de l'île Bylot. D'un autre côté, la différence des habitats utilisés par les espèces en période d'hivernage pourrait contribuer à la variation interspécifique des stratégies migratoires. Par exemple, certaines espèces migratrices se retrouvent strictement en milieu terrestre (plectrophane lapon, bécasseau de Baird et bécasseau à poitrine cendrée), côtier (bécasseau maubèche, tournepierre à collier et pluvier argenté) ou pélagique (plongeon du Pacifique, labbes et phalarope à bec large) en période de non-reproduction, ce qui diminue le chevauchement spatial entre les espèces. De plus, nous avons observé une grande divergence des stratégies migratoires entre certaines espèces d'un même genre taxonomique (ex. *Gavia* - plongeons, *Pluvialis* - pluviers et *Calidris* - bécasseaux). Cela suggère qu'une forte flexibilité évolutive des traits migratoires (Helbig, 2003; Winger et al., 2012) pourrait contribuer à augmenter la variabilité interspécifique des stratégies migratoires à l'échelle de la communauté. Ainsi, au sein du réseau de migration, une forte variabilité intraspécifique et interspécifique des stratégies migratoires pourrait générer un nombre élevé de connexions migratoires avec une faible connectance.

La position géographique d'une communauté par rapport aux principaux corridors de migration pourrait influencer la structure de son réseau de migration. L'île Bylot se situe à la jonction des voies migratoires de l'Atlantique-Amériques et de l'Atlantique-Est, et relativement près de la voie migratoire du centre des Amériques (voir **Figure 0.2** pour la distribution des corridors de migration). La majorité des espèces de l'île Bylot se retrouvent dans le corridor de migration de l'Atlantique-Amériques et du centre des Amériques et quelques espèces de limicoles et les labbes empruntent le corridor de migration de l'Atlantique-Est. On ne retrouve qu'une seule espèce migrant du côté Pacifique (Plongeon du Pacificique) et aucune espèce ne migre vers l'Asie ou l'Océanie pour la période de non-reproduction. Ainsi, la localisation de l'île Bylot à la jonction de plusieurs corridors de migration pourrait favoriser un nombre plus élevé de connexions migratoires, une connectance plus faible et contribuer à la formation de modules au sein du réseau de migration. Les patrons migratoires à l'échelle des communautés ont été peu décrits, toutefois, selon des résultats préliminaires, les espèces migratrices d'une communauté de la toundra située au nord de l'Alaska (*Arctic Wildlife Refuge*) semblent se répartir sur un gradient longitudinal encore plus étendu, avec des espèces migrant vers chacun des continents pendant la période de non-reproduction (**Figure 0.8** ; Sullender 2019). Cette communauté est notamment située à la jonction de nombreux corridors de migration : Pacifique-Amérique, centre des Amériques et Asie orientale-Australie, et près du corridor de migration du centre de l'Asie. Nous proposons alors l'hypothèse que plus une communauté se situe à la jonction de nombreux corridors de migration, plus son réseau de migration est étendu et présente une faible connectance et une forte modularité. La position d'une communauté par rapport aux grandes barrières écologiques globales pour les espèces migratrices (chaînes de montagnes, océans, golfes, calottes polaires et déserts) pourrait ainsi influencer la structure de son réseau de migration. De par la convergence des corridors migratoires vers les pôles, cela pourrait générer des réseaux de migration plus étendus en Arctique que dans les milieux boréaux ou tempérés.

Les compromis effectués par les espèces migratrices afin de maximiser leur efficacité énergétique pourraient expliquer la forte connexion observée entre la communauté arctique de l'île Bylot et les écorégions tempérées d'Amérique du Nord. La migration saisonnière semble représenter une stratégie adaptative afin de maintenir une fidélité à un site de reproduction au sein d'environnements saisonniers (Winger et al., 2019). Les espèces migratrices visent généralement à minimiser la distance de migration et les coûts de thermorégulation tout en visant à maximiser l'accès aux ressources pendant la période de non-reproduction (Somveille et al., 2015, 2018, 2019). Pour les espèces migratrices arctiques, rejoindre les milieux tempérés de l'hémisphère nord pourrait alors représenter un compromis intéressant entre la distance de migration, le climat et l'accès aux ressources. Toutefois, le compromis optimal pourrait varier selon les traits des espèces (Somveille et al., 2019). Par exemple, les limicoles présentent des adaptations morphologiques, physiologiques et métaboliques pour le vol de longue distance (Kersten and Piersma, 1987; Minias et al., 2015), ce qui peut influencer le compromis optimal. Pour ces oiseaux adaptés au vol de longue distance, maximiser l'accès aux ressources en profitant de l'été austral, malgré une distance de migration plus élevée, pourrait selon Henningsson and Alerstam (2005) représenter un statégie optimale. La maximisation de l'efficacité énergétique des individus migrateurs pourrait ainsi représenter un mécanisme structurant au sein des réseaux de migration des communautés, générant de fortes connexions migratoires entre les écosystèmes arctiques et tempérés de l'hémisphère nord.

Les caractéristiques de l'habitat au sein d'une communauté pourraient agir comme un facteur déterminant pour l'exposition aux perturbations environnementales des espèces migratrices à travers leur cycle annuel. Dans les écosystèmes de toundra, la végétation basse crée un paysage ouvert où, durant la saison de reproduction, la plupart des espèces s'alimentent et détectent leurs prédateurs au sol. Considérant l'adaptation des espèces migratrices aux caractéristiques des habitats de la toundra, nous proposons que ces espèces tendent à rechercher des caractéristiques d'habitats similaires en période de non-reproduction. En support, à l'échelle du globe, les espèces migratrices de longue distance tendent à maintenir une niche environnementale similaire au cours de leur cycle annuel (Zurell et al. 2018, mais voir Somveille et al. 2019). Toutefois, les milieux ouverts avec une végétation basse à l'extérieur de l'Arctique sont représentés par les prairies naturelles et les terres agricoles. Ainsi, les contraintes évolutives associées à l'habitat de reproduction des espèces migratrices de la toundra pourraient les prédisposer à une exposition aux perturbations environnementales associées aux prairies naturelles et aux milieux agricoles. Suivant cette logique, les espèces migratrices se reproduisant dans une communauté boréale pourraient se retrouver davantage exposées aux perturbations environnementales associées aux milieux forestiers pendant la période de non-reproduction. À l'échelle du globe, les Amériques et l'Europe-Afrique montrent une distribution latitudinale similaire des superficies cultivées avec une forte proportion dans les milieux tempérés de l'hémisphère nord (Potapov et al., 2022). Nous proposons alors l'hypothèse que les communautés toundriques de l'Amérique du Nord et de l'Europe présentent une exposition relativement élevée aux perturbations d'origines agricoles.

4.15 Limites

La réalisation d'études empiriques à l'échelle d'une communauté nécessite souvent l'intégration de sources de données variées, avec une incertitude plus élevée associée à l'aire de non-reproduction, l'abondance et la biomasse de certaines espèces. Dans certains cas, nous avons eu recours à des données de haute précision et représentativité présentant ainsi une relativement faible incertitude. Par exemple, les suivis d'individus équipés de dispositifs de géolocalisation directement au site d'étude ont permis de définir l'aire de non-reproduction de certaines espèces. Nous avons également utilisé des données issues de suivis systématiques spécifiques afin d'estimer la densité d'individus ou de nids de plusieurs espèces. Dans d'autres cas, nous avons eu recours à des données moins précises et représentatives, comme les cartes de répartition pour définir l'aire de non-reproduction de plusieurs espèces, ou les suivis de nids et les observations opportunistes pour estimer l'abondance et la biomasse au site d'étude. Ainsi, pour certaines espèces, il y a une plus grande incertitude associée à l'aire d'hivernage, l'abondance et la biomasse estimée, mais celle-ci n’a pas été formellement quantifiée. Cette lacune constitue un obstacle à l’évaluation de l’incertitude associée aux métriques du réseau de migration, ce qui complique les comparaisons futures avec d’autres sites à travers l’Arctique. Néanmoins, nous estimons que répéter l’exercice avec un jeu de données optimal, fondé sur des informations de haute précision et représentativité pour l’ensemble des espèces de la communauté, ne devrait pas modifier qualitativement les patrons généraux observés, tels que le nombre élevé (c.-à-d. des centaines) de connexions migratoires maintenues entre l’île Bylot et des écorégions distantes, la faible connectance du réseau, la présence de modules, les fortes connexions avec les écorégions terrestres tempérées, et l’exposition relativement élevée aux perturbations d’origine agricole. En ce sens, en considérant uniquement les espèces pour lesquelles des individus du site d’étude ont été suivis à l’aide de dispositifs de localisation (GPS ou géolocalisateurs), nous avons observé que ces espèces occupent 97 écorégions différentes durant la période de non-reproduction. De plus, à titre d’analyse de sensibilité, nous avons observé que le nombre total d’écorégions et la connectance du réseau demeurent robustes face au retrait aléatoire d’espèces (**Figure 4.15**).

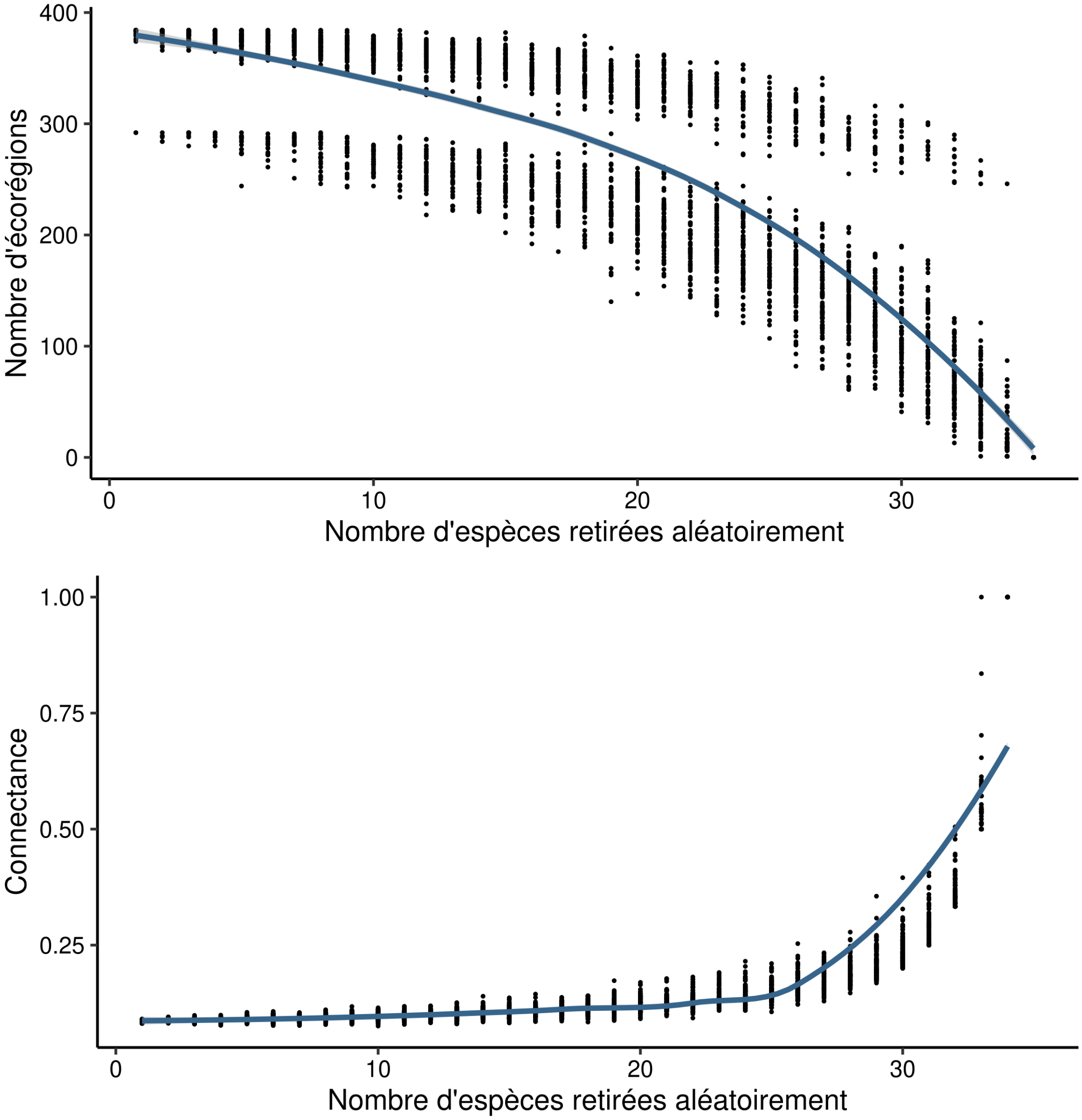


Figure 4.15 – Nombre total d'écorégions (en haut) et connectance (en bas) du réseau de migration de l'île Bylot en fonction du nombre d'espèces retirées aléatoirement. La courbe bleue correspond à un ajustement par régression polynomiale locale (fonction *loess*).

L'utilisation de sources de données sous-optimales pourrait toutefois influencer quantitativement certains patrons spécifiques observés, notamment le rôle structurel de certaines espèces ou écorégions dans le réseau de migration de l'île Bylot. Par exemple, l'utilisation de cartes de distribution des espèces, raffinées avec les corridors de migration des populations de l'est de l'Arctique canadien, tend à surestimer le nombre d'écorégions dans lesquelles une espèce se trouve en période de non-reproduction (voir **Figure 1.11**). Des espèces comme le faucon pèlerin, présentant une répartition très étendue, pourraient ainsi surestimer le nombre absolu d'écorégions occupé en période de non-reproduction (voir **Annexe 1**). Il semble toutefois que les faucons pèlerins d'un même site arctique puissent se répartir sur un large gradient latitudinal et longitudinal (Gosler et al., 2012; Mattox and Restani, 2014). En raison de l'absence d'incertitude associée à l'aire de non-reproduction de plusieurs espèces migratrices, et donc au rôle structurel des écorégions dans le réseau de migration de l'île Bylot, nous avons évité de présenter les résultats pour des écorégions spécifiques. Cette approche aurait pourtant permis d'identifier les écorégions où les efforts de conservation en dehors de l'Arctique devraient être ciblés. En revanche, à l'échelle de la communauté, il est peu probable que le nombre de connexions migratoires maintenues entre l'île Bylot et des écorégions distantes soit d'un ordre de grandeur différent (c.-à-d. des centaines), compte tenu de la grande diversité des stratégies migratoires. De même que pour l'abondance des espèces, nous pourrions observer une diminution ou une augmentation de l'abondance moyenne de certaines espèces si chacune des espèces était suivie de façon systématique à travers le site d'études. Par contre, il serait surprenant que l'ordre de grandeur de l'abondance des espèces (c.-à-d. dizaines, centaines, milliers ou dizaines de milliers d'individus) change drastiquement en utilisant des données de plus grande qualité. De plus, les espèces présentant les plus grandes abondances et biomasses dans la communauté sont suivies de façon systématique (c.-à-d. oie des neiges, lemmings, plectrophane lapon, bécasseau de Baird, labbe à longue queue, renard arctique, bernache de Hutchins et pluvier bronzé).

L'identification de modules au sein d'un réseau nécessite l'utilisation d'algorithmes, et le choix de celui-ci peut influencer la composition ainsi que le nombre de modules détectés (Beckett, 2016). Étant donné que la représentation par réseau proposée dans cette thèse repose sur une définition novatrice des nœuds et des arêtes, il demeure incertain quel type d'algorithme de modularité serait le plus adapté au réseau de migration d'une communauté, et si le développement d'un algorithme spécifique tenant compte de la nature saisonnière des mouvements migratoires est préférable. L'impact du choix de l'algorithme de modularité pourrait être plus marqué dans les régions où plusieurs espèces se chevauchent en période d'hivernage, comme en Amérique du Nord et dans le sud de l'Amérique du Sud.

4.16 Perspectives de recherche future

Perspectives empiriques

La comparaison de réseaux de migration de différentes communautés le long d'un gradient latitudinal pourrait révéler des patrons biogéographiques globaux. Bien que la caractérisation du réseau de migration de l'île Bylot demeure descriptive, elle constitue un point de repère pour formuler des hypothèses générales sur la structure des réseaux de migration des communautés terrestres arctiques.

Il est probable que la structure des réseaux de migration des communautés varie selon la latitude, en raison du gradient latitudinal du nombre, de la proportion et des traits des espèces migratrices (Newton and Dale, 1996; Somveille et al., 2013; Ganter et al., 2013; Saulnier-Talbot et al., 2024). La diminution progressive de la richesse spécifique des espèces migratrices aviaires entre 40 et 80°N (Newton and Dale, 1996; Somveille et al., 2013) pourrait générer un gradient latitudinal de la connectance des réseaux de migration des communautés. La proportion d'espèces côtières et marines au sein des communautés d'oiseaux augmente progressivement des milieux tempérés jusqu'au Haut-Arctique (Newton and Dale, 1996; Piersma, 2007). Étant donné que plusieurs espèces côtières ou marines, comme les limicoles et les labbes, effectuent des migrations transhémisphériques, il est probable que l'importance des connexions migratoires transhémisphériques et des connexions migratoires avec des écorégions côtières et marines augmente avec la latitude. Comme mentionné à la section précédente, la convergence des corridors de migration vers les pôles pourrait générer des réseaux de migration plus étendus avec une plus faible connectance et une plus forte modularité avec la latitude. De même qu'effectuer des comparaisons de réseaux de migration de communautés le long d'un gradient longitudinal permettrait de tester si la localisation d'une communauté par rapport aux corridors de migrations globaux augmente l'étendue de son réseau de migration et influence la connectance et la modularité. Effectuer la caractérisation de réseaux de migration le long d'un gradient latitudinal permettrait d'évaluer comment les réseaux de migration de différentes communautés sont interreliés par le biais de régions communes situées dans d'autres biomes et utilisées par les espèces migratrices. Identifier l'interconnectivité de communautés utilisées pour la reproduction des espèces migratrices par le biais d'aires de non-reproduction permettrait ainsi d'évaluer si les perturbations environnementales se produisant en milieux tempérés ou tropicaux représentent le même risque de cascade spatiale pour les communautés boréales, subarctiques, arctiques et de l'extrême Haut-Arctique (**Figure 4.16**).

Dans le cadre de cette thèse, nous avons caractérisé la structure des connexions migratoires de la communauté en nous appuyant sur la distribution spatiale des espèces ainsi que sur leur abondance et leur biomasse moyennes, en faisant abstraction des variations interannuelles. Toutefois, certaines espèces présentent de fortes fluctuations interannuelles de biomasse (Legagneux et al., 2012; Moisan et al., 2025*a*), tandis que d'autres montrent des variations interannuelles de leur distribution hivernale (Robillard et al., 2018). Il serait donc pertinent de quantifier dans quelle mesure ces variations interannuelles modifient la structure du réseau de migration à l'échelle de la communauté.

Le concept de réseau de migration des communautés est transférable à d'autres types d'écosystèmes, sous réserve de certaines considérations. Premièrement, l'aire d'étude doit idéalement être suffisamment étendue pour inclure le domaine vital de plusieurs individus des espèces présentant les plus grands domaines vitaux au sein de la communauté, afin de représenter adéquatement la dynamique trophique à l'échelle du paysage. Deuxièmement, ce concept est particulièrement adapté à des aires d'étude caractérisées par une composition spécifique relativement homogène et spatialement circonscrite. Les écorégions constituent ainsi un cadre pertinent, car leurs limites géographiques correspondant souvent à des transitions relativement abruptes dans la composition des espèces (Smith et al., 2018). À des échelles spatiales plus fines, le concept peut également s'appliquer à des aires bien délimitées par des barrières naturelles au mouvement des animaux, telles que des îles (p. ex. l'île Bylot), des lacs, des rivières, des cavernes ou des chaînes montagneuses, permettant ainsi de circonscrire spatialement une communauté. En revanche, l'application du concept à des aires d'étude dépourvues de limites géographiques claires, situées au sein de vastes écosystèmes tels que des régions forestières ou les milieux océaniques, pourrait nécessiter des adaptations conceptuelles supplémentaires.

La modélisation de cascades spatiales via les espèces migratrices nécessitera également une meilleure compréhension de la sensibilité des espèces migratrices aux différentes perturbations environnementales à travers leur cycle annuel. Mettre en relation des tendances de populations locales ou régionales avec l'exposition de différentes perturbations dans des approches multi-dimensionnelles pourrait représenter une avenue à explorer pour quantifier la sensibilité des espèces à de multiples perturbations à travers leur cycle annuel. De plus, déterminer la capacité biotique des espèces sur leur aire de reproduction et de non-reproduction permettrait d'évaluer si un changement dans la capacité biotique d'une aire de non-reproduction devrait moduler le flux d'individus vers les aires de reproduction. Parallèlement, il serait essentiel de mieux comprendre la propagation de perturbations au sein des réseaux trophiques, ce qui pourrait se traduire entre autres par le développement de modèles mécanistiques de réponse fonctionnelle comprenant plusieurs espèces (Beardsell et al., 2022).

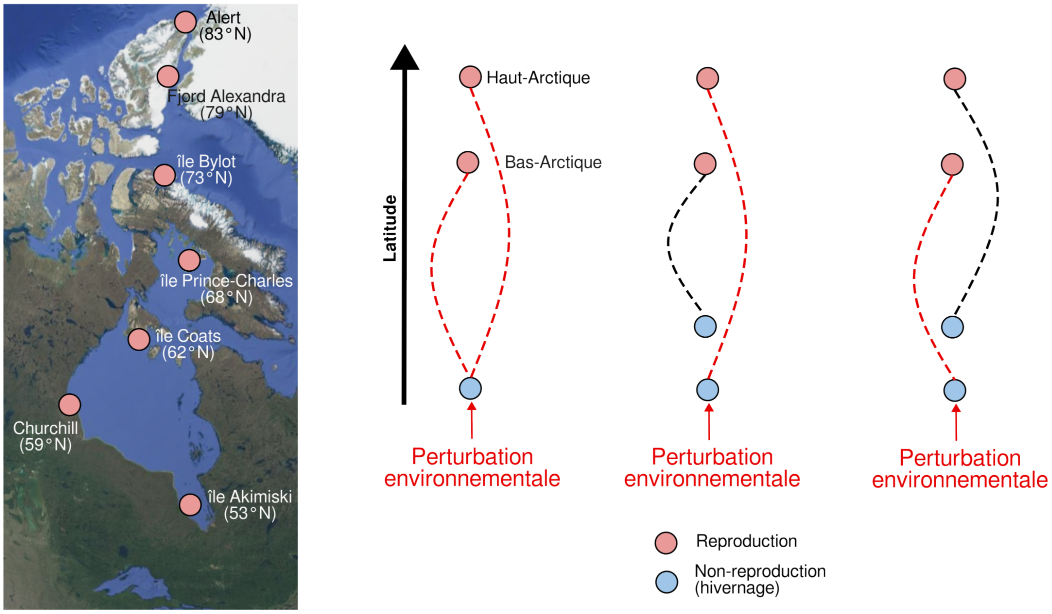


FIGURE 4.16 – Carte de sites potentiels pour caractériser et comparer les réseaux de migration le long d'un gradient latitudinal (gauche) et schéma illustrant la propagation de perturbations environnementales des sites de non-reproduction vers les sites de reproduction selon différents patrons de connexion (droite).

Il serait également pertinent d'utiliser le cas d'études de l'île Bylot afin de déterminer les facteurs et contraintes influençant la structure du réseau de migration de la communauté. Par exemple, mettre en lien la phylogénie, la niche climatique et environnementale, les traits des espèces ou les relations interspécifiques avec les connexions migratoires maintenues par les espèces afin d'évaluer l'influence relative de ces facteurs sur la structure du réseau. De même qu'une approche mécanistique de la migration (voir Somveille et al. 2018) pourrait être envisagée pour mettre en lumière l'importance relative des mécanismes sous-jacents aux patrons observés dans le cadre de cette thèse. Cette avenue de recherche permettrait ainsi une meilleure compréhension des mécanismes façonnant la structure des réseaux de migration à l'échelle des communautés.

Perspectives méthodologiques

Le développement d'une méthode standardisée afin de définir le réseau de migration d'une communauté représente une avancée méthodologique essentielle pour le futur de ce domaine de recherche. L'intérêt grandissant de la communauté scientifique pour la connectivité migratoire a mené des initiatives à grande échelle telle que l'*Atlas de la connectivité migratoire* (Project, 2025) et l'*Atlas de la migration des oiseaux eurasiens et africains* (Spina et al., 2022), ce qui pourrait nettement faciliter la transférabilité de l'approche proposée à plusieurs autres sites à travers le globe dans un futur proche.

Perspectives théoriques

L'approche présentée dans cette thèse permet de caractériser les connexions migratoires au sein d'une communauté, offrant une représentation statique de la structure du réseau de migration, mais sans en évaluer la dynamique. Il est donc nécessaire d'adapter l'approche proposée pour intégrer les interactions trophiques au sein de la communauté, afin de modéliser la propagation de cascades spatiales via les espèces migratrices. Il existe des approches mathématiques pour modéliser la propagation de cascades spatiales occasionnées par les mouvements de dispersion et d'alimentation des organismes au sein de métacommunautés (García-Callejas et al., 2019). Toutefois, aucune approche ne permet actuellement de modéliser la propagation de cascades spatiales générées par des mouvements saisonniers et bidirectionnels des organismes. Les systèmes hybrides permettent de modéliser la dynamique d'un système à plusieurs états, comme les variations saisonnières de la structure (c.-à-d. la topologie) d'un réseau trophique (Saavedra et al., 2016; Hutchison et al., 2020), et constituent ainsi une avenue prometteuse pour intégrer la migration dans l'étude des métacommunautés. Le défi consiste surtout à relier conceptuellement et mathématiquement la dynamique trophique au sein de la communauté durant une saison donnée (p. ex. la reproduction) à la répartition des espèces dans les différentes communautés occupées lors d'une autre saison (p. ex. la non-reproduction) et finalement à l'exposition aux perturbations (**Figure 4.17**).

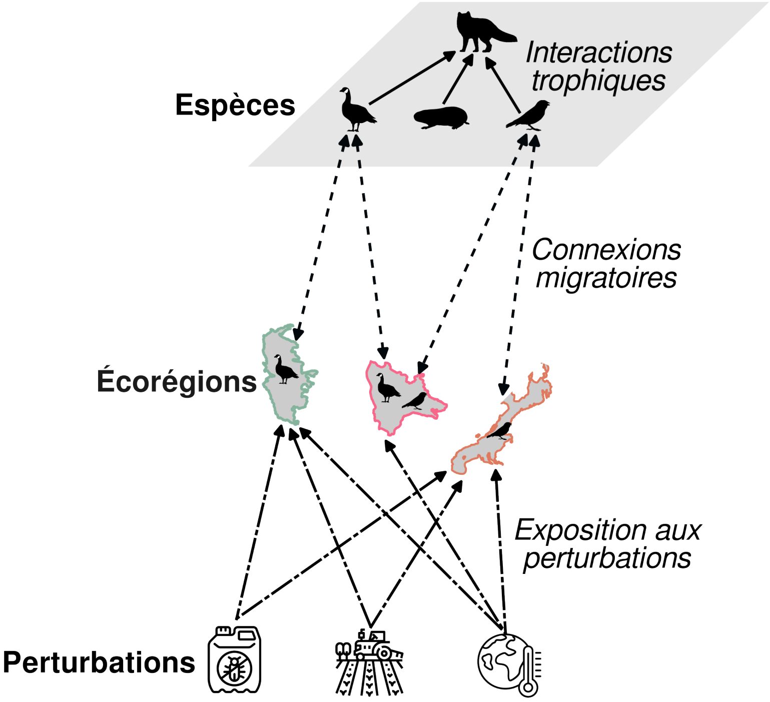


Figure 4.17 – Représentation schématique d'un réseau de migration intégrateur reliant des perturbations environnementales externes à la dynamique d'un réseau trophique focal.

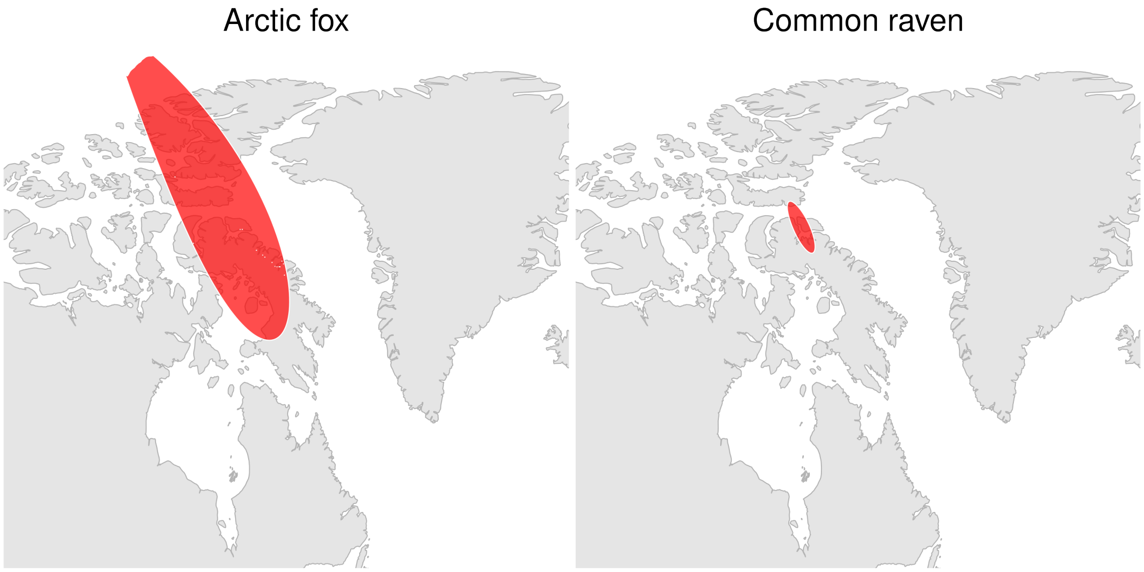
4.17 Conclusion générale

Les espèces migratrices saisonnières agissent comme un agent de couplage entre les communautés et les écosystèmes du globe (Bauer and Hoye, 2014), permettant ainsi la propagation de perturbations environnementales. Polis, Anderson et Holt ont d'ailleurs mentionné en 1997 dans leur article iconique sur la connectivité écologique que « les écologistes sont désormais conscients et conscientes que les dynamiques sont rarement confinées à une zone focale et que des facteurs extérieurs à un système peuvent considérablement influencer (voire dominer) les patrons et les dynamiques locaux ». Toutefois, dans les décennies suivantes, la migration a tout de même été peu abordée à l'échelle des communautés. Dans cette thèse, nous avons proposé un cadre original afin d'étudier les patrons de migration au sein des communautés. Nous avons révélé la complexité du réseau de connexions migratoire maintenu par l'ensemble des espèces migratrices d'une communauté de vertébrés, ce qui met en évidence la forte interconnectivité d'un écosystème terrestre arctique avec le reste du globe *via* la migration. Enfin, nous avons montré que les espèces migratrices d'une communauté peuvent être exposées à des pressions environnementales contrastées lorsque l'on considère leur destination migratoire. Par conséquent, nous souhaitons souligner l'importance d'adopter une perspective globale pour mieux comprendre la structure et la dynamique des écosystèmes et des communautés comportant des espèces migratrices. Toutefois, il s'agit d'un défi considérable en écologie, car il est difficile de relier une perturbation environnementale survenant dans un écosystème aux changements observés dans une communauté ou un écosystème situé à des milliers de kilomètres.

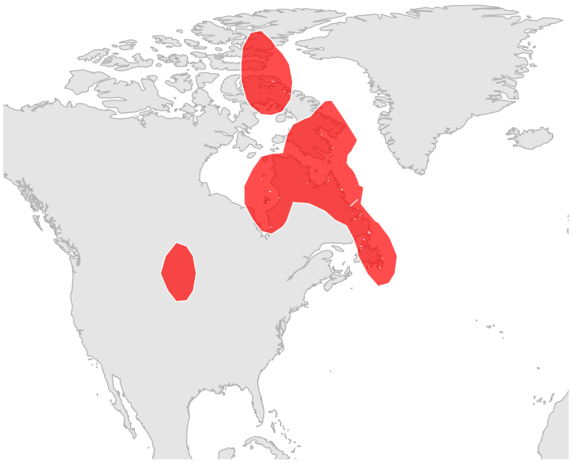
ANNEXE I

NON-BREEDING RANGE OF VERTEBRATE SPECIES IN THE BYLOT ISLAND COMMUNITY

Partial migrant and resident



Raptors and cranes



Snowy owl

Rough−legged hawk

Peregrine falcon

Sandhill crane

Jaegers and gulls

Long–tailed jaeger

Parasitic jaeger

Glaucous gull

Ducks and loons

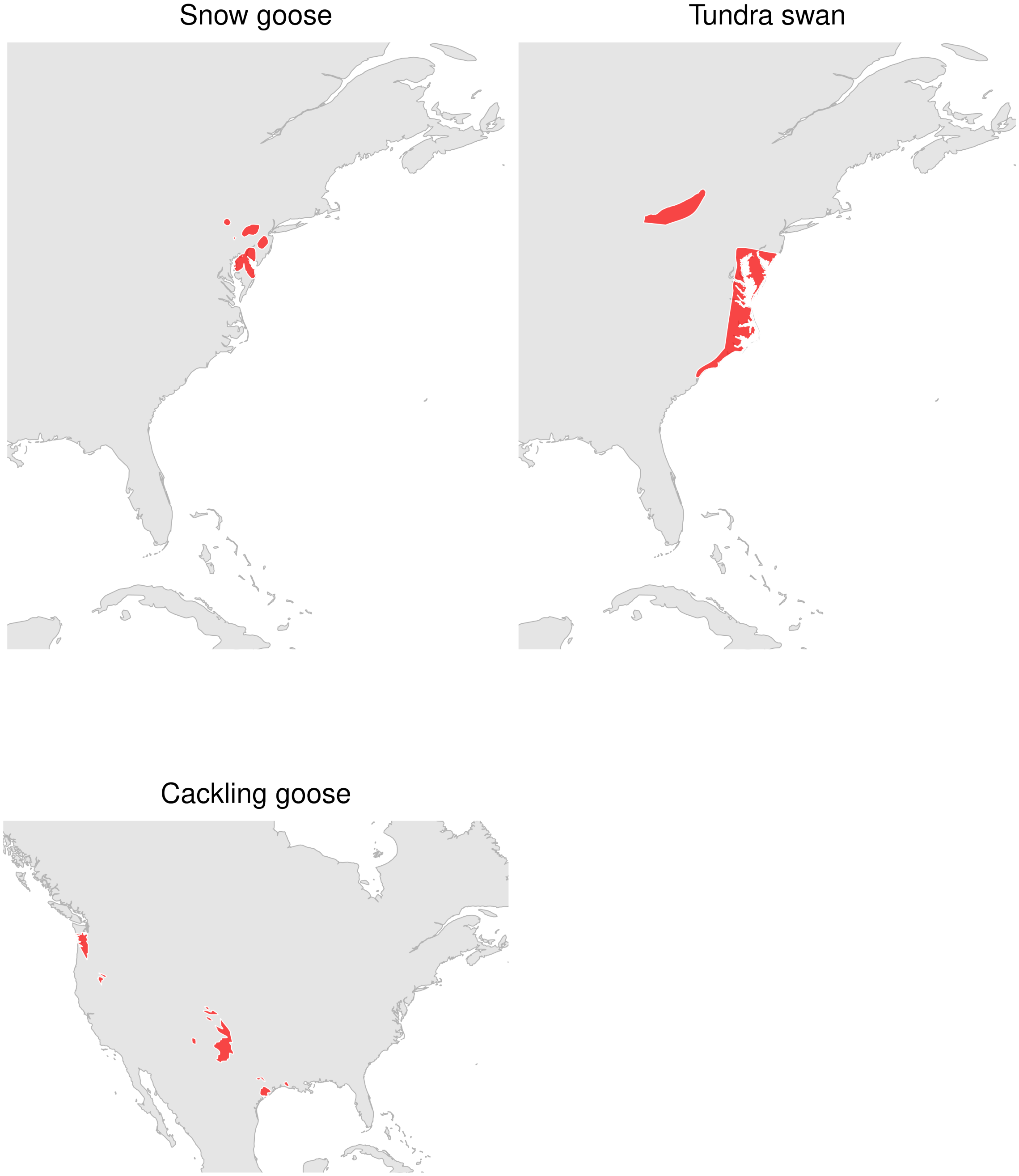
Long–tailed duck

King eider

Red–throated loon

Pacific loon

Geese and swans



Passerines

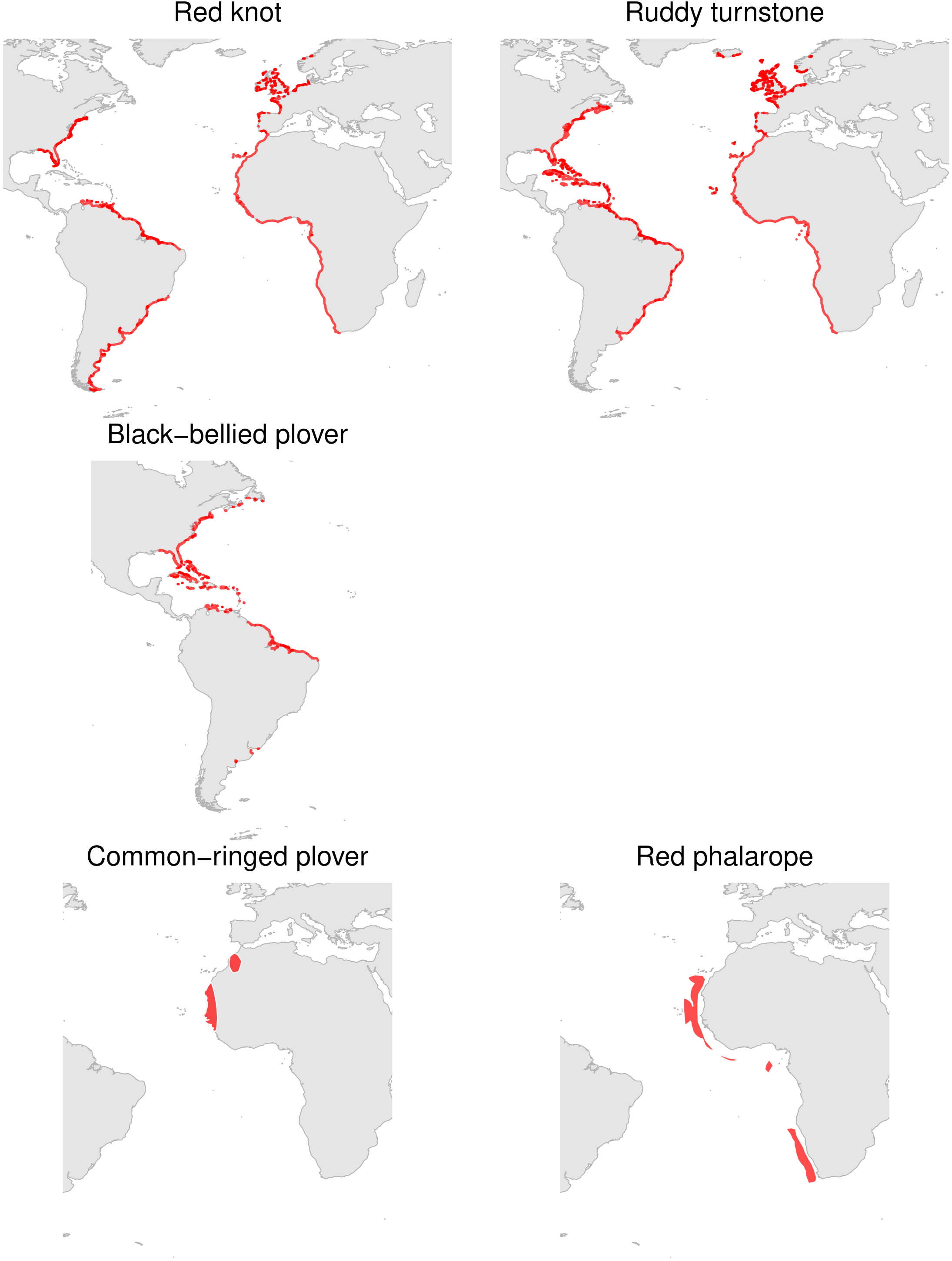
Lapland longspur

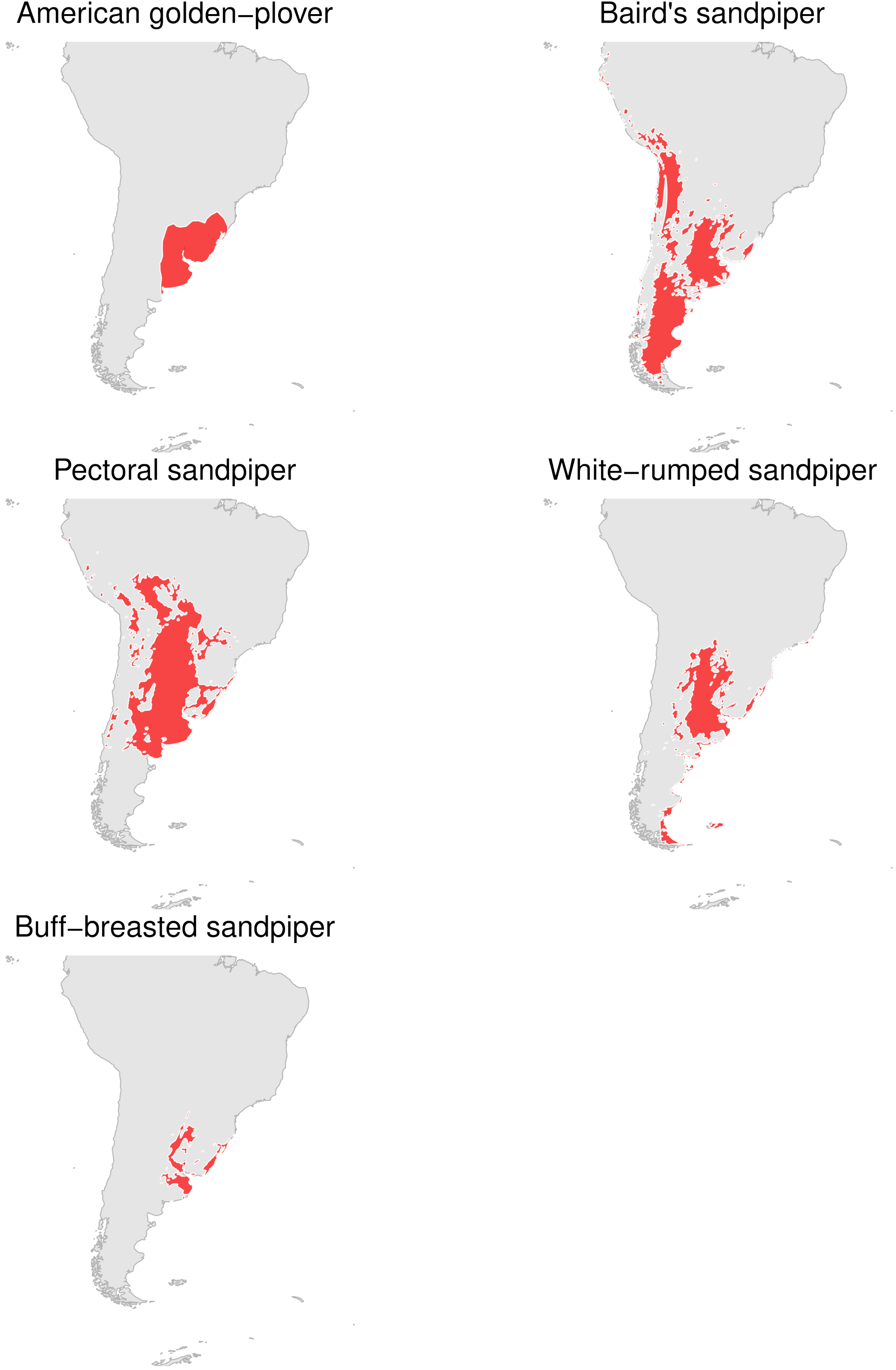
Snow bunting

Horned lark

American pipit

Shorebirds (coastal or marine)





Shorebirds (terrestrial)

American golden–plover

Baird's sandpiper

Pectoral sandpiper

White–rumped sandpiper

Buff–breasted sandpiper

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